Striking the metapopulation balance

Mathematical Models & Methods Meet Metapopulation Management

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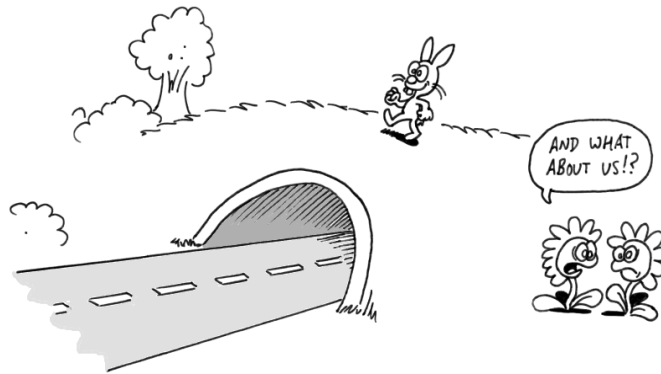# Part IV. Methods improving the quality of model predictions *145*

Introduction

There are two buzz words in nature management: fragmentation and connectivity. Not only (rail)roads, but also agricultural, residential and industrial areas fragment previously connected (or even continuous) habitat. Common sense tells us that the answer to habitat fragmentation is defragmentation and hence much effort is put into building corridors, of which fauna crossings are just one example. Corridors are conduits connecting two pieces of habitat through an environment of hostile non-habitat. As such, the use of corridors need not be restricted to the animal kingdom; plants can also use them as stepping-stones for their seeds, enabling them to colonize distant habitat. Although corridors may not only act as conduits but also as habitat, filters or even as barriers (Hess & Fischer 2001), in most cases they are constructed primarily for their conduit function. Connectivity is nowadays taken to its extreme in the "Ecologische Hoofdstructuur" (Ecological Main Structure) in The Netherlands. This is a plan in operation to create an extensive ecological structure by connecting a substantial part of the remaining "natural" habitat, which includes conduits of decommissioned farmland bought by the government. Similar plans exist in other parts of the world.

Needless to say, there are good reasons for building corridors and plans involving them. Yet, there are some valid arguments against connecting everything (see Shafer 2001 for a recent review from a conservationist's perspective). The risk of spreading of infectious diseases through these corridors is one of the most prominent arguments (Hess 1994, Hess 1996b). The spread of the effects of (natural) catastrophes such as fire is another. But even when dismissing such negative effects of connectivity, there may be other mitigating measures that are much more efficient (and less expensive) than building corridors. The question whether this is the case and how alternatives should be compared stimulated the work for this thesis.

A theory that is well suited for predicting the effects of fragmentation is metapopulation theory. As almost every text on metapopulations will tell you, this theory was conceived by Richard Levins in 1969-1970 (Levins 1969, Levins 1970), although its roots may be found in earlier work (e.g. Wright 1940, Andrewartha & Birch 1954, Den Boer 1968). The core of the theory is the following observation. Populations are assumed to live in distinct habitat fragments, called patches. These local populations can go extinct relatively quickly, but immigration from other patches can lead to recolonization of empty patches. Thus, the whole population of populations, the metapopulation, can potentially persist if these recolonizations outweigh the extinctions of local populations. In a sense, the population spreads the risk of extinction by spatial separation.

A balance between several opposing processes, or between costs and benefits, quickly calls for mathematical modelling when verbal arguments cannot cope with the complexity of

Attention deficiency

the problem anymore, and any outcome, positive or negative, seems possible. Metapopulation theory is far from being an exception to the rule: many a model has been developed and much insight has been gained. According to Hanski (1999) there are three basic models on which all other metapopulation models are grounded: the Levins model (which Levins himself calls the migration-extinction model in Levins & Culver 1971), the two-population model and the lattice model. Most of this thesis centers around the Levins model, occasionally containing the spatial aspect of the lattice model; the two-population model is not represented anywhere in this thesis, or it must be the inclusion of local dynamics in chapter 2.

Why this bias towards the Levins model? The Levins model comprises a simple and conceptually clear metaphor of what one aims to model. By putting all local dynamics into a single extinction parameter, the model enables one to focus clearly on metapopulation dynamics. Likewise it can be claimed that its implicit instead of explicit spatial character allows a clear focus on the effects of dispersal (Wennergren et al. 1995). Yet, to make models influence management, which is concerned with spatially explicit questions such as where to put an ecoduct and what patch to favor in a conservation program, these models must be spatially explicit as well. Therefore the second part of this thesis (chapters 5-8) involves models incorporating spatial configuration.

Not unimportantly, any such bias is bound to be partly irrational; every scientist has his or her pet ideas or models (Hanski 1999) and mine happens to be the Levins model, and even more so its stochastic, spatially explicit versions. A(n irrational) preference for a particular (type of) model need not be disadvantageous, as long as this preference is not universal and as long as its shortcomings are kept in mind. Undoubtedly, a similar irrationality caused the Kuhnian paradigm shift from island biogeography (McArthur & Wilson 1967) to metapopulation dynamics which is not a large shift at all considering their similarities (Hanski 1999).

I will now briefly describe the Levins model and refer to chapter 2 for a more concise description. In the Levins model the world consists of infinitely many patches that are all alike and homogeneously mixed (i.e. no specific spatial location and all equally accessible

from one another). Patches can be either occupied by a population or empty; local dynamics are not considered. The state of the system is described by the fraction of occupied patches p. Population become extinct with rate e and dispersers from occupied patches colonize empty patches (of which the fraction is given by $1 - p$) with rate c. The dynamics of p are described by the following differential equation:

$$\frac{dp}{dt} = cp\left(1 - p\right) - ep. \tag{1}$$

Hence, ep is the fraction of patches becoming empty per unit of time and $cp\left(1 - p\right)$ is the fraction of patches becoming occupied per unit of time. This equation has two equilibria, denoted by p^*. One is the trivial equilibrium, $p^* = 0$. The other is given by

$$p^* = 1 - \frac{e}{c}. \tag{2}$$

This equilibrium is only biologically realistic and different from the trivial equilibrium if $\frac{c}{e} > 1$. This condition is also the condition for global stability of the equilibrium. If $\frac{c}{e} \leq 1$, the trivial equilibrium is globally stable. Defining $R_0 = \frac{c}{e}$, one can write the condition for a non-trivial globally stable equilibrium as

$$R_0 > 1. \tag{3}$$

R_0 is the basic reproduction number and can be interpreted as the expected number of patches colonized during the lifetime of a local population in a virgin environment (i.e. all other patches are empty). If (3) is satisfied, the local population can more than replace itself before it becomes extinct, and thus the population can grow.

In the ensuing chapters of this thesis, armed with this metapopulation theory with an inclination towards stochastic and deterministic, implicitly and explicitly spatial models of the Levins-type, I hope to provide some additional insights that may be useful for meta-population conservation. In this introduction, as most, if not all, introductions written last, I try to glue these chapters together in a coherent framework, supply them with some additional comments, discuss their implications, and look beyond them for interesting current and future developments.

Thesis overview and annotations

The thesis consists of eight chapters and is divided into four parts. Part I, containing only one chapter, can be regarded as a review of fundamental metapopulation processes, set in the context of a persistent problem in conservation science, the SLOSS problem. This problem, of which the acronym stands for Single Large Or Several Small, raises the question whether the optimal design of a habitat network consists of a single large nature reserve or several small reserves. Although this question was initially concerned with biodiversity (which design can contain the largest number of species?), it can be equally well applied to a single species living in a metapopulation for which the question becomes: which design optimizes the persistence of the species?

Studying metapopulation theory

Defined thus, it represents a fine example of opposing processes requiring mathematical modelling. On the one hand, patches must be as large as possible to minimize the risk of local extinction; on the other hand, there must be as many patches as possible to maximize the probability of recolonization and to minimize the risk of simultaneous extinction. Precise mathematical formulation of these thoughts can in principle lead to a solution of the problem. Sometimes the mathematical formulation requires that the question be expressed differently or more clearly. In chapter 1 SLOSS is replaced by the more neutral FLOMS, short for Few Large Or Many Small, because in the chosen framework a single large patch is not really possible (it exists only in a limit).

Which design is optimal turns out, not completely surprisingly, to depend upon the measure one employs for metapopulation persistence. Two measures are introduced: the metapopulation extinction time and the colonization potential which is a type of basic reproduction number (the number of patches colonized by a local population during its lifetime in an environment where all other patches are empty). These measures return in subsequent chapters.

Which design is optimal also depends on how designs with different size and number of patches are compared. In chapter 1 this is done such that the amount of habitat per unit area is constant. This implies that few large patches have larger interpatch distances than many small patches. Ovaskainen (2002a), who also considers two measures of metapopulation persistence, the metapopulation extinction time and the metapopulation capacity (Hanski & Ovaskainen 2000, Ovaskainen & Hanski 2002) which is closely related to the colonization potential, keeps interpatch distance fixed and only requires the amount of habitat to be constant and reaches a different conclusion. Keeping the interpatch distance fixed demands an explicit expression of the metapopulation extinction time while this is not essential in chapter 1. But since Ovaskainen (2002b) has derived such an expression for certain limits, this new development could be applied to the situation in chapter 1 as well, and would make its argument more solid, but it does not affect the qualitative conclusions of this chapter.

The SLOSS debate has been considered highly academic, because the considered patch configurations are far from realistic. One of the few exceptions is an article by Pelletier (2000), which was published in the Journal of theoretical Biology only a month before chapter 1. As a third alternative, next to one large and many small, Pelletier (2000) introduces a mixture, the so-called self-similar patch distribution which supposedly resembles the distribution of managed areas in the United States. For the SLOSS debate to remain fruitful, this type of novelty is crucial.

Part II concentrates on the Levins model. Models are often considered inadequate because the underlying assumptions are thought to be unrealistic. Yet, these assumptions can be formulated in a way that is stronger than necessary for the development of the mathematical model. Therefore, they need to be subjected to careful scrutiny, such that all superfluous elements are eliminated. If the model is still discarded, at least it is so for the right reasons.

In chapter 2 the assumptions of the Levins model are examined. One of the assumptions as it often appears in the literature proves to be too strong: After colonization, the newly born population need not grow to the carrying capacity. It is sufficient if local dynamics are fast enough for a steady population size distribution to be established. It follows that patches need not all have the same extinction and colonization rates, but merely that these form a steady distribution depending on the population size distribution. The extinction and colonization rates in the Levins model are weighted averages over these distributions. Although this does not make the model much more realistic, it does remove restrictions on more realistic extensions of the Levins model. Two such extensions are studied in chapter 2, and one in chapter 3 (which could easily have been an additional section of chapter 2 if history had not decided otherwise).

The first extension in chapter 2, involving the rescue effect, and the one in chapter 3, dealing with the Allee effect, are attempts at a more careful and more mechanistic formulation of already existing models. Although the conclusions remain basically the same in these new formulations, they provide more insight in the responsible processes and are scientifically and aesthetically more satisfactory. The latter argument may seem insignificant, but one only needs to remember Einstein's revolutionary paper on special relativity (Einstein 1905) to know that this can make a difference. Obviously, I do not claim that the alternative models have quite the same status as Einstein's theory, but I want to stress that aesthetics may be a guide to find the appropriate model.

The second extension of the Levins model in chapter 2 incorporates preference for occupied or empty patches in the Levins model. Preference for occupied patches may arise because of conspecific attraction (Smith & Peacock 1990, Ray et al. 1991, Vos et al. 2000); preference for empty patches seems plausible for territorial species (but see Stamps 1991). Preference for empty patches is shown to increase patch occupancy; preference for occupied patches lowers patch occupancy.

Ray et al. (1991) also model conspecific attraction, but there are two differences with the approach in chapter 2. First, when Ray et al. (1991) model the rescue effect simultaneously, they use a discrete-time model thus complicating comparison with the continuous-time model of chapter 2. Second, in chapter 2 preference for occupied or empty patches depends on the available fraction of occupied and empty patches which is not the case in Ray et al. (1991) where a fixed fraction of propagules is assumed to settle on occupied patches. In other words, if there are almost no occupied patches, empty patches are colonized anyway in chapter 2, but only partly in Ray et al. (1991). The latter approach is reasonable if conspecific attraction causes individuals to leave patches, whereas the former is more appropriate if conspecific attraction only influences the settlement of dispersers, but does not initiate dispersal. Chapter 2 briefly studies patch preference and the rescue effect simultaneously as well, because it is not *a priori* evident how the rescue effect interferes with patch preference.

On the one hand, empty patches should be preferred because colonization of empty patches is the only way in which the metapopulation can reproduce. On the other hand, additional colonization of occupied patches prolongs survival of the local population due to the rescue effect. It turns out that the effects are almost additive as far as patch occupancy is concerned. This could, however, be quite different if the metapopulation extinction time is taken as a measure of metapopulation persistence. It would also be interesting to examine the consequences of adding the Allee effect of chapter 3 to this system, because then colonization is not guaranteed, implying a cost to preference for empty patches.

Most metapopulation models, particularly Levins-type models, are only used to study equilibria. The last chapter of part II, chapter 4, deals with non-equilibria and their consequences for metapopulation management, using both the Levins model and its stochastic counterpart. These non-equilibria are created by imposing sudden changes in patch number and the colonization and extinction parameters on systems in equilibrium. One of the most striking results is that if we want to counteract the effects of habitat loss or increased dispersal resistance, the optimal conservation strategy is not to restore the original situation (that is, to create habitat or decrease resistance against dispersal), but rather to improve the quality of the remaining habitat in order to decrease local extinction rate. Optimality here pertains to metapopulation extinction time computed using the stochastic model. Chapter 4 also tells us that using the relaxation time of the deterministic Levins model as a surrogate for the metapopulation extinction time is not always warranted, which is not totally surprising, yet still somewhat disappointing, because the metapopulation extinction time is often hard to compute.

In writing chapter 4, my co-author Kees Nagelkerke and I initially viewed the Levins model in two different ways. To enable comparison with the stochastic model (with an explicitly finite number of patches) we wrote the Levins model as

$$\frac{dn}{dt} = cn\,(N - n) - en \tag{4}$$

where n refers to the occupied patches, N to all patches, c is the colonization rate, and e is the local extinction rate. My co-author considered the parameter N and the variable n in (4) to stand for the *density* of patches in the landscape. This interpretation, in which the total number of patches is infinite, is similar to the interpretation in papers where the effect of habitat destruction is studied (e.g. May 1991, Nee & May 1992, Hanski et al. 1996, Hess 1996a, Amarasekare 1998, Etienne 2000, chapter 3).

In contrast, I regarded the Levins model here simply as the deterministic limit of the stochastic model presented in chapter 4, where N and n represent the number of patches (interestingly, Levins himself used the second interpretation in 1969 (Levins 1969), the first in 1970 (Levins 1970) and both in 1971 (Levins & Culver 1971)). That is, as the number of patches in the stochastic model approaches infinity, the *expected* patch occupancy approaches the equilibrium patch occupancy of the deterministic Levins model, and the probability that the metapopulation becomes extinct approaches 0 (assuming that the metapopulation is deterministically viable). In this interpretation, there is a one-to-one correspondence between parameters in the deterministic and the stochastic model.

As long as the number of patches remains constant, our interpretations are practically the same. Difficulties arise when one wants to study the effect of habitat loss as in the references just cited. In my view, this evidently implies a reduction in the number of patches and hence the viability of the metapopulation. In my co-author's interpretation, this could imply either that the density of patches stays the same (the system of infinitely many patches is simply reduced at the edges) which has no effect on metapopulation viability, or that the patch density decreases (random patch destruction) which entails a decrease in metapopulation viability only if propagules may settle in unsuitable habitat, empty or occupied (see chapter 2).

Now, in comparing deterministic and stochastic Levins models, we were, among other things, interested in the effect of pure reduction of system size, which has, as stated above, no effect on metapopulation viability in the deterministic model, but does have some effect in the stochastic model. However, this could only be brought about by simultaneously reducing N and enlarging c in the stochastic model of chapter 4. We eventually refrained from doing so, and adopted (more or less) my interpretation accepting that a reduction in N entails both a direct (due to a reduction in colonization opportunities) and an indirect (due to a reduction in system size making stochastic extinction more probable) effect on metapopulation viability. Yet, it illustrates that precise mathematical formulation both demands and provides a clearer notion of what is modelled.

Chapter 4 forms a bridge between part II and III: it introduces the stochastic approach used in the chapters following it and it already provides us with a rule of thumb for metapopulation conservation as we stated above. In part III rules of thumb that can guide management of metapopulations play a central role. First, in chapter 5, rules of thumb are derived on the abstract level of colonization and extinction probabilities. Then, in chapter 6, some of these rules are tested on the less abstract level of two landscape characteristics that often mainly determine the probabilities of colonization and extinction, viz. patch size and interpatch distance.

The rules of thumb generated in chapter 5 can be summarized as: to optimize metapopulation extinction time, decreasing the risk of local extinction is preferable over increasing colonization probability and this should generally be done in the least extinction-prone patches; if changing local extinction risk is impossible, then increasing the colonization probability between the two least extinction-prone patches is most preferable. When extinction and colonization are related to patch size and interpatch distance in chapter 6 by mechanistic submodels of the corresponding processes, the last two of these rules transform into: the preferred strategies to optimize the metapopulation extinction time and the basic reproduction number are, firstly, increasing the size of the largest patch (which is least extinction-prone) and, secondly, decreasing the effective interpatch distance between the two largest patches. These rules are less strongly supported than those of chapter 5, and the first is even reversed if absolute (instead of relative) increases in patch size are considered. The reason for this is that in the mechanistic submodel for local extinction a large patch requires a large increase in size to substantially alter its local extinction probability. Since it is not *a priori* clear whether increases in patch sizes must be compared on an absolute or a relative basis, final conclusions cannot be drawn. Thus, chapters 5 and 6 are two parts of a trilogy, which would be completed

by a socio-politico-economic chapter taking into account e.g. the costs of habitat creation in relation to the size of the patch to which habitat is added. That is, it would then be *almost* completed, because there should also be an additional section on the important biological question how ecoducts and the like change the effective interpatch distance; this is usually merely hidden in the parameters. Although the trilogy is not complete, at least more light has been shed on the range of possible final conclusions and, more importantly, the conditions under which they are valid.

Whereas the first three parts of this thesis deal with general models of hypothetical meta-populations, and are somewhat academic, part IV concentrates on (statistical) methodology assisting in making model predictions, illustrated by two real case studies. Chapter 7 shows how the (relative) impact of human interventions can be predicted despite data of poor quality, for two amphibian species threatened by the reinstatement of an old railway track, using un-certainty analysis. Again, the measure employed, in this case metapopulation extinction time and the occupancy of each local population, plays a crucial role in deciding which scenario of human interventions is most preferable. It is also noted that the optimal scenario may differ for different species which aggravates the decision making process, because species must then be assigned a certain quantity representing their importance. Furthermore, the most important source of uncertainty is not the uncertainty in the effects of the railway track on extinction and colonization, as one might expect, but the uncertainty due to the inherent stochastic nature of the model combined with the uncertainty about the default parameter settings.

Chapter 8 demonstrates how Bayesian inference using Monte Carlo Markov Chain simu-lations can help in obtaining (estimates of posterior) probability distributions of meta-population model parameters based on a dataset, typical in metapopulation studies: a few years of data of occupancy (presence or absence) of the tree frog in 202 patches with many missing data. Parameter estimation methods were available before for such datasets (and surely formed a source of inspiration for this new method), but none of them could use all information in the dataset as well as provide a joint probability distribution of the parameters rather than a point estimate. Such a joint probability distribution is necessary for model pre-dictions that take into account the uncertainties about the model parameters. It does take some time to compute, however, so much that it would not have been possible within a reasonable time until recently. Therefore, the appendix of chapter 8 also supplies an efficient algorithm.

In moving from parts I and II to parts III and IV we can see a switch from continuous-time models to discrete-time models. This is not a coincidence: continuous-time models are usually easier to analyze and thus appear in more theoretically inclined texts, whereas discrete-time models are easier to interpret and easier to link to real-life situations and data and thus show up in more practically oriented accounts. One of the arguments, pertaining to realism, to opt for discrete-time models is the possibility of using two separate phases for extinction and colonization (see chapter 5).

Similar arguments may lead one to question whether the rescue effect and the Allee effect can be modelled in continuous time at all (as in chapters 2 and 3). Ray et al. (1991) claimed that rescue cannot occur in infinitesimal time and therefore used a discrete-time model (see

above). Taking their claim to a more general level that relates to both the rescue effect and the Allee effect, the impact of immigrants on population dynamics may not be appropriately modelled in continuous time; the colonization success may be a function of the sum of all immigrants that have arrived in a patch during the dispersal season (see chapter 6 for an example where this can be calculated relatively easily). Yet, apart from the fact that this can also be fully taken into account in a continuous-time model - which admittedly does make it much more difficult - I believe that chapters 2 and 3 show that such detail can be avoided.

In moving from parts I and II to parts II and IV we can also see a switch from spatially homogeneous (or even spatially implicit) to spatially heterogeneous models. Again, this is not a coincidence for the same reasons as stated above. Although the former models are very valuable for understanding metapopulation dynamics, I believe, along with e.g. Gotelli & Kelley (1993) and Fahrig & Merriam (1994), that spatially explicit models with variable patch size and quality are necessary for establishing helpful guidelines for metapopulation conservation. At the same time, I am reserved about adding even more detail, because it inevitably entails a loss of generality, and often requires unwarranted assumptions. Only in specific case studies, a tailor-made model is appropriate, and even then I would advise to have Ockham's razor handy.

Implications

What does this thesis contribute to metapopulation theory and to metapopulation management? Being aware of the fact that I may not be the right person to answer this question, I will endeavor to provide an answer, at the risk of being pretentious.

As far as metapopulation theory is concerned, I hope to have drawn attention to some underexposed aspects (the necessity of a careful definition of the SLOSS problem and the constant realization that different measures may yield different conclusions). Furthermore, I hope to have shown how existing models may be adjusted to a more satisfactory form that can be more easily extended (by incorporating the rescue and Allee effects into the Levins model). I also hope to have built more solid foundations and intermodel connections (by formulating more precise assumptions of the Levins model and examining the extensions that result when one of these assumptions is violated, by comparing the stochastic and deterministic versions of the Levins model, and by studying different modifications of the discrete-time stochastic model) and to have made some fairly original additions to the theory (patch preference, non-equilibria).

As far as metapopulation management is concerned, I would be content if due to my work those responsible for metapopulation management thought twice before they decided upon, for example, building an ecoduct. At the same time, I would be disappointed if they followed the rules of thumb mindlessly. Along with many skeptical scientists, particularly biologists, I do not believe (anymore) that there are rules of thumb upon which can be relied unconditionally. Yet, far from disposing of them altogether, I think they are very important; their value lies in summarizing a large part of our knowledge, the importance of which evidently increases with the robustness of the rules, and in provoking discussions. These discussions

already commence in chapters 5 and 6, and are hopefully taken up by others. If the reactions to presentations that I have held about this topic and the many requests for reprints (a large fraction of which comes, interestingly, from researchers working at national parks and zoos) are representative, I dare say that this will not be any problem. The discussions should deal with the many assumptions underlying the rules of thumb, when these assumptions are (approximately) valid and when they are clearly violated, and the extent to which such violations entail a change in the rules of thumb.

Furthermore, I would be pleased if uncertainty analysis of metapopulation model predictions became standard, especially in situations where expert judgment is the most significant source to parameterize a model. I hope that chapter 7 makes clear that there are sophisticated yet easily understandable and implementable techniques. Likewise, I would be satisfied if our Bayesian parametrization method were in vogue, in cases where data are available. With the example of a non-standard incidence function model, I hope to have demonstrated its generality.

Current and future developments

A thesis is never finished. There are many subjects that I would have liked to work (more) on. Here I want to name a few of them in arbitrary order, and discuss their (biological) relevance and my expectations of their influence on metapopulation theory and metapopulation management.

Time delay

By time delay I do not mean timelags that arise when systems are brought out of equilibrium (chapter 4). Rather, I refer to delays in colonization caused by seed banks (Perry & Gonzalez-Andujar 1993) or delays in animals noting changes in the landscape (such as a newly built corridor). Seed banks may represent a vital but easily ignored phase in colonization. In an extreme case, the metapopulation may appear to be extinct, while seeds are just waiting for the right time to germinate. Seed banks may thus be the evolutionary answer to wildly fluctuating environments. The impact of time delays caused by seed banks could be studied in a Levins-type model, using either delay differential equations, or an additional state variable and its differential equation.

One of the rules of thumb in chapter 6 dictates that the effective interpatch distance between the largest patches should be diminished. An ecoduct may establish this. Yet, if the patches are very large, it may take some time before the ecoduct is put to use by the inhabitants of the patches. With such a potential time delay in mind, the rule of thumb may be inappropriate if time is running out. Hence, I advocate testing the rules of thumb for robustness to such time delays.

Reintroduction

In cooperation with Michiel Wallis de Vries of the "Vlinderstichting" (Butterfly Foundation) in The Netherlands, I have modelled the fate of the metapopulation species *par excellence*, the Glanville fritillary (*Melitaea cinxia*) in Flanders, Belgium. We also considered some scenarios where the species was reintroduced in a few patches. It became very clear that reintroduction without changing the landscape (defragmentation, habitat creation) is a waste of energy, but also that an ambitious plan to refurbish the landscape stands no chance if the initial state of the system bears the risk of immediate extinction. In our case study, only one patch out of 17 (or more after habitat restoration) was occupied, so such plans must be accompanied by active reintroduction in other patches.

Evidently, this has to do with timelags in the system, which are the topic of chapter 4. Interestingly, the prediction in this chapter that the metapopulation reacts most slowly to changes in the colonization rate was confirmed in the case study: improving local conditions, particularly in the patches where the species still remained, was crucial and of much greater importance than creating connections from this patch to neighboring patches. This all suggests rules of thumb of when and where reintroduction is optimal which the reader can concoct himself. Testing the robustness of these rules of thumb seems worthwhile.
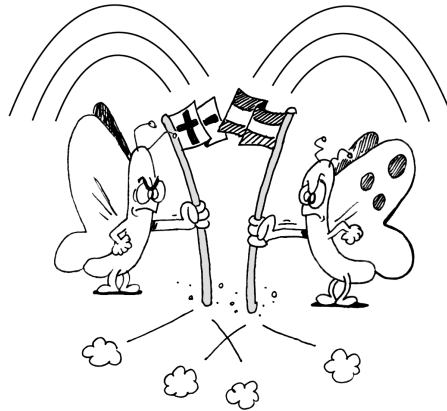
Escape effect

Correlation between extinctions and colonizations in general demand careful examination. One such correlation is the escape effect: due to deteriorating circumstances dispersers leave their home patch *en masse* thereby letting the population go extinct and found new colonies elsewhere. Such a correlation can be accounted for in the Levins model or the incidence function model by making extinction and colonization (partly) depend on a single parameter (perhaps patch area; see Ovaskainen 2002a) measuring the risk of extinction due to the escape effect. I expect that it might result in viability of an otherwise doomed metapopulation, because extinctions are accompanied by colonizations.

Although such a model is academically already intriguing, empirical support for the escape effect adds arguments for studying it. Such evidence is available. Kuussaari et al. (1996) already note that emigration increases with decreasing population size and Crone et al. (2001) find a negative value of the parameter b of the incidence function model in some years which means that emigration increases with decreasing patch size. Because emigration is usually assumed to increase with increasing patch size, this may be a sign of a threshold phenomenon: below and above a threshold patch size, emigration increases with decreasing respectively increasing patch size. Therefore, the escape effect might not always show up in b if there are many large patches that contribute heavily to a positive value of b; hence instead of using the standard incidence function model like Crone et al. (2001), a modified incidence function model with different b parameters for small and large patches could be a first step towards unravelling this phenomenon. A complicating matter is that the escape effect may also occur in large patches, because it really depends on population size rather

than patch size. Of course, population size can be modelled explicitly, but the question arises then whether there are data that match the complexity of the resulting model.

Multiple species

All the models in this thesis are single-species models. The results could evaporate when interactions between species are considered. Much work has already been done on multiple-species extensions of the Levins model (Levins & Culver 1971, Slatkin 1974, Hanski 1983, Sabelis et al. 1991, Nee & May 1992, Nee et al. 1997, Taneyhill 2000, Nagelkerke & Menken 2002) and many more extensions are conceivable, for example, competition and predator-prey interactions with an Allee effect acting on one or both species, as we announce in chapter 3. For single-species models, Bascompte & Solé (1996) showed that patch occupancy is lower and the extinction threshold is higher in spatially explicit models than in spatially implicit models. It remains to be seen whether this is also true for multiple-species models. A multiple-species incidence function model could help us extract vital parameters from multiple-species data, such as those in Van der Meijden & Van der Veen-Van Wijk (1997) and Lei & Hanski (1998).

Competitive colonization

It may turn out that in many cases multiple-species models are not warranted, particularly for competitive interactions. Gutiérrez et al. (2001), for example, recently argued that competitive interaction may be a rarity. They observed that four very similar butterfly species sharing the same host plant showed very different metapopulation structures suggesting that each species belongs to an independent metapopulation. Apparently, even for these similar species, habitat requirements are so subtle, that competitive interactions do not really exist; our speculations about such interactions just stem from a lack of knowledge.

Infectious disease

As I mentioned in the beginning of this introduction, one of the most prominent counterarguments in the discussion about corridors is the spread of infectious diseases (which is in fact a special case of a multiple-species interaction). Hess (1994, 1996b) showed with a modified Levins model that this objection must be taken seriously: often the fraction of occupied patches will have an optimum as a function of connectivity above which the disease benefits more from connectivity than the host. However, Gog et al. (2002) demonstrated that this model is very sensitive to the addition of an external source of infection (e.g. alternative hosts); with low rates of external infection the optimum already disappears. I also worked on this problem using the discrete-time stochastic model of chapter 5 and concluded that in a fraction of 0.03 to 0.35 of parameter space a global or (possible) local optimum of the metapopulation extinction time exists, which does not seem negligible (unpublished results). This calls for further investigation.

A downside to connectivity

Interestingly, this is a topic where the mathematical theory of infectious diseases and metapopulation theory, however similar their paradigm models (SIS-model and the Levins model, respectively) may be, differ in their approaches. Mathematical epidemiologists start out with local spread of the disease and add spatial arrangement in patches (e.g. Park et al. 2001), whereas metapopulation theorists begin with a metapopulation model and enrich it with a disease (e.g. Hess 1996b).

Suitable habitat

In models, our ability to distinguish suitable from unsuitable habitat is simply assumed, because metapopulation theory relies heavily on this assumption. But, if habitat requirements are so subtle as suggested above, how can we determine which patches are suitable and which are not? Not only may some suitable patches be actually unsuitable, but unsuitable, or previously unobserved patches could turn out to be suitable (see Akçakaya & Atwood 1997 for a habitat suitability model). Presence of a population seems evidence of suitability, but perhaps

the population is on its way to extinction because the habitat is no longer suitable, and presence at one time does not guarantee suitability at some other time when the patch is empty. Absence of a population provides no evidence at all. Any well-trained metapopulation theorist would hasten to teach us that empty habitat should not be interpreted as being unsuitable. However, it should neither been instantly regarded as temporarily empty, but surely suitable habitat.

That the suitability of patches may change over time, is recognized (Johnson 2000, Keymer et al. 2000, Amarasekare & Possingham 2001) and is even known to account for some cases of metapopulation dynamics (Stelter et al. 1997). In contrast, the uncertainty about suitability itself has not received so much attention. Yet, it seems fairly straightforward to incorporate in parameter estimation methods (like that of chapter 8), similarly to the incorporation of false observations of presence or absence (Moilanen 2002).

Defining patch boundaries

Matrix

In all of the models I have used, the matrix, i.e. the habitat surrounding the patches, is simply treated as unsuitable habitat, an unavoidable obstacle for dispersers, an obvious simplification of reality (Wiens 1997). Recent articles in *The American Naturalist* put the matrix on the agenda of both empirical and theoretical metapopulation research (Ricketts 2001, Vandermeer & Carvajal 2001), because it may substantially affect metapopulation persistence. As stated earlier in this introduction, corridors not only facilitate dispersal, but they can also function as suitable habitat for foraging and even reproduction. This then suggests that we can manipulate the longevity of a metapopulation by changing the matrix, which surely warrants a closer examination of the matrix.

One objective is incorporation in spatially explicit models. The influence of the matrix on dispersal success seems to be relatively easily accounted for. In incidence function models, for example, this can be done by using the effective instead of geometrical interpatch distance. Perhaps a measure should be developed analogous to the permittivity ε and permeability μ in

physics (describing a material's response to an applied electric or magnetic field respectively) to calculate the effective distance. Another option in incidence function models is to let the parameter that describes the average dispersal distance (α^{-1} in chapter 8) to take different values in spatial locations of different matrix types. Data of good quality may then allow for estimation of these parameters.

A matrix also offering opportunities for populations to establish (temporarily), is more difficult to model, because it challenges the distinction between patches and matrix, if the population supporting matrix cannot be treated as lower quality extensions of existing patches or as stepping stones. This may eventually give way to a new paradigm.

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Part I

A basic problem

1

On optimal size and number of reserves for metapopulation persistence

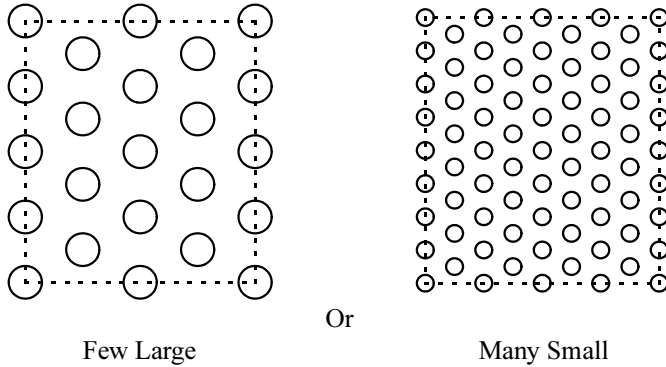RAMPAL S. ETIENNE & J.A.P. HEESTERBEEK

Abstract

Habitat fragmentation is generally believed to be detrimental to the persistence of natural populations. In nature management one therefore tends to prefer few large nature reserves over many small nature reserves having equal total area. This paper examines whether this preference is warranted in a metapopulation framework with circular reserves (patches) by formulating the dependence of metapopulation persistence on the size and number of reserves, which both depend on reserve radius if the total area is kept constant. Two measures of metapopulation persistence are used: R_0, the number of patches colonized by an occupied patch during its lifetime as an occupied patch, and T_e, the expected time to extinction. These two measures are functions of the extinction and colonization rates of the metapopulation. Several mechanisms for the extinction and colonization processes are formulated from which the dependence of these rates on reserve radius is calculated. It turns out that T_e generally increases with reserve radius for all mechanisms, which supports the preference of few large reserves. However, R_0 supports this preference only in the case of some special, rather unrealistic, mechanisms. In many other, more realistic, cases an intermediate reserve size exists for which metapopulation persistence measured by R_0 is optimal.

Introduction

Habitat fragmentation is generally believed to be detrimental to the persistence of plant and animal populations (e.g. Forney & Gilpin 1989, Gonzalez et al. 1998). Indeed, there are several mechanisms by which species may suffer from habitat fragmentation, such as in-

creased local extinction risk because of the larger impact of demographic and environmental stochasticity on smaller habitat patches; however, there are also (although fewer) mechanisms by which they may gain from it, such as recolonization of empty habitat patches by dispersers from still occupied patches (for more pros and cons of fragmentation see Verboom et al. 1993, Burkey 1996, and Discussion). The cumulative effect of these opposing mechanisms should therefore be studied, but this has scarcely been done. Thus, in nature management one still faces the question whether or to what degree fragmentation is harmful. The (main aspect of this) problem can be restated more neutrally and more precisely in the following way: given a fixed amount of area A_{tot} for nature reserves, what reserve size A_{res} and hence what corresponding number $N_{\text{res}} = \frac{A_{\text{tot}}}{A_{\text{res}}}$ of reserves of this size are optimal for conservation purposes, that is, offer the best chances for the species to persist? This question is the central question in this paper where two different measures of persistence will be used (R_0 and T_{e}; see the next section).

As stated, this question is similar to a problem commonly known as the SLOSS (single large or several small) problem, but contrary to the SLOSS problem, it allows intermediate solutions. To distinguish the question studied in this paper from the SLOSS problem and yet emphasize their close relationship, we will refer to the question in this paper as the FLOMS (few large or many small) problem (Figure 1).

Or

Few Large   Many Small

Figure 1. The FLOMS-problem for a hexagonal patch configuration: which configuration is optimal for metapopulation persistence, few large patches (FL) or many small patches (MS)? Here $R_{\text{MS}} = \frac{1}{2} R_{\text{FL}}$, but in both cases $L = 4R$. This implies that the amount of patch area within the dotted rectangle is the same in both cases. The area outside the dotted rectangle is not the same in both cases, but this difference will become smaller for a larger number of patches inside the dotted rectangle.

This paper differs from most of the SLOSS literature in another respect as well. The SLOSS debate has been concerned mostly with the question of which reserve configuration provides the largest biodiversity, i.e. species richness (e.g. Quinn & Harrison 1988, Baz &

Garcia-Boyero 1996); hence it is essentially a multiple-species debate. This paper, however, focuses on single species for which the optimal configuration (size and number of reserves) needs to be determined. Stacey et al. (1997) come closer to the question posed in this paper, because they compare few large populations with many small populations with the same total number of individuals using a single-species stochastic simulation model, and they conclude that if there is some connectivity an intermediate number of populations is optimal, that is, gives the longest mean time to extinction. However, keeping the total number of individuals constant is essentially different from fixing the total amount of reserve area.

We study the FLOMS problem here in a metapopulation setting with local extinctions in and recolonizations of identical circular patches in a lattice, which seems the most minimal setting in which the FLOMS problem makes sense. The aim of this paper is to explore several mechanisms for extinction and colonization in order to see how they scale with patch radius R, and hence to examine how patch radius affects the persistence of the metapopulation, in Hanski's (1991) words, to study their "compensatory effects".

We will discuss the implications and limitations of this approach for nature management at the end of the paper.

Methods

Metapopulation model assumptions and measures of persistence

The FLOMS problem can be stated as follows: is it better for metapopulation persistence to have a few large (FL) patches or many small (MS) patches, where the size and number of patches are such that the total habitable area A_h is the same in both cases? Two aspects of this question deserve scrutiny. The first is: how can a fair comparison between FL and MS be made? The second is: what does "better for metapopulation persistence" mean?

As regards the first aspect, in comparing an MS scenario and an FL scenario the only difference between FL and MS should be a difference in scale. This means that the patch configuration (i.e. *relative* patch positions) must be the same in both cases. However, this does not completely specify the *absolute* patch positions. So another assumption is needed. It seems most natural to assume then that not only the total habitable area is the same for MS and FL, but also that on the scale of several patches the habitable area *density* is the same. Therefore, a sufficiently large number of patches (for the MS case *and* the FL case) is required to meet this criterion.

To facilitate computations, we will make the following assumptions to be discussed later on:

1. All patches are identical (in size, shape, quality etc.) and they are circular with radius R.
2. The patches form a regular lattice with each patch having n nearest neighbors at equal center-to-center distance L. We will present results for a hexagonal lattice ($n = 6$) and

a square lattice ($n = 4$); see Figure 1. For other values of n some modifications of the formulae may be needed.

Figure 1 shows two scenarios with a hexagonal lattice of circular patches: one with a few large patches (lattice distance L_{FL}, patch radius R_{FL}) and one with many small patches (lattice distance $L_{\mathrm{MS}} = \frac{1}{2}L_{\mathrm{FL}}$, patch radius $R_{\mathrm{MS}} = \frac{1}{2}R_{\mathrm{FL}}$), but both with $\frac{R}{L} = \frac{1}{4}$. In this setting the scale parameter which differs between the FL and MS cases is the patch radius R. The FL and MS cases have equal area density because one can show that the total habitable area inside the dotted rectangle is given by $\frac{16\pi}{8\sqrt{3}}\frac{R^2}{L^2}$ in both cases. If one includes patches at the edges in full, the total habitable area is not exactly the same for FL and MS. Therefore, we assume that the number of patches is sufficiently large to make these edge effects negligibly small.

Let us move on to the second aspect of the question above: what does "better for metapopulation persistence" mean? The word "persistence" is used here in its informal, nonmathematical sense which is approximately equivalent to "survival". To answer the question we employ two measures of metapopulation persistence; "better for metapopulation persistence" then means a higher value of these measures.

The first measure is the expected time required by the metapopulation to reach extinction. This expected time to metapopulation extinction will be denoted by $T_{\mathrm{e}}^{\mathrm{meta}}$ or just T_{e}. Because larger patches have larger interpatch distances (see Figure 1), the probability that a patch will be able to colonize another patch will become smaller with increasing patch size, and the expected extinction time T_{e} of the metapopulation will become an increasing function of the expected time to local extinction $T_{\mathrm{e}}^{\mathrm{local}}$:

$$T_{\mathrm{e}} := T_{\mathrm{e}}^{\mathrm{meta}} \sim T_{\mathrm{e}}^{\mathrm{local}} \text{ for large } R. \tag{1}$$

As a second measure of metapopulation persistence we use the basic reproduction ratio R_0 which can be interpreted as the colonization potential of an occupied patch. More precisely, it is the average number of successful dispersers produced by a single occupied patch before its extinction, successful meaning that the dispersers reach a new (empty or occupied) patch and settle there. In short, R_0 is the number of colonizations from a single occupied patch. We call it a colonization potential because it bears some similarities to the population potential (Pooler 1987). R_0 reflects the capacity of the metapopulation to return to its original configuration after a disturbance to a very low occupation level. The benefits and limitations of R_0 as a measure of metapopulation persistence will be discussed later.

Suppose that a patch with local extinction time $T_{\mathrm{e}}^{\mathrm{local}}$ colonizes other patches at a constant rate c. Then R_0 equals the product of c and $T_{\mathrm{e}}^{\mathrm{local}}$:

$$R_0 = cT_{\mathrm{e}}^{\mathrm{local}}. \tag{2}$$

For the lattices studied here, R_0 is the same for every patch (ignoring edge effects), so the colonization potential of the entire metapopulation can be represented by the R_0 of a single patch.

The FLOMS problem can now be stated more precisely as the question of how the measures of persistence, T_{e} and R_0 depend on patch radius R. Therefore, we will formulate several plausible mechanisms for $T_{\mathrm{e}}^{\mathrm{local}}$ and c, and derive expressions for these parameters

as a function of patch radius R. Since the objective is only a comparison of R_0 and T_e for the FL and the MS cases, it suffices to know how the colonization and extinction parameters *scale* with R, i.e. proportionality constants are irrelevant.

We will derive these expressions for the hexagonal and square patch configurations described above using some assumptions which simplify computations, and present the results for this simple case. Then we will discuss how the results may be affected when these assumptions are relaxed. The assumptions, in addition to the two assumptions above, are the following:

3. There is no influence of dispersal on local population size (neither by emigration, nor by immigration; see however the remark made in the section about dispersal after depletion).
4. Spatial correlation of local extinction times plays no role in metapopulation persistence.
5. The colonization rate is constant and can be split up into c_{out} and c_{in}:

$$c = c_{out} c_{in} \tag{3}$$

where the parameter c_{out} is the emigration rate (the number of dispersers produced per unit time) per occupied patch, and the quantity c_{in} is the probability that a disperser reaches a patch and settles successfully. Then

$$\frac{R_0}{c_{in}} = c_{out} T_e^{local} \tag{4}$$

is the number of dispersers produced by an occupied patch during its lifetime as an occupied patch, and

$$R_0 = c_{out} c_{in} T_e^{local} \tag{5}$$

is the fraction of those dispersers eventually settling successfully.

6. Local populations are almost always at carrying capacity which is an increasing power function of R. More precisely, we will assume that populations grow quickly to the carrying capacity K, the maximum number of individuals a patch can sustain, and remain there most of the time. We will assume that $K \geq 1$, and that K scales linearly with area, that is,

$$K = C_1 R^2 \tag{6}$$

with $C_1 := \frac{1}{R_{min}^2}$ with R_{min} being the minimum patch radius to sustain one individual (here after C_i, with i any integer, will denote a species-specific and/or system-specific constant). Equation (6) is supported both theoretically and empirically (Kindvall & Ahlén 1992, and references therein, Hanski 1997). However, other empirical data do not display any significant relationship with R (Kindvall & Ahlén 1992, and references therein, Manne et al. 1998), while Hanski et al. (1996) find that

$$K \sim R. \tag{7}$$

Nevertheless, it will turn out that any positive power of R will suffice to reach the same qualitative conclusions.

Mechanisms for $T_{\mathrm{e}}^{\mathrm{local}}$

Local extinction can be due to demographic and environmental stochasticity, catastrophes and genetic processes such as random drift and inbreeding depression (Shaffer 1981). Here only demographic and environmental stochasticity are studied, although the impact of catastrophes (Wardle et al. 1997, Spiller et al. 1998) and genetic processes (Boecklen 1986, Frankham & Ralls 1998, Saccheri et al. 1998) can obviously play a role as well.

Demographic stochasticity
Using a stochastic differential equation with only demographic stochasticity, Foley (1997) derives the following dependence of the expected time to local extinction $T_{\mathrm{e}}^{\mathrm{local}}$ on patch radius R:

$$T_{\mathrm{e}}^{\mathrm{local}}(R) \sim e^{\varepsilon R^2} \tag{8}$$

with $\varepsilon^{-\frac{1}{2}}$ the characteristic radius of extinction. Foley (1997) finds that ε is proportional to $\frac{\alpha}{\mathrm{Var}(\alpha_1)}$. Here α is the (mean) net overall reproduction rate, and α_1 is the (mean) net reproduction rate for one individual; $\mathrm{Var}(\alpha) = \frac{\mathrm{Var}(\alpha_1)}{N}$, where N is the number of individuals. Equation (8) is valid as long as $\frac{\alpha}{\mathrm{Var}(\alpha_1)} \ln K$ is sufficiently large, K being the carrying capacity.

Environmental stochasticity
Using a stochastic differential equation with environmental stochasticity Foley (1997) derives

$$T_{\mathrm{e}}^{\mathrm{local}}(R) \propto e^{2\frac{\alpha}{\mathrm{Var}(\alpha)} \ln C_1 R^2} - 1 - 2\frac{\alpha}{\mathrm{Var}(\alpha)} \ln C_1 R^2 \tag{9}$$

with α again being the net overall reproduction rate.

If $\frac{|\alpha|}{\mathrm{Var}(\alpha)} \ln C_1 R^2$ is large and α negative, then (9) approaches

$$T_{\mathrm{e}}^{\mathrm{local}}(R) \propto \ln C_1 R^2. \tag{10}$$

For small $\frac{|\alpha|}{\mathrm{Var}(\alpha)} \ln C_1 R^2$ with α positive or negative (9) reduces to (see also Goodman 1987):

$$T_{\mathrm{e}}^{\mathrm{local}}(R) \propto (\ln C_1 R^2)^2, \tag{11}$$

which entails that $R_{\min}$ is indeed a threshold.
For large $\frac{|\alpha|}{\mathrm{Var}(\alpha)} \ln C_1 R^2$ with α positive (9) behaves according to

$$T_{\mathrm{e}}^{\mathrm{local}}(R) \propto R^{\mu} \tag{12}$$

with $\mu = 4\frac{\alpha}{\mathrm{Var}(\alpha)}$. See also Figure 2. Foley (1997) gives estimations of $\frac{\alpha}{\mathrm{Var}(\alpha)}$ which are usually between 0 and 1, but occasionally just below zero or very large.
Assuming environmental stochasticity but without a stochastic differential equation, Allen et al. (1992) also derive (12) where μ ranges between 1 and 2. Hanski uses (12) and reports μ-values of 0.92, 1.82, 4.60 for shrews (Hanski 1997) and 1.002, 2.118, 1.580 for butterflies

(Hanski 1992). Using the population viability analysis package ALEX (Possingham et al. 1992, Possingham & Davies 1995), Day & Possingham (1995) report a relationship similar to (12) with $\mu = 1$.

