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Predicting the rate of spread of introduced animals and plants

Rob Hengeveld & Frank van den Bosch

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This paper includes an estimate of what we need to know for predicting the spreading rates of introduced animal and plant species. The models although catching the principal aspects of the spreading process, still prove to be too simple. Yet even in their initial state of development, they require an amount of biological and environmental information that cannot be reasonably supplied. However, as such, they can indicate the kind of information needed to make statistical prediction reliable. These models also indicate the limits of prediction beyond which extrapolations from simpler models should not be made. It thus appears that the limits of prediction are very restrictive about the fate of species accidentally or deliberately introduced into an area.

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In this paper, I discuss a model describing the rate of invasion of animal species, together with a couple of its recent extensions. Under certain conditions, this model can also be applied to plant species. Because these models are mathematically analytical, and because they contain only biologically interpretable and measurable parameters, they can show the limitations to predictions. The limitations are not so much set by the complexity of the mathematics involved, as by the possibility of requiring the biological information needed for estimating the values the parameters take. These values are partly intrinsic to the species and partly the result of the response of species to the intensities of environmental variables. The part intrinsic to the species implies that it is not possible to generalise results obtained in one species to any other species. The ecologically determined part of the species' response means that we cannot generalise the result obtained under one set of environmental conditions to another set, even within the same species.

On top of this, the models show that the rate of spread is also conditioned by the spatial characteristics of the environment.

Ecologists are used to thinking in terms of sets of interacting factors, species and processes, forming dynamic systems. The present paper fits this tradition. However, it applies this attitude to the autecology of single species, instead of to sets of species, i.e. communities. The analytical models discussed here can only be formulated for single-species processes, not for those within communities. The risk incurred to other, native species by introducing a species cannot be calculated from analytical models.

Two statistical rules

In connection with predicting invasion rates statistically, there are two topics of research interest: 1) the search for intrinsic properties of species distinguishing them from other non-invader species, and 2) the search for rules expressing the risk of a species becoming a harmful invader once introduced into a foreign area.

The search for intrinsic properties making a species an invader as distinguished from those of non-invaders has failed. There are neither species intrinsically determined to be invaders, nor intrinsic non-invaders. This search was for properties related to fast reproduction and rapid dispersal (e.g. Baker 1965, 1974, Ehrendorfer 1965). Fast reproduction can be accomplished, for instance, by great numbers of seeds or eggs being produced per plant or per female animal. Reproduction can also be non-generative, such as by the ease of growing out as a new plant from branches or from rhizomes broken up with plowing or with the removal of the 'exotic weed', or by parthenogenesis in e.g. aphids. Rapid dispersal can be accomplished in several ways due to the morphology of the propagules (e.g. winged seeds, planktonic larvae, rapid flight of nomadic animals, human transport by tractors, ship, cargo,

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or through connecting rivers or lakes by digging canals). Another type of properties could have been ecological: ruderals as a group might more likely contain invaders than, say, forest species (e.g. Grime 1986, Simberloff 1981) yet other ones would be genetical (Gray 1986) or geographical (e.g. Rejmanek 1995).

These studies pose several difficulties. Some invaders, weeds or pests may indeed have a high reproductive potential, but others produce only a few seeds or eggs (the collared dove *Streptopelia decaocto* lays only two eggs per clutch) in their life time. Furthermore, a high reproductive potential also occurs within the 'group' of non-invaders, such as mushrooms, the herring *Clupea harengus* or the cod *Gadus callarias*. Moreover, in part of their range, a species with a high reproductive potential can be a noxious weed, whereas in another part nearby, it fails to reproduce because the seeds do not germinate. *Rhododendron ponticum*, for example, is a very aggressive weed in Britain, but in continental Europe its seeds fail to germinate.

Obviously, a combination of traits could also distinguish invaders from non-invaders, in one species one set of traits being distinctive and in another species another set. As it is not known beforehand which set applies to which species, this approach does not give predictive results either.