With respect to the joint effect of both environmental and demographic stochasticity, Foley (1997) notes that adding demographic stochasticity to environmental stochasticity hardly affects the dependence of $T_{\mathrm{e}}^{\mathrm{local}}(R)$ on R. This is due to the marginal effect of demographic stochasticity when population number is high.

Figure 2. Graphs of the extinction rate $e := \frac{1}{T_{\mathrm{e}}^{\mathrm{local}}}$ as a function of the rescaled patch radius $R' := \frac{2|\alpha|}{\mathrm{Var}(\alpha)} \ln C_1 R^2$ for environmental stochasticity. The solid curve represents the full relationship of equation (9) for negative α (thick curve) and positive α (thin curve). The dotted curves are the approximations. A. thick curve: (9), $\alpha < 0$, dotted curve: (10). B. thick curve: (9), $\alpha < 0$, thin curve: (9), $\alpha > 0$, dotted curve: (11). C. thin curve: (9), $\alpha > 0$, dotted curve: (12).

Mechanisms for $c_{\mathrm{out}}(R)$

For the dispersal rate from a patch $c_{\mathrm{out}}(R)$ several mechanisms can be imagined, such as dispersal due to the avoidance of competition, a constant fraction of dispersers, or resource depletion. A more phenomenological approach uses a maximum distance of dispersal. Let us take a closer look at these options.

Avoiding competition

Assume that the population is at carrying capacity where any excess reproduction does not vanish because of competition as in the logistic growth model, but it vanishes because of dispersal to avoid competition (Hansson 1991). This may be valid for territorial species. If the net reproduction rate is again denoted by α, then $c_{\text{out}}(R)$ is given by

$$c_{\text{out}}(R) = K\alpha \propto R^2, \tag{13}$$

again assuming that (6) holds.

Constant fraction of dispersers

If a constant fraction φ of the population disperses (e.g. juveniles leave a patch at the end of the season), and the population is assumed to be at carrying capacity which obeys (6), then

$$c_{\text{out}}(R) = K\varphi \propto R^2, \tag{14}$$

which is similar to (13).

Dispersal after depletion

If a patch is left only when the resources are depleted (Bell 1991, Hansson 1991), then for dispersal to come about, the resource recovery rate must be lower than its depletion rate. If this is indeed the case, then the dispersal rate is proportional to the number of organisms present in the patch, which itself is presumably proportional to this resource threshold and hence to area by assumption. Therefore,

$$c_{\text{out}}(R) \propto R^2, \tag{15}$$

which is similar to (13) and (14). If the patch is left by (almost) all organisms at the same time, then extinction and colonization become correlated, which alters expression (2) to $R_0 = Kc_{\text{in}} \propto R^2 c_{\text{in}}$ which will turn out not to affect the results of this paper qualitatively. However, this correlation between extinction and colonization may cause extinctions between patches to become correlated; in that case one of the assumptions above is violated, which may well affect the results of this paper.

Maximum distance of dispersal

Another approach, suggested by Vos et al. (1999), is based on the assumption that dispersers are only produced in an outer strip or ring of the patch. If R_{s} is the width of the outer strip of each circular patch, then $c_{\text{out}}(R)$ is proportional to the number of organisms living in this strip, and hence to the area of this strip (assuming e.g. constant density within the strip), which is $\pi R^2 - \pi(R - R_{\text{s}})^2$. Then,

$$c_{\text{out}}(R) = \begin{cases} C_2 R R_{\text{s}} \left(2 - \frac{R_{\text{s}}}{R}\right) & \text{for } R \geq R_{\text{s}} \\ C_2 R^2 & \text{for } R \leq R_{\text{s}} \end{cases} \tag{16}$$

where C_2 is a constant. So, assuming $R \geq R_{\text{s}}$, $c_{\text{out}}(R) \propto R$. This linear behavior with a threshold is qualitatively similar to diffusion with logistic growth. Indeed, in the latter case

one can show that the density of organisms is at the carrying capacity, except for a strip near the edge of the patch, which has an approximately constant width. Equation (16) seems to be supported by Woodroffe & Ginsberg (1998), who remark that patch edge size rather than population size determines the dispersal rate.

Mechanisms for $c_{\text{in}}(R)$

The probability that a disperser arrives at any patch conditional on leaving a certain patch, $c_{\text{in}}(R)$, involves at least three factors: the behavior (movement pattern, velocity) of the disperser, the risk the disperser runs while dispersing, and the settlement process (patch selection strategy). As far as the first factor is concerned, we will assume that the disperser moves at a constant speed. Two movement mechanisms will be considered: straight walk and random walk. With regard to the second factor, we will assume that there is a constant mortality rate λ. As for the third factor, for each of the two movement mechanisms one or two patch selection strategies will be chosen.

Straight walk
Straight walk is defined as movement at a constant velocity v (constant in magnitude and direction). The patch selection strategies to be discussed are nearest-neighbor dispersal, the "settlement-death" strategy, adapted from Vos et al. (1999) and the "pie-slice" strategy, implicit in Lindenmayer & Possingham (1995). For both strategies we have in a patch configuration with n ($n = 4, 6$) nearest neighbors

$$c_{\text{in}}(R, n) = \sum_i p_{\text{survival}}\left[d_i(R)\right] p_{\text{settlement}}\left[d_i(R), n\right] \tag{17}$$

where $p_{\text{survival}}(d_i)$ is the probability of surviving distance d_i to patch i (center-to-center distance), which is given by

$$p_{\text{survival}}(d_i) = e^{-\lambda_1\left(d_i - \frac{3}{2}R\right)}, \tag{18}$$

and where $p_{\text{settlement}}(d_i, n)$ is the probability of settlement at distance d_i, in which the two patch selection strategies differ. Here i refers to any patch surrounding the patch abandoned by the disperser, and λ_1 is the mortality rate per unit distance: $\lambda_1 = \frac{\lambda}{v}$. One can interpret λ_1^{-1} as the average distance traveled before dying. Expression (18) for $p_{\text{survival}}(d_i)$ is just the survival function with hazard function $\lambda(t = \frac{d_i}{v}) = \lambda$; the presence of $e^{\frac{3}{2}\lambda_1 R}$ in (18) is due to the fact that part of the trip of distance d_i lies within either the patch of origin (R) or the patch of destination (approximately $\frac{1}{2}R$; in fact it is a lower bound); intermediate patches are not considered.

Straight walk and nearest-neighbor dispersal
For nearest-neighbor dispersal, $p_{\text{settlement}}$ is simply

$$p_{\text{settlement}}(d_i, n) = \left\{ \begin{array}{ll} \frac{1}{n} & \text{if patch } i \text{ is a nearest neighbor} \\ 0 & \text{for all other patches.} \end{array} \right. \tag{19}$$

With lattice distance $L \equiv hR$, h being a constant reflecting the total area density which is the same in the FL and MS cases, we arrive at

$$c_{\text{in}}(R, n) = e^{-\lambda_1 R\left(h - \frac{3}{2}\right)}. \tag{20}$$

Straight walk and the settlement-death strategy
The settlement-death strategy assumes that dispersers prefer nearby patches over distant patches, and large patches over small patches. Mathematically:

$$p_{\text{settlement}}(d_i, n) = \frac{A_i e^{-\lambda_2 d_i}}{\sum_i A_i e^{-\lambda_2 d_i}} \tag{21}$$

where A_i is the size of patch i which will drop out from the equation because all patches are identical, and λ_2 is the constant settlement rate per unit distance. λ_2^{-1} can be interpreted as the average distance an individual wants to travel. Evidently λ_2^{-1} may depend on λ_1^{-1}: the willingness of a mouse to cross a large open grass land may be much smaller than its willingness to walk from stepping stone to stepping stone which is presumably safer. In (21) the normalization stems from the assumption that without death settlement will always occur. Although (18) is often used (e.g. MacArthur & Wilson 1967, Hanski 1997, where λ_1 is called α) and will also be used here, it should be noted that Hill et al. (1996) show some empirical data supporting a power function, i.e. $p_{\text{survival}}(d_i, n) \sim d_i^{-\chi}$ where χ is a positive parameter, while Gilpin & Diamond (1976) study various values for the parameter y in the expression $p_{\text{survival}}(d_i) \sim e^{-d_0^{-1} d_i^y}$, d_0 being a constant, and find that $y = 0.553$ fits their data best. However, neither Hill et al. (1996) nor Gilpin & Diamond (1976) provide an explanatory mechanism.

With again lattice distance $L \equiv hR$, $c_{\text{in}}(R, n)$ turns into

$$c_{\text{in}}(R, n) = \begin{cases} e^{\frac{3}{2}\lambda_1 R}\left(\frac{\lambda_2}{\lambda_1 + \lambda_2}\right)^2 & \text{for } (\lambda_1 + \lambda_2)Rh \ll 1 \\[2mm] \frac{n(\lambda_2 Rh)^2 \sin \frac{2\pi}{n}}{2\pi} e^{-\lambda_1 R\left(h - \frac{3}{2}\right) - \lambda_2 Rh} & \text{for } \lambda_1 Rh \gg 1 \text{ and } \lambda_2 Rh \ll 1 \\ & \left(\text{so } \frac{\lambda_2}{\lambda_1} \ll 1\right) \\[2mm] e^{-\lambda_1 R\left(h - \frac{3}{2}\right)} & \text{for } \lambda_2 Rh \gg 1. \end{cases} \tag{22}$$

See appendix A for details of the derivation of these approximations.

Straight walk and the pie-slice strategy
The pie-slice strategy is more spatially explicit. It assumes that dispersers choose a patch to disperse to with a probability proportional to its size as it appears on the horizon of the disperser. This leads to

$$p_{\text{settlement}}(d_i, n) = \frac{f_i \Delta \varphi_i(R, n)}{2\pi}. \tag{23}$$

Here, $\Delta \varphi_i$ is the angle of the horizon covered by patch i, and f_i is the fraction of the patch that is observable (i.e. not blocked from view by another patch) by the disperser from its patch of origin.

One can show (see appendix A) that the following asymptotic expression for $c_{in}(R, n)$ holds:

$$c_{in}(R, n) \approx \frac{n}{\pi} e^{-\lambda_1 R(h - \frac{3}{2})} \arccos\left(1 - \frac{1}{2h^2}\right) \quad \text{for } \lambda_1 Rh \gg 1. \tag{24}$$

No such approximation is possible for small $\lambda_1 Rh$.

Random walk

Random walk (i.e. diffusion) can also be used as an approach to $c_{in}(R)$ (see appendix B). One may use the solution to the stationary ($\frac{\partial x}{\partial t} = 0$) diffusion equation with a sink term $\sigma = -\lambda x$, where x is disperser density and λ again denotes the death rate. Let D be the diffusion coefficient outside the patches, and define $\lambda_1 := \sqrt{\frac{\lambda}{D}}$ which may be interpreted as the mortality rate per unit distance dispersed.

$c_{in}(R)$ is here defined as the quotient of the rate of dispersers entering destination patches and the rate of dispersers leaving the patch of origin, which is $c_{out}(R)$:

$$c_{in}(R) = \frac{\int_{\partial A_{in}} (D\nabla x, d\vec{A})}{c_{out}(R)} \tag{25}$$

where ∂A_{in} denotes the combined boundaries of the destination patches, and $(D\nabla x, d\vec{A})$ is the component of the gradient of the disperser density perpendicular to the destination patch boundary, i.e. the flux over the destination patch boundary. For the pie-slice strategy and sufficiently large $\lambda_1 Rh$, this reduces to (see appendix B)

$$c_{in}(R, n) \approx nR\sqrt{h - \frac{1}{2}} e^{-\lambda_1 R(h - \frac{3}{2})} \arccos\left(1 - \frac{1}{2h^2}\right) \quad \text{for } \lambda_1 Rh \gg 1. \tag{26}$$

Results: $T_e(R)$ and $R_0(R)$

With all functions of (2) having been defined, $T_e(R)$ and $R_0(R)$ can be calculated. Taking all suggested mechanisms for c_{out} into account, one obtains

$$c_{out}(R) \propto R^\gamma \tag{27}$$

with $0 \leq \gamma \leq 2$. Likewise, all dispersal strategies for $c_{in}(R)$ can be summarized as

$$c_{in}(R) \propto \begin{cases} e^{-\lambda_1 R(\beta h - h_0)} & \text{for } \lambda_i Rh \ll 1 \\ R^\nu e^{-\lambda_1 R(h - h_0)} & \text{for } \lambda_i Rh \gg 1 \end{cases} \tag{28}$$

with $\beta = 0$ or 1, $\nu = 0$, 1 or 2, and $h_0 = 1$, $\frac{3}{2}$, or $\frac{3}{2} - \frac{\lambda_2}{\lambda_1} h$; i stands for both 1 and 2. If $\beta = 1$, $\nu = 0$.

Now, with equations (8), (10), (11), (12), (27) and (28) equations (1) and (2) yield the following expressions for $T_e(R)$ and $R_0(R)$:

$$T_{\mathrm{e}}(R) \sim T_{\mathrm{e}}^{\mathrm{local}}(R) \text{ for large } R \propto \begin{cases} e^{\varepsilon R^2} & \left(\frac{\alpha}{[\mathrm{Var}(\alpha)]_1} K \gg 1\right) \\ R^\mu & \left(\frac{\alpha}{[\mathrm{Var}(\alpha)]} K \gg 1\right) \\ \ln C_1 R^2 & \left(\frac{-\alpha}{[\mathrm{Var}(\alpha)]} K \gg 1\right) \end{cases} \tag{29}$$

and

$$R_0(R) = c(R) T_{\mathrm{e}}^{\mathrm{local}}(R) \propto \overbrace{R^\gamma}^{c_{\mathrm{out}}(R)} \times \overbrace{\begin{cases} e^{-\lambda_1 R(\beta h - h_0)} & (\lambda_i R h \ll 1) \\ R^\nu e^{-\lambda_1 R(h-h_0)} & (\lambda_i R h \gg 1) \end{cases}}^{c_{\mathrm{in}}(R)} \times$$

$$\times \overbrace{\begin{cases} e^{\varepsilon R^2} & \left(\frac{\alpha}{[\mathrm{Var}(\alpha)]_1} K \gg 1\right) \\ R^\mu & \left(\frac{\alpha}{[\mathrm{Var}(\alpha)]} K \gg 1\right) \\ (\ln C_1 R^2)^2 & \left(\frac{|\alpha|}{[\mathrm{Var}(\alpha)]} K \ll 1\right) \\ \ln C_1 R^2 & \left(\frac{-\alpha}{[\mathrm{Var}(\alpha)]} K \gg 1\right) \end{cases}}^{T_{\mathrm{e}}^{\mathrm{local}}} \tag{30}$$

where in the $T_{\mathrm{e}}^{\mathrm{local}}$-term the first expression is valid for demographic stochasticity and the others are valid for environmental stochasticity, and $K = C_1 R^2$.

It is easy to see that $T_{\mathrm{e}}(R)$ increases with R for large R, so using this measure of meta-population persistence supports the widely adopted view that habitat fragmentation is harmful. However, this is generally not true if R_0 is used as the measure of metapopulation persistence. Consider the case with only environmental stochasticity. If we make the assumptions that $\lambda_1 > 0$ and $\gamma + \nu > 0$, then we see that there will be an optimal patch size if $R_0(R)$ is used as the measure of metapopulation persistence. As R increases, $R_0(R)$ will sooner or later enter the region for which $\lambda_i R h \gg 1$, where the decreasing exponential term of $c_{\mathrm{in}}(R)$ dominates causing $R_0(R)$ to decrease with R in that region. Mathematically:

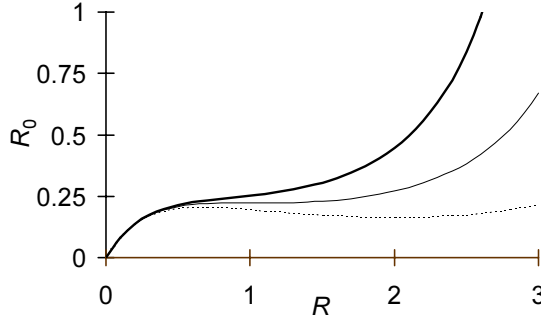$$R_0(R) \propto f(R) R^{\gamma+\nu} e^{-\lambda_1 R(h-h_0)} \quad \text{if } \lambda_i R h \gg 1 \tag{31}$$

where $f(R)$ is a function which increases with R, yet slower than an exponential function.

With only demographic stochasticity, and the same assumptions $\lambda_1 > 0$ and $\gamma + \nu > 0$, we get

$$R_0(R) \propto e^{-\lambda_1 R(h-h_0)+\varepsilon R^2} R^{\gamma+\nu} \quad \text{if } \lambda_i R h \gg 1. \tag{32}$$

It is not difficult to see that $R_0(R)$ will eventually increase monotonically with R, but for $\lambda^2 - 8\varepsilon(\gamma + \nu) > 0$, $\lambda := \lambda_1(h - h_0)$ there are two extrema as Figure 3 shows. This means that for demographic stochasticity, enlarging patch size may cause a (temporary) decrease in $R_0(R)$.

Before discussing the consequences of these findings, let us look at an example. Since in reality there is always some environmental stochasticity and the carrying capacity K of the patch is not extremely small (otherwise we would not regard it as habitable), (12) is the

Figure 3. Plots of $R_0(R) = Ce^{-\lambda R + \varepsilon R^2} R^{\gamma + \nu}$ versus R for several values of $\lambda^2 - 8\varepsilon(\gamma + \nu)$, where $\gamma + \nu > 0$, and $C = 1$: $\lambda^2 - 8\varepsilon(\gamma + \nu) < 0$ (thick solid curve), $\lambda^2 - 8\varepsilon(\gamma + \nu) = 0$ (thin solid curve), $\lambda^2 - 8\varepsilon(\gamma + \nu) > 0$ (dotted curve).

most widely applicable choice for $T_{\mathrm{e}}^{\mathrm{local}}$. Assuming straight walk and the settlement-death strategy (equation (A-1)), we arrive at

$$R_0(R) \propto R^{\gamma + \mu} e^{\frac{3}{2} \lambda R} \frac{S_1(\lambda_1 + \lambda_2)}{S_1(\lambda_2)} \tag{33}$$

which is plotted in Figure 4. The optimum value for $R_0(R)$ occurs when the derivative of $R_0(R)$ with respect to R equals 0:

$$\frac{dR_0(R)}{dR} = 0 \Rightarrow \frac{\gamma + \mu}{R} + \frac{3}{2}\lambda_1 = -\frac{d \ln\left(\frac{S_1(\lambda_1 + \lambda_2)}{S_1(\lambda_2)}\right)}{dR} \tag{34}$$
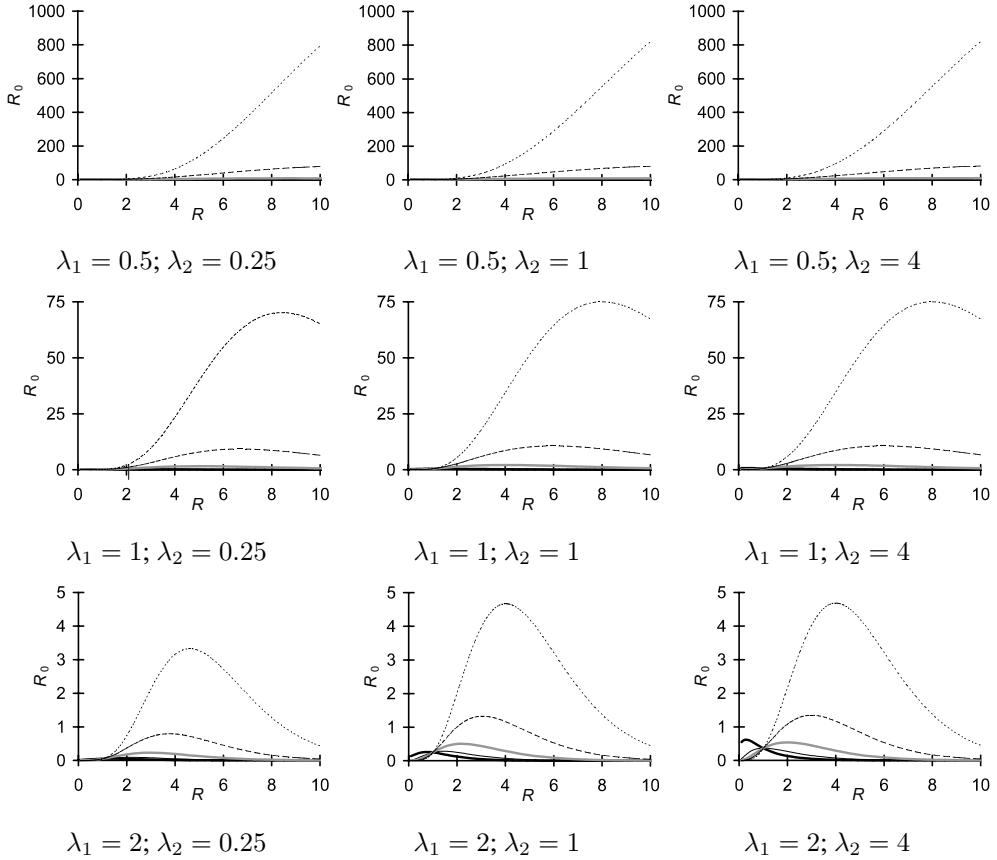
Using (A-2), this leads to the following condition for the optimal radius R_{opt}:

$$\begin{aligned} \frac{R_{\mathrm{opt}}}{\lambda_1^{-1}} &\geq \frac{\gamma + \mu}{h - \frac{3}{2}} \quad \text{for } \gamma + \mu > 0 \text{ and } \lambda_2 R_{\mathrm{opt}} h \gg 1 \\ R_{\mathrm{opt}} &= 0 \qquad \text{for } \gamma + \mu \leq 0 \end{aligned} \tag{35}$$

This optimal radius can indeed be seen in the plots of $R_0(R)$ in Figure 4. For the nearest-neighbor dispersal strategy, the equality sign in the first equation of (35) applies.

Discussion

The results show that two different measures of metapopulation persistence lead to two different opinions on the FLOMS problem if environmental stochasticity with or without demographic stochasticity is assumed. On the one hand, someone who wants to maximize the colonization potential R_0 will advocate an intermediate value of reserve size. On the other hand, someone wishing to postpone metapopulation extinction as long as possible will support maximizing reserve size, because this eventually increases the extinction time T_{e}.

Figure 4. Plots of $R_0(R)$ versus R using environmental stochasticity and the settlement-death strategy for different values of λ_1 and λ_2 and $k := \gamma + \mu$ ($k = 0$ (thick solid curve), $k = 1$ (thin solid curve), $k = 2$ (gray curve), $k = 3$ (dashed curve), $k = 4$ (dotted curve)). Here $h = 2$, but similar results are obtained with higher values of c; R_0 is just smaller and R_{opt} is shifted to the left.

A strong argument of proponents of "the larger, the better" is that computing the exact value of the reserve size which optimizes R_0 may be a difficult task because it depends on species-specific parameters; miscalculations may have large consequences, especially when the calculated optimal reserve size is relatively small. Maximizing reserve size seems much safer in this respect.

However, the conclusion "the larger, the better" is possibly only valid for large R, because T_{e} may have local optima at intermediate values of R. Of course, for any given area, there is a physical limit to the maximum reserve size that can be achieved. It is therefore possible

that one would choose this maximum reserve size in a given area, but that, at least in theory, a smaller size has a larger extinction time. We remark that there is no direct relation between the specific values of R where R_0 and T_e achieve their optimum.

If R_0 is small enough such that the metapopulation is doomed for all R, there is a third possible opinion, which states that there should be a larger amount of habitable area to be distributed, because the main problem in this case is habitat loss, not habitat fragmentation. Habitat fragmentation becomes the basic problem once R_0 ceases to be so small, that is, when a viable metapopulation is theoretically possible.

If the choice of the metapopulation persistence measure leads to disagreement even for a single species, one can expect even more discord when decisions influencing several species simultaneously need to be taken, especially when these species interact either directly or indirectly, for instance in a predator-prey system, or when a species is suffering from an infectious disease. In those cases habitat fragmentation may have additional effects which are difficult, if not impossible, to handle under the assumptions made here (see e.g. Hassell et al. 1991 and Hess 1996).

This discussion is only warranted of course if one accepts the basic reproduction ratio R_0 as a measure of persistence. R_0 has been found to be a useful measure of infectious disease persistence. In that context it is interpreted as the number of individuals which are infected by a single infectious host. It has been shown that there is the following threshold behavior: if $R_0 > 1$ then the disease persists, if $R_0 < 1$ then it cannot persist (Diekmann et al. 1990, Diekmann 1993). An important assumption for this threshold behavior at $R_0 = 1$ is that in the invasion phase, when the number of infected individuals is small, infectious particles do not fall on already infected hosts. If hosts are well mixed (i.e. they move around), this assumption can be reasonable for many infectious agents. Now, it seems natural to use R_0 and its threshold behavior at $R_0 = 1$ in a metapopulation context where patches take the role of hosts and dispersers take the role of spreading infectious particles. The analogous assumption for the threshold behavior at $R_0 = 1$ is then that in the invasion phase, when the patch occupation level is low, dispersers do not arrive in patches that are already occupied. Indeed, there are metapopulation models where this assumption is made, such as the Levins (1969) model, where all patches are supposed to be equally accessible. However, in the present setting, patches are fixed in a lattice and dispersal is distance-dependent, so patches are not equally accessible at all; even in a virgin environment (i.e. all patches except one are empty) dispersers will almost immediately settle in patches which are already occupied. Hence, the criterion $R_0 > 1$ no longer guarantees metapopulation persistence. This criterion would only be valid in the thought experiment in which patches are immediately replaced by a new empty patch every time a disperser arrives. So, the criterion now becomes $R_0 > b$ for a certain $b > 1$. It is, however, an unsolved mathematical problem to determine analytically the value of b for the fixed lattice structure discussed in this paper. For the related contact process with nearest-neighbor dispersal in a square lattice, upper and lower bounds for b have been found analytically (Durrett 1992, Durrett & Levin 1994), while numerical studies give $b \approx 1.65$ when $T_e^{\text{local}} = 1$ (Brower et al. 1978, Mollison 1986) and $b \approx 2.13$ when $c = 1$ (Durrett & Levin 1994). This shows that b depends on the spatial configuration (which determines T_e^{local} and c). Hence b may differ between the FL and MS cases! Thus, the combination of

R_0 and b instead of R_0 by itself needs to be specified to act as a persistence measure, and as the numerical examples above show, this can be done in practical applications.

Nevertheless, there are several reasons why R_0 by itself is worth considering as a persistence measure.

First of all, the condition for deterministic metapopulation *extinction*,

$$R_0 < 1 \qquad\qquad\qquad (36)$$

still holds, because, if less than one disperser sent out by a patch eventually settles in a patch, the metapopulation goes extinct. That is, (36) is a sufficient, but no longer a necessary condition for metapopulation extinction.

Secondly, the overestimation of persistence may not be as severe as it looks. In the case of an infectious disease, every infectious particle falling on an already infected host, is completely wasted; it will not contribute to the persistence of the disease. But in the metapopulation case, dispersers arriving in an already occupied patch can still serve to increase metapopulation persistence by contributing to the local dynamics. In particular, they facilitate the rescue of local populations on the brink of extinction (the rescue effect, Brown & Kodric-Brown 1977, Hanski 1983). In this respect, occupied patches act in a way as if they were empty, and the assumption for the threshold behavior at $R_0 = 1$ is not so severely violated as it seemed at first.

Thirdly, this contribution to local dynamics in the fixed lattice can also be an advantage in the following sense. Suppose that dispersers always arrive in empty patches, thereby satisfying the assumption for the threshold behavior at $R_0 = 1$. Then $R_0 > 1$ may still not lead to metapopulation persistence if there is an Allee effect, that is, if more than one disperser is needed to start off a new local population. On the other hand, in the fixed lattice structure with distance-dependent dispersal the Allee effect will be overcome quickly.

The results of this paper were derived for the most minimal setting in which the FLOMS problem makes sense. It remains to show that the results are qualitatively robust to relaxing the assumptions of this minimal setting. We will discuss the most prominent of them.

The mechanisms for $T_e^{\text{local}}(R)$, $c_{\text{out}}(R)$ and $c_{\text{in}}(R)$

The mechanisms for $T_e^{\text{local}}(R)$, $c_{\text{out}}(R)$ and $c_{\text{in}}(R)$ may be inadequate, especially the ones describing c_{in}. It is evident that the exponential part of $c_{\text{in}}(R)$ for large $\lambda_1 R h$ plays a crucial role in the existence of an intermediate optimal reserve size. If Hill et al. (1996) are right about a power function instead of an exponential function, then there is no finite non-zero optimal reserve size. Therefore, more research is needed to enable models of dispersal and patch selection strategies for different classes of organisms (such as small mammals, birds, butterflies, and plants) that more closely adhere to what these organisms actually do when dispersing.

The power-law behavior of $T_e^{\text{local}}(R)$ for environmental stochasticity as opposed to exponential increase is the other crucial factor for the existence of an optimal reserve size.

However, this behavior is not likely to change if local extinction were modelled in more detail.

As stated before, we used the (in our opinion) most minimal setting in which the FLOMS problem makes sense. This minimal setting comprises only the basics of the metapopulation concept for a single species: local extinction through demographic and environmental stochasticity, and recolonization driven by straight or random dispersal with a mortality risk. Of course, as mentioned previously, there are many more mechanisms by which fragmentation may be harmful or beneficial to metapopulation persistence. These mechanisms not only include single-species effects but also multiple-species effects, such as on the one hand increased local extinction risk because of the Allee effect, edge effects, minimum territory size, loss of key species in a food web and destabilization of mutualistic interactions, and on the other hand reduction of epidemic diseases, risk spreading in stochastic environments (bet hedging), increased genetic diversity, and the emergence of refugia from predators and competitors (Verboom et al. 1993, Burkey 1996). These complicated mechanisms, which cannot be treated easily under the assumptions of this paper, may lead to different conclusions about the optimal size and number of reserves for a metapopulation, and deserve therefore to be studied. The outcome of this paper may serve as a null hypothesis for such further studies.

Variance in patch size and patch distribution

The analysis in this paper does not take variance in patch size and the spatial distribution of patches into account. Variance in patch size was found by Day & Possingham (1995) to be of importance to the metapopulation extinction probability. They compared a scenario involving variable patch size with a scenario assuming equal patch size, where the total area of the eight patches under study is the same in both scenarios. For low colonization rates, systems with variable patch size are least extinction-prone, whereas for high colonization rates equal patch size provides the longest expected lifetime of the metapopulation. Variance in patch distribution has been studied by Adler & Nuernberger (1994), who reported a significant effect of this spatial distribution on metapopulation persistence. Day & Possingham (1995) found only minor effects, but their study was not as extensive as Adler & Nuernberger's and they used a different model.

What could be done in the present set-up to incorporate variance in patch size is to first restate the FLOMS problem by comparing few patches with a large mean patch size and many patches with a small mean patch size, and then to check the behavior of the mean $\overline{R}_0(\overline{R})$ where $\overline{R}$ is the mean patch size. The problem is what mean to choose for $\overline{R}_0$. Possibly, ideas from Gyllenberg & Hanski (1997), who study R_0 in a Levins-type metapopulation model with patches of different sizes, can be used for this purpose.

As far as patch distribution in space is concerned, the analysis in this paper, notably the formulation of the colonization potential which is representative of the entire metapopulation, cannot be extended in a simple way to cover patch configurations other than a regular lattice. It seems impossible to foretell whether the results will be similar or different from the regular pattern.

Influence of dispersal on extinction

The assumption of the absence of the influence of dispersal on local population size and thereby on extinction is too crude. Gyllenberg & Hanski (1992, 1997) have modelled the influence of dispersal on local population size mechanistically. However, the exercise of this paper cannot be repeated for their model because their model explicitly assumes a disperser pool which cannot be made consistent with distance-dependent dispersal (where distance in turn depends on R). Models which incorporate both patch-size-dependent local dynamics and distance-dependent dispersal are needed.

The connection between colonization and extinction may also be due to a different, although related, process. As Woodroffe & Ginsberg (1998) note, patch (edge) size rather than population size determines the dispersal rate, making the patch boundaries (and hence small patches) into population sinks, i.e. $\alpha \leq 0$. In this case Foley's (1997) models for the extinction rate prescribe behavior according to (11) rather than (12), but this does not change the qualitative dependence of R_0 and T_e on R.

Spatial correlation of local extinction times

The influence of spatial correlation of local extinction times on metapopulation persistence has been studied, but the literature suggests that it can go either way. For instance, using a Markovian metapopulation model with a finite number of patches, Akçakaya & Ginzburg (1991) state that "Three Small" may be better than "Single Large" if spatial correlation is not too large. This agrees with the results of Frank & Wissel (1998) who, using a model similar to Akçakaya & Ginzburg's, conclude that the metapopulation extinction time is significantly larger than local extinction time only if the dispersal distance exceeds the correlation length.

In this paper the total habitable area was taken to be constant; changing patch size meant changing patch density simultaneously. This is of course the essence of the FLOMS problem. But the question is whether this problem is relevant, and hence whether the results of this paper are in any way applicable. If one can start from scratch to develop a given (fixed) amount of natural area, FLOMS is indeed the relevant problem, waiving the fact that there are more degrees of freedom for refuge design than just reserve size, such as reserve shape and spatial pattern (see e.g. Wilson & Willis 1975*)*. In practice, however, nature is already present (although declining). Decisions need to be made about where to develop nature (often in exchange for the destruction of habitat elsewhere in favor of roads or buildings), about where to put a corridor, or just about what to do about habitat fragmentation and habitat loss in general. The first issue is predominantly a FLOMS problem, but the second and third may involve much more, one reason being that habitat loss and habitat fragmentation often occur together. It would be advantageous to distinguish the effects of habitat fragmentation from those of habitat loss in a process that involves both, perhaps along the lines of Bascompte & Solé (1996). But this is beyond the scope of this paper which just aimed to provide a view on the FLOMS problem in a minimal setting.

And all in all, most of the arguments above about the consequences of relaxing the assumptions in this minimal setting contribute to the robustness of the qualitative results that R_0 often shows a global optimum, whereas T_e usually does not. Until empirical data or refined models (disperser behavior in particular needs looking into) convincingly show otherwise, one must be very careful in choosing few large instead of many small patches, but also in interpreting this warning as a license to fragment habitat.

Acknowledgments

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Appendix A. Straight walk and exponential decline outside circular patches in a lattice

For the settlement-death strategy with straight walk in a hexagonal ($n = 6$) or square ($n = 4$) lattice, (17), (18) and (21) can be worked out to give

$$c_{\text{in}}(R, n) = e^{\frac{3}{2}\lambda_1 R} \frac{\sum_{k=1}^{\infty} \sum_{l=0}^{\infty} n e^{-(\lambda_1 + \lambda_2)Rh\sqrt{k^2 + l^2 - 2kl\cos\pi(1 - \frac{2}{n})}}}{\sum_{k=1}^{\infty} \sum_{l=0}^{\infty} n e^{-\lambda_2 Rh\sqrt{k^2 + l^2 - 2kl\cos\pi(1 - \frac{2}{n})}}} =: e^{\frac{3}{2}\lambda_1 R} \frac{S_1(\lambda_1 + \lambda_2)}{S_1(\lambda_2)}.$$
(A-1)

Note that h, the constant representing the density of habitable area, must be greater than $\frac{3}{2}$; this is always satisfied, since the patches should not overlap which entails $h > 2$ for $n = 4$ and $h > 12^{\frac{1}{4}} \approx 2$ for $n = 6$.

Approximation of the double sum $S_1(x)$ in (A-1) by its first term leads to

$$S_1(x) \approx n e^{-xRh} \quad \text{for large } xRh \tag{A-2}$$

which is a lower boundary of S_1. Approximation of $S_1(x)$ by the corresponding integral gives

$$S_1(x) \approx \frac{2\pi}{(xRh)^2 \sin\frac{2\pi}{n}} \quad \text{for small } xRh \tag{A-3}$$

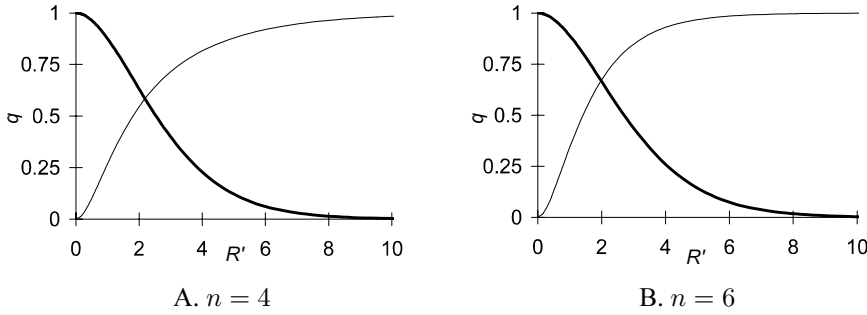which is an upper boundary of S_1. See Figure 5 for an impression of the accuracy of these

approximations. With (A-2) and (A-3) $c_{\mathrm{in}}(R,n)$ can be approximated by

$$
c_{\mathrm{in}}(R,n) = \begin{cases} e^{\frac{3}{2}\lambda_1 R}\left(\frac{\lambda_2}{\lambda_1+\lambda_2}\right)^2 & \text{for } (\lambda_1+\lambda_2)Rh \ll 1 \\ \frac{n(\lambda_2 Rh)^2 \sin\frac{2\pi}{n}}{2\pi}e^{-\lambda_1 R\left(h-\frac{3}{2}\right)-\lambda_2 Rh} & \text{for } \lambda_1 Rh \gg 1 \text{ and } \lambda_2 Rh \ll 1 \\ & \quad\text{(so } \frac{\lambda_2}{\lambda_1} \ll 1\text{)} \\ e^{-\lambda_1 R\left(h-\frac{3}{2}\right)} & \text{for } \lambda_2 Rh \gg 1. \end{cases}
$$
(A-4)

For the pie-slice strategy with straight walk, simple geometry teaches that $\Delta\varphi_i(R,n)$ is given by

$$
\Delta\varphi_i(R,n) = 2\arccos\left(1 - \frac{1}{2h^2 u_i^2}\right)
$$
(A-5)

where $u_i := \frac{d_i}{L}$ is the distance from patch center to patch center expressed in units of the lattice distance L. Note that $\Delta\varphi_i(R,n) \equiv \Delta\varphi_i$ is independent of the size of the patches.

$$ \text{A. } n = 4 \qquad\qquad\qquad \text{B. } n = 6 $$

Figure 5. Plots of approximations (A-2) and (A-3) to S_1 as functions of the rescaled patch radius $R' = xRh$ for $n = 4$ (A) and $n = 6$ (B). The approximations are plotted as quotients q relative to S_1: thin curve: $q(R') = \text{(A-2)}/S_1(R')$, thick curve: $q(R') = S_1(R')/\text{(A-3)}$. S_1 is defined in (A-1).

The fraction f_i depends on whether there are patches in front of patch i, blocking the view from the patch of origin. To facilitate straightforward calculation, we assume that

$$
f_i = \begin{cases} 0 & \text{if patch } i \text{ is entirely unobservable} \\ 1 & \text{if patch } i \text{ is partly or entirely observable} \\ \frac{1-\sum_{j=0}^{i-1}\Delta\varphi_j}{\Delta\varphi_i} & \text{if patch } i \text{ is the furthest patch, } i.e. \text{ if } \sum_{j=0}^{i-1}\Delta\varphi_j < 2\pi \le \sum_{j=0}^{i}\Delta\varphi_j \end{cases}
$$
(A-6)

The unobservable patches are easily found, because the quotient of their coordinates are either the same as that of a closer patch, or $\sum_{j=0}^{m}\Delta\varphi_j \ge 2\pi$ for a patch m which is closer than they are.

The survival probability $p_{\mathrm{survival}}(R)$ can be written in terms of u_i as well:

$$p_{\text{survival}}(R) = e^{-\lambda_1(d_i - \frac{3}{2}R)} = e^{-\lambda_1 R(u_i h - \frac{3}{2})}. \tag{A-7}$$
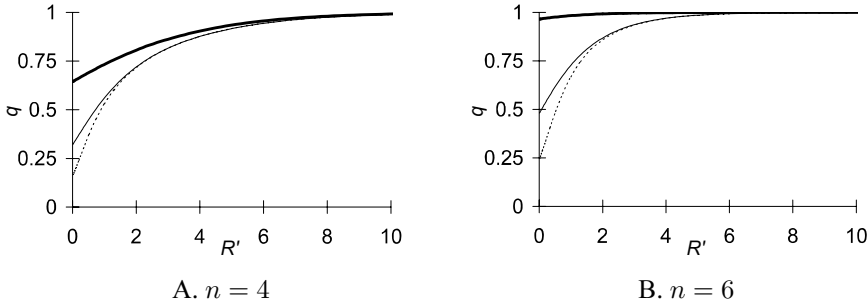
Thus,

$$c_{\text{in}}(R, n) = e^{\frac{3}{2}\lambda_1 R} \sum_i \frac{f_i}{\pi} e^{-\lambda_1 R u_i h} \arccos\left(1 - \frac{1}{2h^2 u_i^2}\right) =: e^{\frac{3}{2}\lambda_1 R} S_2. \tag{A-8}$$

A fairly good approximation to the sum S_2 in (A-8) is its first term for which all f_i and u_i are equal to 1:

$$S_2 \approx \frac{n}{\pi} e^{-\lambda_1 Rh} \arccos\left(1 - \frac{1}{2h^2}\right) \quad \text{for large } \lambda_1 Rh \tag{A-9}$$

as can be seen from Figure 6. No such simple approximation is possible for small $\lambda_1 Rh$ because of the dependence of the arccos term on h, which is also evident from Figure 6. With this approximation (A-8) yields

$$c_{\text{in}}(R, n) \approx \frac{n}{\pi} e^{-\lambda_1 R(h - \frac{3}{2})} \arccos\left(1 - \frac{1}{2h^2}\right) \quad \text{for } \lambda_1 Rh \gg 1. \tag{A-10}$$

Figure 6. Plots of the approximation (A-9) to S_2 as a function of the rescaled patch radius $R' = \lambda_1 Rh$ for $n = 4$ (A) and $n = 6$ (B). The approximation is plotted as a quotient q relative to S_2 for three values of h, that is $q = $ (A-9)$/S_2(R')$. S_2 is defined in (A-8). Thick curve: $h = 2$, thin curve: $h = 4$, dotted curve: $h = 8$.

Appendix B. Random walk and exponential decline outside circular patches in a lattice

Here expressions are derived for $c_{\text{in}}(R)$ using the stationary ($\frac{\partial x}{\partial t} = 0$, x is disperser density) diffusion equation (Carslaw & Jaeger 1959, Crank 1975) with a constant net death rate λ outside circular patches with radius R and diffusion coefficient D,

$$D\left(\frac{\partial^2 x}{\partial r^2} + \frac{1}{r}\frac{\partial x}{\partial r}\right) - \lambda x = 0 \tag{B-1}$$

subject to the boundary conditions

$$\lim_{r \to \infty} x(r) = 0, \tag{B-2}$$

$$\lim_{r' \downarrow R} D \frac{\partial x}{\partial r}\bigg|_{r=r'} = c_{\text{out}}(R). \tag{B-3}$$

The solution is, defining $\lambda_1 := \sqrt{\frac{\lambda}{D}}$,

$$x(r) = \begin{cases} C_1 + C_2 \ln r & \text{for } \lambda_1 = 0 \\ C_3 I_0(\lambda_1 r) + C_4 K_0(\lambda_1 r) & \text{for } \lambda_1 > 0 \end{cases} \tag{B-4}$$

where I_j and K_j are the jth-order modified Bessel functions of the first and second kind. The boundary condition (B-2) requires

$$C_1 = C_2 = C_3 = 0, \tag{B-5}$$

leaving only the solution

$$x(r) = C_4 K_0(\lambda_1 r). \tag{B-6}$$

The second boundary condition (B-3) gives

$$C_4 = -\frac{c_{\text{out}}(R)}{D\lambda_1 K_1(\lambda_1 R)}. \tag{B-7}$$

For (25) with the pie-slice strategy it follows that

$$
\begin{aligned}
c_{\text{in}}(R) &\approx \frac{-\sum_i \lim_{r' \uparrow d_i - \frac{1}{2}R} D \frac{\partial x}{\partial r}\big|_{r=r'} f_i \left(d_i - \frac{1}{2}R\right) \Delta\varphi_i}{c_{\text{out}}(R)} = \\
&= \sum_i \frac{DC_4\lambda_1 K_1\left[\lambda_1\left(d_i - \frac{1}{2}R\right)\right]\left(d_i - \frac{1}{2}R\right) f_i}{c_{\text{out}}(R)} \arccos\left(1 - \frac{1}{2h^2 u_i^2}\right) = \\
&= \sum_i \frac{K_1\left[\lambda_1\left(d_i - \frac{1}{2}R\right)\right]\left(d_i - \frac{1}{2}R\right) f_i}{K_1(\lambda_1 R)} \arccos\left(1 - \frac{1}{2h^2 u_i^2}\right)
\end{aligned} \tag{B-8}
$$

where either $f_i = 1$ for all i, or f_i is given by (A-6), and $\Delta\varphi_i$ and C_4 are given by (A-5) and (B-7) respectively. The term $\frac{1}{2}R$ is subtracted from d_i to account for the fact that part of d_i lies inside the patch of destination. For large $\lambda_1 Rh$ we can replace the sum in (B-8) by its first term and approximate K_1 to get

$$c_{\text{in}}(R) \approx nR\sqrt{h - \frac{1}{2}} e^{-\lambda_1 R(h - \frac{3}{2})} \arccos\left(1 - \frac{1}{2h^2}\right) \quad \text{for large } \lambda_1 Rh. \tag{B-9}$$

Part II

Insights from extensions of the Levins model

2

Local populations of different sizes, mechanistic rescue effect and patch preference in the Levins metapopulation model

RAMPAL S. ETIENNE

Abstract

In this paper three extensions of the Levins metapopulation model are discussed. 1. It is shown that the Levins model is still valid if patches contain local populations of different sizes with different colonization and extinction rates. 2. A more mechanistic formulation of the rescue effect is presented. 3. The addition of preference of dispersers for occupied or empty patches and its consequences for conservation strategies are studied.

Introduction

Space plays a very important role in biology in general and in population dynamics in particular. Yet, incorporating spatial structure in a mathematical model of a biological process has proven to be very complicated. Various approaches to incorporate spatial structure in population dynamics can be taken, one of which is the metapopulation approach (for an overview see Hanski & Gilpin 1997). A metapopulation is a population of several more or less loosely connected local populations with colonization and extinctions of these local populations analogous to births and deaths of individuals in each local population. This system of various populations (often living in discrete habitat patches) coupled by migration can be described in many ways: for example, space can be explicitly or implicitly taken into account and local dynamics can be supposed to play a role, being either identical or different for all local

populations. This leads to a whole range of metapopulation models from the very simple to the very complex. Here we will focus on probably the simplest model of all, the Levins (1969, 1970) model. Despite or perhaps by virtue of its obvious shortcomings, this single-species metapopulation model has proven to illustrate the key processes in metapopulation dynamics, it has been extended to study the effect of additional processes, and it has functioned as the basis of more complex metapopulation models involving for example several species. In this tradition, this paper aims to scrutinize some of the assumptions of the Levins model in order to better understand and extend it, and study its applicability in conservation biology. This requires first an exposition of the model, some of its properties, and its assumptions.

The Levins model

The classical Levins (1969, 1970) metapopulation model can be presented by the following differential equation:

$$\frac{dp}{dt} = cp(1-p) - ep \tag{1}$$

where p is the fraction of occupied patches, c is the colonization rate per occupied patch per empty patch, and e is the extinction rate per patch. The equilibria p^* of this model are

$$p^* = \begin{cases} 0 & R_0 \leq 1 \\ 1 - \frac{1}{R_0} & R_0 > 1 \end{cases} \tag{2}$$

where

$$R_0 := \frac{c}{e} \tag{3}$$

and the relaxation time τ is

$$\tau = \begin{cases} \frac{1}{e(1-R_0)} & R_0 \leq 1 \\ \frac{1}{e(R_0-1)} & R_0 > 1. \end{cases} \tag{4}$$

Both R_0 and τ can be used as (sometimes conflicting) measures of the persistence of a metapopulation (Etienne & Heesterbeek 2000).

The Levins model is said to be subject to the following assumptions (Hanski & Simberloff 1997, Gyllenberg et al. 1997):

1. There is no spatial structure: patches are not assigned a specific location in space and there is no correlation among local dynamics.
2. All patches and all local populations are identical in terms of their local dynamics.
3a. Local dynamics are ignored or local dynamics occur on a much faster time scale than metapopulation dynamics, implying that
3b. Migration has negligible effect on local dynamics.
4. Choice of patches by colonists is random (there is no habitat preference). With assumption 2, this assumption implies that colonization of empty patches occurs by mass action.

From these assumptions it follows that one can consider patches as either occupied or empty.

In this paper we will leave assumption 1 as it is, but we will examine the other assumptions in order, to see how modification of each assumption leads to a Levins-type model that can be compared to the original Levins model described by (1). We will first show that assumption 2 can be relaxed to incorporate local populations of different sizes with different colonization and extinction rates without changing the Levins model qualitatively as long as assumption 3 is maintained. Secondly, we will address assumption 3b in an attempt to remodel the rescue effect mechanistically within the Levins framework. Thirdly, we will substitute the mass action of assumption 4 by a different term which accounts for patch preference and see what its consequences are, especially for conservation purposes.

Different local population sizes

Assume that there are n size classes of local populations (either measured in number or density, i.e. number per unit area) and that an occupied patch with a local population of class i has colonization rate c_i and extinction rate e_i with $i = 1, ..., n$, so we allow for density-dependent colonization and extinction. By a patch of *type i* we will denote a patch with a population of class i. These patches can change from type i into type j with rate α_{ij} by birth or death ($\alpha_{ii} = 0$). By p_i we denote the fraction of patches with a population of size i. So different patch types only differ in the size of the population they contain, not in their habitat quality. In other words, the model is still unstructured as far as patches are concerned, but structured as far as local populations are concerned. Thus, we only relax or reinterpret assumption 2 to allow local populations of different sizes with different colonization and extinction rates. If a newly colonized patch is always of type 1 (1 can then be interpreted as the critical population size below which patches are considered empty), then the differential equations for the p_i become

$$\frac{dp_1}{dt} = \sum_{j=1}^{n} c_j p_j \left(1 - \sum_{j=1}^{n} p_j \right) + \sum_{j=1}^{n} \alpha_{j1} p_j - \sum_{j=1}^{n} \alpha_{1j} p_1 - e_1 p_1 \qquad (5a)$$

$$\frac{dp_i}{dt} = \sum_{j=1}^{n} \alpha_{ji} p_j - \sum_{j=1}^{n} \alpha_{ij} p_i - e_i p_i \quad \forall i \neq 1. \qquad (5b)$$

This is a generalization of Hanski's (1985) model and Hastings' (1991) simplified model which have $n = 2$.

Defining

$$p := \sum_{j=1}^{n} p_j, \qquad (6)$$

we can write down the differential equation for all occupied patches:

$$\frac{dp}{dt} = \sum_{i=1}^{n} c_i p_i (1 - p) - \sum_{i=1}^{n} e_i p_i. \qquad (7)$$

The system defined by (7) and (5b), where p_1 is eliminated using

$$p_1 = p - \sum_{j=2}^{n} p_j, \tag{8}$$

is equivalent to the system consisting of (5a) and (5b).

If we now assume that local dynamics are much faster (i.e. occur on a much shorter time-scale) than metapopulation dynamics, then we can set for all $i \neq 1$

$$\frac{dp_i}{dt} = 0 \;\Rightarrow\; \widetilde{p}_i = \frac{\sum_{j=1}^{n} \alpha_{ji} \widetilde{p}_j}{e_i + \sum_{j=1}^{n} \alpha_{ij}} \tag{9}$$

where $\widetilde{p}_1 = p - \sum_{j=2}^{n} \widetilde{p}_j$ and the ˜ denotes the quasi-equilibrium: the $\widetilde{p}_i$ only depend on time through their dependence on p. We can write (9) in matrix notation, dropping the ˜ for notational simplicity,

$$\begin{aligned} \overrightarrow{p} &= M\overrightarrow{p} + \overrightarrow{p_0} \\ \Rightarrow\; \overrightarrow{p} &= (I - M)^{-1} \overrightarrow{p_0} \end{aligned} \tag{10}$$

where

$$\overrightarrow{p} = (p_1, p_2, ..., p_n)^T \tag{11a}$$

$$\overrightarrow{p_0} = (p, 0, ..., 0)^T \tag{11b}$$

$$M_{1j} = -1 \quad \forall j \neq 1; \quad M_{ij} = \frac{\alpha_{ji}}{e_i + \sum_{j=1}^{n} \alpha_{ij}} \quad \forall i \neq 1, j \neq i; \quad M_{ii} = 0 \quad \forall i. \tag{11c}$$

Because of (11b) we have the following expression for p_i:

$$p_i = \left[(I - M)^{-1} \right]_{i1} p \tag{12}$$

and hence (7) turns into

$$\frac{dp}{dt} = c'p(1 - p) - e'p \tag{13}$$

with

$$e' := \sum_{i=1}^{n} e_i \left[(I - M)^{-1} \right]_{i1} \tag{14a}$$

$$c' := \sum_{i=1}^{n} c_i \left[(I - M)^{-1} \right]_{i1}. \tag{14b}$$

Thus, the Levins model is also valid for systems of patches with different local population sizes and effective extinction and colonization rates given by (14a) and (14b) as long as local dynamics are faster than metapopulation dynamics, immigration into occupied patches does not affect population size, and colonization (occurring by mass action) always turns empty patches into patches which can have only one population size.

Rescue effect

The rescue effect (occupied patches on the brink of extinction are rescued by immigrating dispersers, Brown & Kodric-Brown 1977) can be incorporated in the Levins model in the following way

$$\frac{dp}{dt} = cp(1-p) - ep[1 - r(\gamma)p] \tag{15}$$

where $r(\gamma)$ is a measure of the strength of the rescue effect which depends positively on γ, the rate of further colonization of occupied patches. The rates c and γ are related because colonization of empty patches and further colonization of occupied patches are both driven by migration (i.e. they may both be functions of the migration rate), but c and γ also reflect the impact of immigration on empty patches and on occupied patches respectively, which may be different. To name two possible causes of this difference: Allee effects may hamper the establishment of new colonies in empty patches, but they may not hamper the settlement of new colonists in already occupied patches; or there is a difference in the preference of migrants for occupied or empty patches (this case is treated from a different perspective in the next section).

Equation (15) describes phenomenologically that the local extinction rate decreases with increasing patch occupancy and increasing $r(\gamma)$. Often one sets $r(\gamma) \equiv r$ (Hanski 1983, Hanski & Gyllenberg 1993, Hanski et al. 1996, Gyllenberg & Hanski 1997, see however Ray et al. 1991 and Hess 1996) where r ranges between 0 (no rescue effect) and 1 (full rescue effect). However, it is far from obvious that the rescue effect is independent of the colonization rate γ. The simplest way to model a dependence on γ phenomenologically is a simple linear dependence on γ, i.e. $r(\gamma) \equiv a\gamma$, where $a > 0$ has the dimension of time,

$$\frac{dp}{dt} = cp(1-p) - ep(1 - a\gamma p). \tag{16}$$

This model may be valid for small $a\gamma p$, but is obviously inconsistent for large $a\gamma p$. Two phenomenological models which incorporate a dependence on the colonization rate γ and do behave acceptably for large $a\gamma p$ are, for example,

$$\frac{dp}{dt} = cp(1-p) - ep\exp(-a\gamma p) \tag{17}$$

(see e.g. Hanski & Zhang 1993) and

$$\frac{dp}{dt} = cp(1-p) - ep\frac{1}{1 + a\gamma p}. \tag{18}$$

For small values of $a\gamma p$ both models reduce to (16).

All these models are still quite *ad hoc*; there is no mechanistic basis for them. To derive a mechanistic model for the rescue effect, we start with a model with patches of two types: patches of low population number and patches of high population number. This model differs from the model in the previous section in that the transition between patches of type 1 and type 2 is not only due to birth, but also due to immigration from patches of type i with rate γ_i. Again, γ_i is certainly related to, but may be quite different from c_i. Mass action is now

assumed to apply to immigration into both types of patches. So we address assumption 3b: the effect of migration into occupied patches is no longer neglected, but it is still small to avoid a conflict with assumption 3a which we still need. This results in the following model (Hastings 1991, see also Hanski 1985):

$$
\begin{aligned}
\frac{dp_1}{dt} &= (c_1 p_1 + c_2 p_2)(1 - p_1 - p_2) - (\gamma_1 p_1 + \gamma_2 p_2) p_1 + \\
&\quad + \alpha_{21} p_2 - \alpha_{12} p_1 - e_1 p_1 \tag{19a} \\
\frac{dp_2}{dt} &= (\gamma_1 p_1 + \gamma_2 p_2) p_1 + \alpha_{12} p_1 - \alpha_{21} p_2 - e_2 p_2. \tag{19b}
\end{aligned}
$$

For all occupied patches combined, $p = p_1 + p_2$, we therefore get

$$
\frac{dp}{dt} = (c_1 p_1 + c_2 p_2)(1 - p) - e_1 p_1 - e_2 p_2. \tag{20}
$$

The system of the equations (19a) and (19b) is also adequately described by (20) and (19b) where p_1 is eliminated with $p_1 = p - p_2$. To facilitate comparison with the original Levins model described by (1), let us further assume that low level patches and high level patches are equal in their migration rates ($c_1 = c_2 = c$; $\gamma_1 = \gamma_2 = \gamma$), only differing in extinction rates ($e_2 < e_1$). The assumption that local dynamics are much faster than metapopulation dynamics yields in this case

$$
\begin{aligned}
\frac{dp_2}{dt} &= (p - p_2)(\alpha_{12} + \gamma p) - e_2 p_2 - \alpha_{21} p_2 = 0 \\
&\Rightarrow \quad \widetilde{p}_2 = \frac{\gamma p + \alpha_{12}}{\gamma p + \alpha_{12} + e_2 + \alpha_{21}} p. \tag{21}
\end{aligned}
$$

Substituting this expression and $p_1 = p - \widetilde{p}_2$ into (20) results in

$$
\begin{aligned}
\frac{dp}{dt} &= cp(1-p) - e_1 p \left(1 - \frac{\gamma p + \alpha_{12}}{\gamma p + \alpha_{12} + e_2 + \alpha_{21}} \right) - e_2 p \frac{\gamma p + \alpha_{12}}{\gamma p + \alpha_{12} + e_2 + \alpha_{21}} = \\
&= cp(1-p) - e'' p \tag{22}
\end{aligned}
$$

with

$$
e'' := e_1 \frac{e_2 + \alpha_{21}}{\gamma p + \alpha_{12} + e_2 + \alpha_{21}} + e_2 \frac{\gamma p + \alpha_{12}}{\gamma p + \alpha_{12} + e_2 + \alpha_{21}}. \tag{23}
$$

Without the rescue effect ($\gamma = 0$), we have

$$
e' := e_1 \frac{e_2 + \alpha_{21}}{\alpha_{12} + e_2 + \alpha_{21}} + e_2 \frac{\alpha_{12}}{\alpha_{12} + e_2 + \alpha_{21}}. \tag{24}
$$

which is equivalent to (14a) for $n = 2$. Comparing (23) with (24) shows us that the rescue effect reduces the effective local extinction rate by an amount

$$
\frac{e''}{e'} = \frac{1 + \dfrac{\gamma}{\alpha_{12} + e_2 + \alpha_{21} + \left(\frac{e_1}{e_2} - 1 \right)(e_2 + \alpha_{21})} p}{1 + \dfrac{\gamma}{\alpha_{12} + e_2 + \alpha_{21}} p}. \tag{25}
$$

Hence, the model with rescue effect can also be written as

$$\frac{dp}{dt} = cp\left(1 - p\right) - e'p\frac{1 + \frac{\gamma}{\alpha_{12} + e_2 + \alpha_{21} + \left(\frac{e_1}{e_2} - 1\right)(e_2 + \alpha_{21})}p}{1 + \frac{\gamma}{\alpha_{12} + e_2 + \alpha_{21}}p} \tag{26}$$

which for sufficiently small γp (which was presupposed above to avoid a conflict with assumption 3a) can be approximated by

$$\frac{dp}{dt} = cp(1 - p) - e'p[1 - r(\gamma)p] \tag{27}$$

where the rescue effect is now found to be

$$r(\gamma) := \left(\frac{1}{\alpha_{12} + e_2 + \alpha_{21}} - \frac{1}{\alpha_{12} + e_2 + \alpha_{21} + \left(\frac{e_1}{e_2} - 1\right)(e_2 + \alpha_{21})}\right)\gamma. \tag{28}$$

Thus, the rescue effect can be expressed in the Levins model mechanistically, in terms of the parameters of the local dynamics and the parameter measuring the impact of immigration into occupied patches.

Patch preference

The assumption of mass action (assumption 4) presupposes that all patches are equally accessible and that therefore the colonization of empty patches is proportional to the fraction of empty patches and the fraction of occupied patches. If, however, dispersers have a preference for either empty or occupied patches, assumption 4 is no longer warranted. Let us start with the following generalization of the Levins model:

$$\frac{dp}{dt} = cp\pi_1(p) - ep, \tag{29}$$

where $cp\pi_1(p)$ is the rate of colonization of empty patches. In the original Levins model $\pi_1(p)$ is assumed to be equal to the fraction of empty patches, i.e. $\pi_1(p) = 1 - p$, which expresses that there is no preference for occupied or empty patches. Here, however, we want to allow for such a preference. First we introduce the fraction $\pi_2(p)$ complementary to $\pi_1(p)$, where $cp\pi_2(p)$ is interpreted as the rate of further colonization of already occupied patches. The total rate of colonizations of both empty and occupied patches is simply cp, so obviously,

$$\pi_2(p) = 1 - \pi_1(p). \tag{30}$$

Now, we define the preference parameter $v \geq 0$ (as proposed by Hasibeder 1996 in the context of a malaria transmission model) by

$$\frac{p\pi_1(p)}{1 - p} = v\frac{p\pi_2(p)}{p}, \tag{31}$$

that is, the rate of colonization of empty patches per empty patch is assumed to be v times the rate of colonization of occupied patches per occupied patch. For the original Levins model $v = 1$; $v > 1$ means that empty patches are preferred over occupied patches, $v < 1$ means that this patch preference is reversed. Equations (30) and (31) yield

$$\pi_1(p) = \frac{1-p}{1-p+\frac{p}{v}}. \tag{32}$$

Inserting this expression in (29) we arrive at

$$\frac{dp}{dt} = cp\frac{1-p}{1-p+\frac{p}{v}} - ep \tag{33}$$

which has the equilibria

$$p^* = \begin{cases} 0 & \text{for } R_0 \leq 1 \\ \frac{1-\frac{1}{R_0}}{1-\frac{1}{R_0}\left(1-\frac{1}{v}\right)} & \text{for } R_0 > 1 \end{cases} \tag{34}$$

where R_0 is again given by (3) so it is independent of v as can be expected because R_0 is the number of patches colonized during the lifetime of an occupied patch in a *virgin* environment ($p = 0$) in which patch preference does not matter. We see from (34) that, although the criterion for the existence of a nontrivial equilibrium does not depend on v, the nontrivial equilibrium occupation level does depend on v: it is higher than in the original Levins model (which has $v = 1$) if $v > 1$, and it is lower if $v < 1$. The corresponding relaxation time is smaller than in the original Levins model if $v > 1$ but larger if $v < 1$:

$$\tau = \begin{cases} \frac{1}{e(1-R_0)} & \text{for } R_0 \leq 1 \\ \frac{1}{e\left(vR_0+1-2v-\frac{1-v}{R_0}\right)} & \text{for } R_0 > 1. \end{cases} \tag{35}$$

We now investigate how patch preference varies with habitat loss. To study the effect of habitat loss, the original Levins model has previously been altered to the equation (May 1991, Nee & May 1992, Hanski et al. 1996, Hess 1996)

$$\frac{dp}{dt} = cp(h-p) - ep \tag{36}$$

where h is the fraction of habitable patches. The equilibria of this system are

$$p^* = \begin{cases} 0 & \text{for } R_0 \leq \frac{1}{h} \\ h-\frac{1}{R_0} & \text{for } R_0 > \frac{1}{h} \end{cases} \tag{37}$$

where (3) again applies. We see here that the number of empty patches is independent of h for $h > \frac{1}{R_0}$:

$$h-p^* = \frac{1}{R_0} \tag{38}$$

Because the condition $R_0 > \frac{1}{h}$ (or equivalently $h > \frac{1}{R_0}$) is necessary and sufficient for metapopulation persistence, $h = \frac{1}{R_0}$ is called the eradication or extinction threshold. With

(38) this leads to the Levins rule (Hanski et al. 1996): "A necessary and sufficient condition for metapopulation survival is that the remaining number of habitat patches following a reduction in patch number exceeds the number of empty but suitable patches prior to patch destruction". This rule has been put forward by several authors (Lande 1987, Lande 1988ab, May 1991, Lawton et al. 1994, Nee 1994) and it also has its counterpart in epidemic theory (see e.g. Anderson & May 1991 and Diekmann & Heesterbeek 2000). However, Hanski et al. (1996) showed that the Levins rule no longer holds when the rescue effect is active; applying the Levins rule would lead to metapopulation extinction sooner (i.e. at a higher value of h) than expected from the observed number of empty patches. Moilanen & Hanski (1995) draw the same conclusion from simulation results of a model based on the incidence function model (Hanski 1994), while Lawton et al. (1994) argue for similar consequences of the Levins rule if patches can be temporarily uncolonizable, or if the colonization rates are spatially heterogeneous and patches with high colonization rates are destroyed first. Conversely, Lawton et al. (1994) also contend that if there is no dependence of patch destruction on colonization rate or if patches with low colonization rates are destroyed first, then the Levins rule is a safe conservation strategy: even more patches than proclaimed by the Levins rule can be destroyed without resulting in metapopulation extinction.

We explore here whether the Levins rule holds in the case of patch preference. In this case we have

$$\pi_2(p) = h - \pi_1(p) \tag{39}$$

which together with the analog of (31)

$$\frac{p\pi_1(p)}{h-p} = v\frac{p\pi_2(p)}{p} \tag{40}$$

reduces (29) to

$$\frac{dp}{dt} = cph\frac{h-p}{h-p+\frac{p}{v}} - ep. \tag{41}$$

This model has equilibria

$$p^* = \begin{cases} 0 & \text{for } R_0 \leq \frac{1}{h} \\ h\frac{h-\frac{1}{R_0}}{h-\frac{1}{R_0}\left(1-\frac{1}{v}\right)} & \text{for } R_0 > \frac{1}{h} \end{cases} . \tag{42}$$

Hence the fraction of empty patches in the nontrivial equilibrium is

$$h - p^* = \frac{\frac{h}{vR_0}}{h - \frac{1}{R_0}\left(1-\frac{1}{v}\right)} \tag{43}$$

which increases for decreasing h if $v > 1$ and decreases for decreasing h if $v < 1$. See Figure 1 which also shows the result obtained from the rescue effect model (15) for the nontrivial equilibrium p^* with $r \equiv r(\gamma)$, that is,

$$h - p^* = \frac{1-hr}{R_0 - r} , \tag{44}$$

to facilitate comparison with Hanski et al. (1996). So the warning of Hanski et al. (1996) not to use the Levins rule can also be based on a preference of empty patches over occupied

patches. However if occupied patches are preferred over empty ones, then the Levins rule seems a fairly safe conservation strategy.

Figure 1. The relationship (43) between the fraction of empty patches $h - p^*$ and the fraction of suitable habitat h for the Levins model with patch preference. Here $R_0 = 4$, $v = 2$ for the case in which empty patches are preferred, and $v = 0.5$ for the case in which occupied patches are preferred. $v = 1$ means no preference and is equivalent to the original Levins model. For comparison with the result of Hanski et al. (1996), the curve described by (44) for the rescue effect as in (15) with $r(\gamma) \equiv r = 0.3$ is also plotted. For $h \leq \frac{1}{R_0}$ all curves coincide: the metapopulation is extinct.

It remains to see what happens if both patch preference and the rescue effect are present because patch preference also affects the rescue effect. To study this, let us incorporate patch preference into the rescue effect system from the previous section defined by (19a) and (19b) with $c_1 = c_2 = c$, $\gamma_1 = \gamma_2 = \gamma$ and let the fraction of suitable patches again be denoted by h:

$$\frac{dp_1}{dt} = cph\frac{h - p}{h - p + \frac{p}{v}} - \gamma ph\frac{\frac{p_1}{v}}{h - p + \frac{p}{v}} + \alpha_{21}p_2 - \alpha_{12}p_1 - e_1p_1 \tag{45a}$$

$$\frac{dp_2}{dt} = \gamma ph\frac{\frac{p_1}{v}}{h - p + \frac{p}{v}} + \alpha_{12}p_1 - \alpha_{21}p_2 - e_2p_2. \tag{45b}$$
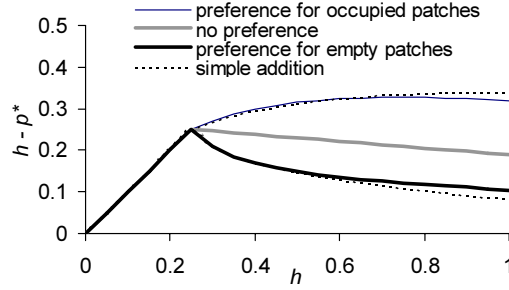
For a small rescue effect, the same approach as above results in

$$h - p^* = \frac{\frac{h}{vR_0}(1 - hr)}{h - \frac{1}{R_0}\left(1 - \frac{1-hr}{v}\right)} \tag{46}$$

for the nontrivial equilibrium p^* with $r \equiv r(\gamma)$ given by (28). See Figure 2 for the combined effect (46) of patch preference and rescue effect. The curves obtained by simply adding the separate effects [i.e. (43) + (44) − (38)] are also shown. For h close to 1, these curves deviate slightly more from the original Levins model than do the curves representing (46), while for h close to $\frac{1}{R_0}$ they deviate slightly less. In other words, for h close to $\frac{1}{R_0}$, patch preference is dominating disproportionally, with the rescue effect taking over as h approaches 1.

Figure 2. The relationship between the fraction of empty patches $h - p^*$ and the fraction of suitable habitat h for the Levins model with both patch preference and rescue effect as in (15) with $r(\gamma) \equiv r = 0.3$. As in Figure 1, $R_0 = 4$, $v = 2$ for the case in which empty patches are preferred, and $v = 0.5$ for the case in which occupied patches are preferred. $v = 1$ means no preference and is equivalent to (44), the result in the original Levins model with rescue effect, so the dotted curve in Figure 1 and the gray curve in this Figure are the same. The solid curves are drawn using (46) while the dotted curves represent simple addition of the curve of the rescue effect and the curves of patch preference of Figure 1. For $h \leq \frac{1}{R_0}$ all curves coincide: the metapopulation is extinct.

Figure 3. The relationship between the fraction of empty patches $h - p^*$ and the fraction of suitable habitat h for the Levins model with both patch preference for occupied patches and rescue effect as in (15) with $r(\gamma) \equiv r = 0.5$ and $v = 0.6$. The curve described by (38) for the original Levins model without patch preference and rescue effect is also shown. For $h \leq \frac{1}{R_0}$ both curves coincide: the metapopulation is extinct.

Thus, the Levins rule still seems a fairly safe conservation strategy when occupied patches are preferred and the rescue effect is weak, but should not be taken seriously when the rescue effect is strong and/or empty patches are preferred. When occupied patches are preferred and

the rescue effect is sufficiently strong, the interesting situation of Figure 3 may arise where the Levins rule is a disastrous instrument when there is little habitat destruction (h close to 1), but a relatively safe guideline when substantial destruction of habitat has already taken place (h closer to $\frac{1}{R_0}$).

Discussion

The first result of this paper shows that the assumption of identical population sizes can be relaxed within the Levins framework. Local populations need not grow quickly to the same carrying capacity, but they should quickly reach a pseudo-equilibrium population size distribution. The c and e in the Levins model can therefore also stand for effective colonization and extinction rates, which are averages over the patches.

Size-structured models reducible to the Levins model have been constructed before (e.g. Gyllenberg & Hanski 1992, Hanski & Zhang 1993, Gyllenberg & Hanski 1997, Casagrandi & Gatto 1999), but they differ from the model presented here in several aspects. Firstly, they all assume a pool of dispersers in which there may be mortality, whereas dispersal is only implicit in our model. Secondly, Hanski & Zhang (1993) and Gyllenberg & Hanski (1992, 1997) model population size as a continuous variable while population size is divided in discrete size classes here. Thirdly, this paper allows transitions from any patch type i to any other patch type j with rate α_{ij}, thus being more general than the papers mentioned which at best allow partial catastrophes (Gyllenberg & Hanski 1992, 1997). Finally, Hanski & Zhang (1993) and Gyllenberg & Hanski (1992, 1997) appeal to a time-scale argument like assumption 3 to make population size *identical* in all occupied patches; in this paper, the time-scale argument is evoked to create a *distribution* of population sizes which only depends on the total number of occupied patches (or, alternatively, on p_1). This distribution allows for an effective extinction rate e' and colonization rate c' not observed in the papers mentioned.

Models describing the rescue effect mechanistically are also no rarity (e.g. Hastings 1991, Gyllenberg & Hanski 1992, Gyllenberg & Hanski 1997, Lande et al. 1998), but none have been reduced to a one-dimensional Levins-type model in order to facilitate comparison with the original Levins model. The second result of this paper demonstrates just this: the rescue effect can be mechanistically incorporated into the Levins model. The phenomenological model (15) appearing in the literature is then seen to be valid for a small rescue effect.

In the model with different local population sizes it was assumed that colonization of empty patches always results in patches containing a population of class 1. This is in line with assumption 3b; as soon as patches reach a size in class 1 immigration is supposed to be unimportant. In the related model for the rescue effect, however, immigration is the vital force driving the rescue effect, so it seems inconsistent that empty patches can become of type 2 purely by immigration only indirectly (through type 1) but not directly. It is possible to incorporate such a direct change in the model, but this does not change the results qualitatively.

The third result of this paper is that patch preference in the Levins model can lead to both higher (if empty patches are preferred) and lower (if occupied patches are preferred)

occupation levels and relaxation times. In the latter case the Levins rule can be applied if the rescue effect is small relative to the occupied patch preference effect, whereas in the former case the Levins rule may lead to extinction at a higher fraction of habitable patches than expected from the observed fraction of empty patches.

The Levins rule is only relevant if (39) holds which means that dispersal to both suitable and unsuitable patches is possible which is the case if dispersers are not able to select suitable habitat, e.g. plants and small animals. This was actually already tacitly assumed in (36). If there is only dispersal to occupied or empty suitable patches but not to empty unsuitable patches (i.e. if dispersers are able to select suitable habitat only, which may apply to birds and larger mammals), then we must insert (30) into (40) and replace $h - p$ by $1 - p$ so we simply get (31). Hence (34) holds; consequently we find no effect of decreasing h on metapopulation survival in this case, provided that, among other things, R_0 does not depend on h. However, this provision needs scrutiny because $R_0 = \frac{c}{e}$ may very well depend on h. For the local extinction rate e, independence of h seems a reasonable assumption to start with, but for the colonization rate c one may have some doubts. If habitat destruction is random, then interpatch distances will increase, so the colonization rate is destined to decrease with decreasing h. In the Levins model the independence of the colonization rate on h is assumed from the outset, because the Levins model is not spatially structured. The warning against the Levins rule should therefore be reinstated because space often does appear to matter.

Although the Levins model is undoubtedly not very realistic biologically, this does not mean that it is irrelevant. Its weakness (its simplicity) is also its strength. As mentioned in the introduction, the Levins model has been frequently used to illustrate the key processes in metapopulation dynamics, processes that are described by the model, as well as processes that it does *not* capture. For instance, the discussion of the Levins rule clearly shows which properties of the model are representative of metapopulation dynamics, and which are due to oversimplification. More generally, by showing that some extensions of the Levins model which violate one (or more) of the assumptions underlying the model can be written as a Levins model with rescaled parameters while others can be cast in a model of the Levins type, this paper has hopefully added some insight into the action radius of the Levins model.

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3

Allee effects in metapopulation dynamics revisited

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Introduction

The paradigm model of metapopulation theory is undoubtedly the Levins (1969, 1970) patch occupancy model in which the habitat consists of many distinct patches, which can be either empty or occupied by a population of the species under consideration. An occupied patch can become empty by extinction of the local population and an empty patch can become occupied after colonization by dispersers from extant populations. This model has been extended in many ways to study the effect of the extension, which often adds more realism to the model, on metapopulation dynamics (Levins & Culver 1971, Slatkin 1974, Hanski 1983, Sabelis et al. 1991, Hanski et al. 1996, Gyllenberg & Hanski 1997, Holt 1997, Nee et al. 1997, Amarasekare 1998, Etienne 2000, Amarasekare & Possingham 2001, Vandermeer & Carvajal 2001). One of the extensions, by Amarasekare (1998), incorporates the Allee effect (e.g. Stephens et al. 1999) into the Levins model. This is an important extension because the Allee effect directly influences colonization and therefore metapopulation persistence. Although the model by Amarasekare (1998) exhibits the desired behavior to some degree, we believe that the incorporation of the Allee effect is rather phenomenological and not entirely satisfactory. We will point out the drawbacks of this model more precisely and then present a more mechanistic alternative model without these drawbacks.

The Levins model

The Levins model is usually written as

$$\frac{dp}{dt} = mp(1-p) - ep \tag{1}$$

where p is the fraction of occupied patches, m is the colonization rate of empty patches, and e is the extinction rate of occupied patches. Defining $\beta := \frac{m}{e}$, this model has the nontrivial equilibrium,

$$p^* = 1 - \frac{1}{\beta} := K. \tag{2}$$

We call this K because of its interpretation as the metapopulation carrying capacity. This equilibrium is stable as long as $\beta > 1$ (if $\beta \leq 1$ the trivial equilibrium $p^* = 0$ is stable).

The Levins model with Allee effect - Amarasekare (1998)

In the Levins model the fraction of occupied patches increases when p is close to 0. Amarasekare (1998) considers this aspect of the Levins model to be invalid in small metapopulations where the metapopulations may suffer a disproportionate reduction in colonization success at low p, that is, an Allee effect. She assumes that there is a threshold occupancy T below which the fraction of occupied patches decreases and above which it increases, and models this as follows:

$$\frac{dp}{dt} = (mp\,(1-p) - ep)\left(\frac{p}{K} - \frac{T}{K}\right) \tag{3}$$

where T is restricted to $0 < T < K$.

This model has the following nontrivial equilibria

$$p^* = T \tag{4}$$
$$p^* = K \tag{5}$$

which are unstable and stable respectively for $\beta > \frac{1}{1-T}$ which is just the condition $T < K$.

Indeed, equation (3) makes the metapopulation shrink when below the threshold occupancy T and makes it grow above it. It has, however, some drawbacks:

1. The model is not defined for $m < e$ because of the restriction $0 < T < K$. Without this restriction, the metapopulation grows for $m < e$ when $p < T$; hence the trivial equilibrium $p^* = 0$ is not stable.
2. It does not reduce to the original Levins model when $T = 0$.
3. The threshold occupancy is set beforehand; it is not a threshold caused naturally by (meta)population dynamics (see also point 4). In contrast, the metapopulation carrying capacity K is set by metapopulation dynamics (see (2)).
4. The term adding the Allee effect is descriptive rather than mechanistic. An Allee effect at the population level in each patch, at the time of colonization, seems to be the only possible cause of an Allee effect at the metapopulation level (apart from Allee-like effects caused by for example the rescue effect, see Gyllenberg & Hanski 1997). This is also the example that Amarasekare mentions. To incorporate the Allee effect into the Levins model without detailed modelling of the local population dynamics, we should then

a. change only the colonization term, and
b. have the threshold be determined naturally by metapopulation dynamics.

The Levins model with Allee effect - our alternative

To come to a more satisfactory formula for the Levins model with Allee effect, we first rewrite the Levins model as

$$\frac{dp}{dt} = m_{\text{out}}pm_{\text{in}}\left(1 - p\right) - ep \tag{6}$$

where we can identify the term $m_{\text{out}}p$ with the flow of dispersers and the term $m_{\text{in}}(1 - p)$ with the probability that a disperser arrives in an empty patch (as opposed to an occupied patch) and colonizes it ($1 - p$ is the probability that a patch is empty); equivalence with (1) is established for $m = m_{\text{out}}m_{\text{in}}$ (see also Etienne & Heesterbeek 2000). We now assume, as seems most realistic, that the Allee effect affects m_{in} and that the strength of the Allee effect depends on $m_{\text{out}}p$. A simple way to model this, is to multiply m_{in} by a function f of $m_{\text{out}}p$. Of this function we require that it contains a parameter determining the strength of the dependence on $m_{\text{out}}p$ and that in one limit of this parameter the model reduces to the Levins model, and that in another limit no colonization is possible. Evidently, there are many possibilities; we chose the rectangular hyperbola model

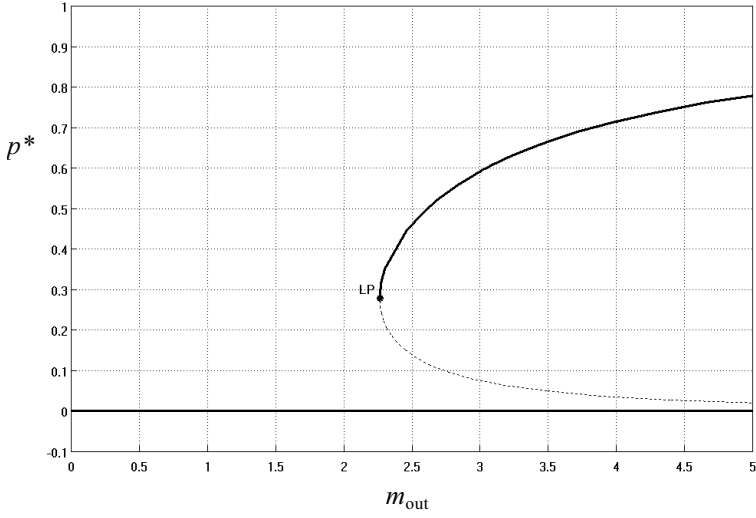$$f\left(m_{\text{out}}p\right) = \frac{m_{\text{out}}p}{m_{\text{out}}p + a}, \tag{7}$$

where a is the parameter determining the strength of the Allee effect. Although this function is descriptive rather than mechanistic, it is so at the population level, not at the metapopulation level as in Amarasekare's model.

As one may have noted, this function f does not have the sigmoidal shape often associated with the Allee effect. It could, however, be interpreted as the result of demographic stochasticity acting on the immigrants (Goel & Richter-Dyn 1974) which is simply that many immigrants have a larger probability of successfully colonizing a patch than a few. This is also considered a type of Allee effect (Lande 1998, Keitt et al. 2001), although not unanimously (Stephens et al. 1999).

With (7) the model becomes

$$
\begin{aligned}
\frac{dp}{dt} &= m_{\text{out}}pm_{\text{in}}f\left(m_{\text{out}}p\right)\left(1 - p\right) - ep = \\
&= m_{\text{out}}pm_{\text{in}}\frac{m_{\text{out}}p}{m_{\text{out}}p + a}\left(1 - p\right) - ep = \\
&= mp\frac{p}{p + \frac{a}{m_{\text{out}}}}\left(1 - p\right) - ep
\end{aligned} \tag{8}
$$

where $\frac{a}{m_{\text{out}}}$ can be interpreted as the occupancy where colonization is at one half of the level it would be at without the Allee effect; setting $a = 0$ reduces the model to the Levins model.

A.

B.

Figure 1. Bifurcation diagrams of the Levins model with Allee effect. A. p^* versus m_{out}. Parameter settings for this diagram are $e = 1$, $m_{in} = 1$, $a = 0.4$. B. p^* versus a. Parameter settings for this diagram are $e = 1$, $m_{in} = 1$, $m_{out} = 3$. The solid curves in both panels are the locally stable equilibria (the trivial equilibrium $p^* = 0$ and the nontrivial equilibrium p_+^*). The dotted curve is the unstable equilibrium p_-^*. The point LP is the limit point where the fold bifurcation occurs (where both nontrivial equilibria disappear when m_{out} is decreased (A) or a is increased (B)).

The nontrivial equilibria for this differential equation are

$$p_{\pm}^* = \left(1 - \frac{1}{\beta}\right)\left(\frac{1}{2} \pm \frac{1}{2}\sqrt{1 - \frac{4\frac{1}{\beta}\frac{a}{m_{\text{out}}}}{\left(1 - \frac{1}{\beta}\right)^2}}\right) \tag{9}$$

with

$$\beta := \frac{m}{e} \tag{10}$$

The nontrivial equilibria can only exist if both $\beta > 1$ and $a < \frac{1}{4}\beta m_{\text{out}}\left(1 - \frac{1}{\beta}\right)^2$, that is, $\beta > 1 + 2\frac{a}{m_{\text{out}}}\left(1 + \sqrt{1 + \frac{m_{\text{out}}}{a}}\right)$; in the limit where a approaches 0 this becomes the Levins condition $\beta > 1$. The highest equilibrium, p_+^*, is stable; the middle equilibrium, p_-^*, is unstable and forms the separatrix between the domain of persistence and the domain of extinction (Figures 1A and 1B). We see that enlarging m_{out} makes the domain of extinction smaller and the equilibrium occupancy larger. At the same time, reducing m_{out} can result in sudden extinction of the metapopulation. Similarly, lowering a is beneficial to persistence, while a small increase in a can cause sudden metapopulation extinction.

Amarasekare (1998) also studies the effect of habitat destruction along the lines of Hanski et al. (1996) who introduce the parameter h which presents the fraction of patches with suitable habitat remaining after habitat destruction. Modifying our model (8) in the same spirit leads to

$$\frac{dp}{dt} = mp\frac{p}{p + \frac{a}{m_{\text{out}}}}(h - p) - ep \tag{11}$$

with nontrivial equilibria

$$p_{\pm}^* = \left(h - \frac{1}{\beta}\right)\left(\frac{1}{2} \pm \frac{1}{2}\sqrt{1 - \frac{4\frac{1}{\beta}\frac{a}{m_{\text{out}}}}{\left(h - \frac{1}{\beta}\right)^2}}\right). \tag{12}$$

Again, p_+^* is stable and p_-^* is unstable when they exist; the condition for existence is $\beta > \frac{1}{h} + \frac{2}{h^2}\frac{a}{m_{\text{out}}}\left(1 + \sqrt{1 + h\frac{m_{\text{out}}}{a}}\right)$ which reduces to the Levins condition $\beta > \frac{1}{h}$ when $a = 0$. The condition can also be expressed as $h > \frac{1}{\beta} + 2\sqrt{\frac{1}{\beta}\frac{a}{m_{\text{out}}}}$. This entails that metapopulation persistence requires more suitable habitat when the Allee effect is active than under the Levins model without Allee effect. We note here that, for habitat destruction to have a detrimental effect, we must assume that dispersers cannot select suitable habitat over unsuitable (destroyed) habitat; if they can, such that all colonization effort is directed at suitable patches, then habitat destruction has no effect whatsoever on the fraction of occupied patches. This is not due to the Allee effect; it is also true in the Levins model (Etienne 2000).

Discussion

We have presented a model which incorporates the Allee effect into the Levins model which does not contain the drawbacks of the existing model of Amarasekare (1998), or to a lesser extent. First, our model is defined for $m < e$. The trivial equilibrium is then globally stable. Second, for $a = 0$ the model reduces to the original Levins model. Third, the threshold is not set beforehand, but follows from the dynamics of the model. This threshold is p^*_-. (The carrying capacity, p^*_+, also follows from metapopulation dynamics). Fourth, the model treats the Allee effect more mechanistically, because it makes the Allee effect act on colonization. The function f responsible for this is, however, still descriptive. A mechanistic basis for this function would involve detailed modelling of local dynamics.

So far, judging from the citation links (Courchamp et al. 1999, Reed 1999, Stephens et al. 1999, Stephens & Sutherland 1999, Wang et al. 1999, Berec et al. 2001, Brassil 2001, Cronin & Strong 2001, Keitt et al. 2001) provided by the Web of Science (October 30, 2001), the model by Amarasekare (1998) has not been used to make any predictions beyond those made by Amarasekare (1998) herself, which still stand in our model. However, in order to study the effects of multiple-species interactions and the Allee effect, we attempted to combine the two-species Levins-type models of Nee et al. (1997) with the Levins model incorporating the Allee effect of Amarasekare (1998), and came across some inconsistencies which can be attributed to the drawbacks in the Amarasekare (1998) model. For instance, let us consider a model with two competing species in which the superior competitor completely excludes the inferior competitor from patches which it occupies and where both species are subject to an Allee effect with different existence thresholds. If, in this model, both the superior and inferior competitor are below their threshold occupancy, the inferior competitor can still grow. Blindly using the combined models anyway would result in interesting, yet incorrect, consequences for metapopulation conservation. For example, in the above-mentioned competition model coexistence would be possible for low and high values of the threshold parameter of the inferior competitor, but not for intermediate values. This must be incorrect because due to the assumption of the competition model that the superior competitor does not "feel" the presence of the inferior competitor, a stronger Allee effect in the inferior competitor can only impede persistence of the inferior competitor. This does not necessarily mean that the Allee effect in two competing species cannot enlarge the domain of coexistence. We are currently examining this using our alternative model and we will present the results elsewhere.

In sum, Amarasekare (1998) undoubtedly made a valuable point in highlighting the Allee effect as an important aspect often ignored in metapopulation dynamics, by a simple extension of the Levins model. Yet, because of its phenomenological character, this model is not fit (and probably not meant) for further extensions. The alternative, more mechanistic, model that we presented here is better suited for this purpose.

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4

Non-equilibria in small metapopulations: comparing the deterministic Levins model with its stochastic counterpart

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Abstract

In this paper we examine, for small metapopulations, the stochastic analog of the classical Levins metapopulation model. We study its basic model output, the expected time to metapopulation extinction, for systems which are brought out of equilibrium by imposing sudden changes in patch number and the colonization and extinction parameters. We find that the expected metapopulation extinction time shows different behavior from the relaxation time of the original, deterministic, Levins model. This relaxation time is therefore limited in value for predicting the behavior of the stochastic model. However, predictions about the extinction time for deterministically unviable cases remain qualitatively the same. Our results suggest that, if we want to counteract the effects of habitat loss or increased dispersal resistance, the optimal conservation strategy is not to restore the original situation (that is, to create habitat or decrease resistance against dispersal), but rather to improve the quality of the remaining habitat in order to decrease local extinction rate.

Introduction

Probably the simplest, and most cited, single-species metapopulation model is the Levins (1969, 1970) model which describes the occupancy of a very large number of identical habitat patches N as a result of colonization and extinction events. This model captures

the essence of metapopulation dynamics: the metapopulation can persist if extinctions of populations in occupied patches are balanced by colonizations of empty patches, and thereby explains the presence of empty but suitable habitat. The Levins model has been invaluable for the understanding of metapopulation dynamics. Many modifications have been examined, such as the incorporation of rescue effect (Hanski 1983, Hanski et al. 1996, Etienne 2000), patch preference effect (Etienne 2000) and Allee effect (Amarasekare 1998), and it has been extended to models involving multiple species interactions (Levins & Culver 1971, Slatkin 1974, Nee et al. 1997), succession (Amarasekare & Possingham 2001), heterogeneous habitat (Holt 1997), the quality of the matrix habitat (Vandermeer & Carvajal 2001) and to structured models containing local population dynamics and dynamics of patch formation and destruction (Gyllenberg & Hanski 1997). These more detailed models have shown the range and hence also the shortcomings of the Levins model.

Although many of the assumptions of the Levins model have been relaxed and explored in the abovementioned studies, the corresponding models are all deterministic, hence not allowing for the important process of stochastic metapopulation extinction in small networks (i.e. small values of N). Models using stochastic differential equations or diffusion equations (Gurney & Nisbet 1978, Saether et al. 1999) can predict the expected time to stochastic extinction, but strictly this is only an approximation (which becomes better as N gets larger), because stochastic differential and diffusion equations treat N as a continuous quantity. Work has also been done on fully stochastic metapopulation models, either analytical models (Gyllenberg & Silvestrov 1994, Day & Possingham 1995, Frank & Wissel 1998, Ovaskainen 2002) or simulation models (for examples see Lindenmayer et al. 1995) in which N is a discrete quantity which may take small values as well. In this paper we will present such a stochastic metapopulation model which can be viewed as a Levins model for any discrete N. Our main aim is to investigate this model's predictions for the expected metapopulation extinction time which we emphasize as a central yardstick for conservation biology. We will focus mainly on relatively small metapopulations, where the deterministic Levins model is expected to be most deficient, but we will also try to give an indication where the models start to coincide approximately.