Thus, for both statistical and methodological reasons, this statistical approach fails to work. We cannot tell conclusively from the intrinsic properties of a species whether or not it might develop as a noxious weed or pest once it is introduced. Indeed, we cannot even tell whether it will settle at all, as it appears from deliberate introductions in biological control (e.g. Simberloff 1986).

The second line of research looks for rules concerning the risk that species will develop into noxious weeds or pests once introduced into a foreign region or continent, independent of their properties. This search resulted in the so-called 10:10 rule.

This rule states that only 10% of the introduced species settle in the new area. Of these settlers, only 10% would develop into a harmful species (Williamson 1993). The risk one runs with introducing a species would therefore be that only 1 in 100 species will become harmful. It then depends on the type of harm incurred whether this is an acceptable risk or not.

In fact, these percentages themselves are rough estimates, not liable to precise prediction. Thus, Williamson (1993) considers the percentage to be lying somewhere between 5 and 20. Instead, Kowarik (1995) suggests a 10:2:1 per cent rule for introduced woody species in Brandenburg, Germany, during the last 200 years. This means that 10% or less of the introduced species began to spread, 2% became established, and 1% may successfully have invaded into the natural vegetation. Still, even these percentages are changing over time: 3% of the introduced species started spreading in 1780, and 7.4% of them in 1990. If it is true that invaders are found more frequently in areas disturbed by humans than in undisturbed, natural areas (Fox & Fox 1986), this last percentage might be expected to increase rapidly in the future. Still, whatever the eventual value, at present it is not a reliable estimate upon which to base rules or predictions.

In short, statistical analyses cannot supply reliable estimations for the success of introduced species in spreading into foreign areas. Apart from this, such analyses cannot predict the rate of spread as they were not designed for this purpose. Both the success rate and the rate of spreading can only be constructed from analytical models. However, these, in turn, suffer from yet other limitations.

An invasion model determining the rate of spread

From a statistical analysis of *Pinus* species, Rejmanek (1995) concluded that, among some factors of lesser importance, small seed mass, a short juvenile period, and a short mean interval between large seed crops are good predictors for the invasiveness of woody species. The first of these three parameters, small seed mass, relates to dispersal capacity, and the other two to the reproductive potential of individual trees. As will be shown below, this finding from a statistical analysis can be understood from results obtained from modelling the rate of invasion.

Fisher (1937) and Skellam (1951), in a population genetical and an ecological context, respectively, modelled invasion rates assuming that individuals move randomly. The diffusing individuals subsequently reproduce, thus fuelling the process by producing new and more individuals. However, this initial reaction-diffusion process still assumed reproduction to take place continually rather than in seasonal batches. The spatial spread would progress in a similar and continuous way. Although this model contains the basic elements - the proper choice of parameters and the proper process structure - it still needed some mathematical refinement and biological justification.

Van den Bosch et al. (1990, 1992) worked out another reaction-diffusion model, allowing for discontinuity in space and time. This model estimated the spatial spread from independent, non-spatial data on a species' life history. The resulting, expected rate of spread can be compared with the observed rate obtained from the field or from a map. As an analytical rather than a simulation model, it can be extended mathematically, thus including consequences of further assumptions as to settlement rate or the degree of spatial heterogeneity of the environment,

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for example. It can also be used for validating the values of the various parameters. This gives insight into the relative importance of those parameters, as well as into the sensitivity of the results to changes in their values.

The basic model structure of the two-dimensional process of spread reads

$$\frac{\partial n}{\partial t} = rn + \tfrac{1}{2}s\left(\frac{\partial^2 n}{\partial x_1^{\,2}} + \frac{\partial^2 n}{\partial x_2^{\,2}}\right)$$

where $n(t_1, x_1, x_2)$ is the population density n at time t at location (x_1, x_2), s is the diffusion constant, and r is the species' intrinsic rate of increase. The reaction (= reproduction) component in this reaction-diffusion equation is rn, and the remainder of the equation represents the diffusion component. Yet, it assumes that the rates of reproduction, mortality and dispersal are independent of the age of the individual, which is biologically unrealistic.