Most of the model studies have thus far focused on equilibria (in deterministic models) or pseudo-equilibria (in stochastic models). Recently, attention has also been paid to non-equilibrium situations (Tilman et al. 1994, Hanski et al. 1996, Nagelkerke 2002). Such non-equilibria are usually thought to arise from recent landscape degradation by humans, but they may equally well originate from landscape restoration (Nagelkerke et al. 2002) and the cause may even be natural landscape change (see e.g. Stelter et al. 1997). Because it takes time for the metapopulation to react to these changes in the landscape, the consequences of severe degradation such as deforestation may not be instantly visible: the metapopulation appears healthy, but is in fact no longer viable (e.g. Heywood et al. 1994, Whitmore 1997). This can result in an extinction debt in biodiversity (Tilman et al. 1994). Similarly, the effect of conservation attempts may be unnoticeable for some time, with the metapopulation looking doomed, but being actually on its way to recovery. Such timelags are evidently important to conservation biology, but, to our knowledge, they have not been studied for small metapopulations. In this paper we will attempt to fill up part of this void by using non-equilibria

as initial conditions, which we create out of equilibria by imposing sudden (negative and positive) changes in patch number, in colonization rate and in extinction rate. Potential time-lags are then naturally accounted for in the expected metapopulation extinction time. The equilibria that we disturb cannot be deterministic equilibria, because sometimes the equilibrium is extinction. Therefore, we adopt a more natural starting-point, the quasi-stationary equilibrium of the stochastic model, which is well defined for both deterministically viable and deterministically unviable systems; as N gets large and the time to metapopulation extinction relative to the local extinction time becomes very large, this quasi-stationary equilibrium more and more resembles the deterministic equilibrium. The changes in patch number, in colonization rate and in extinction rate will be formulated such that they can be compared between different types of degradation/restoration. These changes can be due to, respectively, habitat destruction/creation, increased/decreased dispersal resistance caused by, for example, matrix (i.e. habitat between the patches) deterioration/improvement, and increased/decreased disturbance or habitat quality. The equilibrium situation is then the special case where there is no change in patch number, colonization or extinction rate, that is, the change is zero. We will devote special attention to the consequences of non-equilibrium situations for conservation biology.

Fully stochastic models, including the one we will describe, often have a very high-dimensional state space which makes them analytically intractable and numerically hard to handle, even though there are ways to reduce the dimensionality of the state space substantially (Gilpin & Taylor 1994). Therefore it seems worthwhile to investigate whether properties of the much simpler deterministic models can be used to predict the behavior of stochastic models (this is not obvious, see Gueron 2001). In such an effort, Lehman & Tilman (1997, p. 189-190) compared the metapopulation extinction time calculated with a stochastic simulation model with the stability of the non-trivial equilibrium of the Levins model measured by the eigenvalue corresponding to this equilibrium (this eigenvalue is a measure of the relaxation time, i.e. the time to return to equilibrium). They concluded that the less stable the equilibrium of the Levins model (i.e. the longer the relaxation time), the *shorter* the expected time to extinction. Their explanation is simple: a more stable equilibrium will more strongly drive the system back to equilibrium after a disturbance, away from extinction, so stochastic fluctuations which may cause accidental extinction, are dimmed. However, Lehman & Tilman (1997) only showed a few results, so we interpret their conclusion and explanation as a conjecture which should be tested for robustness in a more extensive study. In this paper, we will perform such a more detailed comparison of the relaxation time of the Levins model and the expected metapopulation extinction time of our stochastic model, and see if indeed the former can teach us something about the latter. Importantly, Lehman & Tilman (1997) only presented results for situations in which the metapopulation is deterministically viable (and in equilibrium), i.e. in which a non-trivial equilibrium exists. For deterministically unviable systems, i.e. in which the equilibrium is extinction, the relaxation time is in fact a direct measure of the metapopulation extinction time, because the deterministic force driving the system back to equilibrium after a disturbance is now pointed towards extinction. One could hypothesize then that for deterministically unviable systems, the relaxation time of the Levins model and the expected metapopulation extinction time of the stochastic

model would more or less coincide. However, note that this implies that, contrary to the case studied by Lehman & Tilman (1997), the expected metapopulation extinction time *increases* with relaxation time. This raises the question what, in general, the relationship will be between the relaxation time of the deterministic Levins model (valid for large continuous N) and the metapopulation extinction time of our stochastic model (for any discrete N). For example, does the relationship indeed change direction between viable and unviable cases? In this paper we will perform a detailed comparison of the relaxation time of the Levins model and the expected metapopulation extinction time of our stochastic model, and see if the former can, at least qualitatively, teach us something about the latter. We will do this for systems in non-equilibrium (with equilibrium being a special case), thus also accounting for timelags. Concerning metapopulations that, after degradation, have become deterministically unviable, Nagelkerke (2002) has done extensive studies of timelags in the Levins model, using the relaxation time as an indicator of the time to metapopulation extinction. Our comparisons make it possible to investigate to what extent his results can be translated to small networks.

In sum, we will briefly review the Levins model and present a stochastic version of the Levins model. We will examine the predictions of this stochastic model for the expected metapopulation extinction time of (small) metapopulations which are disturbed from equilibrium by changes in their patch number, colonization rate and extinction rate. We will compare the expected time to metapopulation extinction to the return time of the Levins model to investigate whether the relaxation time can be a guide for the expected time to metapopulation extinction; for deterministically unviable systems this implies a comparison of the behavior of both models. We will discuss the consequences of our findings for conservation biology, i.e.,which environmental changes most reduce the expected metapopulation extinction time, and what is the best way to prolong metapopulation longevity?

Models

The deterministic model

Let p be the probability of a patch being occupied; hence $1 - p$ is the probability that it is empty. Assume further that an empty patch is colonized with probability rate C whereas an occupied patch goes extinct at probability rate E. C and E may depend on the number of occupied patches. This leads to the following ordinary differential equation:

$$\frac{dp}{dt} = C\left(1 - p\right) - Ep. \tag{1}$$

Let us assume that the extinction rate is constant, $E = e$, and that the colonization rate increases linearly with the number of occupied patches n, $C = cn$. If we define $m = cN$, N being the total number of patches, and let N be large enough to justify setting the probability of a patch being occupied equal to the fraction of occupied patches, that is, $p = \frac{n}{N}$, then this reduces to the familiar Levins model,

$$\frac{dp}{dt} = mp(1-p) - ep \tag{2}$$

where p is then interpreted as the fraction of occupied patches. Multiplying both sides by N gives

$$\frac{dn}{dt} = cn(N-n) - en \tag{3}$$

which we will use to enable comparison with the full stochastic model presented in the next section. The assumption that $p = \frac{n}{N}$ is only reasonable for large N; hence the Levins model can at most be a good approximation of that stochastic model.

The Levins model has the following equilibria:

$$n^* = \begin{cases} 0 & \text{stable for } \frac{cN}{e} \leq 1 \\ N - \frac{e}{c} & \text{stable for } \frac{cN}{e} > 1. \end{cases} \tag{4}$$

For later convenience we define

$$\widetilde{n}^* = N - \frac{e}{c} \tag{5}$$

so $\widetilde{n}^* = n^*$ for $\frac{cN}{e} > 1$. With this definition $\widetilde{n}^*$ is a measure of the viability of the meta-population.

The relaxation time (return time to equilibrium) corresponding to an ordinary differential equation is given by

$$T_{\mathrm{r}} = -\frac{1}{\lambda} \tag{6}$$

where λ is the eigenvalue of the differential equation, linearized around the equilibrium. With this definition the relaxation time measures the time it takes to reduce a disturbance by a factor $\exp(-1)$. Nagelkerke (2002) uses the half-life of a disturbance given by $-\frac{\ln 2}{\lambda}$. For the equilibria (4) the relaxation time is

$$T_{\mathrm{r}} = \begin{cases} \frac{1}{e-cN} = -\frac{1}{c\widetilde{n}^*} & \text{for } \frac{cN}{e} \leq 1 \\ \frac{1}{cN-e} = \frac{1}{cn^*} = \frac{1}{c\widetilde{n}^*} & \text{for } \frac{cN}{e} > 1 \end{cases} \tag{7a}$$

$$= \left| \frac{1}{c\widetilde{n}^*} \right| \tag{7b}$$

$$= \left| \frac{1}{e} \left(\frac{N}{\widetilde{n}^*} - 1 \right) \right|. \tag{7c}$$

For very small $\frac{c}{e}$ ($\frac{c}{e} \ll \frac{1}{N}$) where obviously $n^* = 0$, we note that T_{r} reduces to

$$T_r \approx \frac{1}{e} \left(1 + N\frac{c}{e} \right) \text{ for } \frac{c}{e} \ll \frac{1}{N}. \tag{8}$$

The stochastic model

A stochastic model analogous to the deterministic model is the continuous-time Markov model (Frank & Wissel 1998, Ovaskainen 2002). It describes the probability P_n of n patches

being occupied for all $0 \leq n \leq N$:

$$\frac{dP_n}{dt} = c(n-1)(N-(n-1))P_{n-1} - [en + cn(N-n)]P_n + e(n+1)P_{n+1} \quad (9)$$

with $P_n = 0$ for $n < 0$ and $n > N$; c and e are again the probability rates of colonization and extinction (comparable with (1)) and N is again the number of patches. It is assumed, as in the deterministic model, that in infinitesimal time steps no more than one extinction or colonization event can occur. We can also write (9) in matrix notation,

$$\frac{dP}{dt} = P^T R \quad (10)$$

where P represents a $(N+1)$-dimensional vector containing the probabilities of $n = 0...N$ patches being occupied and R is the $(N+1)$ by $(N+1)$ transition matrix with elements

$$R_{k+1,l+1} = \begin{cases} ke & \text{for } k = l+1 \\ -ke - kc(N-k) & \text{for } k = l \\ kc(N-k) & \text{for } k = l-1 \\ 0 & \text{otherwise.} \end{cases} \quad (11)$$

For example, if $N = 2$, then R is given by

$$R = \begin{pmatrix} 0 & 0 & 0 \\ e & -e-c & c \\ 0 & 2e & -2e \end{pmatrix}. \quad (12)$$

The expected metapopulation extinction time is related to the second largest eigenvalue λ_2 of R (Keilson 1979, Frank & Wissel 1998):

$$T_{\text{ext}}(P^0 = P^*) = -\frac{1}{\lambda_2}. \quad (13)$$

This is the expected extinction time when the initial condition of the system, P^0, is the left eigenvector corresponding to λ_2. This eigenvector, denoted by P^*, represents the most likely distribution of initial states n. The system is then said to be in quasi-stationary equilibrium; it is the equilibrium conditional on non-extinction (the only stationary equilibrium is extinction).

We can also view the process as a birth-death process where extinction corresponds to death and colonization to birth. For a general continuous-time birth-death process in a discrete state space we can write (Goel & Richter-Dyn 1974)

$$\frac{dP_n}{dt} = b_{n-1}P_{n-1} + d_{n+1}P_n - [b_n + d_n]P_n \quad (14)$$

where b_i and d_i are the probability rates of birth and death respectively. If the process is restricted between a lower absorbing state ($n = 0$) and an upper reflecting state ($n = N$) then the expected time to reach the absorbing state if starting in state $n = m$ equals (Goel & Richter-Dyn 1974)

$$T_{\text{ext}}(m) = \sum_{i=1}^{m} \left[\frac{1}{d_i} + \sum_{n=i+1}^{N} \left(\frac{1}{d_n} \prod_{j=i}^{n-1} \frac{b_j}{d_j} \right) \right]. \quad (15)$$

In our case we have

$$d_n = ne \tag{16a}$$

$$b_n = n(N-n)c \tag{16b}$$

which gives

$$T_{\text{ext}}(m) = \sum_{i=1}^{m}\left[\frac{1}{ie} + \sum_{n=i+1}^{N}\left(\frac{1}{ne}\prod_{j=i}^{n-1}\frac{j(N-j)c}{je}\right)\right] =$$

$$= \sum_{i=1}^{m}\left[\frac{1}{ie} + \sum_{n=i+1}^{N}\left(\frac{c^{n-i}}{ne^{n-i+1}}\frac{(N-i)!}{(N-n)!}\right)\right] \tag{17}$$

so from any initial state distribution P^0 we have

$$T_{\text{ext}}(P^0) = \sum_{k=0}^{N} P_k^0 T_{\text{ext}}(k) \tag{18}$$

where P_k^0 is the probability of the system being in state k as before. Thus, if P^0 is the distribution associated with the quasi-stationary equilibrium, (18) yields the same value as (13).

For any state distribution P we can also calculate the expected number or fraction of occupied patches as follows:

$$\langle p \rangle = \frac{\langle n \rangle}{N} = \frac{1}{N}\sum_{k=1}^{N} kP_k. \tag{19}$$

When $\frac{c}{e}$ is small it can be shown (using the appendix of Etienne & Heesterbeek 2001) that the expected extinction time from the pseudo-equilibrium P^* becomes

$$T_{\text{ext}}(P^*) \approx \frac{1}{e}\left[1 + (N-1)\frac{c}{e}\right] \text{ for } \frac{c}{e} \ll \frac{1}{N}. \tag{20}$$

Comparison of (20) with (8) demonstrates that for $\frac{c}{e} \ll \frac{1}{N}$ the expected metapopulation extinction time of the stochastic model more and more resembles the relaxation time of the deterministic model as N grows large, although at the same time the domain for $\frac{c}{e}$ in which the formulae (20) and (8) are valid approximations, becomes smaller with increasing N. So indeed, as hypothesized in the introduction, the relaxation time and the expected extinction time coincide for very unviable metapopulations. The following, heuristically derived, formula which is equal to (20) to first order in $\frac{c}{e}$ turned out, in numerical experiments, to describe $T_{\text{ext}}(P^*)$ even better than (20) for small $\frac{c}{e}$:

$$T_{\text{ext}}(P^*) \approx \frac{1}{e}\left(1 + \frac{c}{e}\right)^{N-1} \text{ for } \frac{c}{e} \ll \frac{1}{N}. \tag{21}$$

When $\frac{c}{e}$ is large, it can be shown (by reformulating the result obtained analytically by Ovaskainen 2002 with which the earlier result obtained numerically by Frank & Wissel 1998

agrees fairly well) that the expected extinction time from the pseudo-equilibrium P^* can be approximated by

$$T_{\text{ext}}(P^*) \approx \frac{1}{e} \frac{(N-1)!}{N} \left(\frac{c}{e}\right)^{N-1} \text{ for } \frac{c}{e} \gg \frac{1}{N}. \tag{22}$$

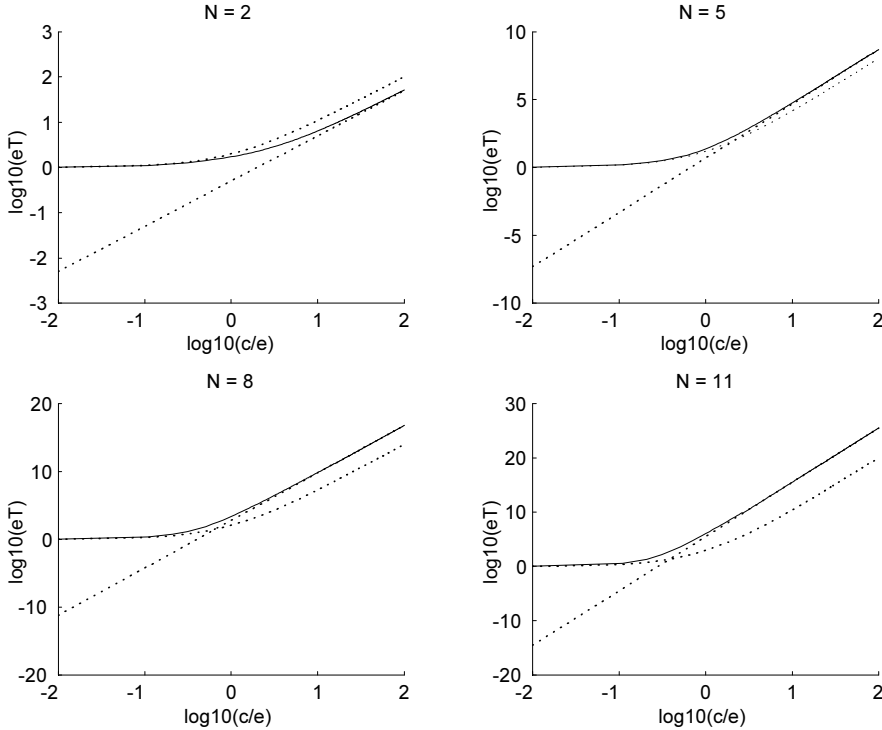For $N = 2$, (20) and (22) are especially easy to prove, because the subdominant eigenvalue of (12) is given by

$$\lambda_2 = -\frac{3}{2}e - \frac{1}{2}c + \frac{(e+c)}{2}\sqrt{1 + \frac{4ec}{(e+c)^2}}. \tag{23}$$

Equations (20) and (22) with 2 substituted for N indeed follow, after a first order Taylor expansion in $\frac{c}{e}$ and a second order Taylor expansion in $\frac{e}{c}$ respectively.

We thus have the following formula:

$$T_{\text{ext}}(P^*) \approx \begin{cases} \frac{1}{e}\left(1 + \frac{c}{e}\right)^{N-1} & \text{for small } \frac{c}{e} \\ \frac{1}{e}\frac{(N-1)!}{N}\left(\frac{c}{e}\right)^{N-1} & \text{for large } \frac{c}{e}. \end{cases} \tag{24}$$

Figure 1 shows plots of $eT_{\text{ext}}(P^*)$ and of its approximations (24) versus $\frac{c}{e}$.

Figure 1. $\log(eT_{\text{ext}})$ as a function of $\log\left(\frac{c}{e}\right)$ for 4 different values of N as calculated by the full model (solid curves) and by the approximations for small and large $\frac{c}{e}$ (dotted curves).

As we already remarked, $T_{\text{ext}}(P^*)$ and T_r are in close agreement for small values of $\frac{c}{e}$ ($\frac{c}{e} \ll \frac{1}{N}$). For large values of $\frac{c}{e}$ ($\frac{c}{e} \gg \frac{1}{N}$) we found close agreement between the equilibrium fraction of patches $p^* = \frac{n^*}{N}$ in the Levins model and the expected fraction of occupied patches in the quasi-stationary equilibrium of the stochastic model, calculated from (19), as long as $\frac{c}{e}$ and N are not too small. This is demonstrated by Figure 2. Thus, Figure 1 and Figure 2 together show the similarities and differences between the stochastic model and the original Levins model.

Figure 2. The expected fraction of occupied patches conditional on non-extinction in the stochastic model (solid curve) and the equilibrium fraction of occupied patches in the Levins model (dotted curve) as a function of $\log\frac{c}{e}$. Here, $e = 1$, but graphs for different values of e are similar.

Let us now assume that the metapopulation with N patches is in quasi-stationary equilibrium. Suppose that then a reduction of the number of patches occurs; let this reduction be ΔN (ΔN is negative). Assuming this reduction to be random, the new initial state distribution, $P^0 = P^{N+\Delta N}$, is related to the old initial state distribution, $P^0 = P^N$, by

$$P^{N+\Delta N} = QP^N \tag{25}$$

with Q an $(N + \Delta N)$-by-N matrix describing the probabilities Q_{ij} that a state with j occupied patches will become a state with i occupied patches which are hypergeometrically distributed, that is,

$$Q_{ij} = \frac{\binom{j}{i}\binom{N-j}{N+\Delta N-i}}{\binom{N}{N+\Delta N}}. \tag{26}$$

Therefore we have

$$T_{\text{ext}}(P^{N+\Delta N}) = \sum_{k=1}^{N} \left(QP^N\right)_k T_{\text{ext}}(k). \tag{27}$$

Instead of patch reduction we may also imagine a sudden patch creation; let the number of patches created be ΔN (ΔN is positive). The new initial state distribution $P^{N+\Delta N}$ is now related to the old initial state distribution P^N by

$$P^{N+\Delta N} = SP^N \tag{28}$$

with S an $(N + \Delta N)$-by-N matrix with

$$S_{ij} = \begin{cases} 1 & j = i \\ 0 & \text{otherwise.} \end{cases} \tag{29}$$

Hence,

$$T_{\text{ext}}(P^{N+\Delta N}) = \sum_{k=1}^{N} \left(SP^N\right)_k T_{\text{ext}}(k). \tag{30}$$

Results

First we will examine whether the relaxation time can be used as an indicator of the expected metapopulation extinction time in a general setting with non-equilibria as initial conditions. Subsequently we will study the effects of non-equilibrium situations more closely from a conservation biological point of view and compare our results with those of Nagelkerke (2002) for the deterministically unviable situation.

The relaxation time as an indicator of the expected metapopulation extinction time

In the spirit of Lehman & Tilman (1997) and Gurney & Nisbet (1978) we start out by comparing systems which have an equal number of occupied patches in equilibrium, that is, systems with equal $\widetilde{n}^*$ given by (5), but different N. Using $\widetilde{n}^*$ instead of n^* enables us to distinguish systems with $n^* = 0$, but different N. If we keep e the same for these systems with equal $\widetilde{n}^*$,

then they must be different in c. We assume a sudden change ΔN in the number of patches; ΔN can be both positive (patch creation) or negative (patch destruction). The deterministic model (2) then predicts that the systems will reach a new equilibrium given by (4) where N is replaced by $N + \Delta N$; the new $\widetilde{n}^*$ then becomes $\widetilde{n}^* + \Delta N$. Note that the fraction of occupied patches $p = \frac{n^*}{N}$ also decreases when N is reduced.

Figure 3. Plots of T_{ext} versus N for different values of ΔN (from $\Delta N = 5$ down to $\Delta N = -19$) and for different values of $\widetilde{n}^*$ which the system has before the change in N. The thin solid curves correspond to negative values of ΔN (patch reduction), the thick solid curves correspond to positive values of ΔN (patch creation), and the dotted curve corresponds to $\Delta N = 0$. The marked curve corresponds to the value of ΔN for which $\widetilde{n}^* + \Delta N = 0$. The thin solid curves do not all start at the lowest value of N because one cannot destroy more patches than there are. Here $e = 1$, but the plots look similar for other values of e.

Figure 3 shows plots of T_{ext} versus N for different values of ΔN and for different values of $\widetilde{n}^*$ (note the double log scale of the y-axis due to the enormous range of T_{ext}). The thin

solid curves correspond to negative values of ΔN (patch reduction), the thick solid curves correspond to positive values of ΔN (patch creation), and the dotted curve corresponds to $\Delta N = 0$. Thus, the dotted curves for $\widetilde{n}^* > 0$ represent the cases considered by Lehman & Tilman (1997). The marked curve corresponds to the value of ΔN for which $\widetilde{n}^* + \Delta N = 0$ and hence coincides with the dotted curve for $\widetilde{n}^* = 0$. We see that this marked curve does not form the demarcation between the cases for which T_{ext} increases with N and those for which T_{ext} decreases with N. Instead, this demarcation curve seems to be the one for which $\widetilde{n}^* + \Delta N = k$ where $k > 4$ for $\widetilde{n}^* < 0$, $k = 4$ for $\widetilde{n}^* = 0$ and $k < 4$ for $\widetilde{n}^* > 0$. This result appears to be independent of e.

From (7c) we can deduce

$$T_{\text{r}} = \frac{1}{e} \left| \frac{N + \Delta N}{\widetilde{n}^* + \Delta N} - 1 \right|. \tag{31}$$
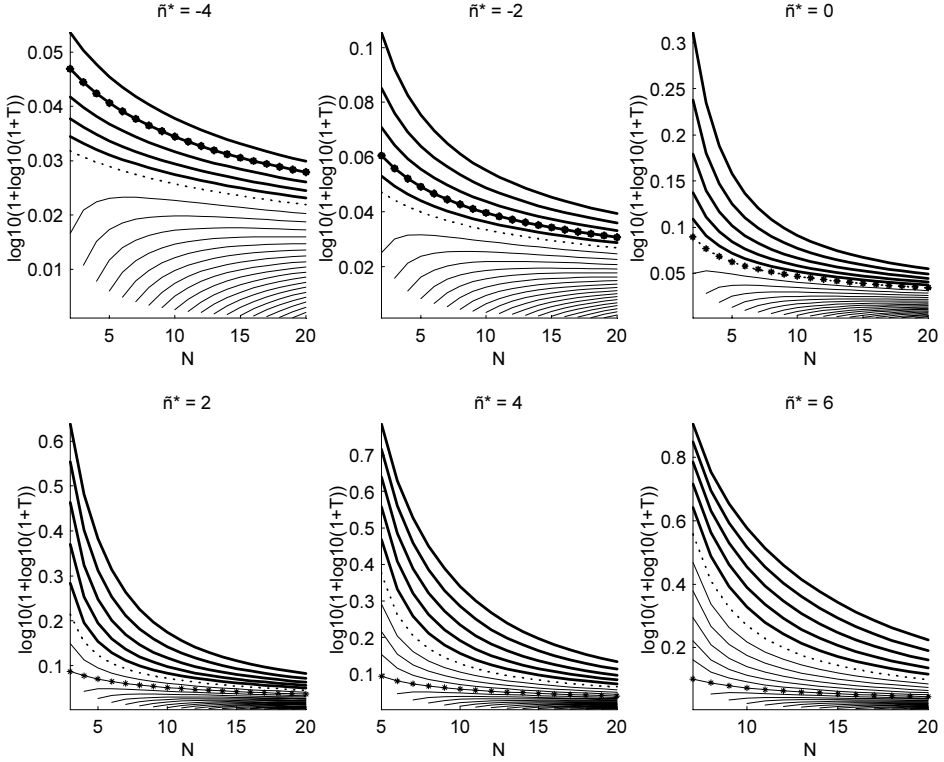
So, larger N implies longer T_{r}. Hence, our results suggest that T_{r} is indicative of T_{ext}: when $\widetilde{n}^* + \Delta N > k$, longer T_{r} coincides with shorter T_{ext}, but when $\widetilde{n}^* + \Delta N < k$, longer T_{r} coincides with longer T_{ext}; note that in between there are cases where the relationship is not completely monotonic. Hence, the expected change in the direction of the relationship between T_{ext} and T_{r} indeed occurs; however the boundary where this change takes place does not exactly coincide with the viability boundary but it is located in the viable part of parameter space.

If we again compare systems with equal $\widetilde{n}^*$ and different N, but now instead of e we take c to be the same (and hence e differs between these systems), then from (7b) we obtain

$$T_{\text{r}} = \frac{1}{c} \left| \frac{1}{\widetilde{n}^* + \Delta N} \right| \tag{32}$$

which tells us that these systems have equal T_{r}. Yet, they have far from equal T_{ext} as Figure 4 demonstrates, although for the unviable case T_{ext} remains quite constant when N changes, especially when N is large. Hence, T_{r} does not summarize T_{ext} well. It is clear that the local extinction rate is an important determinant of T_{ext}. When we plot T_{ext} scaled to the local extinction time $\frac{1}{e}$ on the y-axis (i.e. $e T_{\text{ext}}$), a picture emerges that closely resembles Figure 3 (which was effectively already on the local extinction time scale because all systems had the same e). This implies that, when appropriately scaled, systems with equal $\widetilde{n}^*$ and different N show the following general behavior: for large $\widetilde{n}^*$ or large positive ΔN, the metapopulation extinction time ($e T_{\text{ext}}$) decreases with N, whereas the metapopulation extinction time increases with N for small $\widetilde{n}^*$ or large negative ΔN. Apart from this, there is an interesting feature of the unscaled Figure 4 that we want to remark here: for the unviable case T_{ext} increases with N for large negative disturbances in N implying that the effect of larger N is apparently greater than the effect of larger e that accompanies it.

For sudden changes in c and e instead of in N (see below how we established these), similar results emerge (figures not shown). In sum, we find that T_{r} is not always a reliable measure of T_{ext}: sometimes it is a good indicator (e.g. for the unviable case, as we showed in equation (20) for the very unviable case), sometimes it is not.

Figure 4. Plots of T_{ext} versus N for different values of ΔN (from $\Delta N = 5$ down to $\Delta N = -19$) and for different values of $\widetilde{n}^*$ which the system has before the change in N. The thin solid curves correspond to negative values of ΔN (patch reduction), the thick solid curves correspond to positive values of ΔN (patch creation), and the dotted curve corresponds to $\Delta N = 0$. The marked curve corresponds to the value of ΔN for which $\widetilde{n}^* + \Delta N = 0$. The thin solid curves do not all start at the lowest value of N because one cannot destroy more patches than there are. Here $c = 1$, but the plots look similar for other values of c.

The consequences of timelags for conservation biology

Above we considered changes in patch number. Other possible changes in the environment are those affecting the colonization and extinction rates. Again, we compare systems with equal $\widetilde{n}^*$. But this time we do not reduce or increase the number of patches, but, following Nagelkerke (2002), we change the colonization and extinction rates such that the deterministic equilibrium is changed by the same amount as would be achieved by a change in patch number. This allows us to express the changes in colonization and extinction rates also

in terms of ΔN (this is what we did above). Hence, the changes in c and e are obtained by solving

$$N + \Delta N - \frac{e}{c} = N - \frac{e}{c + \Delta c} \tag{33a}$$

$$N + \Delta N - \frac{e}{c} = N - \frac{e + \Delta e}{c} \tag{33b}$$

for Δc and Δe respectively, which gives Δc and Δe as functions of ΔN:

$$\Delta c\,(\Delta N) = c\left(\frac{1}{1 - \frac{c}{e}\Delta N} - 1\right) \tag{34a}$$

$$\Delta e\,(\Delta N) = -c\Delta N \tag{34b}$$

Figure 5. Effects of applying sudden changes in the parameters N, c and e: relative values of T_{ext} versus equivalent changes in N (thick solid curve), c (dotted curve) and e (thin solid curve) expressed in units of ΔN, for several values of N and $\widetilde{n}^*$ which the system has before the change. The values of T_{ext} are relative to $T_{\text{ext}}(P^*) \equiv T_0$, i.e. the value of T_{ext} when there is no change in N, c or e.

Figure 5 shows the logarithm of the relative expected metapopulation extinction time versus the changes in N, c and e expressed in units of ΔN for several values of $\widetilde{n}^*$ and N

which the system has before the changes in N, c and e. The curve for changes in N does not extend to the left indefinitely, because this would lead to negative values of N; the curves for changes in c and e do not have such a limitation. The general emerging pattern, relative to the case where there is no change, is: T_{ext} is larger when c is decreased than when e is increased, but smaller when c is increased than when e is decreased; T_{ext} is generally smaller when N is changed (both positively and negatively) than when c or e is changed. This suggests, firstly, that increasing habitat quality is better (i.e. results in a larger increase in metapopulation extinction time) than decreasing dispersal resistance, while increasing dispersal resistance is not as bad as decreasing habitat quality, and, secondly, that destroying habitat is generally worse than increasing dispersal resistance or decreasing habitat quality, but creating patches is generally not as good as decreasing dispersal resistance or increasing habitat quality.

This pattern is more complicated than that of the relaxation time in the Levins model for which Nagelkerke (2002) shows that T_{r} is the same for changes in N and e, larger for negative changes in c and smaller for positive changes in c. His derivation comes down to the following: from (7b) and (7c) we get

$$T_{\text{r}}(\Delta c\,(\Delta N)) \;=\; \left|\frac{1}{(c+\Delta c)\,N-e}\right| = \tag{35a}$$

$$=\; \frac{1}{e}\left|\frac{N+\Delta N}{\widetilde{n}^{*}+\Delta N}-1-\frac{\Delta N}{\widetilde{n}^{*}+\Delta N}\right| = \tag{35b}$$

$$=\; \frac{1}{c}\left|\frac{1}{\widetilde{n}^{*}+\Delta N}-\frac{1}{N-\widetilde{n}^{*}}\frac{\Delta N}{\widetilde{n}^{*}+\Delta N}\right| \tag{35c}$$
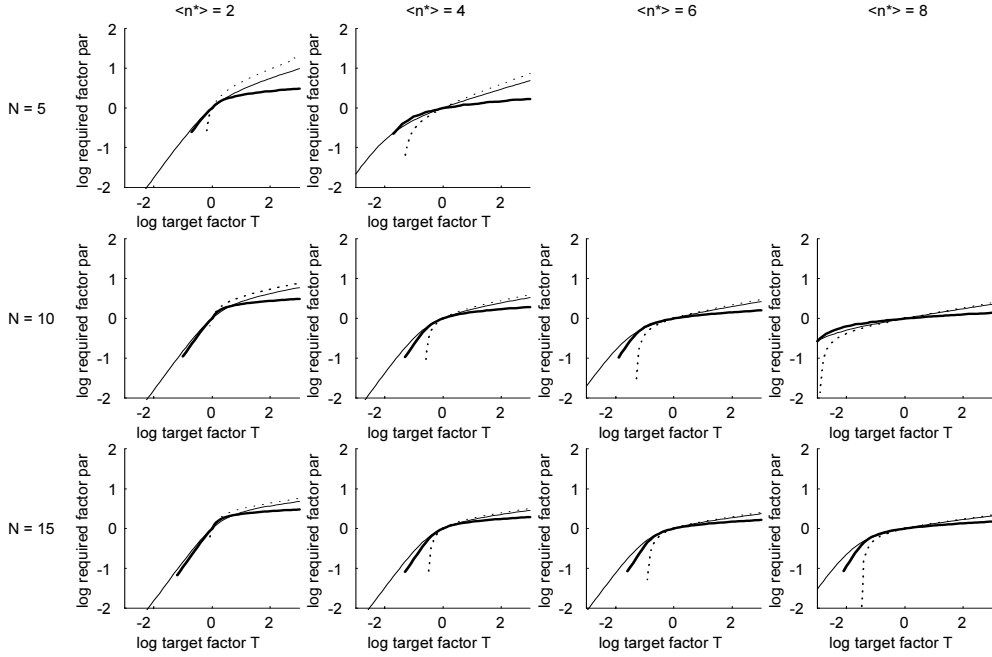
$$T_{\text{r}}\,(\Delta e\,(\Delta N)) \;=\; \left|\frac{1}{cN-e-\Delta e}\right| = \tag{35d}$$

$$=\; \frac{1}{e}\left|\frac{N+\Delta N}{\widetilde{n}^{*}+\Delta N}-1\right| = \tag{35e}$$

$$=\; \frac{1}{c}\left|\frac{1}{\widetilde{n}^{*}+\Delta N}\right|. \tag{35f}$$

and comparing (31) with (35b) and (35e) or, similarly, comparing 32 with 35c and 35f, gives the pattern Nagelkerke (2002) reports. Although this pattern is different from the pattern of Figure 5, we do see that as N and $\widetilde{n}^{*}$ become larger and ΔN is sufficiently small, the curves for changes in N and e in Figure 5 more and more coincide, as in the Levins model. Furthermore, Nagelkerke's (2002) conclusion that metapopulation extinction time is largest when inviability is caused by a decrease in c is also valid for T_{ext} in the stochastic model.

From comparison of the graphs in Figure 5 for the same value of N (for example the four graphs with $N = 10$) we see that systems with large $p^{*} = \frac{n^{*}}{N}$ benefit most from positive changes in c, e and N, but they also suffer most from negative changes: for positive changes $\frac{T_{\text{ext}}}{T_{\text{ext}}(P^{*})}$ is much larger for high values $\widetilde{n}^{*}$ than for low values, but for negative changes $\frac{T_{\text{ext}}}{T_{\text{ext}}(P^{*})}$ is much smaller for high values $\widetilde{n}^{*}$ than for low values (note the change in the scale of the y-axis). Thus, a species which has a high occupancy, has the largest relative change in the metapopulation extinction time (mathematically, it is the most sensitive to changes in the environment!), although it may have the smallest absolute change.

Figure 6. Effects of applying sudden changes in the parameters N (thick solid curve), c (dotted curve) and $\frac{1}{e}$ (thin solid curve): the factor by which the parameter must be multiplied versus the factor by which the T_{ext} of the system in pseudo-equilibrium is multiplied (the target factor), both on a log scale, for several values of N and $\langle n^* \rangle$ which the system had before the change. For N it is an extrapolated factor, because N must obviously be an integer. Here the (initial) value of e equals 1, but other values of e give almost the same curves.

In our approach to compare the effect of changes in the parameters on T_{ext} of the stochastic model we have used expressions for $\widetilde{n}^*$ of the deterministic Levins model. Although this yields simple expressions for these changes, it is more consistent to compare these effects based on the stochastic model only. To do so, we now follow a different procedure to compare the effect of changes in the parameters on T_{ext}: First we choose starting values of the parameters N and e and we calculate the value of c which leads to a predetermined value of the expected number of occupied patches in pseudo-equilibrium, $\langle n^* \rangle = \sum_n n P_n^*$. Assuming this system to be in pseudo-equilibrium we calculate T_{ext}. Then we choose target values of T_{ext} and we calculate the change in the parameters needed to achieve this target T_{ext}. The results of this exercise are shown in Figure 6. The curves for N and c in this figure do not extend infinitely to the left because in the case of N we do not allow all patches to be destroyed and in the case of c there is a limit to the effect of reducing c. We see that to establish

equal change in T_{ext} a much larger change in c is needed than in the other two parameters, particularly if the disturbance is detrimental, hence T_{ext} is least sensitive to changes in c. For detrimental changes this is in agreement with Figure 5, but not for beneficial changes. Also, in contrast to our results above, we see that increasing N is more effective than decreasing e and that, in general, increasing e is worse than decreasing N. Note, however, that for larger values of N and $\langle n^* \rangle$ the curves for beneficial changes in c, e and N become closer and closer. That the curves for changes in c and e become closer, is to be expected from (22) because the value of $\frac{c}{e}$ then strongly determines T_{ext}.

Figure 7. The effects on the expected metapopulation time of restoring the original situation at time $t = t'$ after detrimental changes in N (thick solid curve), c (dotted curve), and e (thin solid curve) at $t = 0$, relative to the value of T_{ext} which the system would have had if no disturbance had taken place at $t = 0$, for several values of N and $\langle n^* \rangle$. The initial disturbance in N is a reduction of 4 patches; the initial disturbances in c and e are such that they lead to the same value of T_{ext} without restorative action. The gray curve gives the horizontal assymptote of all three curves which is equal to $T_{ext}^{\text{no restoration}}$ divided by $T_{ext}^{\text{no disturbance at } t=0}$. Here $e = 0.1$ (before the disturbance), but other values of e give similar graphs. The values of T_{ext} were: 470 (top row), 84, 492, 2224 (middle row), 64, 146, 841 (bottom row). Note the linear scale in the relative T_{ext} whereas we used a log scale in previous figures.

Although our results show that decreasing c does not influence T_{ext} as much as do increasing e and decreasing N, increasing c also does not influence T_{ext} as much as do decreasing e and increasing N according to Figure 6. Since conservation efforts are often directed at bringing disturbed systems back in their original state, one may wonder what happens to T_{ext} when such efforts are made. To study this, we can do the following. We choose the parameters of the metapopulation as above, reduce N at $t = 0$ by a predetermined number (e.g. 4 patches) thus degrading the metapopulation, and bring N to its original value at some time $t = t'$. For this restored system we calculate the expected extinction time at $t = 0$ relative to the expected extinction time the system would have had without the degradation. We repeat this procedure for c and e instead of N where the initial disturbances in all three parameters are such that they would result in the same value of T_{ext} if no restorative action were taken (or, equivalently, taken at $t = \infty$). This recipe leads to Figure 7.

This figure shows that the effect for the changes in the three parameters are rather similar. Only if both N and $\langle n^* \rangle$ are initially small, the discrepancy is substantial. In that case, restoration, if carried out only a short time after the degradation, is most effective when c is concerned. Apparently, because of the relatively slow response to decreases in c, such decreases are fairly reversible. So, if the only conservation option is to bring back the system in its original state, particularly the effects of decreases in c can be well countered if action is taken rather promptly. For larger t and larger N, however, restoring c can be somewhat less effective than restoring e and N. Our explanation is that then the system, settled down in its new pseudo-equilibrium, responds relatively slowly to *in*creases in c. It is also interesting to note that negative disturbances in N cannot be completely undone, even at $t = 0$ right after the initial disturbance; over longer time, however, this disadvantage of changes in N disappears.

Discussion

We have found that some properties of the Levins model which do have a well-defined counterpart in the stochastic model are fairly good approximations, even for relatively small patch numbers. As expected, the fit improves when the number of patches increases. Those properties are (I) the relaxation time for systems that have been made deterministically unviable and (II) equilibrium patch occupancy. For instance, in both the Levins model and in its stochastic version, extinction after an increase in dispersal resistance occurs much slower than after other kinds of degradation. Results of Nagelkerke (2002) concerning timelags to extinction in the Levins model therefore, in a qualitative sense, also apply to small networks. Further, our conjecture that the relationship between the deterministic relaxation time and the expected metapopulation extinction time is negative for viable systems but positive for unviable ones is validated in a broad sense, but the relation only becomes negative for strongly viable systems. However, it is clear that otherwise the deterministic relaxation time of the Levins model is not a good indicator of the expected time to metapopulation extinction. The expected extinction time may vary widely between systems that have equal relaxation times. Hence the conjecture, based partially on Lehman & Tilman (1997), that relaxation time would be a good

guide for stochastic extinction time, has its limits. The assertion, made by Lehman & Tilman (1997) and also by Gurney & Nisbet (1978), that of systems with equal n^* those with low occupancy will go extinct sooner, is only true for metapopulations that are not too small and have not been degraded recently. Hence, even the results for the specific case studied these authors do not hold universally.

We have found more interesting implications for conservation biology. First, species having a high relative patch occupancy have the largest relative change in the metapopulation extinction time when changes in the environment are made. Second, for the two approaches that we employed to compare changes in the parameters N, c and e (see Figure 5 and Figure 6), the results suggest two rules, if we treat c as a measure of dispersal resistance and e as a measure of habitat quality. 1. Improving habitat quality is a better strategy to elongate the existence of the metapopulation than decreasing dispersal resistance, while increasing dispersal resistance is not as bad as lowering habitat quality. 2. Destroying habitat is generally worse than increasing dispersal resistance. Rule 1 creates the interesting suggestion that conservationists who have the opportunity to undo (some of) the higher metapopulation extinction risk caused by increased dispersal resistance, should not try to partially restore the old situation (i.e. build ecoducts or reroute highways), but they should rather invest in improving local habitat quality, unless of course this option is much more expensive or unless it is impossible for other reasons. This strong influence of the habitat quality through the extinction parameter most probably lies in the observation that even for an unconnected metapopulation, its ultimate extinction can be postponed by suspending local extinction (see also Etienne & Heesterbeek 2001). Third, for very small metapopulations with a high occupancy, if detrimental effects of a change in a parameter are counteracted by changing it back to its original value after some time, a decrease in dispersal resistance is the most reversible of the three types of landscape degradation, but only for a relatively short time. For metapopulations that are larger or have a lower occupancy, this effect is less pronounced, and may even be reversed when restoration is postponed longer. Destroying patches always has some impact, even if this destruction is immediately undone, but this disadvantage of a change in patch number compared to changes in extinction and colonization rates disappears over longer time.

While our two approaches agree on the impact of changes in the extinction rate relative to the changes in the colonization rate, they differ on the impact of changes in patch number. The first approach suggests that patch destruction is the worst of all disturbances, and patch creation is least effective of all conservation efforts, whereas the second approach suggests that patch destruction is intermediate between defragmentation and lowering habitat quality, and that patch creation is the most effective conservation strategy. Evidently, this must be due to their different ways of defining equivalent changes in the parameters. In our first approach the criterion was the effect on $\tilde{n}^*$ thus facilitating comparison with the deterministic model, while in our second approach it was the effect on T_{ext}. Hence, depending on one's choice of the way different changes in the environment should be compared, completely different conservation strategies are possible! We see the second approach as preferable, because the expected time to extinction is a central yardstick concerning conservation of metapopulations, as we noted in the introduction. Also, the expected time to metapopulation extinction is the natural measure in the stochastic model, as is the occupancy in the deterministic model.

A problem that still remains is: how do we compare the required changes in the parameters? If, for example, the result is, that c must be increased by 200% whereas e must only be decreased by 20% to achieve the same expected metapopulation extinction time, does this mean that it is more efficient to go for the latter? The bottom-line would be to make comparisons on a financial basis as already hinted at above: what is the cheapest way to increase the expected metapopulation extinction time to a certain value? Answering this question requires knowledge about the effect of management efforts on extinction and colonization probabilities (Etienne & Heesterbeek 2001) which is often not readily available, or at least rather unreliable. The answer may also depend on factors not captured by our models such as spatial and temporal heterogeneity in the parameters.

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Part III

Rules of thumb for metapopulation management

5

Rules of thumb for conservation of metapopulations based on a stochastic winking-patch model

Rampal S. Etienne & J.A.P. Heesterbeek

Abstract

From a theoretical viewpoint nature management basically has two options to prolong metapopulation persistence: decreasing local extinction probabilities and increasing colonization probabilities. This article focuses on those options with a stochastic single-species metapopulation model. We found that for most combinations of local extinction probabilities and colonization probabilities, decreasing the former increases metapopulation extinction time more than does increasing the latter by the same amount. Only for relatively low colonization probabilities is an effort to increase these probabilities more beneficial, but even then, decreasing extinction probabilities does not seem much less effective. Furthermore, we found the following rules of thumb: 1. If one focuses on extinction, one should preferably decrease the lowest local extinction probability. Only if the extinction probabilities are (almost) equal, should one prioritize decreases in the local extinction probability of the patch with the best direct connections to and from other patches. 2. If one focuses on colonization, one should preferably increase the colonization probability between the patches with the lowest local extinction probability. Only if the local extinction probabilities are (almost) equal, should one instead prioritize increases in the highest colonization probability (unless extinction probabilities and colonization probabilities are very low). The rules of thumb have an important common denominator: the local extinction process has a greater bearing on metapopulation extinction time than colonization.

Introduction

Ever since Levins (1969, 1970) presented his well-known metapopulation model, it has been clear that the key processes in single-species metapopulation dynamics are local extinction

and (re)colonization. For nature management of single-species metapopulations this has the important consequence that attempts to prolong metapopulation persistence can either be directed toward decreasing the probability of local extinction or toward increasing the probability of colonization. The former may be achieved by, for instance, improving habitat quality or size (cf. Klok & De Roos 1998), whereas the latter is often attained by building corridors or stepping stones (Schultz 1998). However, corridors may affect local extinction probability as well, both positively (by the rescue effect; Brown & Kodric-Brown 1977) and negatively (by a leakage or dilution effect; Allen et al. 1992). Likewise, improving habitat quality may have positive and negative effects on the ability to generate colonists or be colonized (a better-quality patch might attract more immigrants and it could produce more colonizers due to higher reproduction [see e.g. Hanski 1994, Vos et al. 2001]; or such a patch might sustain a larger population and thus offer less incentive to disperse). These diverse processes make it difficult to answer the practical question of whether, given a limited budget, improving habitat or building corridors (or perhaps a combination of the two) is the best option for metapopulation management. As a first step toward answering this question, we will investigate the problem on the level of local extinction and colonization probabilities: will metapopulation persistence benefit most from a small change in colonization probabilities or from an equally small change in local extinction probabilities? We will also study variations to this theme: if one focuses on local extinction probabilities in a network of patches, which patch should receive most attention, and similarly if one focuses on colonization probabilities between patches, which connection between which patches deserves most attention? The setting of this study is a single-species stochastic winking-patch (terminology of Verboom et al. 1993) or patch occupancy (terminology of Gosselin 1998) metapopulation model in discrete or continuous time. With this model, the answers to the above questions are straightforward for special cases in which the values for the colonization and local extinction probabilities are known exactly. However, these probabilities are usually only vaguely known, for example in terms of "high" and "low". Therefore, this article aims at providing rules of thumb, in the spirit of Wilson & Willis (1975) and Frank & Wissel (1998), rather than precise answers to the questions above.

The model

Discrete time

Consider a single-species metapopulation distributed over n patches that can be either occupied or empty. Assume that there is a discrete phase in which local population dynamics take place but no dispersal. After this "extinction phase" there is a "colonization phase". This separation of phases has been suggested by several authors (Akçakaya & Ginzburg 1991, Hansson 1991, Sabelis et al. 1991, Burgman et al. 1993). During the extinction phase, the

population in each occupied patch i has an extinction probability e_i, and during the colonization phase, dispersers from each occupied patch i can colonize an empty patch j with colonization probability c_{ij}. For the most part of this article, all these probabilities are considered to be independent, that is, we assume that extinctions and colonizations are not correlated. This means for example that we do not incorporate the rescue effect (Brown & Kodric-Brown 1977, Etienne 2000). We will also briefly study a model with correlated extinctions; other, probably less important, correlations require detailed models of dispersal and local dynamics that are beyond the scope of this article.

Because every patch is either occupied (denoted by 1) or empty (denoted by 0), the metapopulation is in any of 2^n states. For example, for $n = 2$, these states are (patch 2, patch 1) = (0,0), (0,1), (1,0), (1,1); for $n = 3$, these states are (patch 3, patch 2, patch 1) = (0,0,0), (0,0,1), (0,1,0), (0,1,1), (1,0,0), (1,0,1), (1,1,0), (1,1,1). We will order these states lexicographically as in these examples (this is why the order of the patches may seem a bit odd at first) and number them so that, for example, for $n = 2$ the states (0,0), (0,1), (1,0), (1,1) correspond, respectively, to 1, 2, 3, 4.

With the extinction and colonization probabilities given, we now describe the dynamics of the metapopulation, i.e. the changes in its state. We follow Day & Possingham (1995) and Akçakaya & Ginzburg (1991), but see also Gyllenberg & Silvestrov (1994), who present a similar discrete-time model but without separation of extinction and colonization phases. Suppose that $n = 2$ and the metapopulation is in state (patch 2, patch 1) = (0,1). From this state the metapopulation can reach state (1,1) if the first patch does not go extinct and if it subsequently provides colonists to the second patch to make it occupied. These two events occur with probability $(1 - e_1)c_{12}$ because we have assumed independence. If we now define M_{24} to be the probability that the metapopulation changes from state 2 ($\equiv (0,1)$ in the lexicographical ordering) to state 4 ($\equiv (1,1)$), then $M_{24} = (1 - e_1)c_{12}$. Similarly, we can define M_{ij} as the transition probability that the system moves from state i to state j. For any pair of states i and j one can calculate the transition probability as above. The $2^n \times 2^n$ matrix M thus defined is the Markov transition matrix of the metapopulation system with n patches. For $n = 2$ the transition matrix M is given by

$$M = \begin{pmatrix} 1 & 0 & 0 & 0 \\ e_1 & (1 - e_1)(1 - c_{12}) & 0 & (1 - e_1)c_{12} \\ e_2 & 0 & (1 - e_2)(1 - c_{21}) & (1 - e_2)c_{21} \\ e_1 e_2 & (1 - e_1)e_2(1 - c_{12}) & (1 - e_2)e_1(1 - c_{21}) & M_{44} \end{pmatrix} \quad (1)$$

where

$$M_{44} = (1 - e_1)e_2 c_{12} + (1 - e_2)e_1 c_{21} + (1 - e_1)(1 - e_2). \quad (2)$$

If $e_i = e$ and $c_{ij} = c$ for all i and j, then matrix M can be simplified to an $(n + 1) \times (n + 1)$ matrix P, the elements P_{kl} of which are transition probabilities to go from any state with k occupied patches to any state with l occupied patches. They are given by (see appendix A)

$$P_{kl} = \sum_{i=0}^{\min(k,l)} \binom{k}{i}(1 - e)^i e^{k-i} \binom{n - i}{l - i} \left[1 - (1 - c)^i\right]^{l-i} \left[(1 - c)^i\right]^{n-l} \quad (3)$$

in which the terms $\binom{y}{x}$ are combinatorials.

For large n the assumption of equal c is very unrealistic. Patches are usually colonized by their neighbors, not by distant populations. We can easily incorporate these thoughts in the model by replacing $(1-c)^i$ in (3) by $(1-c_s)^{i_s}$ where $i_s := \frac{i}{n}\min(s,n)$, thus allowing a maximum of s occupied patches to contribute (equally) to colonization. (Below, we will use $s = 8$ − so we will be concerned with c_8 − which is quite arbitrary, but is motivated by the number of neighbors of a patch in a lattice.) The subscript s is added to c for no other reason than to distinguish this adjusted model from the original one. We remark here that this adjusted model assumes that occupied patches do not form clusters, but are randomly distributed in space, which is not true for nearest-neighbor colonization. If one wants to be strict, one should use the general model at the cost of a much higher dimension, or aggregate patches into a single patch ending up with a much lower dimensional metametapopulation.

Day & Possingham (1995) and Akçakaya & Ginzburg (1991) do not describe the case in which extinctions are correlated (Akçakaya & Ginzburg 1991 do incorporate it in their model but do not specify how). In appendix A we derive the following analogue of (3) with extinctions correlated with parameter $\rho := \frac{\sigma^2}{1+\sigma^2}$, based on an underlying normal distribution:

$$
\begin{aligned}
P_{kl} \;=\; & \sum_{i=0}^{\min(k,l)} \binom{k}{i} \left(\int_{-\infty}^{\sqrt{1+\sigma^2}\,\Phi^{-1}(e)} \right)^{k-i} \left(\int_{\sqrt{1+\sigma^2}\,\Phi^{-1}(e)}^{\infty} \right)^{i} N_k[\overrightarrow{y}, \overrightarrow{0}, Y(\rho)] d\overrightarrow{y} \;\times \\
& \times \binom{n-i}{l-i} \left[1 - (1-c)^i \right]^{l-i} \left[(1-c)^i \right]^{n-l}
\end{aligned}
\tag{4}
$$

where $N_k[\overrightarrow{y}, \overrightarrow{0}, Y(\rho)]$ is the k-dimensional normal distribution of the k-dimensional variable $\overrightarrow{y}$ with zero mean and (co)variance matrix $Y(\rho) = \sigma^2 J + I$, with J a k-by-k matrix with all elements equal to 1 and I the k-by-k identity matrix; $\left(\int_\alpha^\beta \right)^i$ is short-hand for repeating the integration $\int_\alpha^\beta$ i times.

One can show (see e.g. Halley & Iwasa 1998) that the second largest eigenvalue λ_2 of the transition matrix (M or P) is a measure of the expected extinction time of the metapopulation:

$$
T_{\text{ext}} = \frac{1}{1 - \lambda_2}.
\tag{5}
$$

This extinction time is an average over the extinction times of all initial states, where each state is weighed according to the so-called quasi-stationary distribution (Darroch & Seneta 1965, Gilpin & Taylor 1994, Gosselin 1998) which is the probability distribution of states for a system in pseudo-equilibrium.

The expected metapopulation extinction time T_{ext} is the measure of persistence used in this article. Other measures, such as the basic reproduction number R_0 are also possible, and may lead to different conclusions (for comparison of these measures in a general metapopulation setting, see Etienne & Heesterbeek 2000).

Continuous time

If instead of a discrete-time Markov process, a continuous-time Markov process is used,

then one uses extinction and colonization rates (probabilities per unit of time) instead of probabilities. To keep the model simple and for reasons that become clear later on, we will only study the case where all extinction rates are equal and all colonization rates are equal and we will denote these rates by e_r and c_r respectively. Then one can write down the differential equation for the probability Q_x of x patches being occupied:

$$\frac{dQ_x}{dt} = R_{x-1,x}Q_{x-1} + R_{x+1,x}Q_{x+1} - (R_{x,x-1} + R_{x,x+1})Q_x \tag{6}$$

where $R_{k,l}$ is the rate of transition from k occupied patches to l occupied patches and where it is assumed that in infinitesimal time steps no more than one extinction or colonization event can occur. In matrix notation:

$$\frac{d\vec{Q}}{dt} = \vec{Q}R, \tag{7}$$

where $\vec{Q}$ represents an $(n + 1)$-dimensional vector containing the probabilities of $x = 0...n$ patches being occupied and R is the $(n + 1)$-by-$(n + 1)$ transition matrix with elements

$$R_{kl} = \begin{cases} ke_r & \text{for } k = l + 1 \\ -ke_r - kc_r(n - k) & \text{for } k = l \\ kc_r(n - k) & \text{for } k = l - 1 \\ 0 & \text{otherwise.} \end{cases} \tag{8}$$

For example, if $n = 2$, then R is given by

$$R = \begin{pmatrix} 0 & 0 & 0 \\ e_r & -e_r - c_r & c_r \\ 0 & 2e_r & -2e_r \end{pmatrix}. \tag{9}$$

The expected metapopulation extinction time is related to the second largest eigenvalue λ_2 of R (Keilson 1979, Frank & Wissel 1998):

$$T_{\text{ext}} = -\frac{1}{\lambda_2}. \tag{10}$$

The extinction and colonization rates can be converted to probabilities using

$$e = 1 - \exp(-e_r), \tag{11a}$$
$$c = 1 - \exp(-c_r), \tag{11b}$$

because $\exp(-e_r)$ and $\exp(-c_r)$ are the probabilities of a patch not having become extinct and not having colonized after one time-step.

Using the model for rules of thumb in nature management

As announced in the introduction, we will focus on several questions that are important for nature management. First we will study whether a metapopulation benefits (in terms of the

expected extinction time) most from a small change in colonization probabilities or from an equally small change in local extinction probabilities. We will then ask two more detailed questions: 1. If one focuses on local extinction probabilities, extinction of which patch should receive most attention? 2. If one focuses on colonization probabilities, colonization between which pair of patches deserves most attention? The answers to these two questions depend on the particular metapopulation structure; therefore, we study two extreme structures for each question to gain insight in the system and then we try to generalize to some rules of thumb. We first use the uncorrelated discrete-time model to obtain these answers and regard the continuous-time model and the correlated discrete-time model as test models to see how robust these answers are to changes in model structure. The changes in model structure that we consider are relatively small, so robustness of our results to these changes is definitely not sufficient to conclude overall robustness. Yet, models which are very dissimilar in model structure (and hence seem a better test of robustness) are much more difficult to gauge. Therefore, we restrict ourselves to our relatively small deviations in model structure. Robustness to these deviations may not be sufficient, but it is certainly necessary.

Should one decrease local extinction probability or increase colonization probability?

We first consider the situation in which all local extinction probabilities are equal ($e_i = e$ for all i) and all colonization probabilities are equal ($c_{ij} = c$ for all i and j); this means that we can use matrix P. If we decrease the local extinction probability e by a small amount Δe, or increase the colonization probability c by a small amount Δc, then we can ask whether decreasing local extinction probability yields a larger metapopulation extinction time than increasing the colonization probability. Because $T_{\text{ext}}(e, c)$ increases monotonically with increasing c when e is fixed, and with decreasing e when c is fixed, it suffices to look for the pairs (e, c) for which

$$-\Delta e \left. \frac{\partial T_{\text{ext}}}{\partial e} \right|_{(e,c)} = \Delta c \left. \frac{\partial T_{\text{ext}}}{\partial c} \right|_{(e,c)} . \qquad (12)$$

These pairs (e, c) then form the boundary in (e, c)-space between regions in (e, c)-space where T_{ext} benefits more from a decrease in e and regions where T_{ext} benefits more from an increase in c.

It remains to choose appropriate changes in e and c, that is, to choose Δe and Δc. We will assume that

$$\Delta e = \Delta c \qquad (13)$$

and discuss the reasons for this choice and consequences of other choices at the end of this article. This choice allows us simply to compare the derivatives in (12).

Numerical calculations gave graphs pictured in Figure 1A. It can be shown analytically (see appendix B) that the curves of Figure 1A-C cross the ($c = 0$)-axis at $e = 1 - \frac{1}{n-1}$. This means that for small c and $e > 1 - \frac{1}{n-1}$ it is always better to decrease local extinction probability than to increase colonization probability. This can be understood intuitively as follows: if e is close to 1, a large contribution to the metapopulation extinction time comes

from rapid local extinction in all patches before recolonization even gets the opportunity to increase the metapopulation extinction time. Therefore, a change in the colonization probability has only a small influence. When n increases, the probability of local extinction in all patches together decreases, so the effect of recolonization increases resulting in a higher upper bound for e when c is small.

Figure 1. The pairs (e,c) satisfying (12) and (13) for several values of n (A-C), and (e,c)-pairs estimated from data (D). A. The discrete-time model: above the lines decreasing e increases the metapopulation extinction time more than increasing c; below these lines the opposite applies. B. The continuous-time model: between the lines decreasing e increases the metapopulation extinction time more than increasing c; below the lower and above the upper lines the opposite applies. The line $c = e$ is drawn

[Figure 1 cont'd] for convenience; the lines appear to converge to this limit as n approaches infinity. C. The discrete-time model for $n = 5$ with correlated extinctions for several values of the correlation parameter ρ. D. Maximum likelihood estimates of the parameter combinations (e,c) and (e,c_8) from turnover data for several meta-populations. The pairs (e,c) and (e,c_8) corresponding to the same metapopulation are connected by a line; its lower end is (e,c) and its upper end is (e,c_8). The models used to estimate (e,c) and (e,c_8) are the (uncorrelated) discrete-time model and its analog for a limited number of 8 patches contributing to colonization. The letters denote the source of the turnover data. These are, with the number of patches: a. Briers & Warren (2000) - 68; b. Eber & Brandl (1994, 1996) - 513; c. Hanski et al. (1994) - 50; d. Lei & Hanski (1998) - 50,22; e. Harrison et al. (1988) - 59; f. Hecnar & M'Closkey (1997) - 160; g. Hill et al. (1996) - 69; h. Kindvall & Ahlén (1992) - 110; i. Morrison (1998) - 129; j. Nürnberger (1996) - 51; k. Smith & Gilpin (1997) - 78; l. Sutcliffe et al. (1997) - 14; m. Thomas & Harrison (1992) - 16,20; n. Van der Meijden & Van der Veen-Van Wijk (1997) - 102,79; o. Villard et al. (1995) - 51. Although the data sets are of different quality, we have not included a measure of the error in the parameter estimates, because they are intended for illustrative purposes only.

From Figure 1A one can conclude that if nothing is known about e and c, the results suggest that one should aim at decreasing e rather than at increasing c, because the region in (e, c)-space in which increasing c is favored is substantially smaller than the region where decreasing e is preferred. If we know that the colonization probability is (very) low and the extinction probability is smaller than $1 - \frac{1}{n-1}$, then increasing c is the better option. The latter addition makes clear that a hasty conclusion that one should increase c when the metapopulation is most extinction-prone is not warranted.

To investigate the robustness of these results to model structure, we repeated the analysis with slightly modified models. First, we considered the adjusted model with a maximum of 8 patches contributing to colonization. For this model we get similar results, but the curves of Figure 1A lie a bit higher for $n > 8$ (but still do not rise above $c_8 = 0.3$) and do not appear to go down again for large n, but instead seem to become independent of n.

Second, we considered the model in continuous-time. The results are shown in Figure 1B. The main difference between Figure 1A and Figure 1B is the presence of a second region favoring changes in c that is absent in Figure 1A. This is caused by the difference in the nature of the underlying models. When c is close to 1, colonization is almost certain, so all patches are almost always occupied. Therefore, metapopulation extinction can almost only come about if extinctions occur in all patches within a very short time interval, so that recolonization cannot take place. In the discrete-time model there is a finite period in which all patches can go extinct together, so decreasing e always has some impact, even for the extreme case $c = 1$. In the continuous-time model simultaneous extinctions were assumed to be impossible, so metapopulation extinction can only occur by subsequent extinctions of all patches without recolonizations in between. Hence, if $c = 1$, metapopulation extinction is impossible, so decreasing e has no effect whatsoever. This makes it plausible that for values of c only a little smaller than 1, decreasing e has hardly any influence, while increasing c

brings the system even closer to the situation where a change in e has no effect. Another difference between Figure 1A and 1B is that in Figure 1A for fixed e the corresponding value of c initially increases as n increases, but then starts to decrease at some value of n (which depends on e), whereas in Figure 1B the values of c below the line $c = e$ keep increasing with n; they seem to approach the line $c = e$. This elevation of the curves occurs because increasing c changes colonization probabilities for all $n(n-1)$ pairs of patches, whereas decreasing e only changes extinction probabilities of n patches, a difference of a factor $n - 1$ in favor of increasing c. In the discrete-time model there is an opposing force in favor of decreasing e, which dominates for large n: the probability of local extinction always benefits from decreasing e, whereas the probability of a patch being colonized does not gain much from increasing c when n is quite large. This opposing force is (almost) absent in the continuous-time model. The continuous-time model thus yields results similar to the discrete-time model: decreasing e is the preferred strategy unless c is small and $e < 1 - \frac{1}{n-1}$ (see appendix B). However, the continuous-time model favors increasing c when n becomes large ($n > 30$) or when c is quite large.

Third, to gain understanding of possible effects of correlated extinctions on the results, we repeated the analysis for $n = 5$ using the discrete-time model with correlated extinctions (4) for several values of the correlation parameter ρ. The resulting Figure 1C shows that correlation between extinctions makes the region in (e, c)-space in which increasing c is favored become smaller with increasing ρ. More generally, we expect that correlation strengthens the effect of decreasing the local extinction probability.

Finally, we examined what happens when we drop the assumption of equal e and equal c. We considered 1000 sets of randomly chosen e_i and c_{ij} (i.e. drawn uniformly from one of several choices of intervals, e.g. $0 < e_i, c_{ij} < 1$ or $0 < e_i < 1 - \frac{1}{n-1}; 0 < c_{ij} < 0.2$) for the case $n = 5$ and determined, in the spirit of (12), whether or not

$$-\sum_{i=1}^{n} \Delta e_i \left. \frac{\partial T_{\text{ext}}}{\partial e_i} \right|_{(\overrightarrow{e}, \overrightarrow{c})} > \sum_{i,j \neq i}^{n} \Delta c_{ij} \left. \frac{\partial T_{\text{ext}}}{\partial c_{ij}} \right|_{(\overrightarrow{e}, \overrightarrow{c})} \tag{14}$$

with

$$\Delta e_i = \Delta c_{ij} \tag{15}$$

and $(\overrightarrow{e}, \overrightarrow{c})$ denoting the entire set of extinction and colonization probabilities. This could be interpreted as a comparison between changes in patch habitat quality and matrix (between-patch) habitat quality. The results show that the left-hand side of (14) is almost always greater than the right-hand side, even for $0 < e_i < 0.5; 0 < c_{ij} < 0.2$ (Figure 2). Only if the e_i do not differ much (for example all equal) and the c_{ij} are small (for example $0 < c_{ij} < 0.2$), is the right-hand side greater for a substantial number of the 1000 sets (58.9% in the example, see also Figure 2, D). But, more importantly, when extinction changes are favored, it is by a factor of up to 500, while when colonization is more important, it is by only a twofold difference at most.
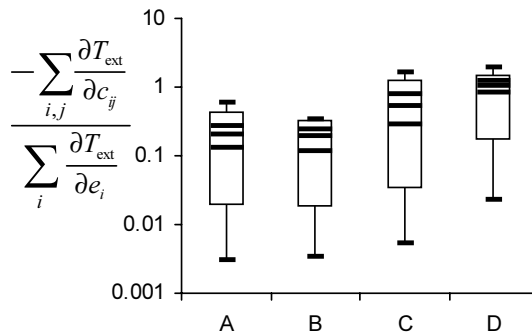
Until now we have compared decreasing e and increasing c on the metapopulation level: all probabilities participated. We can also make the comparison on a local level: for example comparing decreasing e_i with increasing $\sum_j (c_{ij} + c_{ji})$, i.e. a comparison between lowering extinction risk and raising disperser input and output of a patch. We did this in the 1000 sets

for the $n = 5$ case we have just discussed, and found that the results are qualitatively the same: decreasing the extinction probability is far more effective than increasing the sum of colonization probabilities for any patch.

> *First Rule of Thumb.* From all these results we induce the following rule of thumb: To increase metapopulation extinction time, decreasing local extinction probability is preferred over increasing colonization probability; this is strengthened if extinctions are correlated.
> Only if the colonization probabilities are (very) low and the extinction probabilities are almost equal and smaller than $1 - \frac{1}{n-1}$ or if the colonization probability is high and colonization occurs continually is increasing the colonization probability preferred.

Thus, if we have no knowledge about the extinction and colonization probabilities of a particular metapopulation we need to manage, the rule of thumb proposes that we decrease the extinction probability. This reasoning is based on the assumption that, if any further knowledge is lacking, all combinations of e and c are equally likely. In Figure 1D we have plotted the most likely combinations of (e,c) and (e,c_8) of several species, estimated from data on the number of extinctions and colonizations using, respectively, (3) and (3) with $(1 - c)^i$ replaced by $(1 - c_8)^{i8}$. It is evident that values of e smaller than 0.5 and c_8 (which is more realistic than c, particularly in large metapopulations) smaller than 0.2 are most common, so it seems that the exception mentioned in the rule applies to these metapopulations. However, while it is clear that metapopulation management should (also) be based on data, we caution that calculations from data should not be followed blindly (see Discussion).

Figure 2. Boxplots of the sensitivity to colonization relative to the sensitivity to extinction ($\sum_{i,j}^{n} \frac{\partial T_{\text{ext}}}{\partial c_{ij}} / \sum_{i}^{n} \frac{\partial T_{\text{ext}}}{\partial e_i}$) for 1000 sets of randomly chosen e_i and c_{ij}-values ($c_{ij} \neq c_{ji}$) with A. $0 < e_i, c_{ij} < 1$; B. $0 < e_i < 1, 0.4 < c_{ij} < 0.6$; C. $0 < e_i < 0.5$, $0 < c_{ij} < 0.2$; D. $0 < e_i = e < 1, 0 < c_{ij} < 0.2$. Other intervals yielded similar plots. The lower bound of the box is the 2.5th percentile (so 25 sets have a lower value of the sensitivity to colonization than this), the upper bound is the 97.5th percentile and the lines in the box denote the 25th, 50th and 75th percentiles. The ends of the vertical lines above and below the box are the maximum and minimum.

In which patch should the local extinction probability be decreased?

To address this question we consider two extreme situations in both of which we look for that patch i for which a small decrease Δe_i in the local extinction probability results in the largest increase in the metapopulation extinction time, i.e. we look for that patch i for which

$$-\Delta e_i \frac{\partial T_{\text{ext}}}{\partial e_i} \qquad (16)$$

is largest. In the first situation all colonization probabilities are equal ($c_{ij} = c$ for all i and j), but the local extinction probabilities e_i are allowed to differ. In the second situation all local extinction probabilities are equal ($e_i = e$ for all i), but the colonization probabilities c_{ij} are allowed to differ. We make the assumption, analogous to (13), that Δe_i is the same for all i, so in fact we look for the patch i for which $\frac{\partial T_{\text{ext}}}{\partial e_i}$ is largest.

In the first situation ($c_{ij} = c$ for all i and j) we numerically calculated $\frac{\partial T_{\text{ext}}}{\partial e_i}$ for 1000 sets of randomly chosen e_i ($0 < e_i < 1$) for various values of c and n. Since calculations for large n are very time-consuming we restricted ourselves to $n \leq 7$. The results indicate that the metapopulation extinction time is mostly affected by a change in the smallest e_i. In all sets, this result was found.
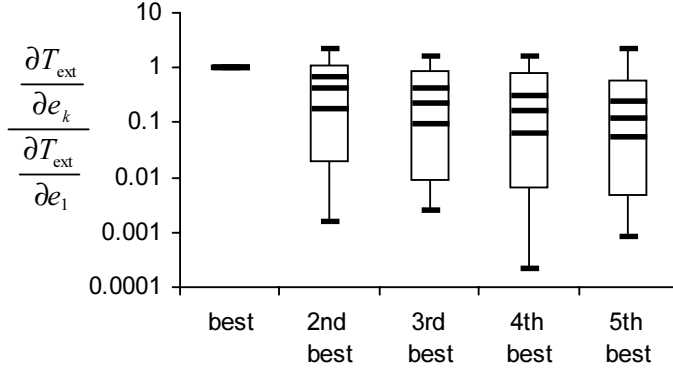
This result can be understood as follows. We have for the discrete-time model

$$
\begin{aligned}
T_{\text{ext}}(c = 0) &= \tfrac{1}{\min_j(e_j)}; & \left.\frac{\partial T_{\text{ext}}}{\partial e_i}\right|_{c=0} &= \begin{cases} -T_{\text{ext}}^2(c=0) & \text{if patch } i \text{ has the smallest } e_i \\ 0 & \text{for all other patches} \end{cases} \\
T_{\text{ext}}(c = 1) &= \tfrac{1}{\prod_{j=1}^{n} e_j}; & \left.\frac{\partial T_{\text{ext}}}{\partial e_i}\right|_{c=1} &= -\tfrac{1}{e_i} T_{\text{ext}}(c=1)
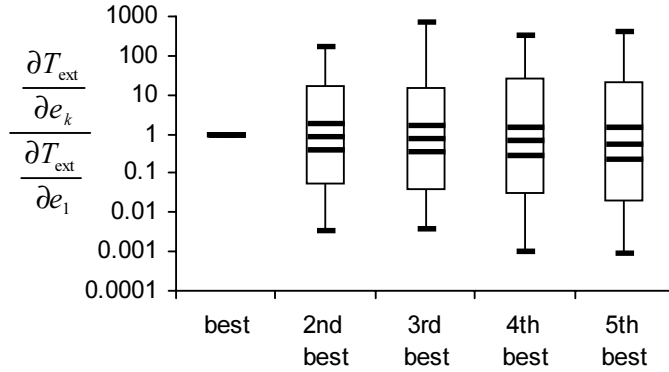\end{aligned}
$$

$$(17)$$

In both cases we find that $\frac{\partial T_{\text{ext}}}{\partial e_i}$ is largest in absolute value for the patch i with the smallest value of e_i. Because T_{ext} is monotone in e_i and c, it is not to be expected that this will be different for intermediate values of c.

In the second situation ($e_i = e$ for all i) we numerically computed $\frac{\partial T_{\text{ext}}}{\partial e_i}$ for 1000 sets of randomly chosen c_{ij} ($0 < c_{ij} < 1$) for various values of e and $n \leq 7$. The results indicate that, in general, the largest influence on metapopulation extinction time is obtained by a change in the e_i of the best-connected patch, i.e. a change in the local extinction probability of that patch i for which $\sum_j (c_{ij} + c_{ji})$ is largest. This means that for $n = 2$ there would be no preference between the patches, which was indeed the case in the calculations. To give some idea of how well this criterion works, the percentage of sets for which this criterion indeed picked the right patch (the patch for which decreasing the local extinction probability prolongs metapopulation persistence most), exceeded 70% for all values of n we studied ($n \leq 7$). Moreover, decreasing the extinction probability of the worst connected patch is almost never the best option to prolong metapopulation persistence. No significant trend for different values of e was observed nor was there any significant change if values for c_{ij} were restricted to a smaller interval than between 0 and 1 with a different mean than 0.5 (we chose $0 < c_{ij} < 0.2$ and $0.8 < c_{ij} < 1$, and $0.4 < c_{ij} < 0.6$ for comparison). However, there is a significant drop in the percentage for which the criterion picks the right patch when n

increases, but this is simply due to the presence of more patches competing for the position of best connected patch. If we allow a patch to be the right patch if it belongs to the top 20%, say, of best connected patches, then there is no such decrease. When we set $c_{ij} = c_{ji}$, the percentage of correct picks became even higher than with $c_{ij} \neq c_{ji}$.

A. kth best means kth smallest e_i

B. kth best means kth largest $\sum_j (c_{ij} + c_{ji})$

Figure 3. Boxplots of $\frac{\partial T_{\text{ext}}}{\partial e_k} / \frac{\partial T_{\text{ext}}}{\partial e_1}$ with k denoting the kth best patch, kth best meaning (A) kth lowest extinction probability or (B) kth largest sum of colonization probabilities, for the 1000 sets of randomly chosen e_i and c_{ij}-values. Here, $0 < e_i, c_{ij} = c_{ji} < 1$, but boxplots for the other intervals of the parameters mentioned in the text look very similar.

Thus, the results suggest that to increase metapopulation extinction time, one should decrease the lowest local extinction probability or the local extinction probability of the best connected patch, i.e. the patch i for which $\sum_j (c_{ij} + c_{ji})$ is largest. Evidently, in a situation where all parameters may differ, the patch with the lowest extinction probability will gener-

ally not be the best connected patch. To study the trade-off between "lowest extinction probability" and "best connected" we considered the case $n = 5$ and calculated $\frac{\partial T_{\text{ext}}}{\partial e_i}$ for 1000 sets of randomly chosen e_i and c_{ij} for several intervals of these probabilities ($0 < e_i < 1$, $0 < c_{ij} < 1$; $0 < e_i < 1$, $0 < c_{ij} < 0.2$; $0 < e_i < 0.5$, $0 < c_{ij} < 1$; $0 < e_i < 0.5$, $0 < c_{ij} < 0.2$) where we chose $c_{ij} = c_{ji}$ for simplicity, thereby getting the strongest effect of $\sum_j (c_{ij} + c_{ji})$. We found that "lowest extinction probability" very strongly dominates over "best connected", i.e. largest $\sum_j (c_{ij} + c_{ji})$. In the four above-mentioned parameter intervals we observed that for 94.6%, 98.2%, 95.2%, and 96.5% of the sets, decreasing the e_i of the patch with the lowest e_i gave the largest $\frac{\partial T_{\text{ext}}}{\partial e_i}$. For the patch with the largest $\sum_j (c_{ij} + c_{ji})$, these percentages were 21.4%, 18.9%, 21.2% and 20.0% which is insignificant because for $n = 5$ a total indifference to $\sum_j (c_{ij} + c_{ji})$ would give 20%. Figure 3 gives an impression of the relative differences in $\frac{\partial T_{\text{ext}}}{\partial e_i}$ for the patch with the lowest extinction probability, the second lowest extinction probability and so on, and for the patch with the best connections, the second best connections and so on. We can see from Figure 3A that sometimes choosing the patch with the lowest extinction probability is not the optimal choice, but the difference with the real optimum is always relatively small, whereas choosing a patch with the second lowest extinction probability may already differ up to a factor of 1000 with the real optimum. In Figure 3B we indeed observe that choosing the best-connected patch does not guarantee at all that one is even close to the real optimum.

Second Rule of Thumb. Summarizing we find the following rule of thumb, given that we focus on extinction: To increase metapopulation extinction time, one should preferably decrease the lowest local extinction probability. Only if the extinction probabilities are (almost) equal should one preferably decrease the local extinction probability of the best-connected patch, i.e. the patch i for which $\sum_j (c_{ij} + c_{ji})$ is largest.

Between which patches should the colonization probability be increased?

To address this question we consider the same two extreme situations as above, but now we look for that pair of patches i and j for which a small increase Δc_{ij} in the colonization probability results in the largest increase in the metapopulation extinction time, i.e. we look for that combination of patches i and j for which

$$\Delta c_{ij} \frac{\partial T_{\text{ext}}}{\partial c_{ij}} \tag{18}$$

is largest. We make the assumption, analogous to (13) and (16), that Δc_{ij} is the same for all combinations of i and j, so in effect we look for the patches i and j for which $\frac{\partial T_{\text{ext}}}{\partial c_{ij}}$ is largest.

In the first situation ($c_{ij} = c$ for all i and j) we numerically calculated $\frac{\partial T_{\text{ext}}}{\partial c_{ij}}$ for 1000 sets of randomly chosen e_i for various values of c and $n \leq 7$. The results suggest that one should always "put one's money on" increasing that c_{ij} between the patches i and j with the lowest extinction probability, i.e. the i and j for which $e_i + e_j$ (or $e_i e_j$) is minimal. Moreover, no difference between $\frac{\partial T_{\text{ext}}}{\partial c_{ij}}$ and $\frac{\partial T_{\text{ext}}}{\partial c_{ji}}$ was observed. In all sets this result was found.

Figure 4. The percentage of cases (out of 1000) in which increasing the highest (best), median and lowest (worst) colonization probability c_{ij} has the largest impact on the metapopulation extinction time for $n = 5$, several e and all c_{ij} randomly chosen in the range A. $0 < c_{ij} < 1$, B. $0.4 < c_{ij} < 0.6$, C. $0 < c_{ij} < 0.2$, D. $0.8 < c_{ij} < 1$. For simplicity, $c_{ij} = c_{ji}$ is chosen.

In the second situation ($e_i = e$ for all i) we numerically computed $\frac{\partial T_{\text{ext}}}{\partial e_i}$ for 1000 sets of randomly chosen c_{ij} for various values of e and $n \leq 7$. For these computations, matters are more complicated than above. To simplify somewhat, we chose $c_{ij} = c_{ji}$. Then, in general, an increase in the largest c_{ij} has the greatest impact on the metapopulation extinction time unless the c_{ij} are all very small and e is small (Figure 4). In the latter case, the smallest c_{ij} has the greatest impact (Figure 4C). Furthermore, as e increases, the percentage of sets in which the largest c_{ij} is indeed the one with the largest impact on T_{ext}, increases significantly up to a certain value of e after which it decreases. This final decrease can be understood following a line of reasoning used earlier. When e is very large, metapopulation extinction occurs before colonization even gets the opportunity to prolong metapopulation longevity; therefore, there is no strong preference for increasing any particular colonization probability as e becomes very high.

A. kth best means kth smallest $e_i + e_j$

B. kth best means kth largest c_{ij}

Figure 5. Boxplots of $\frac{\partial T_{\text{ext}}}{\partial c_k} / \frac{\partial T_{\text{ext}}}{\partial c_1}$ with k denoting the kth best, kth best meaning (A) the c_{ij} with the kth smallest value of $e_i + e_j$ or (B) kth highest colonization probability c_{ij}, for the 1000 sets of randomly chosen e_i and c_{ij}-values. Here, $0 < e_i, c_{ij} = c_{ji} < 1$, but boxplots for the other intervals of the parameters mentioned in the text look very similar. Because $c_{ij} = c_{ji}$ and $\frac{\partial T_{\text{ext}}}{\partial c_{ij}} = \frac{\partial T_{\text{ext}}}{\partial c_{ji}}$, the number of possible values for k equals 10.

Thus, the results suggest that to increase metapopulation extinction time, one should increase either the colonization probability between the patches with the lowest extinction probability or the highest colonization probability (unless extinction probabilities and colonization probabilities are very low). Naturally, in a situation where all parameters differ, the colonization probability between the patches with the lowest extinction probability will generally not be the highest. To study the trade-off between "between the lowest extinction probabilities" and "highest colonization probability", we considered, just as for the previous question, the case $n = 5$ and calculated $\frac{\partial T_{\text{ext}}}{\partial c_{ij}}$ for 1000 sets of randomly chosen e_i and c_{ij} for several intervals of these probabilities ($0 < e_i < 1$, $0 < c_{ij} < 1$; $0 < e_i < 1$, $0 < c_{ij} < 0.2$;

$0 < e_i < 0.5, 0 < c_{ij} < 1; 0 < e_i < 0.5, 0 < c_{ij} < 0.2$), where we chose $c_{ij} = c_{ji}$ for simplicity. We found that "between the lowest extinction probabilities" strongly dominates over "highest colonization probability". In the four above-mentioned parameter intervals we observed that for 83.0%, 90.0%, 56.0%, and 92.2% of the sets, increasing the c_{ij} of the connection between the patches with the lowest e_i gave the largest $\frac{\partial T_{\text{ext}}}{\partial c_{ij}}$. For the connection with the largest c_{ij}, these percentages were 14.3%, 12.4%, 21.1% and 9.8% which is not significant. Figure 5 gives an impression of the relative differences in $\frac{\partial T_{\text{ext}}}{\partial c_{ij}}$ for the connection between the two lowest extinction probabilities, between the two second lowest extinction probabilities and so on, and for the patch with the highest colonization probability, the second highest colonization probability and so on.

> *Third Rule of Thumb*. Recapitulating, the following rule of thumb can be formulated, given that we focus on colonization: To increase metapopulation extinction time, one should preferably increase the colonization probability between the patches with the lowest extinction probability. Only if the extinction probabilities are (almost) equal should one preferably increase the highest colonization probability (unless extinction probabilities and colonization probabilities are very low).

Discussion

The results of this article lead to three rules of thumb. First, for most combinations of the local extinction probability e and the colonization probability c, a decrease in e will increase the metapopulation extinction time more than would a comparable increase in c. This suggests that, in general, one should focus on decreasing e rather than on increasing c, even more so when extinctions are correlated. This preference for lowering extinction probability is in agreement with general conclusions in the literature (e.g. Goel & Richter-Dyn 1974, Drechsler & Wissel 1998). Second, if one focuses on decreasing local extinction probability, then one should generally select the patch with the lowest local extinction probability; only if the extinction probabilities are (almost) equal should one generally select the patch with the best direct connections in terms of the largest value of $\sum_j (c_{ij} + c_{ji})$. We expect that the latter criterion only works if indirect connections do not vary much between patches such that the sum of direct connections are a good proxy for overall connectivity. Third, if one focuses on increasing colonization probability, then one should generally select the colonization probability between the patches with the lowest extinction probability; only if the extinction probabilities are (almost) equal should one select the highest colonization probability, or at least not the lowest.

We stress that the rules of thumb should be treated with caution (as should all rules of thumb). We will discuss some of their limitations below. But first we want to remark that these rules of thumb show an important similarity that may be more robust than the rules of thumb themselves: extinction appears as a more dominant process than colonization. The main reason for this is presumably that extinction is not only important on a generation basis (i.e. affecting the number of patches colonized by an occupied patch during its lifetime as

an occupied patch), but also in real time (see also Goel & Richter-Dyn 1974; Diekmann & Heesterbeek 2000), both of which are important for the expected metapopulation extinction time. In contrast, colonization plays a part only on a generation basis. If an alternative measure of metapopulation persistence is used − such as R_0 (the mean number of patches colonized by an occupied patch in an otherwise empty environment) and its related, computationally simpler, measures of colonization potential (Etienne & Heesterbeek 2000) and metapopulation capacity (Hanski & Ovaskainen 2000), or the mean occupancy − the dominance of extinction might disappear. The measure to be used depends on our management goals and the metapopulation in question. The variable R_0 (or colonization potential or metapopulation capacity) is a measure of the resilience of the metapopulation after a catastrophe (fire, drought, disease), while patch occupancy stresses abundance, not just presence of a species. We chose the expected time to metapopulation extinction as a measure of persistence because of its easy interpretation and its connection with real time (in which we live), but we remark that it may be fairly useless in specific cases, e.g. when catastrophes are likely to occur on a time-scale shorter than the metapopulation extinction time. Furthermore, we need to stress that the expected metapopulation extinction time depends on the initial state. We took as our initial state the quasi-stationary state, which was said to represent pseudo-equilibrium. Pseudo-equilibrium seems to be the most neutral starting-point for deriving rules of thumb for metapopulations in general. One may wonder whether mathematical pseudo-equilibrium corresponds to the ecological pseudo-equilibrium we have in mind, but without a clearly better alternative, the choice seems fair, especially if we remember that only changes in the metapopulation extinction time were studied instead of predicted values for the metapopulation extinction time itself.

From the common denominator in the rules of thumb − local extinction is more important than colonization − it would seem that one could conclude that the metapopulation approach to management is not very effective: it seems better to manage a single extinction-proof patch and regard the other patches as a bonus, i.e. a mainland-island setting. Add to this the risks of increasing colonization (e.g. facilitating spread of pathogens) and one may have a fairly strong case for a dismissive attitude toward building corridors and stepping stones. We do not fully subscribe to this opinion. First of all, as we noted above, the conclusion may be valid only if we use the expected metapopulation extinction time as a measure of persistence, which is debatable on scientific and other grounds; a high patch occupancy may be politically more defensible than a long time to metapopulation extinction due to survival in only a few (perhaps distant) patches. Second, as the data shown in Figure 1D indicate, most metapopulations have low colonization probabilities, in which case matters are subtler. Third, such an opinion disregards the fact that increasing colonization is still beneficial, albeit not as beneficial as decreasing extinction in most cases, and nature managers may not always have the option to maintain a mainland or even diminish local extinction risk at all, especially in a very fragmented landscape. In that situation they should have some idea whether they should, for example, improve some existing corridors or build new corridors. So, we think that our results should dim the enthusiasm for connectivity and restore the interest in local habitat management, but they should not lead to rejection of the metapopulation approach; we need to keep working at multiple scales.

We noted that Figure 1D, with values of (e,c) and (e,c_8) calculated from data, calls into question our first rule of thumb that we should focus on decreasing e rather than on increasing c. However, the data may not represent classical metapopulations and the models used in the calculations assume equal e and c across patches, which is obviously far from realistic. Moreover, recalling Figure 2, we see, first, that if increasing c is preferred, decreasing e is not much less successful than increasing c and, second, that if one chooses to increase c based on incorrect information, we may be far from the optimal situation achieved by decreasing e. In sum, we feel that Figure 1D warns us to be cautious in using the rule of thumb, but no more than that.

When we compared the effect of small changes in the probabilities (i.e. Δe, Δc, Δe_i, Δc_{ij}) we assumed that they were equal. Especially when comparing changes in e and changes in c, we may be comparing apples and oranges; they only have in common that they are probabilities in the same way that apples and oranges are both fruits. A fair comparison seems only possible on the level of effort, or indeed, money: if we are to choose between putting a certain amount of effort or money x on increasing c or decreasing e, we need to know Δe and Δc as functions of x. A similar procedure should be followed with respect to comparisons between the Δe_i's and between the Δc_{ij}'s. Unfortunately, such a function is not easily formulated. One may try to relate the extinction and colonization probabilities to measurable quantities such as patch area (A_i) and interpatch distance (d_{ij}); see e.g. Gyllenberg & Silvestrov (1994) who put $e_i = \exp(-A_i)$ and $c_{ij} = \exp[-A_i \exp(-\frac{d_{ij}}{d_c})]$ with d_c the characteristic dispersal distance, in a discrete-time model similar to the model of this article, but without separation of extinction and colonization phases. Yet, even if area and interpatch distance are considered sufficient to describe extinction and colonization, these relationships are debatable. Moreover, we still require expressions of ΔA_i and Δd_{ij} as functions of x. Therefore, we deliberately chose to stay on the level of extinction and colonization probabilities, thus avoiding these relatively arbitrary choices of the functional forms. And in fact, there is an alternative option that might incorporate some aspects of a function relating Δe and Δc to x on this probability level: comparing transformed changes. For example, we could compare a change in the local extinction probability for all patches together with a change in the colonization probability for all connections together (i.e. all $n(n-1)$ pairs of patches), that is, we could require

$$n\Delta e = n(n-1)\Delta c. \tag{19}$$

Such a comparison will strengthen the effects of decreasing e, because Δc will be smaller than Δe for $n > 2$. Another example is to compare relative changes in the parameters instead of absolute ones, that is, we could require

$$\frac{\Delta e}{e} = \frac{\Delta c}{1-c}, \tag{20}$$

which is a mathematical formulation of the intuition that it will be more difficult to change e when its value is small than when it is large, and analogously, that it will be more difficult to change c when its value is close to 1 than when it is close to 0. The consequence for Figure 1 is that all the lines lie a little higher, start higher for small e and end on the $c = 0$-axis at larger values of e, namely at $e = 1 - \frac{1}{n}$. So this choice would weaken the first rule of thumb, but the region in (e, c)-space where increasing c is better than decreasing e is still smaller than

the remaining region. For the second and third rules of thumb, the requirement analogous to (20) becomes

$$\frac{\Delta e_k}{e_k} \quad = \quad \frac{\Delta e_l}{e_l}, \tag{21a}$$

$$\frac{\Delta c_{ij}}{1 - c_{ij}} \quad = \quad \frac{\Delta c_{kl}}{1 - c_{kl}} \tag{21b}$$

for each i,j,k and l. This may again have a weakening effect on the rules of thumb. Yet, as stated above, (20) is a mathematical formulation of an intuition, and it is questionable whether we should trust intuitions in this case. For example, well-connected patches may be much easier to connect than poorly-connected patches precisely because of the fact that they are well-connected: the infrastructure may allow for more connectivity. So, unless Δe and Δc as a function of x are known, both (13) and (20) seem quite arbitrary, and we chose the simpler of the two.

Another feature of our analysis needs some attention here. All our randomly generated sets of probabilities were based on the uniform distribution, albeit on several different intervals. Ideally, we should have used extinction and colonization probabilities in real landscapes for real species, but if we knew these for so many different landscapes and species, most of this article would be superfluous. Since determining these probabilities is not an easy task, we are left to use some distribution of these probabilities that we think is fairly realistic. Yet, without strong arguments for a particular distribution, we chose the (arguably) simplest one: the uniform distribution. Encouraged by the limited effect of different intervals, we conjecture that different choices still support our conclusions but in a different degree.

In this article we have only explored three of many questions that may be raised in management of metapopulations. There are many more combinations of changes (in particular a combination of an increase in colonization probability and a decrease in extinction probability) than those we investigated; we tried to pick those that are both simple and useful. Also, we restricted our study to small changes in the parameters, although successive small changes or one large change could lead to different optima. Another interesting option would have been to study the effects of increasing the number of patches, but this discrete change is difficult to compare with small continuous changes in the probabilities (e.g. how to allocate colonization and extinction probabilities to a newly added patch). Furthermore, we examined some modifications of the main model, but many more are conceivable (multiple species, explicit local dynamics, catastrophes). Nevertheless, we believe that this article is a first step toward finding optimal strategies for nature management of metapopulations. The rules of thumb could act as guidelines or null hypotheses that need testing in particular cases and could steer further research, either with different models (e.g. using graph and percolation theory; see e.g. Keitt et al. 1997, Bunn et al. 2000, Urban & Keitt 2001) or more detailed models, or ideally with empirical data. To our knowledge no such model-based null hypotheses were available before. In addition, we feel that the processes underlying metapopulation dynamics have been somewhat disentangled and that new light has been shed on the complexity of the remaining entanglement.

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Appendix A. Derivation of equations (3) and (4)

In this appendix we give the derivation of equations (3) and (4). Let us start with (3). The transition from k to l occupied patches can take place though $k - i$ extinctions to the intermediate state of i occupied patches, and subsequently through $l - i$ colonizations to the final state l:

$$P_{kl} = \sum_{i=0}^{\min(k,l)} p_{ki} p_{il} \tag{A-1}$$

where i is bounded by the initial number of occupied patches k on the one hand (no new occupied patches can arise after extinction), and by the final number of patches l (there can be no more patches after extinction than there can be after colonization). Assuming extinctions to be uncorrelated, extinction of $k - i$ patches has probability e^{k-i}. If $k - i$ patches go extinct, i patches do not go extinct, which happens with probability $(1 - e)^i$. There are $\binom{k}{i}$ different ways in which $k - i$ patches can go extinct. Hence,

$$p_{ki} = \binom{k}{i}(1 - e)^i e^{k-i}. \tag{A-2}$$

Colonization of $l - i$ patches by the remaining i patches has a probability of $1-$ (the probability of not being colonized by i patches), that is, $\left[1 - (1 - c)^i\right]^{l-i}$. If l patches are occupied in the end, then $n - l$ patches have not been colonized by the i patches remaining after extinction, and this has probability $\left[(1 - c)^i\right]^{n-l}$. There are $\binom{n-i}{l-i}$ ways of $l - i$ empty patches being colonized if there are $n - i$ empty patches. Hence,

$$p_{il} = \binom{n - i}{l - i} \left[1 - (1 - c)^i\right]^{l-i} \left[(1 - c)^i\right]^{n-l}. \tag{A-3}$$

If we have correlated extinctions, then (A-2) is no longer valid. Instead we suppose that it becomes

$$p_{ki} = \binom{k}{i} f(e, k, i, \rho) \tag{A-4}$$

for some function f that describes the probability of $k - i$ patches going extinct and i patches not going extinct when extinctions are correlated with some measure of correlation ρ. To find an expression for f we need knowledge of the mechanism that correlates the extinctions. Because this mechanism may be very complicated and our main goal is to get some insight in how any correlation in extinctions might change our results, we use a more phenomenological approach yielding an explicit expression for f.