Van den Bosch et al. (1990, 1992) estimated the net rate of reproduction R_0, using a Leslie matrix. This matrix contains information on the proportion of the initial organisms still alive in various age classes. For each age class, the fertility rate can be estimated. The summed products of the proportion alive with the fertility rate gives an estimate of R_0. The mean age of reproduction is

$$\mu = \frac{1}{R_0}\alpha\int_0^\infty L(a).m(a).da$$

where α is the proportion of females in the population.

The dispersal component is expressed by the variance of the marginal density of the contact distribution

$$\sigma^2 = \int_0^\infty\int_0^\infty x_1^{\,2}D(x_1,x_2)dx_1,dx_2$$

where D is the diffusion coefficient. (NB: a marginal density is a two-dimensional density distribution integrated into the density of a one-dimensional distribution. A contact distribution is the distribution of distances covered by propagules from their starting point).

The expected rate of invasion, C_{exp}, then becomes

$$C = (\sigma/\mu)\sqrt{2\ln R_0}$$

Thus C_{exp} can be calculated using information from parameters the values of which can all be estimated in the field. This calculated rate of invasion or range expansion agrees sufficiently well with the observed rate for the various species studied (van den Bosch et al. 1992). Therefore, no additional parameters are needed for reconstructing these expected rates. Moreover, the invasion velocities could be calculated from parameter values estimated in the region of origin, so that circular reasoning was avoided.

This implies that the conditions of both the region of origin and the region colonised were similar, as assumed. As the equations used assume density independence within the invasion wave, the effects of possible density-dependent processes in the region of origin not included in the model are small relative to effects of the processes that were included. The only exception to this was found in the house sparrow *Passer domesticus* colonising North America. There, the net rate of reproduction was much higher than under density-dependent conditions in Europe from where this species was introduced (van den Bosch et al. 1992).

This model also assumes that the species settles permanently in the area of first breeding. This applies to virtually all plant species, to sedentary animal species, as well as to many bird and mammal species. This model is therefore not applicable to, for example, the Africanised or killer bee *Apis mellifera scutellata* introduced into South America and now spreading into North America (see Hengeveld 1992). When nests are considered individuals, these can split. After this, the parts can abscond, each dispersing into another area. Also, the site before absconding can change continually, the nest moving considerable distances. For cases like these, other models have to be formulated.

Model validation

The good fit between the expected and calculated rates of spread in all cases to which the model has been applied so far, shows that the model reflects the process mechanism adequately, and that the parameters chosen are indeed the main ones operating. Yet, particularly for practical reasons, it is interesting to know which parameters or parameter values determine the spreading rate most.

To this end, I altered data for both the survival rate and the rate of dispersal. I used the most detailed data available, i.e. those of the collared dove having immigrated into Europe during the present century. Then, I compared the effects that these alterations have on the expected spreading velocities (Hengeveld 1992).

In the field, the highest mortality rate in the collared dove occurs after the juvenile stages. Thus, the percentage change in mortality increases from 30 or 40% in the early stages of the individuals to 50% in the later stages. This mortality rate can artificially be taken constant, at say, 50%, implying a greater juvenile mortality. This results in a lower net rate of reproduction, that is $R_0 = 0.74$ instead of the observed rate of $R_0 = 1.33$. This reduces, in turn, the expected spreading rate from 56.3 km per year to 32.4 km.

Similarly, the observed dispersal distances can be altered into different, hypothetical ones. Thus, a change in short-distance dispersal results in changes of a few kilometres covered per year. However, very slight changes in long-distance dispersal greatly affect dispersal rates of

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tens of kilometres per year. Long-distance dispersal, therefore, seems the most sensitive parameter determining the invasion rates.

Of course, these data are, in fact, difficult to compare. The results are, namely, all expressed in the same dimension, kilometres per year, which makes them comparable. In contrast, those concerning alterations in life history are not. Therefore, the comparisons show some intuitive parameter weighting only.