We postulate that the extinction of each occupied patch j is governed by a stochastic variable y_j and that extinction occurs unless y_j exceeds some critical or threshold value y_j^c. We assume further that each y_j can be written as $y_j = \mu_j + u + \varepsilon_j$ where μ_j is a constant and u and ε_j are normally distributed variables with zero mean and variances σ^2 and 1 respectively. This entails that y_j is also normally distributed with mean μ_j and variance $1 + \sigma^2$. All y_j have u in common, so u (or equivalently σ^2) measures the strength of the correlation. To obtain a correlation measure with a value between 0 and 1, we define $\rho :=$

$\frac{\sigma^2}{1+\sigma^2}$. Suppose we have k occupied patches. From the construction of the y_j it follows that the vector $\overrightarrow{y} = (y_1, y_2, ..., y_n)$ is a k-dimensional normally distributed variable with mean vector $\overrightarrow{\mu} = (\mu_1, \mu_2, ..., \mu_k)$ and covariance matrix $Y = \sigma^2 J + I$, where J is a k-by-k-matrix with all elements equal to 1 and I is the k-by-k identity matrix.

We can now relate the extinction probability e_j to the variable y_j in the following way:

$$e_j = P\left(y_j < y_j^c\right) = \Phi\left(\frac{y_j^c - \mu_j}{\sqrt{1+\sigma^2}}\right) \Rightarrow$$

$$y_j^c - \mu_j = \sqrt{1+\sigma^2}\Phi^{-1}\left(e_j\right) \tag{A-5}$$

where $\Phi(x)$ is the cumulative standard normal distribution in one dimension. Now we want to calculate the probability $f(e_1...e_k, k, i, \rho)$ that certain patches go extinct while others do not. If we number the patches such that patches $1...k - i$ are the ones that go extinct and $k - i + 1...k$ do not, this probability f is given by

$$f(e_1...e_k, k, i, \rho) = P_k\left(y_j < y_j^c \text{ for } j \leq k - i \text{ and } y_j > y_j^c \text{ for } j > k - i\right) =$$
$$= P_k\left(y_j - \mu_j < y_j^c - \mu_j \text{ for } j \leq k - i \text{ and } y_j - \mu_j > y_j^c - \mu_j \text{ for } j > k - i\right) =$$
$$= \int_{-\infty}^{\sqrt{1+\sigma^2}\Phi^{-1}(e_1)} ... \int_{-\infty}^{\sqrt{1+\sigma^2}\Phi^{-1}(e_{k-i})} \int_{\sqrt{1+\sigma^2}\Phi^{-1}(e_{k-i+1})}^{\infty} ... \int_{\sqrt{1+\sigma^2}\Phi^{-1}(e_k)}^{\infty} \Bigg($$
$$N_k[\overrightarrow{y}, \overrightarrow{0}, Y]\Bigg) d\overrightarrow{y} \tag{A-6}$$

where we have attached the subscript k to P to denote that the probability concerns k events, $N_k[\overrightarrow{y}, \overrightarrow{0}, Y]$ is the normal distribution in k dimensions with zero mean and covariance matrix Y, and we have used (A-5). If we now substitute $e_j = e$ for all j and use (A-4) in (A-1) we get the required equation (4).

We remark that to facilitate numerical calculation of the integral in (A-6), one can use Ihm's (1959) formula which in this case reads

$$\int_B N_k[\overrightarrow{y}, \overrightarrow{0}, Y]d\overrightarrow{y} = \frac{1}{\sigma\sqrt{2\pi}}\int_{-\infty}^{\infty} e^{-\frac{1}{2}\frac{z^2}{\sigma^2}}\int_B N_k[\overrightarrow{y} - z\overrightarrow{d}, \overrightarrow{0}, I]d\overrightarrow{y}dz \tag{A-7}$$

with B the k-dimensional domain of integration and $\overrightarrow{d}$ a k-dimensional vector with all elements equal to 1. Furthermore one can use the fact that, since we have $e_i = e$,

$$P_k\left(y_j < y_j^c \text{ for } j \leq k - i \text{ and } y_j > y_j^c \text{ for } j > k - i\right) = \tag{A-8}$$

$$= \sum_{h=0}^{i}\binom{i}{h}(-1)^h P_{k-i+h}\left(y_j < y_j^c \text{ for } j \leq k - i + h\right) \tag{A-9}$$

with, evidently, $P_0\left(y_j < y_j^c \text{ for } j \leq 0\right) = 1$ and $P_1\left(y_j < y_j^c \text{ for } j \leq 1\right) = e$, which means that if there are n patches we only have to compute $n - 1$ integrals to get all possible values p_{kl}.

Appendix B. The value of e satisfying (12) and $c = 0$

In this appendix we will show that the curves of Figures 1A-B cross the $(c = 0)$-axis for $e = 1 - \frac{1}{n-1}$. First we note from (5) and (10) that in the discrete-time case

$$\frac{\partial T_{\text{ext}}}{\partial x} = \frac{\partial}{\partial x}\left(\frac{1}{1-\lambda_2}\right) = \frac{1}{(\lambda_2 - 1)^2}\frac{\partial \lambda_2}{\partial x} \tag{B-1}$$

and that in the continuous-time case

$$\frac{\partial T_{\text{ext}}}{\partial x} = -\frac{\partial}{\partial x}\frac{1}{\lambda_2} = \frac{1}{\lambda_2^2}\frac{\partial \lambda_2}{\partial x} \tag{B-2}$$

where x denotes any one of the two parameters e and c. Thus we see that in both cases the equality

$$\left.\frac{\partial T_{\text{ext}}}{\partial e}\right|_{(e,c)} = -\left.\frac{\partial T_{\text{ext}}}{\partial c}\right|_{(e,c)} \tag{B-3}$$

is equivalent to the equality

$$\left.\frac{\partial \lambda_2}{\partial e}\right|_{(e,c)} = -\left.\frac{\partial \lambda_2}{\partial c}\right|_{(e,c)}. \tag{B-4}$$

Below we will use the following result from Caswell (1989): for a matrix A with elements a_{ij}, left eigenvector $\overrightarrow{w}$ and right eigenvector $\overrightarrow{v}$ and a parameter x, we have

$$\frac{\partial \lambda_2}{\partial x} = \sum_i \sum_j \frac{\partial \lambda_2}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial x} = \frac{1}{\overrightarrow{v}\cdot\overrightarrow{w}}\sum_i \sum_j \overline{w}_i v_j \frac{\partial a_{ij}}{\partial x} \tag{B-5}$$

where the dot represents the inner product and the bar represents the complex conjugate.

Discrete time

For any n, when $c = 0$ the second largest eigenvalue λ_2 of P is $(1 - e)$ and it has right eigenvector $\overrightarrow{v} = (0, 1, ..., k, ..., n)^{\text{T}}$ if $e \neq 0, 1$ ($k = 0, 1, ..., n$), and left eigenvector $\overrightarrow{w} = (-1, 1, 0, ..., 0)$. In this case Caswell's formula gives

$$\left.\frac{\partial \lambda_2}{\partial x}\right|_{c=0} = \frac{1}{\overrightarrow{v}\cdot\overrightarrow{w}}\sum_i \sum_j \overline{w}_i v_j \left.\frac{\partial P_{ij}}{\partial x}\right|_{c=0} =$$

$$= \frac{\sum_{j=0}^n \left(-v_j \left.\frac{\partial P_{0j}}{\partial x}\right|_{c=0} + v_j \left.\frac{\partial P_{1j}}{\partial x}\right|_{c=0}\right)}{(0, 1, ..., k, ..., n)^{\text{T}}\cdot(-1, 1, 0, ..., 0)} =$$

$$= \sum_{j=1}^n j \left.\frac{\partial P_{1j}}{\partial x}\right|_{c=0} = \frac{\partial}{\partial x}\sum_{j=1}^n jP_{1j}\Bigg|_{c=0} =$$

$$
= \quad \frac{\partial}{\partial x} \sum_{j=1}^{n} \sum_{i=0}^{1} \left\{ \binom{1}{i} (1-e)^i e^{1-i} \binom{n-i}{j-i} \left[1 - (1-c)^i\right]^{j-i} \left[(1-c)^i\right]^{n-j} j \right\} \Bigg|_{c=0} =
$$

$$
= \quad \frac{\partial}{\partial x} \left\{ (1-e) \sum_{j=1}^{n} \binom{n-1}{j-1} c^{j-1} (1-c)^{n-j} j \right\} \Bigg|_{c=0} =
$$

$$
= \quad \frac{\partial}{\partial x} \left\{ (1-e) \sum_{j=0}^{n-1} \binom{n-1}{j} c^j (1-c)^{(n-1)-j} (j+1) \right\} \Bigg|_{c=0} =
$$

$$
= \quad \frac{\partial}{\partial x} (1-e) \left[1 + (n-1)c\right] \Bigg|_{c=0} \tag{B-6}
$$

where in the last line properties of the binomial distribution are used.

Now,

$$
\frac{\partial \lambda_2}{\partial e} \Bigg|_{c=0} = -1 \left[1 + (n-1)c\right]\big|_{c=0} = -1 \tag{B-7}
$$

and

$$
\frac{\partial \lambda_2}{\partial c} \Bigg|_{c=0} = (1-e)(n-1)|_{c=0} = (1-e)(n-1) \tag{B-8}
$$

so condition (12) is satisfied in $c = 0$ if

$$
e = 1 - \frac{1}{n-1}. \tag{B-9}
$$

Continuous time

When $c = 0$ the second largest eigenvalue is $\lambda_2 = -e_r$ which has right eigenvector $\vec{v} = (0, 1, ..., k, ..., n)^{\mathrm{T}}$ if $e \neq 0, 1$ ($k = 0, 1, ..., n$) and left eigenvector $\vec{w} = (-1, 1, 0, ..., 0)$. Again we can compute the derivative of λ_2 with respect to a parameter x (e_r or c_r) in this case:

$$
\frac{\partial \lambda_2}{\partial x} \Bigg|_{c=0} = \frac{1}{\vec{v} \cdot \vec{w}} \sum_i \sum_j \overline{w}_i v_j \frac{\partial R_{ij}}{\partial x} \Bigg|_{c=0} =
$$

$$
= \sum_{j=0}^{n} \left(j \frac{\partial R_{1j}}{\partial x} \Bigg|_{c=0} \right) = \frac{\partial}{\partial x} \sum_{j=0}^{n} j R_{1j} \Bigg|_{c=0} =
$$

$$
= \frac{\partial}{\partial x} \left[-e_r + c_r(n-1)\right] \Bigg|_{c=0}. \tag{B-10}
$$

First we observe that from (11a) and (11b) it follows that

$$\frac{dc_r}{dc} = \frac{d}{dc}\left[-\ln\left(1-c\right)\right] = \frac{1}{1-c}, \tag{B-11a}$$

$$\frac{de_r}{de} = \frac{d}{de}\left[-\ln\left(1-e\right)\right] = \frac{1}{1-e}. \tag{B-11b}$$

Because

$$\left.\frac{\partial\lambda_2}{\partial c}\right|_{c=0} = \left.\frac{\partial\lambda_2}{\partial c_r}\frac{dc_r}{dc}\right|_{c=0} = \left.\frac{1}{1-c}\frac{\partial}{\partial c_r}\left[-e_r + c_r(n-1)\right]\right|_{c=0} = n-1 \tag{B-12}$$

and

$$\left.\frac{\partial\lambda_2}{\partial e}\right|_{c=0} = \left.\frac{\partial\lambda_2}{\partial e_r}\frac{de_r}{de}\right|_{c=0} = \left.\frac{1}{1-e}\frac{\partial}{\partial e_r}\left[-e_r + c_r(n-1)\right]\right|_{c=0} = -\frac{1}{1-e} \tag{B-13}$$

(12) is satisfied in $c = 0$ for $e = 1 - \frac{1}{n-1}$.

6

Optimal metapopulation conservation strategies concerning patch area and interpatch distance

RAMPAL S. ETIENNE

Abstract

Metapopulation theory teaches that the viability of metapopulations may be enlarged by decreasing the probability of extinction of local populations, or by increasing the colonization probability of empty habitat patches. In a metapopulation model study it has recently been found that reducing the extinction probability of the least extinction-prone patch and increasing the colonization probability between the two least extinction-prone patches are the best options to prolong the lifetime of a metapopulation. In this article we examine with a more detailed model whether this translates into enlarging the largest patch and reducing the interpatch distance between the largest patches. We found that this is indeed the case in general, but there are some significant exceptions.

Introduction

Fragmentation of habitat is considered a major threat to species persistence. Populations in the fragments are much more prone to extinction than in large continuous habitat unless the fragments are so well connected that fragments can be frequently recolonized from other fragments. The metapopulation concept (Levins 1969, Levins 1970) describes the balance of local extinctions and recolonizations whereby a species can persist much longer in the entire network of fragments (called patches) than in any single patch. This insight has led to the attitude that fragmentation should be counteracted by increasing connectivity, for example by constructing corridors (ecoducts) or stepping stone patches. Although this is indeed beneficial to metapopulation persistence according to standard metapopulation theory, it is not neces-

sarily the optimal action to take against fragmentation. As Etienne & Heesterbeek (2001) showed, local extinction has a greater bearing on metapopulation persistence (as measured by the expected time to extinction) than colonization, which suggests that *a priori* the opposite holds: local, intrapatch, action is more effective than global, interpatch, action. However, their analysis was fully in terms of extinction and colonization probabilities which a nature manager can only influence indirectly by altering landscape characteristics such as patch area (or patch quality) and (the effective) interpatch distance. In terms of these landscape characteristics, Etienne & Heesterbeek (2001) remark, matters might be different, because a change in one such landscape characteristic may affect both extinction and colonization probabilities simultaneously, and presumably to different extents. In particular, the local extinction probabilities of patches of different sizes may react differently to changes in patch size.
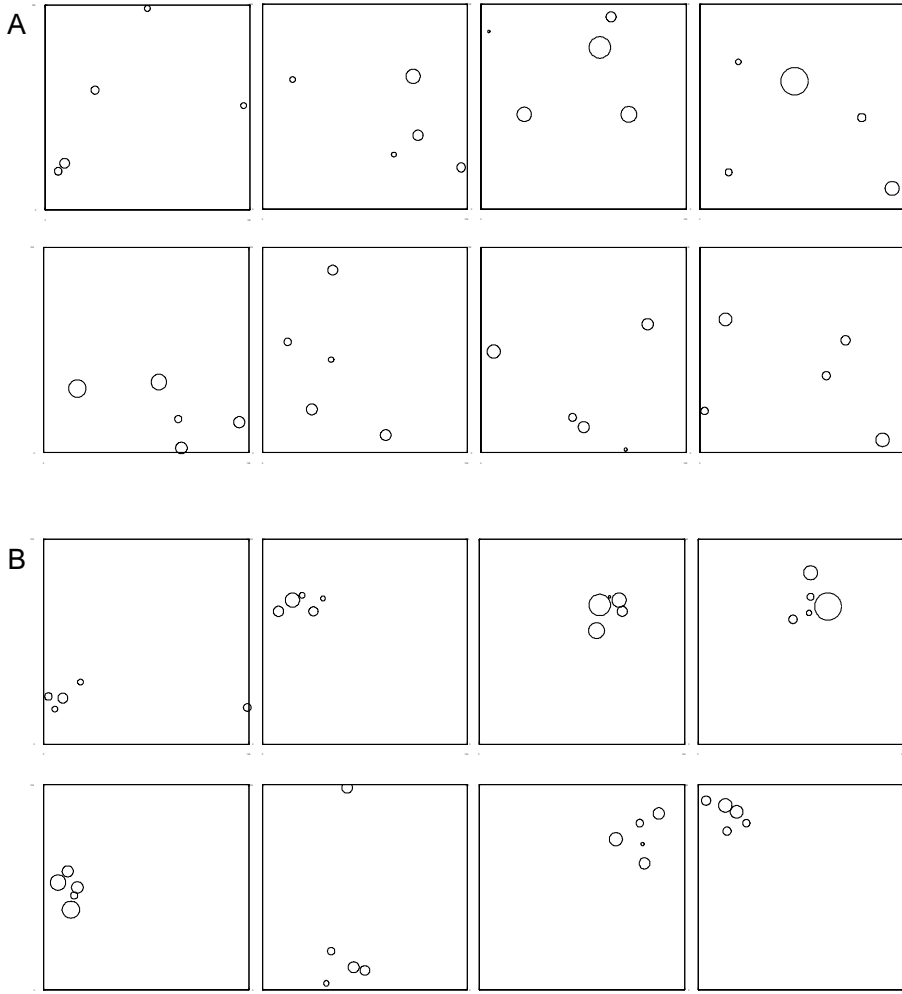
It is not completely obvious, however, how extinction and colonization probabilities are related to landscape characteristics, because a variety of processes may underlie these relationships (see Etienne & Heesterbeek 2000 for a few simple examples). Especially our knowledge of dispersal is still rather limited which aggravates establishing these relationships. Furthermore, in taking action, the financial picture is a very important, yet highly uncertain and variable, aspect as well. Hence, practical questions, such as "is it better to enlarge patches or decrease (the effective) interpatch distance", "which patch should be enlarged", and "which distance should be decreased", seem to allow for an answer only in single cases. General answers, rules of thumb, which are very useful if time and money are limited, have not been provided.

In this paper we will try to fill this gap by constructing artificial landscapes for which we determine the conservation strategy which is optimal for metapopulation persistence, employing two measures of metapopulation persistence, one measuring the longevity of an existing metapopulation and one measuring the resilience of a species in a network when only one patch is initially occupied. We will use the two above-mentioned landscape characteristics (patch area and interpatch distance), and we will link them to the local extinction and colonization probabilities in several ways. We chose patch area and interpatch distance, because these are thought to be the most important landscape characteristics for the metapopulation processes of local extinction and colonization (Hanski 1999a). In our analysis, patch area may also be interpreted as patch quality which is the third major player in the metapopulation field (Thomas et al. 2001), although the exact link with extinction and colonization is less well studied.

Methods

Generating artificial landscapes

Although there are many sophisticated ways of generating landscapes including fractals (Johnson et al. 1992, Andrén 1994, Hargis et al. 1998, Meisel & Turner 1998, Hokit et al. 2001), for our purposes a simple algorithm suffices. We used a 128 by 128 grid each cell of which

Figure 1. Examples of artificially generated landscapes. A. Randomly distributed patches. B. Extremely clustered patches ($\sigma = 10$).

can be the center of a circular patch. We first chose the number of patches ($n = 5$) and then assigned each patch a patch area according to a lognormal probability distribution (Hanski & Gyllenberg 1997) with mean $\log A_m$ and standard deviation $\log r_A$. We chose one combination, ($\log A_m = \log 25$, $\log r_A = \log 2.5$) which yields patch areas which are usually larger than the minimum patch area (see below), but sufficiently small so that the metapopulation approach is warranted (local extinction probabilities should not be too small, see below). The first patch is then placed randomly anywhere in the grid. The second patch is placed in

the grid according to a Gaussian probability distribution centered around (but not in) the first patch. By changing the value of the standard deviation, σ, of this distribution, we can tune the amount of clustering of patches; we picked 10, 20, 40 and ∞ (uniform). For the other patches this is repeated with the probability distribution being the normalized sum of contributions from all patches already placed in the grid. For an example of the landscapes generated in this way, see Figure 1. For the resulting landscapes centroid distances and edge-to-edge distances can easily be calculated. We used the latter which seems biologically more realistic, but we believe that using the former would not change our results qualitatively.

Model: Metapopulation processes

Consider a single-species metapopulation distributed over n patches, which can be either occupied or empty. Assume that there is a discrete phase in which local population dynamics take place, but no dispersal. After this "extinction phase" there is a "colonization phase". This separation of phases has been suggested by several authors (Hansson 1991, Sabelis et al. 1991, Akçakaya & Ginzburg 1991, Burgman et al. 1993). During the extinction phase, the population in each occupied patch i has an extinction probability e_i and during the colonization phase, dispersers from all occupied patches can colonize an empty patch i with colonization probability c_i which depends on the occupied patches j. For the most part of this paper, all these probabilities are considered to be independent, that is, we assume that extinctions and colonizations are not correlated.

Because every patch is either occupied (denoted by 1) or empty (denoted by 0), the metapopulation is in any of 2^n states. For example, for $n = 3$, these states are (patch 3, patch 2, patch 1) = (0,0,0), (0,0,1), (0,1,0), (0,1,1), (1,0,0), (1,0,1), (1,1,0), (1,1,1). We will order these states lexicographically as in these examples.

With the extinction and colonization probabilities given, we now describe the dynamics of the metapopulation, i.e. the changes in its state. We follow Day & Possingham (1995) and Akçakaya & Ginzburg (1991). See also Gyllenberg & Silvestrov (1994) who present a similar discrete-time model, but without separation of extinction and colonization phases; we found in a brief investigation of this model that it behaves very similarly. Suppose that $n = 2$ and the metapopulation is in state (patch 2, patch 1) = (1,0). From this state the metapopulation can reach state (1,1) if the second patch does not go extinct ánd if it subsequently provides colonists to the first patch to make it occupied. These two events occur with probability $(1 - e_2)c_1(2)$, because we have assumed independence of extinction and colonization. If we now define M_{34} to be the probability that the metapopulation changes from state 3 ($\equiv (1,0)$ in the lexicographical ordering) to state 4 ($\equiv (1,1)$), then $M_{34} = (1 - e_2)c_1(2)$. Similarly, we can define M_{ij} as the transition probability that the system moves from state i to state j. For any pair of states i and j one can calculate the transition probability as above. The $2^n \times 2^n$ matrix M thus defined is the Markov transition matrix of the metapopulation system with n patches. For $n = 2$ the transition matrix M is given by

$$M = \begin{pmatrix} 1 & 0 & 0 & 0 \\ e_1 & (1-e_1)\,(1-c_2(1)) & 0 & (1-e_1)\,c_2(1) \\ e_2 & 0 & (1-e_2)\,(1-c_1(2)) & (1-e_2)\,c_1(2) \\ e_1e_2 & (1-e_1)\,e_2(1-c_2(1)) & (1-e_2)\,e_1(1-c_1(2)) & M_{44} \end{pmatrix} \quad (1)$$

where

$$M_{44} = (1-e_1)\,e_2c_2(1) + (1-e_2)\,e_1c_1(2) + (1-e_1)(1-e_2). \quad (2)$$

One can show (see e.g. Halley & Iwasa 1998) that the second largest eigenvalue λ_2 of the transition matrix (M) is a measure of the expected extinction time of the metapopulation:

$$T_{\text{ext}} = \frac{1}{1-\lambda_2}. \quad (3)$$

This extinction time is an average over the extinction times of all initial states where each state is weighed according to the so-called quasi-stationary distribution (Darroch & Seneta 1965, Gilpin & Taylor 1994, Gosselin 1998, Pollett 1999) which is the probability distribution of states for a system in quasi-equilibrium. For any probability distribution q_i over the states i the expected extinction time can be calculated as

$$T_{\text{ext}}(q) = \sum_i q_i \left((I-R_M)^{-1}\,\overrightarrow{I} \right)_i \quad (4)$$

where R_M is the matrix which results when the first row and the first column are deleted from M and $\overrightarrow{I}$ is a vector of length $2^n - 1$ whose entries are all equal to 1.

The expected metapopulation extinction time T_{ext} is one of the two measures of metapopulation persistence used in this paper. The other measure follows from the reproduction matrix G (Gyllenberg 2002). This matrix consists of elements G_{ij} which give the probability that occupancy of patch j is produced by patch i (if occupied) after one time-step, where all other patches are empty. G_{ii} is then the probability of patch i not going extinct: $G_{ii} = 1 - e_i$, and the G_{ij} are the probabilities that patch j is colonized by patch i: $G_{ij} = c_j(i)$. Hence for $n = 2$ we have

$$G = \begin{pmatrix} 1-e_1 & c_2(1) \\ c_1(2) & 1-e_2 \end{pmatrix}. \quad (5)$$

The dominant eigenvalue of this matrix, R_0, is called the basic reproduction ratio. It can be shown that if a "typical" local population is placed in an otherwise empty set of patches, this will lead to an initially growing metapopulation if and only if $R_0 > 1$. The left eigenvector corresponding to R_0 is the stationary type-distribution of newly colonized patches, and a "typical" local population means a population sampled from this distribution. Because n may be small and because colonization usually decreases with distance which causes clustering of occupied patches, even after only one time-step the patch network no longer satisfies the conditions for initial growth anymore. Hence, R_0 may be of very limited practical use. Yet, we include it, because it is a measure of invasion rather than of longevity (such as T_{ext}), so the two measures together give a broader picture of overall metapopulation persistence. A measure comparable to R_0 is the metapopulation capacity (Hanski & Ovaskainen 2000).

Model: Relations with landscape characteristics

We assume first, fairly realistically, that the carrying capacity of a patch K_i is proportional to its area A_i with proportionality constant ρ. We furthermore assume, following Hanski (1999a), that the local extinction probability e_i in a patch of area A_i takes the form

$$e_i = \min\left[1, \left(\frac{A_0}{A_i}\right)^x\right] \tag{6}$$

where A_0 is the minimum required patch area and x is a parameter which measures the strength of environmental stochasticity and demographic stochasticity: the larger the value of x, the weaker is the environmental stochasticity. For pure demographic stochasticity and sufficiently large A_i, one can show that the local extinction probability actually declines exponentially with area for both exponential growth with a ceiling and logistic growth (Foley 1997, Andersson & Djehiche 1998), but this can be mimicked heuristically by taking large x. For environmental stochasticity or pure demographic stochasticity with small K_i the power-law dependence (6) can indeed be derived (Goel & Richter-Dyn 1974, Foley 1997, see also Hanski 1999b). The values of x that we will use are listed in Table I; they cover a realistic range of values (Foley 1997). Because only the value of A_i relative to A_0 matters, we can view their ratio as a new variable or, equivalently, set $A_0 = 1$. The latter interpretation has the advantage that the grid resolution is precisely such that one grid cell has area A_0.

Deriving expressions for the colonization probability is more difficult, because it involves the still poorly understood dispersal behavior. Let us start with the target patch in which m immigrants arrive. We define a successful colonization as the event that the population reaches a certain critical level

$$N_c = \frac{3}{\log R_0^{\text{local}}} \tag{7}$$

before going extinct (which is then a relatively rare event), where R_0^{local} is the local (within-patch) basic reproduction ratio. The probability of this event equals (Goel & Richter-Dyn 1974)

$$C_i(m) = 1 - \left(\frac{1}{R_{0,i}^{\text{local}}}\right)^m. \tag{8}$$

This formula assumes asexual reproduction. In sexual reproduction, Allee effects in mate finding may reduce the probability of colonization for small m. This is modelled phenomenologically by a sigmoidal curve in the incidence function model (Hanski 1994). A mechanistic model along the lines of (8) incorporating the Allee effect can be constructed, but it requires more detailed assumptions (e.g. on monogamous or polygamous reproduction, the process of mate finding and its relation to patch size). However, such a detailed model is neither necessary nor warranted within the scope of this paper (see Discussion). For simplicity we also assume that $R_{0,i}^{\text{local}}$ is the same for all patches, regardless of their size, which is not unreasonable because patch size is not a likely to be a limiting factor for the initial growth of a population.

We will now derive a formula for the number of immigrants m. Let us assume that the number of emigrants is proportional to the carrying capacity, and thus to the area of a patch

with proportionality constant $b\rho$. If an emigrant disperses in a random direction, then the probability that it heads for patch i with area A_i equals the fraction of the horizon that this patch occupies (the so-called pie-slice algorithm, see Etienne & Heesterbeek 2000). If we assume that patches do not overlap on the horizon, this fraction equals $\frac{\sqrt{A_i}}{d_{ij}}\pi^{-\frac{3}{2}}$. If the probability that dispersers actually disperse as far as d_{ij} declines exponentially with distance, i.e. $e^{-\alpha d_{ij}}$ with α^{-1} the average dispersal distance, then the average number of immigrants arriving at patch i is

$$m = \sum_j \pi^{-\frac{3}{2}} b\rho A_j \sqrt{A_i} \frac{e^{-\alpha d_{ij}}}{d_{ij}}. \tag{9}$$

In principle we should have used a joint probability distribution for all the m_i and summed over all possible distributions of the emigrants over the patches, but numerical experiments with such a model seldom led to metapopulation extinction times which differ largely from those calculated with the model we have just described. Table I lists the values of the parameters we introduced; they are chosen such that they are both realistic and consistent with the values of the other parameters and that they do not cause numerical problems.

Table I. Parameter values used in calculating the optimal conservation strategy. The second column contains the default parameter values; the other columns contain alternative values used in replacing one default parameter value at a time.

parameter	values				
$\log A_m$	$\log 25$				
$\log r_A$	$\log 2.5$				
A_0	1				
σ	10	20	40	∞	
x	0.5	1	1.5	2	
α^{-1}	4	8	16	32	64
R_0^{local}	1.1	1.5	2	4	
$b\rho A_0$	0.1	1	10		

Model: Output

As we mentioned above, our two measures of metapopulation persistence are T_{ext} and R_0. We will evaluate these measures for each of 1000 landscapes in which we increase the area of the largest patch by 10%. We then calculate the required changes in the areas of the other patches which would result in the same values of the measures (starting from the original landscape, i.e. as it was prior to the enlargement of the largest patch). Similarly, we evaluate these measures for each landscape in which we decrease the interpatch distance between the two largest patches by 10% and compute the required changes in the distance between all other pairs of patches which result in the same values of the measures. As we stated above, the results by Etienne & Heesterbeek (2001), in terns of extinction and colonization probabilities
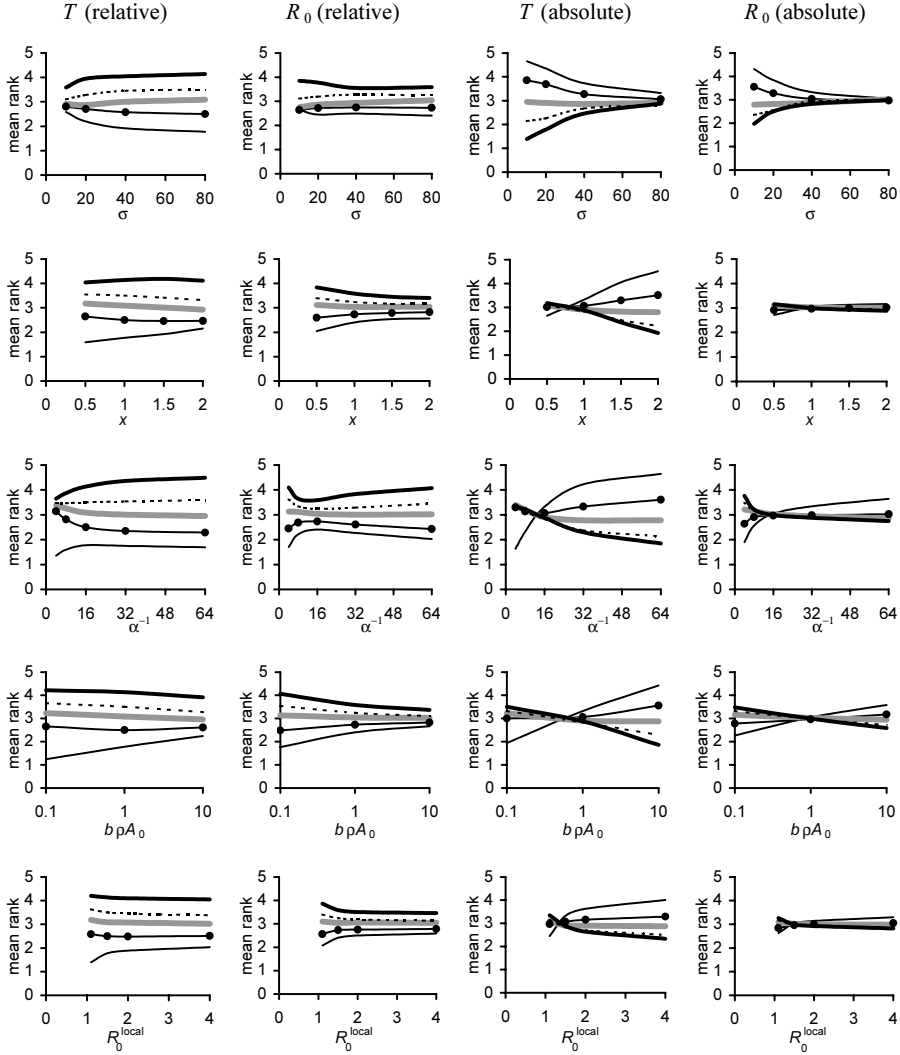
suggest that the required changes will often be larger. However, in terms of patch area and interpatch distance, matters may be different, because, for instance, the extinction probability is least sensitive to changes in patch area for large patches according to our model (formula (6)).

In finding the required changes in patch area and interpatch distance, we did not modify the landscape. Evidently, changing patch area would realistically result in different edge-to-edge interpatch distances; it is even conceivable that two or more patches merge into a single large patch. Because merged patches lead to a totally different landscape causing discontinuities in our measures of metapopulation persistence which are not necessarily realistic, we refrained from implementing this. Changes in patch area should be interpreted as changes in the effective patch area which is a result of geographical area (which remains unaltered) and patch quality. Similarly, changing interpatch distance would be realized by moving patches, thus modifying other interpatch distances as well. Moving patches is of course generally impossible, so a change in interpatch distance should be interpreted as a local change in α, or in other words, in the effective interpatch distance. One may envisage that corridors create such changes (although, admittedly, corridors may lead to local changes in α in other places as well). We furthermore believe that the value of 10% is sufficiently large to be realistic and sufficiently small that the above-mentioned second order changes are negligible in most cases; in the cases where they are not, the required change is probably so large that it is not realistic in itself.
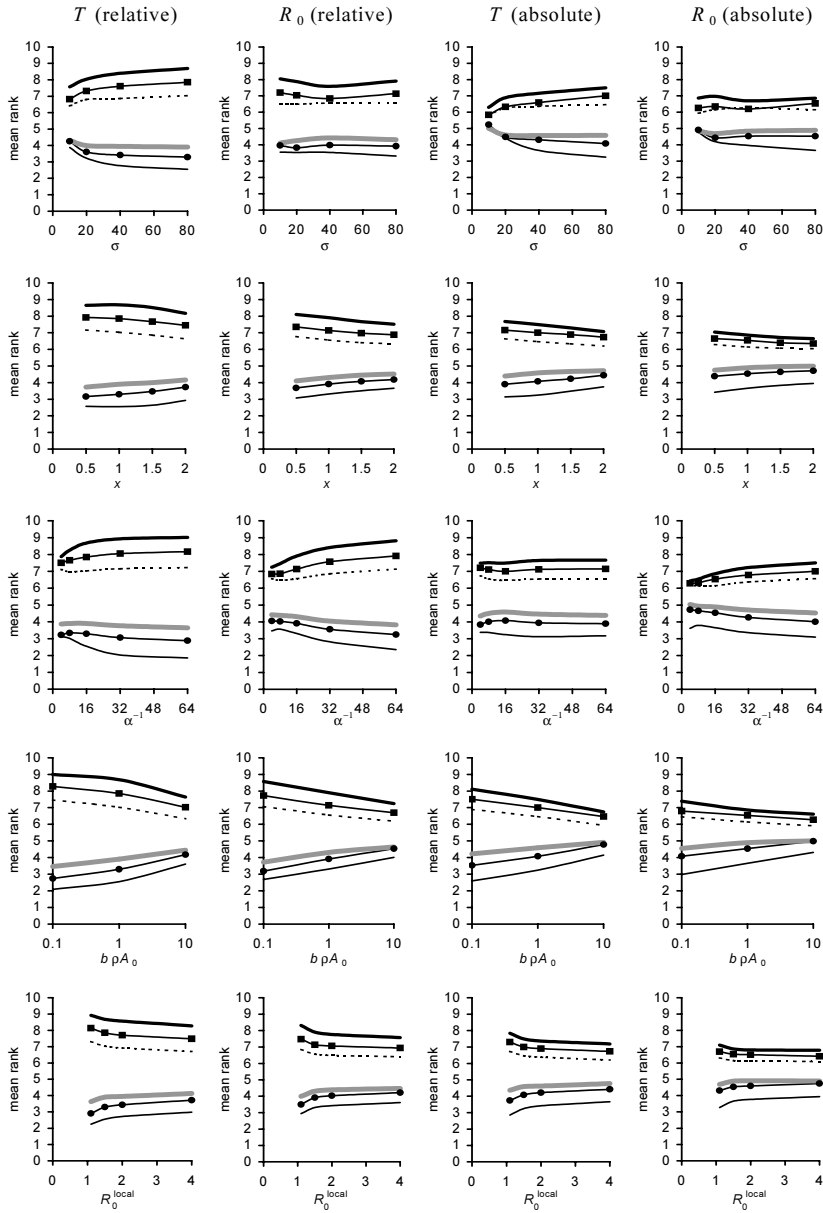
Results

The required changes in patch areas and interpatch distances which the yield same values of the measures are ranked according to their size: if the required change in patch area is the smallest, the patch receives rank 1, if it is the largest it receives rank 5 (there are 5 patches in our simulations) and similarly for the interpatch distance. At the same time, patches are ordered according to their patch area and interpatch distances according to the sum of the sizes of the patches it connects. The mean rank over 1000 landscapes for the largest patch, the second largest patch etc. and for the interpatch distance between the two largest patches, the two second largest patches etc. can then be calculated. The results are summarized in Figures 2 and 3. The required changes are ranked in two ways: relative (i.e. in percentages) and absolute.

In Figure 2 we see that for both measures enlarging the largest patch is the best option for all parameter values, if relative area changes are compared. If absolute area changes are compared, however, the opposite holds: enlarging the smallest patch is the best option for many, but not all parameter values and for R_0 the discrepancies are minor. Enlarging the largest patch is more strongly supported in landscapes with low demographic stochasticity (small values of x) and low patch clustering (large values of σ; for practical purposes the parameter σ is given the value 80 for the completely random case where σ is actually infinite) and for species with small dispersal distances (small α^{-1}), low emigration (small $b\rho A_0$) and low productivity (small R_0^{local}), but note that there are some subtleties in the relationship with

Figure 2. Mean rank of the patches versus each of the parameters of Table I for the largest patch (thin solid curve), second largest patch (solid curve with filled circles), third largest patch (gray curve), fourth largest patch (dotted curve) and fifth largest (= smallest) patch (thick solid curve). Rank 1 is given to a patch if the required change in patch area is smallest, rank 2 is assigned if the required change is the second smallest, etc. The mean rank is the average over all 1000 landscapes. It is calculated for each of the two measures, T_{ext} and R_0, where the required change is compared in two ways: relative (i.e. percentage of the area) and absolute (i.e. area size). The parameter σ is given the value 80 for the completely random case where σ is actually infinite.

Figure 3. Mean rank of the interpatch distances versus each of the parameters of Table I for the interpatch distance between the two largest patches (thin solid curve), the two second largest patches (solid curve with filled circles), the two third largest patches (gray curve), the two third smallest patches (dotted curve), the two second smallest

[Figure 3 cont'd] patches (solid curve with filled squares) and the two smallest patches (thick solid curve); the sum of the patch areas is used to define "two ... largest". Rank 1 is given to an interpatch distance if the required change in interpatch distance is smallest, rank 2 is assigned if the required change is the second smallest, etc. The mean rank is the average over all 1000 landscapes. It is calculated for each of the two measures, T_{ext} and R_0, where the required change is compared in two ways: relative (i.e. percentage of the distance) and absolute (i.e. distance itself). The parameter σ is given the value 80 for the completely random case where σ is actually infinite.

dispersal distance (α^{-1}). This suggests that the largest patch is especially important when the patches are relatively isolated. This makes sense, because in this situation colonization is infrequent and the metapopulation becomes extinct when the least extinction-prone patch does.

These results can be illustrated by the following examples. If one is considering adding, say, a hectare of habitat to one existing patch, then one should do this with the smallest patch. If the decision concerns improving patch quality in one patch, then the largest patch is a better candidate. Adding a strip of, say, 100 m of habitat around a patch is an act which lies between an absolute and a relative addition, and any patch can be chosen, although we conjecture that the largest patch already prevails, particularly when the patches are relatively isolated.

In Figure 3 we see that for both measures reducing the interpatch distance between the two largest patches is the most fruitful option, regardless of whether the required changes are compared in a relative or absolute way, although in the latter case, the trend is less manifest. Reducing the interpatch distance between the two largest patches is more strongly supported in the same cases as listed above for changes in patch area, except one: for species with large dispersal distance (large α^{-1}) the trend is now stronger instead of weaker.

In these figures we also see that R_0 and T_{ext} behave similarly in most cases. This suggests that R_0 can be used as a proxy for T_{ext} for this type of comparison between changes in patch areas and interpatch distances. This is particularly interesting for larger networks in which computing T_{ext} is a difficult and time-consuming, if not impossible task.

Thus, although some general rules of thumb can be extracted from these findings, they are not as strongly supported as those found by Etienne & Heesterbeek (2001). Patch size does not fully determine the outcome of the type of comparisons we made. There is, however, not a simple characteristic of the landscape that does better in this respect according to our examination of the results; connectivity of a patch evidently does play a role, but this role is by no means decisive.

Discussion

We have found the following rule of thumb: in general the best strategies for metapopulation management are enlarging the largest patch and reducing the (effective) distance between the two largest patches; an important exception to this rule is the case where absolute changes

in patch area are compared, for which enlarging the smallest patch is the best option in most cases. The second part of the rule is in line with Frank (1998) who finds that connecting patches may be disadvantageous if emigrants are lost to patches of no importance. The rule also agrees with the results of Drechsler & Wissel (1998) which downplay the role of connectivity.

Although our results increase our insight into the sensitivity of the metapopulation to alterations in its configuration, a definite rule of thumb still requires knowledge of the amount of effort needed to establish these alterations, as noted by Etienne & Heesterbeek (2001). If this is fairly constant across all patch sizes and interpatch distances, then our results give an indication of where the emphasis should be put in metapopulation management.

The question which always arises in simulation studies such as this, is whether artificially generated landscapes are representative of real ones. As Tischendorf (2001) remarks, there is no general answer to this question, because there is no general pattern in realistic landscapes. Nevertheless, he finds that correlations between landscape indices and ecological response variables are similar in artificial and real landscapes, implying that using artificial landscapes is not *a priori* meaningless. As we studied different degrees of clustering, we aimed to cover a range of possible landscapes, and we believe that our conclusions therefore hold quite generally.

Evidently, our model of the colonization probability depends on our assumptions and specific choices, particularly of the dispersal mechanism, where others may be equally possible (e.g. density-dependent emigration, different relationships with interpatch distance, more detailed immigration). Yet, firstly, it captures the essential dependencies on the areas of the patches of origin and destination and their interpatch distances (Hanski 1999a), and, secondly, more detailed models would no longer be in line with the full metapopulation model (patch occupancy model, no explicit local dynamics) and their predictive power is questionable (Moilanen & Hanski 1998). Still, one aspect missing in our model deserves mentioning. Correlated extinctions are major potential threats to the robustness of the results of metapopulation models (Harrison & Quinn 1989, Hanski 1991, Moilanen 1999, Etienne & Heesterbeek 2001). Incorporating correlation in a simulation model is easy, but calculating explicit expressions for quantities such as M_{41} in our model is very difficult. One can proceed along the lines of Etienne & Heesterbeek (2001) making the correlation matrix dependent on interpatch distances. This method involves multi-dimensional integrals which are computable to the required accuracy in a reasonable time only for homogeneous networks (in which all patches and interpatch distances are equal).

Still, these considerations impel us to be careful in using the rule of thumb (as we should with all rules of thumb). If in a particular case sufficient resources are available for extensive research, this should always be preferred. If such resources are not available, our results suggest guidelines as to how to proceed with at least some underpinning.

Acknowledgments

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Part IV

Methods improving the quality of model predictions

7

Ecological impact assessment in data-poor systems: a case study on metapopulation persistence

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Abstract

Assessment of the effects of human interventions on metapopulations is a core task for conservationists. In this paper we demonstrate with a case study how this can be done for situations where data are scarce, and time is lacking to produce them, but where some expert knowledge is available.

The case study involves two amphibian species, great crested newt (*Triturus cristatus*) and natterjack toad (*Bufo calamita*) in the nature reserve "the Meinweg" in The Netherlands for which plans are developed to reinstate an old railway track called the "Iron Rhine".

We assess the effects of this railway track and its proposed alternatives (resulting in 5 scenarios) on several metapopulation persistence measures (the metapopulation extinction time and the occupancy times of the patches) for both species using a relatively simple discrete-time stochastic (Markov chain) metapopulation model. The parameters of this model are extinction and colonization probabilities which we quantify using expert knowledge and some extrapolated data. Because of our uncertainty about the resulting parameter values and hence about the model predictions, we perform a Monte Carlo uncertainty analysis on the model output. This provides us with an estimate of the probability distribution of the model predictions and with insight into the contribution of each distinguished source of uncertainty to the uncertainty about the model outcome.

In this case study we are fortunate enough to find that there is one scenario which optimizes all measures of persistence for both species simultaneously. This may not always be the case.

Introduction

Extensive regulations have been developed to ensure that economic growth and development are compatible with the long term conservation of biodiversity. On the European Union level EU legislation on the protection of biodiversity is implemented in the Directive on the Conservation of Wild Birds (79/409/EEC (O.J. L103, 25.4.79)) and the Directive on the Conservation of Natural Habitats of Wild Fauna and Flora (92/43/EEC (O.J. L206, 22.7.92)). It is to be expected that an increasing number of assessments will be necessary to decide whether diverse human activities are compatible with the protective regulations. The prediction of ecological impacts is often hampered by incomplete knowledge and understanding of relevant ecological processes and responses to different types of impact. Limited time and budgets seldom allow for the development of predictive models suited to the situation, let alone for extensive collection of sufficient quantified data which are needed to parameterize these models. However these facts should not be used as an excuse to predict no ecological impacts at all. Unfortunately, the majority of impact studies are of a qualitative and descriptive nature, indicating that impacts may occur, but not estimating their probability (Treweek 1996). This limits the role of ecological impact assessment in decision making. In this paper we present a method how human impact can be assessed using a predictive model on metapopulation viability, even though quantified knowledge on population dynamics and ecological impacts is limited.