Apart from the differences in their effects on the expected invasion rates, these results can still be important in a more general way. The alterations made artificially can also be effected ecologically in the field under different conditions. The results, therefore, clearly show that the intrinsic part of the determination of the invasion rates is small relative to the ecological part. Invasiveness is not an intrinsic property, but mainly an effect of ecological processes. Small changes in the rates of mortality or fertility can increase or decrease the net rate of reproduction significantly. A slight increase in reproduction rate results in population growth, both numerically and spatially. When it grows in space, a species automatically becomes an invader, whereas before, it could have been stable or could have retreated from part of its range. Because conditions affecting net rate of reproduction are changing continually in various ways, species invasiveness changes continually as well. Invasiveness changes independently of a species' intrinsic properties such as their potential of maximum number of seeds, eggs, etc. The same reasoning holds, of course, for animals. Because correlative methods isolate one or a few properties from their ecological context, they are bound not to work.

On the other hand, Rejmanek's (1995) results are interesting because they hint at the most sensitive parts of the processes determining a species' potential invasiveness. Apart from its scientific interest, this is significant in connection with the feasibility of prediction.

Scientific and practical interest of the model

The success and wide applicability of this model make it scientifically interesting. Mathematically, it is sound and further, more detailed models can be derived from it. Its methodology is mechanistic instead of descriptive, the latter being characteristic of ecological modelling (Hengeveld 1994b). Their mechanistic nature makes the results predictive, and, hence testable. When the match between the expected and observed rates is too small, one can infer that either the species does not meet the assumptions as in the Africanised bee expanding in the Americas, or that the data used for parameter estimation in some way are faulty, as in the house sparrow spreading into North America. In other types of models, such as in simulation models, either the model structure or the parameter choice could have been faulty as well.

Apart from these mathematical and methodological advantages, a third advantage is that the model is biologically realistic. It contains the principal parameters framed into a model structure similar or identical to the process in the field.

Therefore, this model can be of great practical value. At the same time, however, we have to realise that there are very strict limits to its practicability. The limitations result not so much from limitations due to mathematical complexity, as from the limited feasibility to estimate all parameter values needed. Moreover, here too, we have to realise that the parameter values are partly intrinsically determined and partly ecologically. Without exactly knowing the ecological contribution under the conditions the species is going to meet when immigrating into the area still foreign to it, we cannot realistically determine the parameter values in advance.

Still, realising this, the model has been extended into two main directions, that of settlement risk, and that of invading into ecologically non-uniform space. This has been done for two reasons: 1) when we have to predict in practice from results of correlations, we need to know which parameters are closest to the process mechanism, as well as to know the most sensitive ones in this mechanism; 2) when we have to take practical measures, we have to do this with the smallest risk. This risk can be estimated intuitively from knowledge of some details of the process mechanism.

Continental spread

When a species invades an area because it extends its range naturally, or because it is accidentally or deliberately introduced, it may settle there in all sorts of biotopes. In these biotopes, its survival rate may, moreover, be exceptionally high. This, together with other characteristics, can also be quite different, the species then reproducing poorly and occurring in a few, marginal biotopes only. Allowing for these kinds of differences implies that the equation for calculating the expected invasion rate C_{exp} be adjusted. The new equation now reads:

$$C = \sqrt{2\alpha\sigma^2\psi\phi}$$

This equation allows for the rate of settlement Ψ and for the amount of suitable biotopes ϕ available. In other words, we now assume that the species cannot find enough suitable biotopes, and, if it finds one, that it may not be able to settle in it permanently.

As the next step of adding biological realism to the model, we can assume that the survival rate of the settlers

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has to be specified (ε). Also, depending on the rate of reproduction, the fraction δ of long-distance dispersal to dispersal over short distances can be important. Finally, the part of the year during which reproduction can take place, T, also determines the rate of spread, the longer the species can reproduce, the more offspring it will get, and the higher the invasion rate will be. Including these parameters into the process, the equation now reads (van den Bosch et al. 1995; see also Hengeveld 1994a)

$$C = \sqrt{2\alpha\sigma^2\psi\phi}.T - \frac{1}{2\sqrt{2}}\sqrt{\frac{\alpha}{\phi}\sigma^2}.\ln\left(\frac{1}{\varepsilon}\right)$$

Despite their biological realism, these models are not practical for the quantitative prediction of the rates of success of an introduction or of its spreading rate, however. This is because the values of all these parameters are exceedingly difficult to measure in the field. Moreover, these measures do not hold once and for all, but they vary in space and in time. We obviously have trespassed the limits of feasible parameter estimation by far.

Invading into an ecologically non-uniform area

It is realistic to assume that mortality relates to the amount of suitable area available in a region or continent. Thus, the less suitable the area in this way, the higher the mortality.

We can now assume that the individuals, when they search at random in space for suitable area, are following a Gaussian distribution with variance δ. This variance increases at a rate ω over time T. The fraction of suitable area is δ, and the mortality rate during dispersal ψ. The rate of settlement is then the product ψ δ, and the risk of dispersal in ecologically non-uniform areas ψ/ω. Thus, this risk is small when ω is large, when ψ is small, or when both conditions are met in a certain combination. The rate of spread can now be modelled as

$$C = \frac{1}{2\mu}\frac{1}{\sqrt{\delta + \psi/\omega}}\sqrt{2\ln\left(\frac{\delta}{\delta + \psi/\omega}\hat{R}_0\right)}$$

The result is that the rate of traversing an ecologically non-uniform area is non-linear, depending on the fraction δ of suitable area (Fig. 1). The location of the maximum of this non-linear relationship is determined by the risk of dispersal ψ/ω in combination with δ. For different risks, therefore, different fractions of suitable area are most favourable. On the other hand, the value of δ always needs to be relatively high, i.e. higher than 20% of the area to be colonised. With lower percentages, the area soon becomes impenetrable (Fig. 2). The highest spreading rates, though, are typically found when the proportion suitable

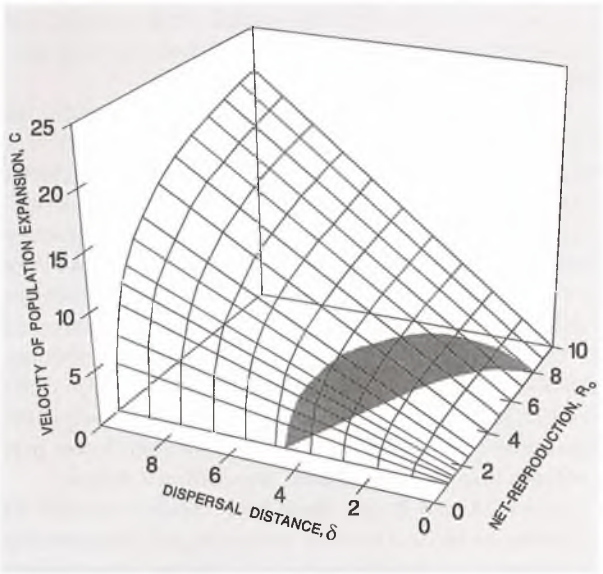


Figure 1. Invasion rate C plotted as a function of both net reproduction rate R_0 and dispersal distance δ. The increasing function results for invasions happening under uniform conditions. C shows a maximum for non-uniform conditions, in this case $R_0 = 8$ and invasion risk $\psi/\omega = 0.01$.