Although many detailed simulation models are available to calculate the viability of a metapopulation, such as METAPHOR (Vos et al. 2001), ALEX (Possingham & Davies 1995), RAMAS (Ferson & Akçakaya 1990, Akçakaya 1994) and VORTEX (Lacy 1993), these models have a large number of parameters which increases rapidly with the number of patches constituting the metapopulation (see also Lindenmayer et al. 1995). Values for these parameters are characteristically hard to find. Simpler models, such as the incidence function model (Hanski 1994, Hanski 1999, Vos et al. 2000), also exist which may have a more tractable number of parameters, but they still need data for parametrizing, which must be spatio-temporal because of the inherent nature of metapopulations (spatially extended, turnover of patches due to extinctions and recolonizations). Important work is done on parameter estimation of such models using data with missing values (Moilanen 1999, O'Hara et al. 2002, Ter Braak & Etienne 2002), but unfortunately even such poor data are lacking in many cases.

Even though quantified knowledge on population dynamics and ecological impacts may be lacking, experts are often able to state ranges (minimum and maximum) and the most likely value of model parameters, particularly if there are only a few parameters. This enables predictions of the range of model outcomes using uncertainty analysis techniques. Furthermore, when assessing human impacts, the main interest often lies in comparing effects of different scenarios (Hanski & Simberloff 1997). It is likely that such a relative ranking of scenarios is less sensitive to uncertainty in (some of) the parameters than an absolute prediction (Akçakaya et al. 1995, Akçakaya & Atwood 1997, Akçakaya & Raphael 1998, Beissinger & Westphal 1998). Dealing with uncertainty in input data, by making explicit to what extent this could alter the impact conclusions, can be a powerful tool to increase the role of ecological impact assessment in decision making.

In this paper, we will perform such an uncertainty analysis on a simple, spatially structured stochastic metapopulation model assessing the effects of a railway bisecting the habitat network of two amphibian species. We will start with a description of the setting of this case study. Then we will outline the model, and sketch the methods of the uncertainty analysis. Subsequently we will present the results and discuss them in the light of the expected ecological impact.

The Habitats and Birds Directive in "the Meinweg"

The Meinweg is a nature reserve in The Netherlands of about 1600 ha mainly consisting of heathland and forest. In 1994 The Meinweg was designated as a special protection zone under the European Birds Directive and since 1998 it has gained protection from the European Habitats Directive as well. The latter declaration was based on the presence of five types of habitat, four animal species and one plant species: greater mouse-eared bat (*Myotis myotis*), great crested newt (*Triturus cristatus*), brook lamprey (*Lampetra planeri*), weatherfish (*Misgurnus fossilis*), large white-faced darter (*Leucorrhinia pectoralis*).and floating water-plantain (*Luronium natans*). The members of the European Union are committed by the Habitats Directive to guarantee maintenance or restoration of natural habitats and species of wild fauna and flora "at favorable conservation status". This is defined in the Habitats Directive as: "(1) population dynamics data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats, and (2) the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and (3) there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis". Furthermore the Habitat Directive requires that "any plan or project not directly connected with or necessary to the management of the site but likely to have a significant effect thereon, either individually or in combination with other plans or projects, shall be subject to appropriate assessment of its implications for the site in view of the site's conservation objectives".

The Belgian government has requested The Netherlands to reactivate the "Iron Rhine", an international railway for the transport of goods from Belgium to Germany. As the Iron Rhine bisects the protected Meinweg area, the reactivation calls for an assessment of its ecological impacts. An impact assessment study has been carried out for five bird, three reptile, two amphibian and one mammal species, which are either explicitly mentioned in the Birds and Habitats Directive or considered representative for the protected habitats (Wieman et al. 2000). Several scenarios were considered: (0) the null scenario of the current situation without trains, (1) reactivation of the historical route with low train frequency, (2) reactivation of the historical route with high train frequency, (3) high train frequency on the historical route mitigated by screens, (4) an alternative railroad to the north of the Meinweg (the A1 route) and (5) an alternative railroad to the south of the Meinweg (the A2 route); see also Figure 1. The possible impact of these scenarios on the viability of the metapopulation network of these species was assessed. In this paper we will focus on the impact assessment study for the two amphibian species: the great crested newt (*Triturus cristatus*) and the natterjack toad (*Bufo calamita*).

A.

B.

Figure 1. The networks of the great crested newt (A) and the natterjack toad (B) in and around National Park "the Meinweg" near the city of Roermond, The Netherlands. The inset shows the location of the Meinweg in The Netherlands. The circles denote the habitat patches; white means unoccupied, black means occupied; the size corresponds to the ability to sustain a small, medium, or large population. The historical route of the railroad and the two alternatives are shown; for the natterjack toad patch 13 is split up by the A2 route.

Effects of railroads on amphibian populations

A quantified cause-effect relationship between railroads and train intensity on the one hand and their impact on species distribution and viability of amphibian populations on the other hand is lacking. From extrapolation of known effects of roads to railroads, the following negative impacts might be expected: habitat loss, mortality, barrier effects and disturbance.

The loss of suitable habitat is an obvious effect of the creation of a new railroad. For amphibians the impact of habitat loss will be most pronounced when the reproduction habitat is lost. However, the loss of (part of) the terrestrial habitat may also have a negative impact on the population.

Figure 2. Migration and dispersal in amphibians and the effect of a railroad thereupon (based on Grossenbacher 1981). Reproduction takes place in water which is often separated from the terrestrial summer and winter habitat by unsuitable habitat. In spring, adult individuals migrate from the winter habitat to the reproduction water (1) and subsequently to the summer habitat (2). The newly metamorphosed individuals disperse from the reproduction water to the summer habitat (3). In fall, adults and juveniles migrate from summer to winter habitat; wintering in water habitat is also possible (4). Apart from these seasonal movements, there are undirected movements within the habitat (5) and dispersal to other habitat (6). The railroad may affect all these movements (shown here for some of them) by acting as a barrier or by adding a risk of mortality to crossing individuals due to trains.

Barrier effects and mortality caused by railroads and trains will impact the spatial relationships within and between amphibian populations. As is illustrated in Figure 2, amphibians use both aquatic and terrestrial habitat that are often spatially separated. Amphibians might encounter a railroad during seasonal migrations between the different habitat parts and during

daily movements in their terrestrial habitat, and when dispersing to new sites. For roads the recent work of Hels & Buchwald (2001) illustrates a direct relationship between traffic intensity and the probability that crossing individuals get killed. Vos & Chardon (1998) found that the number of roads weighted for traffic intensity lowered the probability of moorland ponds being occupied by moor frogs (*Rana arvalis*). There are some studies that indicate that mortality and barrier effect also hold for railroads. Krummenacher & Meier (1989) encountered a large number of dead amphibians on the track Rekingen-Zurzach in Switzerland, where the railroad bisects the terrestrial habitat from the reproduction water. They observed that animals sheltered under the rails during the day and subsequently were killed by the weight of passing trains. In addition, air turbulence from passing trains might cause some mortality, which is also known from car traffic (Scholte 1982). However, observations on this effect are not consistent. Wolf (1993) observed that common toads (*Bufo bufo*) which were hurled away up to 120 cm by passing trains, continued their movements apparently unhurt. However, in Switzerland localities are known where large numbers of train victims were recorded, as a result of air turbulence of passing trains (personal communication S. Zumbach). Barandun (1991) observed that especially common frogs (*Rana temporaria*) were likely to get killed, because of their specific behavior. This species leaps when trains approach and as a consequence gets caught in the air turbulence. There are some observations that indicate that railroads have a barrier effect for passing amphibians. Crawling animals such as toads and newts are, unlike frogs, unable to climb over rails which are 15 cm high. Wolf (1993) studied the behavior of individually marked common toads that had to cross a railroad to reach their reproduction water. Animals were observed to move several hundreds of meters along the rails before they found a passage between rails and ballast. Lehmann (1989) observed that great crested newts made a detour during seasonal migration towards their reproduction water. Individuals moved in the rails over a maximum distance of 500 m, before they crossed the rails at a railroad crossing. On average toads changed direction five times during their search, and time spent trying to cross a railroad can take many hours (Wolf 1993) up to several days (Barandun 1991). During this time amphibians are extra sensitive for predation and unfavorable weather conditions.

Little is known about the effects of disturbance by noise on amphibians. There are some indications that traffic noise might disturb communication for species for which advertisement calls are part of the reproduction process (Barrass 1986, 1993). This might influence the reproductive behavior of the natterjack toad; however, there are no field observations indicating such effects.

In sum, habitat loss, extra mortality and barrier effects are considered to have negative effects on the viability of local populations and population networks. The extinction probability of local populations will increase due to habitat loss and increased mortality. The colonization probability of suitable habitat will be reduced as the number of dispersers is lowered by the barrier effect and extra mortality. Lower colonization probability and higher local extinction probability both contribute to a decrease in viability of the metapopulation as a whole. As the cause-effect relationships are not quantified, the ecological impact of these effects is necessarily based on expert judgement and has a high level of uncertainty.

Methods

Model

Consider a single-species metapopulation distributed over n patches each of which can be either occupied or empty. Assume that there is a discrete phase in which local population dynamics take place, but no dispersal. After this "extinction phase" there is a "colonization phase". This separation of phases has been suggested by several authors (Akçakaya & Ginzburg 1991, Burgman et al. 1993, Hansson 1991, Sabelis et al. 1991). During the extinction phase, the population in each occupied patch i has a local extinction probability e_i and during the colonization phase, dispersers from each occupied patch i can colonize an empty patch j with colonization probability c_{ij}. All these probabilities are considered to be independent, that is, we assume that local extinctions and colonizations are not correlated. This means for example that we do not incorporate the rescue effect (Brown & Kodric-Brown 1977, Etienne 2000); see Akçakaya & Ginzburg (1991) and Etienne & Heesterbeek (2001) for a similar model with correlated extinctions.

Because each patch is either occupied (denoted by 1) or empty (denoted by 0), the metapopulation is in any of 2^n states. For example, for $n = 2$ these states are (patch 2, patch 1) = (0,0), (0,1), (1,0), (1,1); for $n = 3$, these states are (patch 3, patch 2, patch 1) = (0,0,0), (0,0,1), (0,1,0), (0,1,1), (1,0,0), (1,0,1), (1,1,0), (1,1,1). We will order these states lexicographically as in these examples and number them so that, for example, for $n = 2$ the states (0,0), (0,1), (1,0), (1,1) correspond to respectively 1, 2, 3, 4.

With the extinction and colonization probabilities given, we now describe the dynamics of the metapopulation, i.e. the changes in its state. We follow Day & Possingham (1995) and Akçakaya & Ginzburg (1991), but see also Gyllenberg & Silvestrov (1994) who present a similar discrete-time model, but without separation of extinction and colonization phases. Suppose that $n = 2$ and the metapopulation is in state (patch 2, patch 1) = (0,1). From this state the metapopulation can reach state (1,1) if the first patch does not go extinct ánd if it subsequently provides colonists to the second patch to make it occupied. These two events occur with probability $(1 - e_1)c_{12}$ because we have assumed independence. If we now define M_{24} to be the probability that the metapopulation changes from state 2 ($\equiv (0,1)$ in the lexicographical ordering) to state 4 ($\equiv (1,1)$), then $M_{24} = (1 - e_1)c_{12}$. Similarly, we can define M_{ij} as the transition probability that the system moves from state i to state j. For any pair of states i and j one can calculate the transition probability as above. The $2^n \times 2^n$ matrix M thus defined is the Markov transition matrix of the metapopulation system with n patches. For $n = 2$ the transition matrix M is given by

$$M = \begin{pmatrix} 1 & 0 & 0 & 0 \\ e_1 & (1-e_1)(1-c_{12}) & 0 & (1-e_1)c_{12} \\ e_2 & 0 & (1-e_2)(1-c_{21}) & (1-e_2)c_{21} \\ e_1 e_2 & (1-e_1)e_2(1-c_{12}) & (1-e_2)e_1(1-c_{21}) & M_{44} \end{pmatrix} \quad (1)$$

where

$$M_{44} = (1 - e_1)\, e_2 c_{12} + (1 - e_2)\, e_1 c_{21} + (1 - e_1)(1 - e_2). \qquad (2)$$

Suppose that we start in state i. We can write this state also as a column vector $\vec{s}$ with 2^n elements with zeros everywhere except in position i where we have a 1; for $n = 2$, for instance, we have $\vec{s} = (0, 0, 1, 0)^T$ if the initial state is state 3 ($\equiv$ (1,0)). If we now multiply the transpose of M with $\vec{s}$ then we get the probability distribution over the states in the next time step. From M one can in principle calculate with explicit analytical formulae characteristics of the model such as the mean time to metapopulation extinction or the mean time of occupancy of a patch, which are global and local measures of the conservation status of the species in the network respectively. However, because the dimensions of M are 2^n by 2^n, M becomes intractably large even for a relatively small number of patches ($n > 10$). Having 14 and 15 patches for the two studied species in the Meinweg, we therefore chose to simulate stochastically the extinction and colonization dynamics using exactly the same model ingredients as in the model described above, starting from a certain initial state of the system. If we repeat these simulations sufficiently often, we obtain a frequency distribution of properties such as the metapopulation extinction time and the patch occupancy time, of which the averages converge to the values which would be obtained directly from the explicit analytical formulae. This frequency distribution has the important advantage that it enables comparison of the inherent randomness of the model to the uncertainties in the model parameters, as we will see below.

Uncertainty analysis

One of the most generally applicable methods for uncertainty analysis is Monte Carlo sampling (see e.g. Saltelli et al. 2000). This is a simple but powerful method, only limited by computational efficiency: one first needs to specify the uncertainty about the model parameters and, when applicable, about initial and boundary conditions. The uncertainty is specified in the form of probability distributions of these quantities. Then one samples values of the uncertain quantities from these distributions, runs the model with these values and records the model output. Iterating this many times yields a frequency distribution of the model output. Moreover, if the sampling is performed in a structured way, one can apply statistical analyses to the sample, to obtain information about the contributions of the input uncertainties to the output uncertainty.

Definition of the network
For both species all suitable reproduction sites in the Meinweg and its surroundings were derived from detailed habitat maps in combination with field visits. For the relatively mobile natterjack toad (Günther & Meyer 1996) all reproduction sites within 3 km from each other were considered to belong to the Meinweg habitat network. Sinsch (1992) found a maximum dispersal distance of 2.6 km. For the less mobile great crested newt (Van der Sluis et al. 1999, Thiesmeier & Kupfer 2000) all reproduction sites within 1.5 km from each other were considered to belong to the Meinweg habitat network. As is shown in Figure 1B, the

metapopulation network of the natterjack toad consists of 14 reproduction sites, of which 10 sites are occupied. The distribution of the 15 suitable reproduction sites for the great crested newt in the Meinweg is highly fragmented, consisting of 4 separate population networks of which 10 are occupied (Figure 1A).

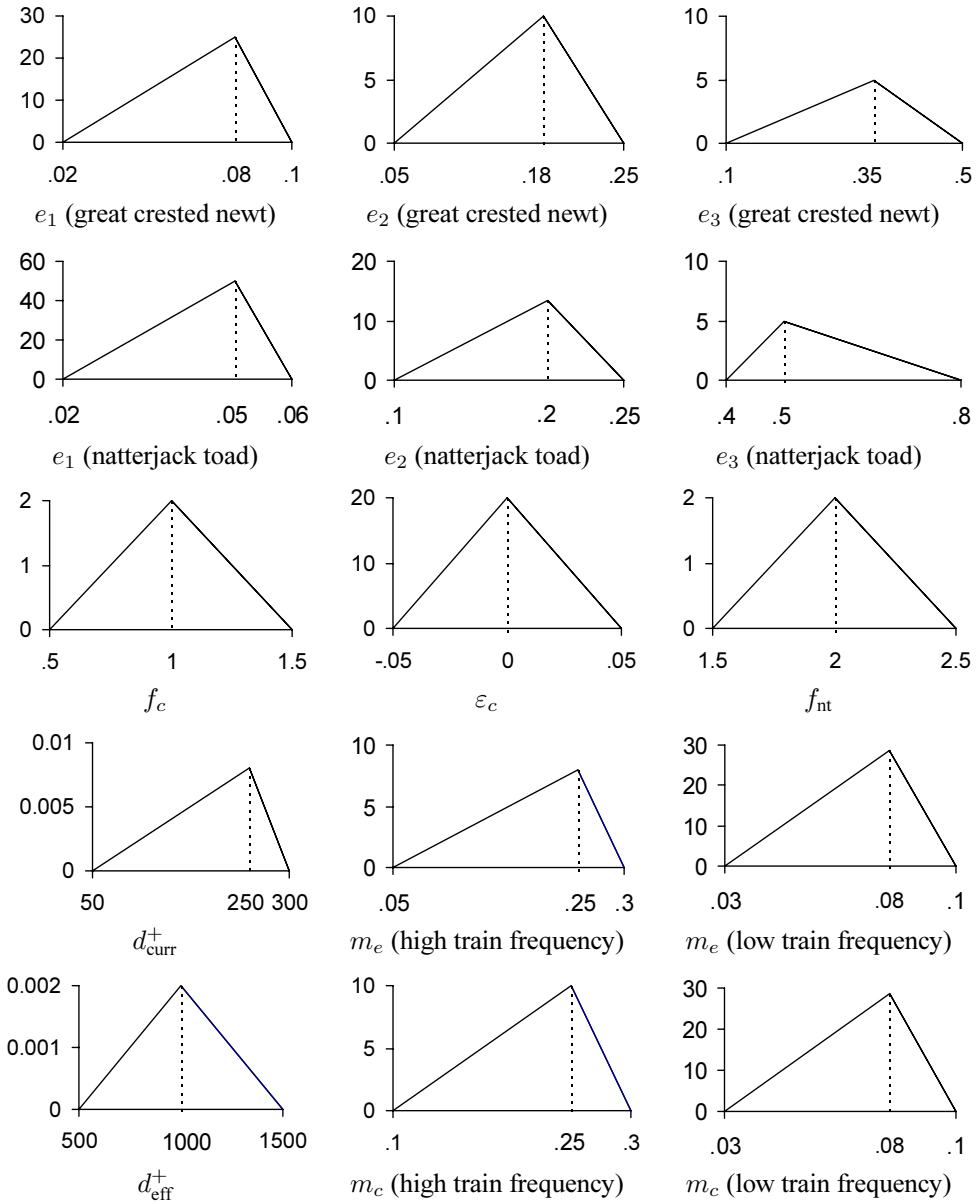**The initial state of the metapopulation**
Information on the present distribution of the two amphibian species were obtained from local herpetologists who have followed the distribution of these species in the area for many years. Therefore we assumed no uncertainty concerning the present distribution of the populations, i.e. the initial state of the metapopulation.

Parameters describing the current situation
Although there are methods to estimate model parameters from occupancy data (Verboom et al. 1991, Hanski 1994, Sjögren-Gulve & Ray 1996, Ter Braak et al. 1998, Moilanen 1999, O'Hara et al. 2002, Ter Braak & Etienne 2002), the available occupancy data were too limited for these methods (only 14 or 15 ponds and incomplete and inaccurate turnover data). Therefore we estimated the uncertainty distributions of the extinction (e_i) and recolonization (c_{ij}) parameters using the literature. We estimated the most likely value for each parameter and defined the minimum and maximum values, which together specify a triangular probability distribution (Figure 3).

Amphibians are sensitive to environmental variation (Pechmann et al. 1991). In unfavorable years, e.g. when desiccation of reproduction water occurs, reproduction may fail completely (Griffiths & Williams 2000). Extinctions of local populations are regular events in amphibian metapopulations, especially when populations are small (Sjögren 1991, Hecnar & M'Closkey 1996, Marsh & Trenham 2000, Vos et al. 2000). As data from the literature about extinctions are scarce and since it is not clear how these may be extrapolated to the Meinweg area, the uncertainty intervals of the extinction probabilities are large (see Figure 3). Three extinction probabilities were distinguished, corresponding to the classification of ponds capable of containing large, medium and small populations. This classification was based on the experience of the local herpetologists. For the great crested newt, large means $N > 50$ where N is the number of reproductive units, medium means $10 < N < 50$, and small means $N < 10$. For the natterjack toad, large means $N > 1000$, medium means $100 < N < 1000$, and small means $N < 100$.

The population dynamics of the great crested newt are relatively well studied (e.g. Miaud 1991, Arntzen & Teunis 1993, Miaud et al. 1993, Baker 1999). Several simulation models on crested newt persistence in subdivided populations exist (Halley et al. 1996, Griffiths & Williams 2000). Although no direct comparison of model parameters is possible because of the different model structures, our extinction probabilities (Figure 3) appear to be within range. Halley et al. (1996) predict that small populations (< 10 females) have a very high extinction risk and can only persist in close range of a source of immigrants, whereas large populations (> 100 females) could persist at larger distances (i.e. < 1.5 km from a source). Griffiths & Williams (2000) show the large impact of environmental stochasticity, defined

Figure 3. Uncertainty distributions of the model parameters, i.e. each graph shows the probability density versus the parameter value. The model parameters are: the extinction probabilities of large, medium and small populations (e_1, e_2 and e_3), the correction factor in the colonization probability (f_c), the noise superimposed upon the colonization probability (ε_c), the extrapolation factor from great crested newt to

[Figure 3 cont'd] natterjack toad (f_{nt}), the additional distance needed to cross the historical, unmaintained, railroad (d_{curr}^+) and to cross a maintained railroad (d_{eff}^+), the effect of extra mortality on the extinction probability (m_e) and on the colonization probability (m_c).

as recruitment failure caused by drought, resulting in large extinction risks, even for large populations.

Much less is known about the population dynamics of the natterjack toad. Although the estimated natterjack toad population sizes are much larger than for the great crested newt, extinction probabilities in relation to population size are considered to be higher for the natterjack toad. The natterjack toad is a species of a dynamic environment, using shallow water with none or hardly any vegetation as breeding sites and very open sandy fields for its terrestrial habitat (Strijbosch 1979, 1980, Beebee 1983, Sinsch 1998). These shallow waters have a considerable risk of desiccation before metamorphosis, in which case reproduction fails completely (Beebee 1983, Sinsch 1998). Also reproduction sites may become unsuitable for the natterjack with increasing vegetation succession. In the Meinweg study area, some of the populations can be found in the sandy parts of gravel pits quarries and on bare sand bodies at building sites.

Because the distributions of the extinction probabilities (Figure 3) overlap and larger populations should always have lower extinction probability than smaller populations, we changed the ranges of the distributions depending on the extinction probabilities already drawn in the Monte Carlo sampling: for example, if we drew first the extinction probabilities for the small populations, and their maximum exceeded the minimum extinction probability of the medium-sized populations, then we set the minimum extinction probability of the medium-sized populations equal to the maximum of the extinction probabilities of the larger populations; we also adjusted the mode to this value if the new minimum became larger than the mode. Since this procedure depends on the order in which probabilities are drawn, we repeated this for all possible permutations of (large, medium, small) using the same set of seed values for each permutation, and then we used the average of the computed extinction probabilities over all permutations.

The colonization probability of the great crested newt was based on colonization data of newly created ponds in The Netherlands (Van der Sluis et al. 1999). Regression analysis gave the following relationship between colonization probability and distance to the nearest reproduction site:

$$c_{ij} = a_1 e^{-a_2 d_{ij}}, \tag{3}$$

with $a_1 = 0.3415$ and $a_2 = 0.000883$ m^{-1}. The colonization probability between ponds calculated using this formula overestimates the true colonization probability consistently, because it also involves contributions to colonization from other occupied patches. To correct for this, we multiplied c_{ij} by $r_c = 0.75$; hence $c_{ij} = r_c a_1 e^{-a_2 d_{ij}}$. The uncertainty about c_{ij} for a certain distance d_{ij} is then caused by the uncertainty in r_c, regression errors, and the uncertain extrapolation to an area different from the area where the data were collected. To take all these uncertainties into account, we assumed the mode of the probability distribution of c_{ij}

to be $r_c a_1 e^{-a_2 d_{ij}}$ and the minimum and maximum 50% and 150% of this mode respectively; hence the correction factor f_c ranges between 0.5 and 1.5. Distances between reproduction sites are also uncertain if these sites are located on opposite sides of the railroad. Although there are more openings between rails and ballast for the historical unmanaged railroad than in a managed situation, dispersers need to walk some additional distance d^+ to cross at a suitable gap between rails and ballast. We estimated the extra distance in the unmanaged current situation, d_{curr}^+, to range from 50 to 300 m with a mode of 250 m (Figure 3). Finally, on the uncertainty in c_{ij} resulting from uncertainties in f_c and d_{curr}^+, we superimposed some noise ε_c to incorporate individual deviations from the regression curve (Figure 3).

We did not have data to estimate the colonization probability for the natterjack toad. The natterjack toad is a more mobile species (Blab 1986, Günther & Meyer 1996), able to find new suitable habitat over larger distances than the great crested newt. As noted above, Sinsch (1992) observed a dispersal distance of 2.6 km, about twice the dispersal distance of the great crested newt. Therefore, we assumed that the colonization probability for the natterjack toad was given by (3), but with $a_2 = 0.000883/f_{\text{nt}}$, where f_{nt} is an extra correction factor for the natterjack toad of which the distribution is given in Figure 3. Because the maximum dispersal distances of the great crested newt and the natterjack toad are not expected to exceed 1500 m and 3000 m respectively (Blab 1986, Günther & Meyer 1996, Van der Sluis et al. 1999, Thiesmeier & Kupfer 2000), we cut off the colonization probability at these distances. These maximum dispersal distances were coupled to the value of c_{ij} without noise, such that a higher curve than the mode extends beyond 1500 m (3000 m), while a lower curve is cut off at a distance shorter than 1500 m (3000 m).

Parameters describing railroad effects
The five scenarios and their estimated effects on the amphibian populations are summarized in Table I. Amphibian populations close to the railroad are exposed to extra mortality risks in their terrestrial habitat and during seasonal migrations (Figure 2). For the more mobile natterjack toad we considered all populations within 1000 m of the railroad to be exposed to this extra mortality risk. For the less mobile great crested newt the impact zone is estimated to be 400 m. For the scenarios with high train frequency (two trains per hour) we assumed a 25% increase in extinction probability (m_e) for all populations within the impact zone. For the scenario with low train frequency (66\% train reduction) we reduced the extra extinction risk accordingly to 8%. The reduction of the colonization probability (m_c) of ponds on opposite sides of the railroad, due to extra mortality of dispersers, was estimated at 25% for high and 8% for low train frequency. As the exact values of m_e and m_c are unknown, the uncertainty distributions are wide (Figure 3).

The barrier effect of a well maintained railway track is high, because gaps between tracks and ballast, large enough to cross for the amphibian species, will be scarce. This effect is translated into an increase in distance between ponds at opposite sides of the track, due to the additional distance that individuals have to move during their search for a suitable gap. We added an additional distance of 1000 m to the distance between ponds at opposite sites of the track ($d_{\text{eff}}^+ = 1000$ m) with a fairly large range (Figure 3). Because the colonization probability is directly related to the distance between ponds, the added distance will lower

Table I. Overview of the five scenarios and their estimated effects on the amphibian populations. The uncertainty intervals of the estimated effects are given in Figure 3. *The impact zone is 1000 m for the natterjack toad and 400 m for the great crested newt. **In the present situation the historical railroad still exists.

	Scenario 0 present situation (historical route, no trains)	**Scenario 1** historical route low train frequency	**Scenario 2** historical route high train frequency	**Scenario 3** historical route high train frequency mitigated by screens	**Scenario 4** A1 route high train frequency north of the Meinweg	**Scenario 5** A2 route high train frequency south of the Meinweg
increased extinction risk caused by extra mortality	-	8% for populations in impact zone*	25% for populations in impact zone*	-	25% for populations in impact zone*	25% for populations in impact zone*
reduced probability of colo- nization caused by extra mortality	-	8% for populations on opposite sides of the track	25% for populations on opposite sides of the track	-	25% for populations on opposite sides of the track	25% for populations on opposite sides of the track
reduced probability of colo- nization caused by barrier effect	distance between ponds on opposite sides of the track increased by 250 m**	distance between ponds on opposite sides of the track increased by 1000 m	distance between ponds on opposite sides of the track increased by 1000 m	no colo- nization between ponds on opposite sides of the track	distance between ponds on opposite sides of the track increased by 1000 m	distance between ponds on opposite sides of the track increased by 1000 m
increased extinction risk caused by habitat de- struction	-	-	-	-	-	large re- production site of the natterjack toad split up into 2 smaller ones

colonization probabilities. The screens that are placed along the historical track in scenario 3 will solve the risk of extra mortality. However the track becomes an absolute barrier dividing the populations in separate networks.

We assumed that the reactivation of the historical track will not cause habitat destruction, not even temporary destruction of habitat, because all reactivating activities will be carried out by a maintenance train using the current track. For the alternative routes A1 and A2 we assumed additional effects of habitat destruction, if the route will cross a reproduction habitat. This is the case for the A2 route, which will bisect a quarry, an important reproduction site of the natterjack toad, resulting in two smaller medium sized populations. The effects of destruction of terrestrial habitat were considered to be already incorporated in the extra extinction probability of populations within the influence zone of the track. The A1 route and the A2 route will have no direct influence on the great crested newt, as the tracks will not bisect the habitat network or come within 400 m from reproduction sites (Figure 1A). Therefore, we did not run scenario 4 and 5 for the great crested newt.

The final source of uncertainty cannot be attributed to parameters: the uncertainty due to the stochastic nature of our model. In our model this uncertainty is generated by sampling random numbers and comparing them with the extinction and colonization probabilities to determine whether or not extinction or colonization takes place. These random numbers can therefore be interpreted as representing the unknown environmental conditions in the future. We assumed, for simplicity, that these are uncorrelated between patches with one exception: we assumed the natterjack toad patches 13a and 13b in scenario 5 to be subject to the same environmental conditions (namely those of patch 13 in the other scenarios), except for an additional noise term.
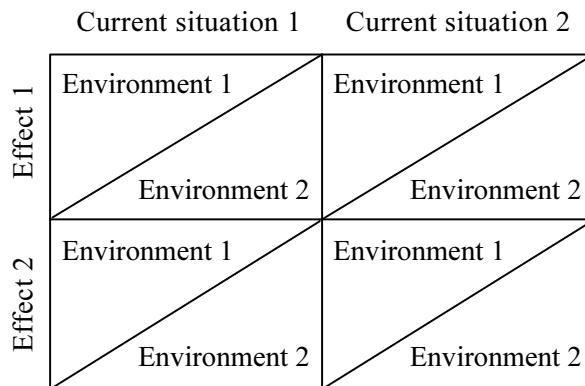
Now that we have specified the input part of the uncertainty analysis, we move to the output part: characterizing the properties of the model output for all the parameter sets drawn by Monte Carlo simulation; the frequency distribution of the output is an estimate of the uncertainty distribution of that output. As mentioned above, we are interested in two measures of the conservation status: the time to metapopulation extinction, $T_{s,M}$ (where s denotes the scenario, M refers to the metapopulation) and the total time that each patch is occupied before the metapopulation becomes extinct, $T_{s,i}$ (where s again denotes the scenario and i denotes the patch), expressed in years. From hereon, $T_{s,i}$ refers to both measures, so i can be the letter M or a number indicating the number of the patch. Both measures are considered relative to the current situation, scenario 0, that is, we consider the quantity

$$\Delta T_{s,i} = \frac{T_{s,i} - T_{0,i}}{T_{0,i}}. \tag{4}$$

To distinguish contributions of the various uncertainties to the uncertainty in $\Delta T_{s,i}$, we divided the uncertainties described above in three classes: uncertainties in the parameters of the current situation, uncertainties in the parameters of the effects, and uncertainty due to the inherent stochasticity of the model, that is, the uncertainty about the local conditions which we termed environmental uncertainty. For estimation of uncertainty contributions of these classes, we conducted the sampling according to a designed experiment. The design we adopted is a classical replicated crossed analysis of variance (ANOVA) design with three random factors, each at two levels. It is depicted in Figure 4. The term "crossed" indicates

that all combinations of the factor levels (eight in our case) are present in one replication of the design. The difference between this design and standard ANOVA designs as used in, for example, agricultural experiments, is that in this design the factors have *random* levels while in the agricultural experiments the factors (e.g. temperature, light and CO_2-concentration) are at *fixed* levels (called treatments). Application of classical and modified ANOVA designs to uncertainty analysis stems from the 1990s (Sobol 1990, Jansen et al. 1994, McKay et al. 1999, Jansen 1999, Chan et al. 2000). This type of uncertainty analysis is called variance-based, because uncertainties and uncertainty contributions are expressed as variances and variance components. In addition, it is sometimes called non-parametric because it does not rely on an estimated parametric relationship between input and output (McKay et al. 1999). The ANOVA is a formal elaboration of the intuitive idea that a factor is important if the model output changes much when that factor assumes new random values while the other factors remain the same.

Figure 4. Experimental design of the uncertainty analysis (one replication). For two random sets of parameters representing the current situation, and two random sets of parameters representing the effects, there are two simulations representing the random environmental conditions, so one replication consists of running the model for a total of 8 combinations. The number of replications was set to 10000.

On the output sample we applied a standard ANOVA decomposition. This results in estimates of the contribution of each class of uncertainties (and their interactions) to the total variance of the output distribution. A useful property of the design we chose, is that it not only enables unbiased estimation of uncertainty contributions, but that it also yields estimates of their accuracy which are robust in not depending on unwarranted assumptions of normality. These accuracy estimates may be used to calculate the smallest number of replications needed for a certain accuracy. In our case, however, a large number of replications posed no problem, so we did not need to calculate the minimum required sample size.

Thus, in each replication we drew two sets of values for the parameters of the current situation, two sets of values for the effect parameters, and two lists of random numbers

representing the environmental conditions for years to come, yielding a total of eight different sets of parameter values. By the nature of our model, we were able to treat the environmental conditions in exactly the same way as the other two causes of uncertainty, unlike, for instance, McKay (1998) who treats these conditions as noise that cannot be kept the same in different model runs. The number of replications of the design was set to 10000 which means that the model was run 80000 times for each scenario.

Results
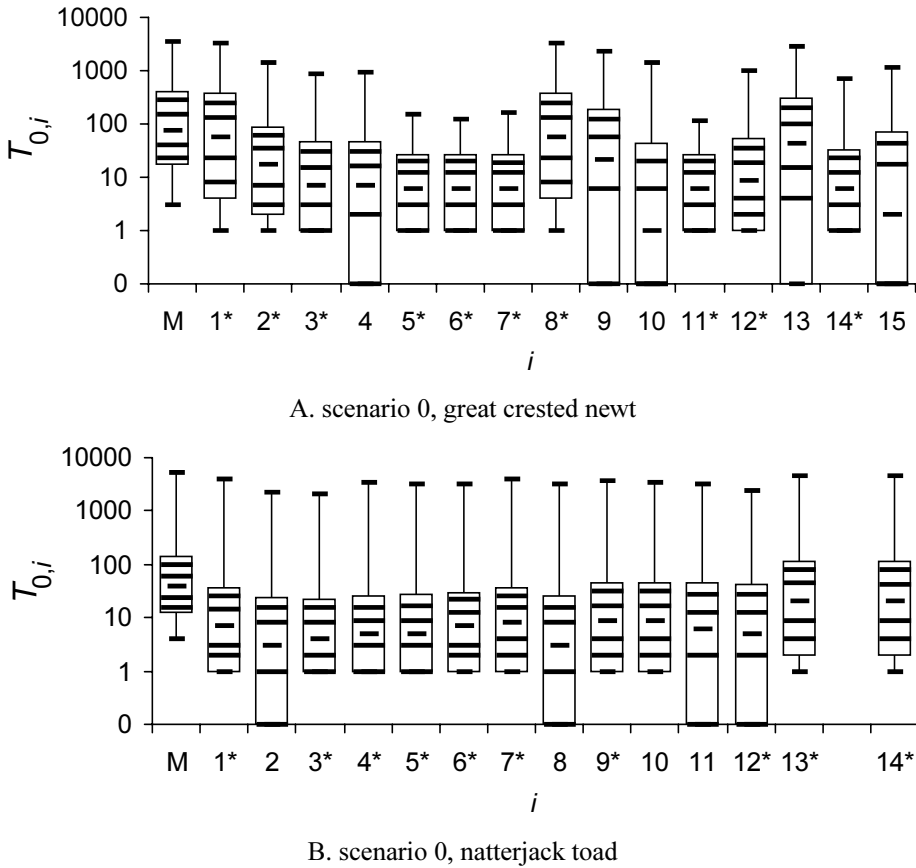
The metapopulation extinction time and the patch occupancy times in the simulations of the present situation, $T_{0,i}$, give insight into the relative importance of the individual patches to the metapopulation as a whole (see Figure 5). For each scenario the distribution of the relative quantities $\Delta T_{s,i}$ as defined by equation (4) is shown in Figure 6.

Figure 5A shows that three patches form the core of the great crested newt metapopulation, namely patches 1, 8 and 13, because their total time of occupancy is of the same order of magnitude as the metapopulation extinction time. When we look at Figure 1A, we see that these patches form a sub-metapopulation relatively distant from the railway track. Hence, we do not expect a substantial influence of putting the railway track to use on the great crested newt metapopulation, but it may have an impact on local populations. We can check this with Figures 6A, B and C. Indeed, the effect on the metapopulation is limited to a maximum of 12% in scenario 3 and patches 1, 8 and 13 are hardly affected at all, but local populations may suffer severely, especially patches 4 and 12.

The natterjack toad metapopulation appears to be fueled by two populations, those in patches 13 and 14, but their importance in Figure 5B is not as pronounced as that of the three core patches of the great crested newt, most probably because the larger dispersal distance of the natterjack toad makes the network more connected. Figure 1B shows the position of these two patches in the network. Their position illustrates that core patches need not be located in the spatial heart of the metapopulation.
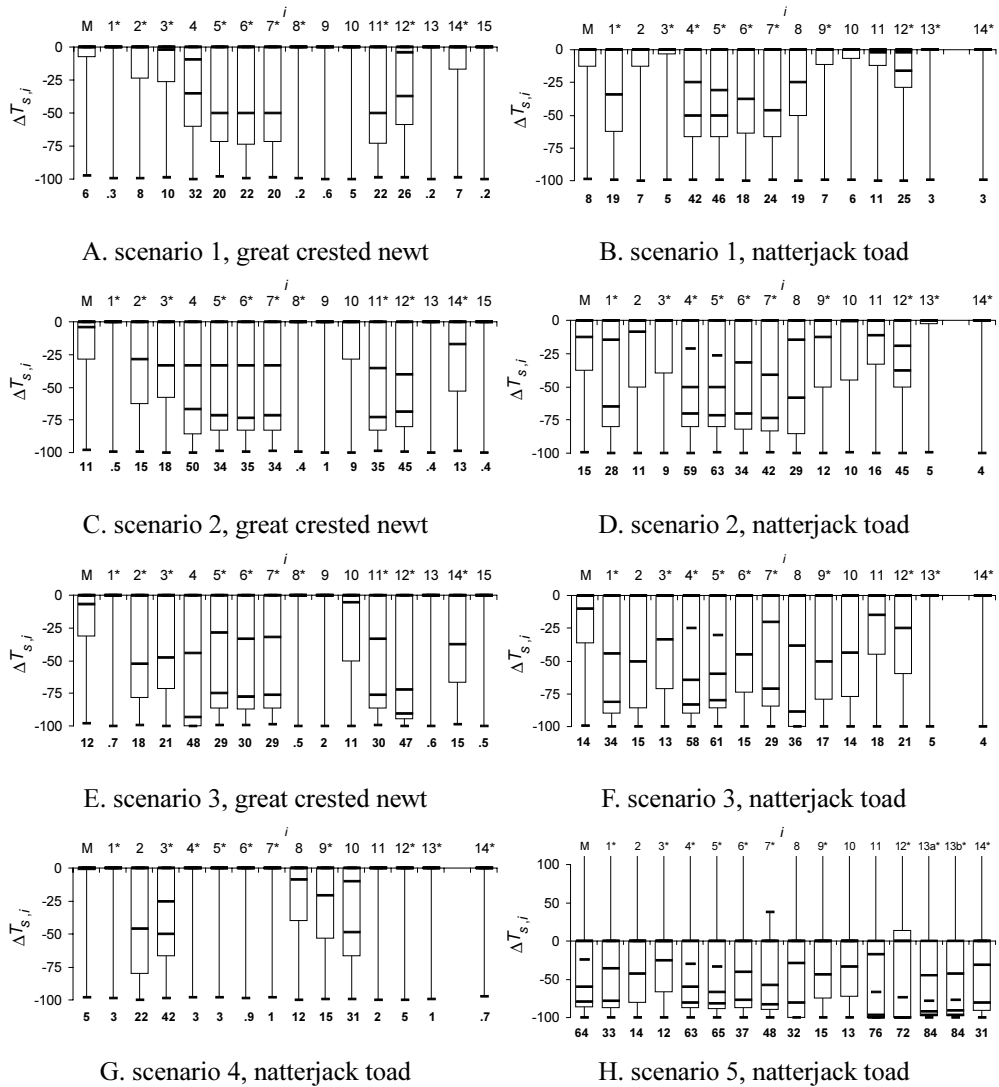
Although screens prevent casualties, they also impede dispersal, which makes their net effect ambiguous: it will be disadvantageous to sink patches which are cut off from their supply, but source patches will mostly benefit. Therefore, screens will only be a better option if the prevention of additional mortality induced by rail traffic outweighs the loss of connectivity. That is, for the metapopulation as a whole; for local sink populations screens may still be more harmful. The natterjack toad, with its larger impact zone and dispersal distance, is subject to additional mortality to a higher degree than the great crested newt, yet it also depends more on the network than the great crested newt does because of its higher extinction probability. A comparison of Figures 6C and D with Figures 6E and F teaches that positive and negative effects of screens fairly balance out, perhaps with a slightly negative effect for the great crested newt and a slightly positive effect for the natterjack toad.

Figure 6H demonstrates that in extreme cases, splitting up a patch may be favorable. We want to stress that these events are very rare: for the metapopulation and all patches but one, this happens with an estimated probability less than 0.2% (for the metapopulation

A. scenario 0, great crested newt

B. scenario 0, natterjack toad

Figure 5. Boxplots of sample distributions of $T_{0,i}$, i.e. the metapopulation extinction time (M) and the patch occupancy times for the current situation (scenario 0). The letter M and the numbers below the plot refer to the total metapopulation and the patch numbers respectively as in Figure 1. An asterisk next to the patch number indicates that the patch was occupied initially. Each boxplot gives the minimum and the maximum of $T_{0,i}$ at the end of the lines, the 5th and 95th percentiles of $T_{0,i}$ as the boundaries of the box, and the 10th, 25th, 50th, 75th and 90th percentiles as horizontal lines inside the box. The shorter horizontal line corresponds to the 50th percentile.

just 0.5%); for patch 12 this occurs with a probability of 5%. At the same time, however, negative effects are much more likely, up to 84% for the split patch, and 72% for patch 12. Although unexpected, the highly improbable event of a positive outcome is not surprising for a metapopulation model. Although patches 13a and 13b are very close to each other and

Figure 6. Boxplots of sample distributions of the relative metapopulation extinction time and patch occupancy times, $\Delta T_{s,i}$, for the great crested newt (A,C,E) and the natterjack toad (B,D,F,G,H) for the scenarios (s) considered: scenario 1 (A,B), scenario 2 (C,D), scenario 3 (E,F), scenario 4 (G), and scenario 5 (H). Scenarios 4 and 5 are only studied for the natterjack toad, as explained in the text. The letter M and the numbers in the plot refer to the total metapopulation and the patch numbers as in Figure 1. An asterisk next to the patch number indicates that the patch was occupied initially. The bold numbers denote the percentile where $\Delta T_{s,i}$ becomes negative, that is, they denote the probability of the scenario having a negative effect on the metapopulation or
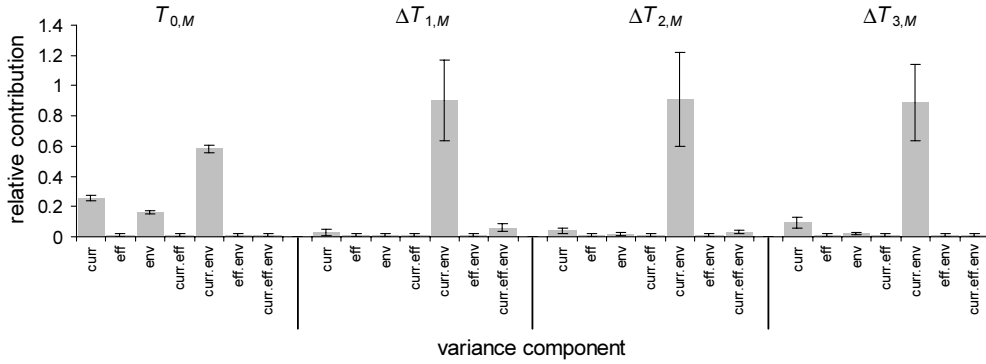
[Figure 6 cont'd] the patch. In scenario 5 patch 13 is split into 2. For very few courses of events, this division is responsible for an increase in patch occupancy time and metapopulation extinction time as the lines above 0 indicate.

their environmental conditions are correlated in our simulations, they need not go extinct simultaneously, because of the additional noise term in these conditions. If one of the patches goes extinct while the other one does not, and the metapopulation experiences a bottleneck episode with low occupancy, the remaining occupied patches may save the metapopulation from untimely extinction.
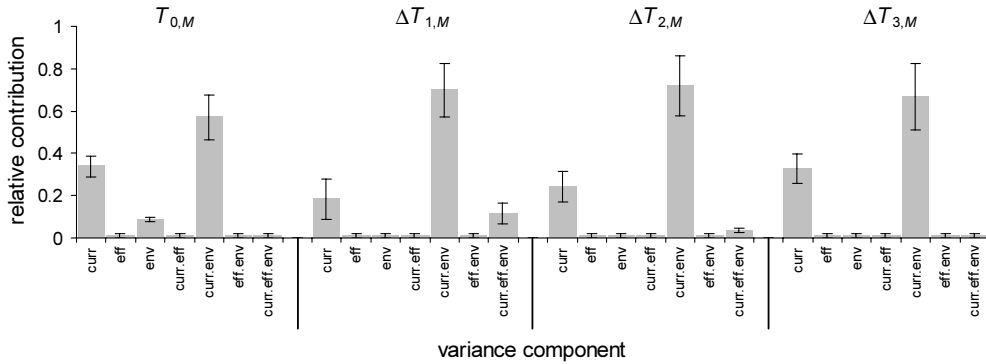
One of the objectives of this study was, evidently, to find the overall least harmful scenario. For the great crested newt, apart from the alternative routes which are expected to have no negative effect as we noted earlier, scenario 1 (restoration of the railway track with low train frequency) seems to be the best. For the natterjack toad scenario 4 (A1 route) is recommended, while scenario 5 (A2 route), despite the rare probability of positive effects, is definitely the worst option. Combining the conclusions for both amphibians, the A1 route is most preferable, except for completely refraining from restoring or building a railway track.