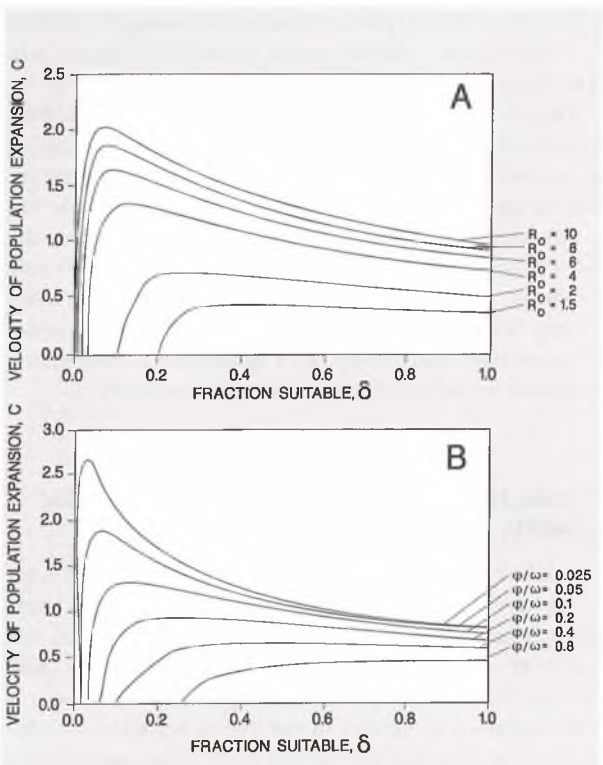


Figure 2. Invasion rate C as a function of the fraction suitable habitat in non-uniform conditions for various values of R_0 (A) and dispersal risk ψ/ω (B). The maximum shifts to the right (more suitable habitat) for both higher reproduction rates and lower dispersal rates.

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area is low, that is when all animals keep moving, not finding a suitable place to live (com. Schroepfer & Engstfeld 1983).

Although this non-uniformity of ecological conditions makes the original model more realistic - in a different way than in the extended model discussed in the previous section - within its context, it is still not entirely realistic. Usually, suitable biotopes are themselves not uniformly distributed within an overall unfavourable area, but they can be clumped. The simplest assumption is that they are randomly distributed, the clumpedness being expressed by the parameter k of the negative binomial distribution. If this is so, the chance of finding a suitable biotope is the smaller, the greater the clumpedness. This implies that the maximum rate of dispersal will shift to even lower percentages than 20% of suitable area within a region.

Figure 2A and B also show how various elements of the invasion process interact, enhancing or compensating each other. It is insufficient to know the net reproduction rate R_0, the dispersal rate or the penetrability δ of the area separately. The values of several parameters together determine a species' invasion velocity and its spatial maintenance process. This once more, although now explicitly, shows that correlations of individual species traits, when taken separate of each other and isolated from their ecological context cannot predict the success and spreading rate of introduced species.

The principal message from these model results is that, as the various parameter values are difficult to obtain, if at all, our predictions should remain crude, qualitative, and intuitive. The models show the limitations set to exact prediction. The second message is that, with the present insight into the process mechanism, we are able to narrow down the range of possible predictions to some extent. Which extent this will be depends on the amount of qualitative knowledge or of quantitative information available on the species and their environments.

Predicting invasion rates using realistic models

It will be clear that, in principle, prediction is feasible using the models mentioned. The only difficulty is to know the ecology of the species, together with the spatial distribution and intensities of their requirements well enough for estimating the various parameter values. It is not so much the number of parameter values to be estimated that prevents the models from being applied, nor their complexity, but it is the mere technicalities of their estimation.

Yet, their message is even stronger than that from the validation experiments of the initial model: the rate of spread, as well as the success rate of the invasion is not determined by properties intrinsic to the species. It depends on the match of ecological requirements of the species among each other and with the characteristics of the species' environment in space what the fate will be of a species introduced into a foreign region.

The degree of information on this match between ecological requirements and environmental attributes determines the predictability of the speed and course of the invasion of an introduced species. Where there is no information, we have to admit not to be able to make any sound, reliable prediction. Everything can happen in that case.

Yet, this conclusion only pertains to the rate of invasion immediately after the introduction taking place. If one wants to include the spatial maintenance process into the prediction, we have to look at another subsequent spatial process as well.

Surviving under non-stationary conditions

Many species live in patchily distributed biotopes. This patchiness varies within a species range, being largest at the range margin and smallest at the centre. Species maintenance within such a patchily distributed biotope can be described by a spatial Markov chain. Within this model, individuals are thought to be continuously on the move. After having crossed an unfavourable and having arrived into a suitable biotope, it can stay there for a time proportional to the suitability of the conditions.

In this set-up, therefore, we distinguish areas with very low staying probabilities from those with high staying probabilities. Stochastically, many individuals accumulate in the suitable areas and only a few animals are found in between. Apart from this, we can define transition probabilities between the suitable areas.

In another way, we can also look at the turnover rate in the composition of all sites in an area with regard to individual animals. This turnover rate is high between the suitable biotopes and low between them. Then, depending on the probabilities relative to each other, we can recognise accumulation areas (populations) within a region and areas of transition where the animals actively disperse. Given a certain, fixed set of probabilities, one obtains a set of fixed populations within the region colonised, despite the fact that the system is highly dynamic because of the permanent flux of individuals. Such an image can apply to many species, although the spatio-temporal scale of movement is specific.

This image is still unrealistic in at least one main aspect: the probabilities are fixed in space. In reality, they are not: the conditions at site A may remain suitable for some time, but then they can turn unsuitable. And the re-

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verse holds for site B somewhere else and not necessarily coinciding with the time that site A deteriorates. In this case, the population of site A evaporates as the conditions deteriorate and another population condenses at site B. This system is dynamic both at the level of the individual, as well as at that where ephemeral populations condense and evaporate.

Species obviously will maintain more easily in regions meeting a uniformly distributed minimum requirement, such as found in weeds and pests in agricultural land. Even then, the species themselves should be spatially dynamic. A very high dynamism can be met, not only by rapid dispersal, high reproductive potential, or both, but also by certain minimum dormancy times, short life cycles, etc. Species that do not meet these environmental requirements cannot spread and maintain after their initial settlement. The basic structure of this kind of model is presently being worked out.

Discussion

The invasion of a species into a foreign area is essentially a demographic process, determined by numbers of propagules produced and their rate of diffusionary dispersal (Hengeveld 1989). These numbers, in turn, are determined by the degree to which specific properties of individuals match with the local conditions under which they live. The difficulty with predicting invasions is how to identify the potential match of the species into an area where it still does not occur.

The mathematical analysis of the process has been developed far beyond the possibility of biological and environmental parameter estimation. This may seem stretching the theory too far relative to its practical testing and application. Yet, the extension of the initial model does not only show the impossibility of precise prediction, but it also shows main elements of the process itself.

It shows, for example, that a certain, relatively high proportion of unsuitable biotope can prevent the progression of the invasion of the introduced species. If, on the other hand, there is information indicating that the conditions are uniformly favourable, we now know that the species is very likely to spread and possibly to maintain at high density levels. Therefore, some basic information on the species' ecological requirements can narrow down the possibility of prediction to a certain, still qualitative estimate of the likelihood of further spread. Conversely, it can also indicate the chance of success of control measures after spread, although these require much further elaboration. Finally, validation experiments can be carried out using these models for estimating which measures will give the greatest success rate of prevention or control. All these estimations, however, depend on the quality of estimations of ecological and environmental parameter values.

The fact that species occur in several types of biotopes, and therefore more uniformly in the centre of their geographical distribution range (e.g. Hengeveld & Haeck 1981, 1982, Hengeveld 1990, Brown 1984), is significant in this context. If some environmental data indicate that a species is introduced into an area with conditions marginal to it, the models now indicate that this also affects its dispersal characteristics, apart from the reproductive ones only. Particularly the spatial ones can prevent the species from any further progression into the area, even when reproduction would be sufficient. If the species, however, is introduced into generally optimal conditions, particularly the resulting greater uniformity of these more favourable conditions will enhance its progress.

The models define the structure of the invasion progress. This means that we can derive how the value of one parameter can enhance or reduce that of another one to a certain extent. Without knowing this structure, this compensatory effect cannot be estimated. Thus, considering, say the average or maximum number of seeds or eggs produced as a predictor of invasion success isolates this trait from its ecological and environmental context. The models discussed define this context. However, they do this differently from the usual way by including environmental characteristics and by relating all relevant ecological parameters to each other within the entire structure of the process mechanism. We can now make a justified choice among potentially significant parameters and identify their relative weights.

Conclusions

One would like to be able to predict exactly what might happen to a species introduced into a new area. This is not possible. The models developed show why this is so. However, the models do narrow the possibilities down to a certain extent. The more ecological and environmental information we include, the narrower the range of possibilities and the closer we get to more precise prediction.

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