Figure 7 shows the contributions of the uncertainties in the three sources we distinguished and their interactions to the total variance in $T_{0,i}$ and $\Delta T_{s,i}$. These contributions are normalized so that they sum to 1. The large contribution of the interaction between the current situation and the environmental conditions is remarkable. This interaction contribution decreases only by a small amount on a logarithmic scale indicating that the interaction is much stronger than a multiplicative interaction. This is not totally surprising since our model possesses a strong interaction between the environmental conditions and the parameter settings. For example, at each time step the probability of local extinction is compared with a random number which represents the local environmental conditions; together they determine whether the local population goes extinct or not. An increase in the local extinction probability due to the railway only affects the local population if it causes the extinction probability to be on the opposite side of the environmental random number. And even then, it only affects the metapopulation if it concerns a core patch and if the metapopulation goes through a bottleneck phase (only one or two patches occupied). Hence, only for very special combinations of the model parameters and the environmental conditions, differences between scenarios arise. If changes only arise for combinations of uncertainty sources, this shows up in the variance contribution of their interaction term. Still, it is somewhat unexpected that the uncertainty about the effects (which together with the parameters of the current situation determine the model parameter settings) do not contribute substantially. Although we would have said beforehand that our uncertainty about the effects is large, this means that their uncertainty is in fact relatively small.

In the introduction it was suggested that the uncertainty in differences between outcomes of different scenarios is smaller than the uncertainty about the outcome of a particular scenario itself. This is indeed the case (results not shown; Figure 7 confirms this in the sense that the relative contribution of uncertainty about the current situation is smaller when scenarios are compared to this current situation).

A. great crested newt

B. natterjack toad

Figure 7. Contributions of three sources of uncertainty and their interactions to the variance in the metapopulation extinction time in scenario 0, $T_{0,M}$, and the metapopulation extinction time in the other scenarios relative to scenario 0, $\Delta T_{s,M}$ (*s*

[Figure 7 cont'd] denotes the scenario) plus their standard errors for the great crested newt (A) and the natterjack toad (B). The contributions are normalized such that they sum to 1. The abbreviations *curr*, *eff*, and *env* stand for the sets of the default population dynamic parameters (as in the current situation), of the effect parameters, and of the inherent model stochasticity (to be interpreted as local environmental conditions). For the great crested newt scenarios 4 and 5 are not studied, as explained in the text.

Discussion

We have demonstrated how a simple metapopulation model in combination with an extensive uncertainty analysis can contribute to ecological impact assessment in data-poor systems. The ranking of the different scenarios proved to be consistent, even though the uncertainty in predicted metapopulation extinction time is large. Because it has been made explicit to what extent uncertainty in the input might alter the outcome of the impact assessment, the results will become more powerful in decision making.

Our relatively simple spatially explicit stochastic metapopulation model possessing the basic ingredients of metapopulation dynamics, extinction and colonization, is fairly easy to parametrize given the unfortunate but typical situation of poor data and fuzzy expert knowledge. Uncertainty analysis on this stochastic model enables us to translate our limited knowledge about the system into uncertainties about the effect of humans interventions. Furthermore, it allows us to distinguish the uncertainty about the effect of properties of the system which we may eventually know exactly and the effect of future environmental conditions influencing the system which we will probably never know. It turns out that these environmental conditions and the default settings of the system together determine the range of possible consequences of human interventions to a large extent. The uncertainty about the railroad effects plays a less substantial role. Still, a further understanding and quantification of species responses to railroads would certainly improve the quality of the assessment.

To assess the impact of human interventions on metapopulations, Monte Carlo uncertainty analysis is a powerful yet seldom used tool. Akçakaya & Atwood (1997), Akçakaya & Raphael (1998), and South et al. (2000) performed uncertainty analyses on the Northern spotted owl (*Strix occidentalis caurina*) metapopulation in the northwestern USA, the California gnatcatcher (*Polioptila c. californica*) metapopulation in California, and the (intended) European beaver metapopulation (*Castor fiber*) in Scotland respectively, but they only used three values (high, medium, low) of the parameters instead of Monte Carlo sampling. So the question remains why Monte Carlo has not yet found a niche in metapopulation applications. One reason which presents itself immediately, is the considerable computer time required for running spatially explicit models. Simulations must be repeated many times to obtain a reliable output uncertainty distribution (often thousands of runs are required), so for time-intensive models, Monte Carlo sampling has not been practically possible until a few years ago and still is not possible in many cases. At the same time, Monte Carlo sampling has been applied successfully in many other scientific fields (see Saltelli et al. 2000). Hence, there

must be other reasons why application to metapopulations has not become customary. One such reason may be that little knowledge is available about the studied systems, so models are only reluctantly used for predictions, not to mention for uncertainty analyses of predictions. However, we believe that, to the contrary, little knowledge and reluctance about using models for predictions call for the use of uncertainty analysis, and we feel that this paper shows that it is also practically possible if the model is not too complicated.

Although our relatively simple model makes uncertainty analysis of its parameters feasible, it bears a different type of uncertainty, namely that of the consequences of its evident simplification of reality (structural or fundamental uncertainty). Local dynamics are simply described by the extinction probability which is only related to population size, whereas there are, evidently, many habitat quality factors that influence extinction probability. Effects of dispersal on the populations of origin and destination are not accounted for, nor does the colonization probability depend on population size (but see below). Possible interactions of the amphibians with other species (for example fish predating the amphibian litter) has been ignored. Detailed dispersal routes are absent, correlations between extinctions are not included, and so forth. Yet, because we have hardly any information about the underlying mechanisms, let alone about the corresponding parameters, building a complex model which appears to resemble reality more closely, is clearly inappropriate, regardless of the difficulty of its uncertainty analysis. In other words: the model should match the available data (Wennergren et al. 1995, Beissinger & Westphal 1998). Also, the uncertainty distributions of the parameters compensate for some of the ignored processes; for example the uncertainty about the extinction probability reflects the fact that there are many factors influencing the extinction probability.

We have, however, tested the robustness of our results to one modification of the model: the dependence of dispersal on population size, because it is believed to be a key element involved in the dispersal process (Hanski 1994). We assumed that equation (3) holds for medium-sized populations and we multiplied the right-hand side of equation (3) by 2 and 0.5 for large and small populations respectively. Although obviously quantitatively different, our results did not change qualitatively at all.

Our results about the contributions of the sources of uncertainty also suggest that even if we had detailed knowledge about the system allowing us to build a complex model, and even if this model could be handled easily in an uncertainty analysis, the inherent stochasticity of the model, representing future environmental conditions, may form a large source of uncertainty. Therefore, the suitability of building such a complex model for predictions is not unquestionable.

This study contains two additional aspects which we feel deserve mentioning. Firstly, its ultimate goal is to find a scenario which is optimal (that is, most beneficial or least harmful) for two species simultaneously. Secondly, we have used different measures by which we assess the optimality of a scenario: the metapopulation extinction time and the occupancy time of each patch conditional on non-extinction of the network relative to the current situation. Fortunately, in this case, there is clearly one scenario which is optimal in all respects for each species (apart from completely refraining from reinstating or building a railway track), namely scenario 4 which has no effects on the great crested newt, and only minor effects on

the natterjack toad for all measures. In general, however, the optimal scenario for one species may differ from the optimal scenario for the other species, and optimality of one measure does not guarantee optimality of the other, despite their being strongly related. Determining the optimal scenario for both species simultaneously then crucially depends on how we weigh the effects of the scenarios on the measures for each species, which is not straightforward at all, and certainly subject to debate. In establishing these weights, uncertainty analysis also plays an essential role. For example, relatively unquestionable effects may receive a larger weight than dubious ones, or a five percent chance of an extreme negative effect of a scenario may result in a weight which practically disqualifies the scenario (note that we would probably act differently if the extreme effect were positive).

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8

Improved Bayesian analysis of metapopulation data with an application to a tree frog metapopulation

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Abstract

Metapopulation models are important tools to predict whether a species can persist in a landscape consisting of habitat patches. Here a Bayesian method is presented for estimating parameters of such models from data on patch occupancy in one or more years. Earlier methods were either ad hoc, or produced only point estimates, or could only use turnover information. The new method is based on the assumption of quasi-stationarity which enables it to use not only turnover data, but also snapshot data. Being Bayesian, the method produces reliable information about the uncertainty of the parameters and model-based predictions in the form of posterior distributions. It is computationally demanding, but considerably faster than a recently developed Bayesian method extended beyond turnover data. The method is compared with existing methods (placed in a Bayesian framework) by fitting an extended incidence function model to a data-set on a tree frog metapopulation with many missing values and by predicting its viability, mean occupancy, and turnover rate after 100 years.

Introduction

Consider the following data-set of the tree frog *Hyla arborea* (Vos et al. 2000): for 202 patches of habitat in Zealand Flanders in The Netherlands presence and absence of the tree frog have been recorded for the years 1981, 1982, 1983 and 1986. How can these data help us to predict the viability of the species in the landscape?

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[1] Both authors are recognized as jointly contributing to first authorship.

Metapopulation theory has been very valuable for understanding the presence and absence of a species in habitat patches within a landscape. Its basis was laid down in the earliest and probably simplest metapopulation model, the Levins (1969, 1970) model: each population occupying a habitat patch runs the risk of extinction, thereby leaving the patch empty, but empty patches can also be (re)colonized by dispersers from occupied patches. If extinctions and colonizations are in balance, the species - unable to persist at the local patch scale - can persist at the landscape scale.

Although the applicability of the metapopulation concept has been criticized (Harrison 1994), it has been accepted as a useful tool in spatial ecology (Gilpin & Hanski 1991, Hanski & Gilpin 1997, Hanski 1999). The Levins model has been extended in many ways (Hanski 1983, Gyllenberg & Hanski 1997, Nee et al. 1997, Amarasekare 1998, Etienne 2000), providing more insight into important metapopulation processes. At the same time, extensive work has also been done on devising methods to parameterize metapopulation models using data on patch occupancy, making it possible to predict the future of the observed metapopulation, and thus presenting an answer to our initial question. The Incidence Function Model (IFM; Hanski 1994, 1999) was especially constructed for this purpose. The IFM links the landscape characteristics interpatch distance and patch area to colonization and extinction probabilities through partly descriptive (i.e. statistical) and partly mechanistic formulae. It gives the probability of any occupancy pattern in year t given the occupancy pattern in year $t-1$. As such, it is an example of a stochastic patch occupancy model (SPOM; Moilanen 1999) possessing the Markov property. An extended version of the IFM was parameterized using the above-mentioned data-set and sustainability predictions were made with it (Vos et al. 2000). The method employed for estimation of the model parameters (Ter Braak et al. 1998) is based on maximum likelihood and uses both turnover events (that is, extinctions and colonizations from one year to the next) and occupancy data in the first year of the data-set. However, although an improvement upon earlier methods which used only turnover information (Verboom et al. 1991, Sjögren-Gulve & Ray 1996) or only occupancy data (Hanski 1994), it cannot exploit the data completely and accurately. It cannot exploit the data completely because it cannot make use of the last year in the tree frog data-set due to missing data in the two preceding years (1984 and 1985), nor is it accurate because the likelihood it calculates for the occupancy in the first year is, as in Hanski (1994), only a pseudo-likelihood, assuming that the occupancies of the patches in these patches are independent which they are obviously not. The method is also not complete and accurate in another way: it produces point estimates of the parameters and standard errors, whereas for predictions with the parameterized model, a full joint probability distribution of the parameters is necessary to allow proper uncertainty analysis.

Moilanen (1999) developed an estimation method based on a Monte Carlo approach which accounts for missing years in the data by simulating them using the transition probabilities given by the model. The pseudo-likelihood in the first year is avoided by simulating hypothetical occupancy patterns of the preceding year from an equilibrium distribution (see also below). This method can thus exploit the data completely and accurately, but it still produces point estimates, although some effort has been made to calculate the reliability of these estimates. Recently, a Bayesian approach has been taken (O'Hara et al. 2002) which

produces a full joint probability distribution of the parameters and also accounts for missing years, but it only uses turnover information. This would not be problematic if large data-sets with many turnover events were available, but the contrary is often true: the data-set in our example which consists of only four years of data with relatively few turnover events is already considered a high quality data-set.

In this paper we present an improved version of the Bayesian approach of O'Hara et al. (2002) for SPOMs in general which retains all of its features but which also fully uses the occupancy data of the first year, and is more efficient in treating missing data. The pseudo-likelihood problem is circumvented by data augmentation (Tanner & Wong 1987), in particu-lar by adding many preceding years which are treated as missing data. We apply the extended IFM of Vos et al. (2000) to our example data-set to show the differences between the methods in parameter estimation and subsequent sustainability prediction.

Methods

The general stochastic patch occupancy model in discrete time

Consider a network of N habitat patches and make the following assumptions: if a patch i contains a population, this population can go extinct in one time-step with probability E_i, and if the patch is empty, it can be colonized with probability C_i. Denote the state of patch i at time t by $X_i(t)$; for an occupied patch $X_i(t) = 1$, for an empty patch $X_i(t) = 0$. The total state of the system at time t, $X(t)$, then consists of N ones and zeros. The colonization probability at time $t + 1$ usually depends on the state $X(t)$ as this state determines how many dispersers are sent out that may end up in patch i. With regard to the extinction probability, its independence of $X(t)$ seems reasonable, but when the rescue effect (Brown & Kodric-Brown 1977) is active, we have an example in which the E_i do depend on $X(t)$. The extinction and colonization probabilities may also depend on species and landscape characteristics which can be treated either as (observed) variables V or (unknown) parameters Θ in our model. Thus, we have

$$\begin{aligned} E_i \quad &: \quad = E_i[X(t), V, \Theta] \\ C_i \quad &: \quad = C_i[X(t), V, \Theta]. \end{aligned} \quad (1)$$

Below, we will give an example of each function.

Assuming that the Markov property holds that the state of the system is fully determined by the state at the previous time, we can calculate the probability of finding a system in state $X(t+1)$ at time $t+1$ given that it is in state $X(t)$ at time t and conditional on the parameters Θ (and on V which we drop for notational convenience):

$$P[X(t+1)|X(t), \Theta] = \prod_{i=1}^{N} P[X_i(t+1)|X(t), \Theta] =$$

$$= \prod_{i=1}^{N} \begin{cases} 1 - E_i & \text{if } X_i(t) = 1 \text{ and } X_i(t+1) = 1 \\ E_i & \text{if } X_i(t) = 1 \text{ and } X_i(t+1) = 0 \\ 1 - C_i & \text{if } X_i(t) = 0 \text{ and } X_i(t+1) = 0 \\ C_i & \text{if } X_i(t) = 0 \text{ and } X_i(t+1) = 1, \end{cases} \tag{2}$$

and the probability of any sequence of states X starting at time 1 and ending at time T conditional on Θ is then:

$$\begin{aligned} P[X|\Theta] \quad = \quad & P[X(1)|\Theta] \; P[X(2)|X(1), \Theta] \; ... \\ & ... \; P[X(T-1)|X(T-2), \Theta] \; P[X(T)|X(T-1), \Theta]. \end{aligned} \tag{3}$$

The Maximum Likelihood (ML) parameter estimation method aims to find the parameter set which maximizes the likelihood (3). There is one quantity in (3) which is not determined by (2), namely $P[X(1)|\Theta]$. This problem can be circumvented by conditioning on $X(1)$. Instead of $P[X|\Theta]$, we then maximize $P[X(2), ..., X(T)|X(1), \Theta]$ for which we do not need to know $P[X(1)|\Theta]$. However, by conditioning we do not use all information provided by our data-set, which is regrettable, especially for small data-sets.

Without any further assumptions $P[X(1)|\Theta]$ cannot be calculated. However, an assumption that is often made in SPOMs is that of quasi-stationarity: conditional on non-extinction the probability that the system is in a particular state is independent of time. Hanski (1994) used the quasi-stationarity assumption to estimate the parameters of the IFM. He defined J_i to be the quasi-stationary probability that patch i is occupied. Then, by quasi-stationarity,

$$\begin{aligned} J_i \quad &= \quad J_i \, (1 - E_i) + (1 - J_i) \, C_i \Rightarrow \\ J_i \quad &= \quad \frac{C_i}{C_i + E_i}, \end{aligned} \tag{4}$$

where C_i and possibly E_i (see above) are functions of $X(1)$. He proceeded by claiming that the quasi-stationary probability P_{qs} of the system being in state $X(1)$ is given by

$$P_{\text{qs}}[X(1)|\Theta] = \prod_{i=1}^{N} J_i^{X_i(1)} \, (1 - J_i)^{1 - X_i(1)} . \tag{5}$$

However, both (4) and (5) are at best approximations. First, the colonization and extinction probabilities are calculated on the basis of $X(1)$ instead of $X(0)$ (which is unknown) and therefore the independence of the $X_i(1)$, as assumed in (5), is not warranted. Hence, the calculated likelihood is only a pseudo-likelihood (Ter Braak et al. 1998). Second, in the first line of (4) conditioning on non-extinction is omitted, which is only a good approximation for systems with a very long time to extinction. Third, in (4) it is also assumed that E_i and C_i are constant over time, which they are not in general, because they usually depend on the evolving states at the other patches. The last difficulty can be partly avoided by assuming that the colonization and extinction probabilities depend on the time average of the states, i.e. on the J_i, and then implicitly solving (4) for all J_i. Yet, this assumption is not generally true. Despite its shortcomings, we will use (5) to obtain initial estimates for our method.

Moilanen (1999) incorporated the quasi-stationarity assumption in his Monte Carlo approach by simulating the system for a long time, e.g. K time steps, (and repeating this if the

simulations led to extinction before $t = K$), thus generating many states Y_i which together form an approximation of the quasi-stationary distribution:

$$
\begin{aligned}
P_{\mathrm{qs}}[X(1)|\Theta] &= \sum_Y P[Y, X(1)|\Theta] = \sum_Y P[X(1)|Y, \Theta]\, P[Y|\Theta] \approx \\
&\approx \frac{1}{K} \sum_{i=1}^{K} P[X(1)|Y_i, \Theta]
\end{aligned}
\tag{6}
$$

where the sum is over all possible states Y. Terms involving $P[Y_i|\Theta]$ drop out on the right-hand side of (6) because the simulation series is self-weighing, i.e. each Y_i is generated in the simulation series with the required probability $P[Y_i|\Theta]$. Although (6) is sufficient to calculate $P_{\mathrm{qs}}[X(1)|\Theta]$, Moilanen (1999) also imposed an additional condition on the parameter values which he called turnover limitation. This apparently improved the results if K is not very large (a large K is computationally very costly). By doing so, Moilanen (1999) was actually combining his maximum simulated likelihood method with another estimation method, termed the method of moments (Bowman & Shenton 1985; for a related application see Snijders & Van Duijn 1997).

Below, we will present our alternative to calculate $P_{\mathrm{qs}}[X(1)|\Theta]$ which partly resembles (6), but is tailored to our Bayesian approach.

Bayesian inference using Markov Chain Monte Carlo simulation

In Bayesian data analysis (see e.g. Gelman et al. 1995) we use probability distributions to express our uncertainty about parameter values. If information about the parameters becomes available, for example in the form of a data-set, we can use this information to update our probability distributions using Bayes' formula which is,

$$
P[\Theta|X] = \frac{P[X|\Theta]P[\Theta]}{P[X]}
\tag{7}
$$

where Θ represents the parameters and X the available information. The probability distributions before updating, $P[\Theta]$ in equation (7), are called the prior distributions, whereas the probability distributions after updating, $P[\Theta|X]$ in (7), are called the posterior distributions. The prior distributions may contain all our (fuzzy) prior knowledge about the parameters. A simple way to choose a prior distribution is to choose realistic limits and then assuming a uniform probability distribution between these limits, but any other distribution is possible, as long as it reflects our prior knowledge.

The idea of Markov Chain Monte Carlo (MCMC) simulation is to let the parameters perform a random walk in parameter space according to a particular Markov chain, which, importantly, has nothing to do with the Markov property of our metapopulation model. The Markov chain is set up in such a way that its stationary distribution is the posterior distribution we are looking for. A useful algorithm for setting up the Markov chain is the Metropolis-Hastings (MH) algorithm (Metropolis & Ulam 1949, Metropolis et al. 1953, Hastings 1970). In the terminology of Gelman et al. (1995) the MH-algorithm reads:

1. Choose a starting estimate Θ^0 for parameters Θ.

For $u = 1...$ repeat steps 2-4:

2. Choose a candidate point Θ^* (proposal) from a jumping distribution $J_u[\Theta^*|\Theta^{u-1}]$.

3. Calculate the acceptance ratio (D denotes data)

$$r = \frac{P[\Theta^*|D]}{P[\Theta^{u-1}|D]} \frac{J_u[\Theta^{u-1}|\Theta^*]}{J_u[\Theta^*|\Theta^{u-1}]}. \tag{8}$$

4. Take

$$\Theta^u = \left\{ \begin{array}{ll} \Theta^* & \text{with probability } \min(r, 1) \\ \Theta^{u-1} & \text{otherwise} \end{array} \right. . \tag{9}$$

The Θ^u with $u > u_{\text{con}}$ now constitute the posterior distribution for Θ, u_{con} being the point where the process is believed to have converged; the period up to this point is called the burn-in period. The efficiency of the algorithm depends largely on the choice of the jumping distribution. If there is more than one parameter, all parameters can be sampled simultaneously from a joint jumping distribution after which the entire set of parameters is either accepted or rejected, but they can also be sampled and accepted/rejected (updated) one by one by alternate sampling conditional on the remaining parameters. Any intermediate combination is also possible: several small subsets of parameters can be sampled one by one. Efficiency guides our choice.

With the MH algorithm missing data can be easily dealt with: they are treated as parameters. Just as for the model parameters, proposals are generated for missing data given the existing data. The MCMC method thus simulates the joint distribution of model parameters and missing data. By looking at just the distribution of the model parameters in the simulation output, the missing data are integrated out (or rather summed out, if this phrase existed). This process of adding data to the existing data-set is known as data augmentation (Tanner & Wong 1987).

Bayesian analysis of metapopulation data using a SPOM

With a general SPOM as defined above and an occupancy data-set such as the Vos et al. (2000) data-set we can perform the MCMC simulation using the MH-recipe once we have chosen a jumping distribution and once we have found a solution to the problem involving $P[X(1)|\Theta]$. Although there is no conceptual distinction between model parameters and missing data in the MH algorithm, it is convenient to alternate between sampling the model parameters and sampling values for the missing data. For the jumping distribution of the model parameters (after appropriate transformations) we choose a multivariate normal distribution centered on the current parameter values and with variance-covariance matrix $c\Sigma$ where c is a scale factor, set to a value such that the resulting acceptance probability lies between 0.3 and 0.4 (Gelman et al. 1995). For Σ we can use a variance-covariance matrix of the estimated model parameters as found in another parameter estimation method, or we can start with an arbitrary Σ and replace it by the Σ generated by the simulations after some iterations. Evidently, a good choice for Σ speeds up convergence.

Because the jumping distribution is symmetrical, the ratio $J_u[\Theta^{u-1}|\Theta^*]/J_u[\Theta^*|\Theta^{u-1}] = 1$. To calculate r in (8), we then only need to compute the ratio $P[\Theta^*|X]/P[\Theta^{u-1}|X]$. We use X (which is shorthand for all states in all years) instead of D here because we condition on both existing data D and the missing occupancy data in our alternate conditional sampling approach. Using (7) and (3) the required ratio $P[\Theta^*|X]/P[\Theta^{u-1}|X]$ can be expressed in terms of the transition probabilities given in (2) and the probability $P[X(1)|\Theta]$. We remarked above that we cannot calculate the latter probability unless we make further assumptions. We also mentioned that this can be circumvented by conditioning on $X(1)$ as O'Hara et al. (2002) do, but one is then unable to use fully the information in the first year of an occupancy data-set: only the turnover information from the first year to the second year is used, provided the first-year data do not contain any missing data (but note that the first-year data in our example contain missing values!).

Our way to use the first-year information completely, which also overcomes the problem of missing data in this first year, is as follows. First, we assume quasi-stationarity using a Markov property of our model:

$$P_{\text{qs}}[X(1)|\Theta] = \lim_{L\to\infty} P[X(1)|X(-L),\Theta], \text{ for all states } X(-L). \qquad (10)$$

This property says that the state at time 1 is independent of the state in the infinitely far past. Second, we use an equality similar to the first part of (6),

$$P[X(1)|X(-L),\Theta] = \sum_Y P[Y, X(1)|X(-L),\Theta] \qquad (11)$$

where the sum is over all possible sets of states $Y = \{X(-L+1), ..., X(0)\}$. Third, we apply the Markov property of our model that the state at some time is fully determined by the state at the previous time:

$$P[Y, X(1)|X(-L),\Theta] = P[X(-L+1)|X(-L),\Theta] ... P[X(1)|X(0),\Theta]. \qquad (12)$$

Thus, (10), (11) and (12) lead to

$$\begin{aligned} P_{\text{qs}}[X(1)|\Theta] &= \lim_{L\to\infty} \sum_{X(-L+1),...,X(0)} \{P[X(-L+1)|X(-L),\Theta] ... \\ &\qquad ... P[X(1)|X(0),\Theta]\}. \end{aligned} \qquad (13)$$

We can approximate this by taking L to be sufficiently large. In our Bayesian framework we treat Y, the states between times $-L$ and 1, as missing data, which we are able to simulate alternately with the model parameters. As we already remarked above, by just looking at the model parameters, the missing data are effectively integrated out, as required by (11). In this process, $X(-L)$ is an arbitrary state at time $-L$ which is kept fixed. We can initialize the additional "pre-years" $X(-L+1), ..., X(0)$ by either simulating $X(-L+1), ..., X(0)$ using our model with a parameter set Θ^0 starting from some $X(-L)$ - the choice of which should not matter mathematically, but influences the speed of convergence - or by starting at $X(1)$ and simulating backwards to $X(-L)$. We prefer the latter approach because it is better accommodated to the data. This is only to initialize these states; during the MCMC simulation

they are updated according to the MH algorithm, treating these pre-years as missing data. Hence, adding these pre-years is just another example of data augmentation.

We now only need to specify the jumping distribution for the missing data (real missing data as well as the pre-years). We can sample each missing data point separately in the same way as O'Hara et al. (2002). However, this is computationally very costly, especially with many patches and many pre-years. Therefore, we chose to sample missing data points in the same year simultaneously which turned out to be much faster. Details are given in the appendix.

Posterior probability distributions in an uncertainty analysis of model predictions

One of our motives for the Bayesian approach is that it generates a joint posterior probability distribution for the model parameters which can be used as input in an uncertainty analysis of model predictions. Apart from the observation that we should only use iterations after u_{con} to guarantee convergence, we should be aware that the sets of parameters Θ^u are correlated with one another, causing the effective number of simulations to be (much) lower than the actual number.

Case study: the tree frog *Hyla arborea*

We demonstrate our approach using the tree frog *Hyla arborea* data-set and the model in Vos et al. (2000). We briefly describe the system and refer to Vos et al. (2000) for more details. In the western part of Zealand Flanders in The Netherlands, the study area of 250 km^2 contains 1.5% suitable habitat, distributed over 202 patches (each patch is a combination of a pond and surrounding terrestrial habitat). The main variables affecting extinction are patch area A_i (defined as pond area plus terrestrial habitat within 250 m of the pond, in ha) and water conductivity $H_{1,i}$:

$$E_i = (1 - C_i) \min \left(1, \frac{e H_{1,i}^{q_1}}{A^x} \right), \tag{14}$$

where the factor $(1 - C_i)$ accounts for the rescue effect and e, x and q_1 are parameters. The main variables influencing colonization of a patch i are its connectivity S_i and the percentage cover of the water vegetation of the pond $H_{2,i}$:

$$C_i = \frac{1}{1 + \frac{y}{S_i^z H_{2,i}^{q_2}}}, \tag{15}$$

where y, z and q_2 are parameters. The connectivity S_i is given by

$$S_i(t) = \sum_{j \neq i} X_j(t) A_j^b B_{ij} e^{-\alpha d_{ij}} \tag{16}$$

with $X_j(t)$ the occupancy of patch j, d_{ij} the distance (in km) between patches i and j, α a parameter with $\frac{1}{\alpha}$ representing the typical dispersal distance, B_{ij} a variable measuring the barrier between patches i and j ($B_{ij} = 1$ if there are no roads between patches i and j, $B_{ij} = 0.5$ if a road is present) and b is an emigration parameter (e.g. $b = 1$ if emigration is assumed proportional to patch area, $b = 0.5$ if it is assumed proportional to patch perimeter). A technical detail: since H_2 may be 0, Vos et al. (2000) added 1 to it before using it in (15). For consistency, 1 was also added to H_1 before inserting H_1 in (14). We accommodated to this approach.

Our aim was to estimate six parameters: e, x, q_1, y, z and q_2. We kept b and α fixed at their values in Vos et al. (2000), $b = 0.5$ and $\alpha = 2$ km^{-1}. In the Bayesian analyses, e, x, y and z were logarithmically transformed to avoid negative values of these parameters. The priors after transformation were normal distributions with very large standard deviations.

To obtain starting values (Θ^0 in our notation above) for the six model parameters we used the ML method of Ter Braak et al. (1998) on the turnover data. This yielded $e = 0.00296$, $x = 0.296$, $y = 19.34$, $z = 0.133$, $q_1 = 1.105$, $q_2 = 0.367$. With these starting parameters we carried out a preliminary MCMC simulation for the complete data-set where we used the pseudolikelihood based on the incidences J_i of equation (5). From the resulting posterior distribution we extracted the mean parameter values (on the log scale) and the variance-covariance matrix and we used these as Θ^0 and Σ, respectively, in our subsequent MCMC simulations. We set the scale parameter c to $T/[a(T + L)]$ (where a is the number of parameters to be estimated, $a = 6$) which resulted in an acceptance probability between 0.3 and 0.4.

To apply our Bayesian method which fully uses the first-year information, we must choose a number of pre-years and a fixed occupancy pattern in the first pre-year, as indicated by the term $X(-L)$ in equations (10) - (13). In all simulations with pre-years, we initialized the pre-year data by starting at $X(1)$ and simulating backwards to $X(-L)$ using the starting values for the parameters. From theory, we know that the choices of L and $X(-L)$ do not influence the posterior distribution if the number of pre-years is chosen to be large enough. But which number is large enough for our data? To answer this question, we carried out a series of six MCMC simulations in which the numbers of pre-years were 25, 50, 75, 100, 200, and 400.

To check in more detail the possible dependence of the results on $X(-L)$, we carried out replicate simulations for 25 and 100 pre-years with different states in the first pre-year. These simulations used the same starting values for the parameter values (Table I, first row). To check the convergence of the MCMC simulations, we repeated the analysis for four very different sets of starting values using 25 pre-years (Table I). Because of our initialization procedure for the pre-year data, the occupancy pattern $X(-L)$ also differed wildly in these four simulations as we can judge from the number of occupied patches (Table I, last column).

For all our analyses we performed 1000000 MCMC iterations. The first 200000 iterations were used as the burn-in period. From the remaining 800000 iterations, we took a $1/100$ systematic sample. This provided us with 8000 more or less uncorrelated MH-samples on which we based our results.

One of the attractive features of the Bayesian approach is that we can use the sample from the posterior distribution for the model parameters to assess the uncertainty of predictions

made by the model. We explored this feature by predicting the probability of metapopulation survival after 100 years, the fraction of patches that are occupied after 100 years and the turnover rate (expressed as the number of turnover events per patch per year) during these 100 years. As the starting state of the model simulations we selected the year 1986. This year lacks data for five patches. As we treated missing data in the MCMC simulation in the same way as the model parameters, we have posterior distributions for these missing data as well, which we use to obtain the predictions.

Table I. Five different sets of initial parameter values. The first set contains starting estimates obtained from preliminary MCMC simulations. This set is used in further analyses. The other sets are used to check convergence of the MCMC simulations. The last column gives the corresponding number of occupied patches in the first pre-year.

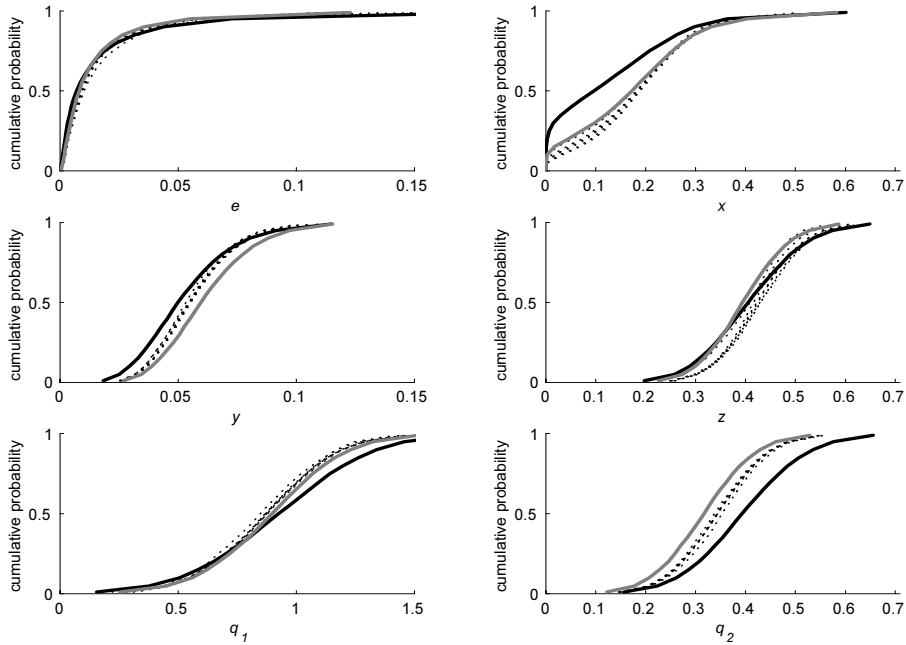| initial parameter set	e	x	y	z	q_1	q_2	# of occupied patches at $-L$
1	0.010	0.088	16.79	0.387	0.852	0.319	20
2	0.1	0.01	10	1	0.3	0.8	78
3	0.2	1	50	2	0.5	0.5	9
4	0.001	0.2	20	0.1	1	1	126
5	1	0.5	15	0.5	0.3	0.2	2

Results

Figure 1 shows the cumulative posterior distributions of the parameters obtained from the following MCMC simulations: one using turnover data only (denoted by TO), one using all data and the J_i-based pseudolikelihood of equation (5) (denoted by AJ), and six using all data and the likelihood of equation (10) for different numbers of pre-years, ranging from 25 to 400 (denoted collectively by AL). For TO and AJ, missing values in the first year were simulated using 25 pre-years. The analyses with 25 pre-years took 20 hours on a Pentium III 1 GHz PC. With 400 pre-years the analysis took about two weeks.

Figure 1 shows that the posterior distributions for TO differ considerably from those for AJ and AL, except for the parameter e, whereas the differences between the posterior distributions for AJ and AL are more subtle. The curves for AJ and AL are steeper than those for TO, showing that AJ and AL were able to extract more information about the parameters from the data than TO. The curves for AL for different numbers of pre-years are very similar. Using 25 pre-years thus appears to be sufficient. When looking at the parameters x and z (Table II) in more detail, we see a small but systematically decreasing trend in z for increasing numbers of pre-years, whereas the parameter x does not show an obvious trend. These results suggest that at this detailed level even 400 pre-years are not sufficient.

The replicate simulations using different states $X(-L)$ showed little influence of the state $X(-L)$ on the results, even with a number of pre-years as low as 25 (Figure 2).

Figure 1. Cumulative posterior probability distributions of the six model parameters using turnover data only (TO, black), all data with the Hanski approximation of the likelihood of the first year (AJ, gray) and all data with different numbers of pre-years (AL, dotted, $25, 50, 75, 100, 200, 400$ pre-years).

From the five simulations which were started with wildly different parameters and very different occupancy patterns in the first of 25 pre-years (Figure 3, solid curves), four yielded very similar results. In the deviating fifth simulation, only two patches were occupied in the first pre-year, much lower than the number of occupied patches in the first year in the data (22) and in the other cases (Table I). This exception shows that with 25 pre-years there is still some dependence of $X(-L)$ on the results. Choosing good starting values for the parameters is thus important to avoid such extreme cases of non-convergence.

The true test whether the differences between TO, AJ and AL matter, is to compare model predictions using the corresponding parameter estimates. Figure 4 shows the cumulative probability distributions of the occupancy after 100 years and the turnover rate during these 100 years obtained using the posterior distributions of the parameters in Figure 1. We can see that TO and AJ overestimate both the expected occupancy and the turnover rate, compared to AL. Hence, the first year of data indeed matters, and it is not completely accounted for by AJ. For all curves, the probability of extinction before 2086 was lower than or equal to 0.001. This is in line with the simulations by Vos et al. (2000) who found no extinctions at all in their 1000 runs (compare with our runs for 8000 different parameter sets). However, our analysis suggests that their estimate of the expected occupancy in 2086 (0.19) is too high; we

Table II. Percentiles and the interquartile range (iq-range, i.e. the difference between the 25th. percentile and the 75th. percentile) of x (A) and z (B). See also Figure 1.

A.

percentile	TO	AJ	AL400	AL200	AL100	AL75
0.05	0.0000120	0.000124	0.00168	0.000773	0.00155	0.00296
0.25	0.00668	0.0715	0.112	0.100	0.104	0.116
0.5	0.097	0.173	0.188	0.184	0.183	0.189
0.75	0.208	0.255	0.253	0.255	0.254	0.258
0.95	0.364	0.403	0.360	0.389	0.376	0.385
iq-range	0.201	0.184	0.141	0.155	0.150	0.142

percentile	AL50	AL25
0.05	0.000668	0.000138
0.25	0.0955	0.0822
0.5	0.182	0.175
0.75	0.259	0.250
0.95	0.394	0.378
iq-range	0.164	0.168

B.

percentile	TO	AJ	AL400	AL200	AL100	AL75	AL50	AL25
0.05	0.257	0.273	0.271	0.301	0.297	0.299	0.303	0.305
0.25	0.341	0.343	0.351	0.371	0.374	0.376	0.377	0.38
0.5	0.405	0.394	0.409	0.417	0.423	0.425	0.429	0.43
0.75	0.475	0.449	0.454	0.463	0.476	0.476	0.483	0.486
0.95	0.574	0.528	0.516	0.539	0.553	0.557	0.563	0.561
iq-range	0.134	0.106	0.103	0.092	0.102	0.100	0.106	0.106

Figure 2 (page 187). Cumulative posterior probability distributions of the six model parameters for two replicate simulations (with different seeds and hence different pre-years) for 100 pre-years (solid curves) and 25 pre-years (dotted curves). The likeness of the pairs confirms that the state in the distant past, $X(-L)$, does not matter.

Figure 3 (page 187). The solid curves represent cumulative posterior probability distributions of the six model parameters for five different sets of initial parameter values (see below) with 25 pre-years. The likeness of four out of five solid curves demonstrates convergence. The fifth, deviating, curve has extreme parameter settings resulting in an extreme state at $-L$ (see Table I). The dotted curves are the results of a simulation for the same extreme initial parameter settings; only the first transition probability, from year $-L$ to year $-L + 1$, is now ignored (see Discussion). The first parameter set contains the mean parameter values (the average is taken at the log scale) of the posterior distributions of a preliminary run on the complete data-set with pseudolikelihood (AJ), as in Figures 1 and 2.
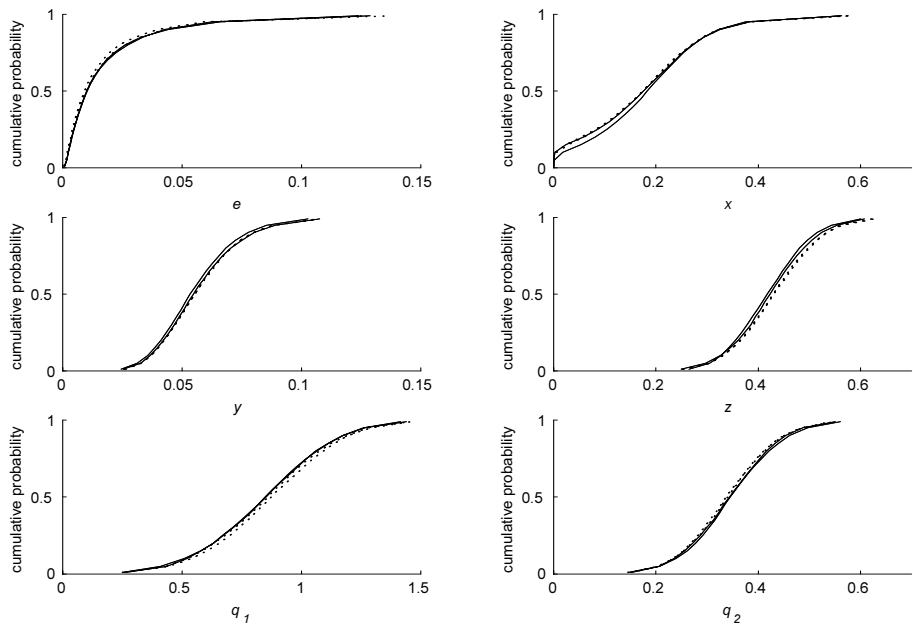
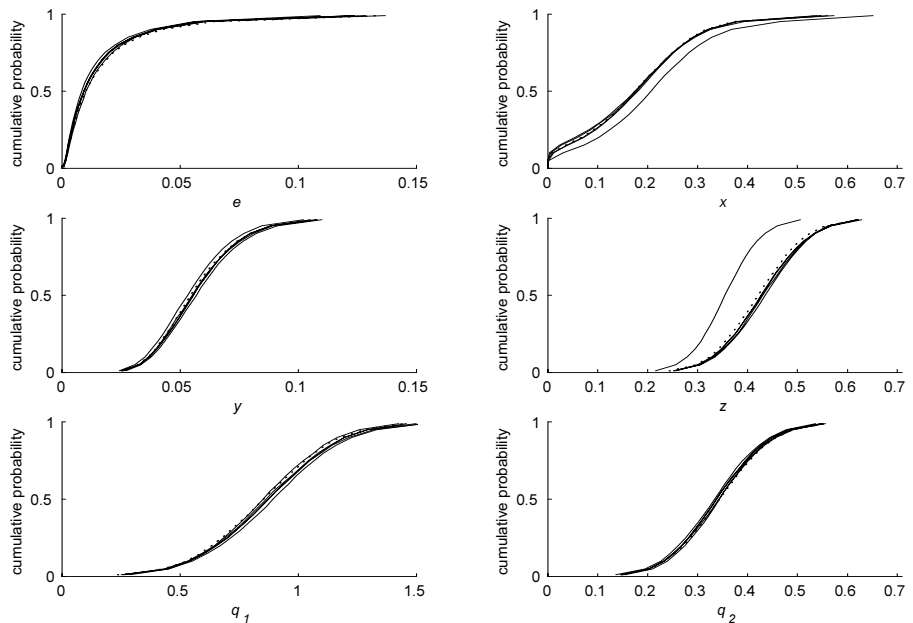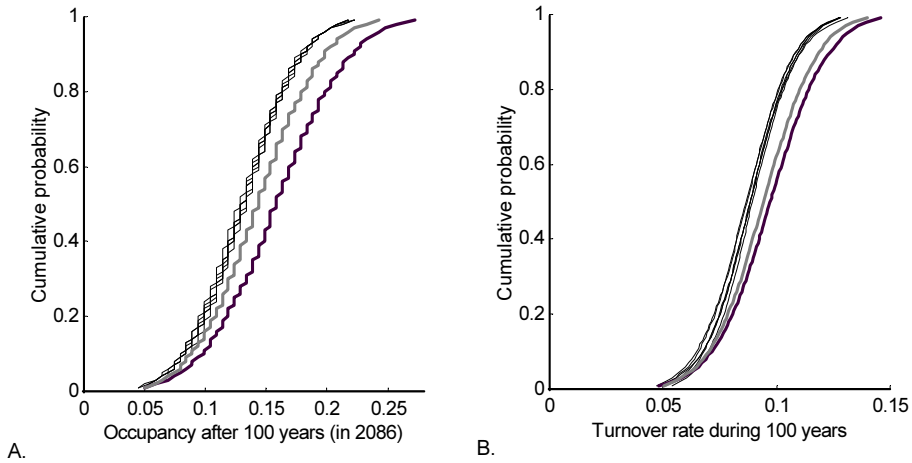**Figure 2**. (Caption on page 186)

Figure 3. (Caption on page 186)

Figure 4. Cumulative posterior probability distributions of the predicted occupancy after 100 years (A) and the turnover rate during these 100 years (B), using turnover data only (TO, thick black curve), all data with the Hanski approximation of the likelihood of the first year (AJ, gray curve) and all data with pre-years for different values of L (AL, thin black curves, $25, 50, 75, 100, 200, 400$ pre-years), exactly as in Figure 1. The results of each curve are based on 8000 simulations which used, in turn, each of the 8000 MH-samples plotted in Figure 1.

found a median of 0.134 with an interquartile range of 0.109 to 0.158 (for 400 pre-years). The 95% posterior interval for the turnover rate (for 400 pre-years) is $[0.059, 0.122]$. The turnover rate in the data (0.114) lies within this interval but close to the upper bound.

Discussion

Our Bayesian method to estimate model parameters from metapopulation data is an improvement upon earlier work in three ways. First, it uses all the data to their full extent (not just turnover data) in a theoretically sound manner. Second, it is considerably faster than the Bayesian method of O'Hara et al. (2002) if this method were extended beyond turnover data. Third, it provides posterior distributions rather than point estimates of the model parameters which can be used as input for uncertainty analyses when making model predictions.

The improvements come at a price which is two-fold. First, despite an efficient implementation, our Bayesian method requires much computing time, especially if L needs to be large. Fortunately, we have seen that moderate values of L (such as 25) can already yield a fairly accurate posterior distribution. Second, it makes the additional assumption that the system is in a quasi-stationary state. This may not always be the case, because convergence to this state may take a long time (Gosselin 1999). Yet, as Moilanen (2000) notes, using only turnover

data may result in the estimation of a trend which does not exist, particularly with a limited amount of data. Taking the first year of data fully into account yielded smaller confidence intervals (e.g. as judged by the interquartile range in Table II) than using the turnover data only. The fact that the confidence intervals are smaller suggests that the information extracted from the first year of data by making the quasi-stationarity assumption is compatible with the turnover information. If this were not the case, the turnover data and the quasi-stationarity assumption would give systematically different contributions to the posterior distribution resulting in a *larger* confidence interval.

Our method requires starting parameter values which are not too extreme. These can be found by a procedure as suggested above. Our results also emphasize that checking convergence is a necessity. At the same time, we argue that deviations such as in Figure 3 can be circumvented in several ways. These are mostly heuristic, so we have not included them in our general method. One of the most promising of them, which is compatible with theory, is dropping the first transition probability, $P[X(-L+1)|X(-L), \Theta]$, in the product of probabilities in (13). The fixed state $X(-L)$ then no longer has a strong influence on the total probability. In Figure 3 the result of this procedure is shown with the dotted curves. Instead of dropping only the first transition probability, we may drop more, as long as there are a sufficient number of transitions in the pre-years left. It remains to be shown rigorously whether this method works in general and what would be the optimal number of terms to be dropped.

In our case study the method using the J_i-based pseudolikelihood to account for the data in the first year fared fairly well. There is no strong bias in the parameter estimates and the confidence intervals are of similar magnitude as in our Bayesian method. The latter is surprising as the J_i-based method disregards the correlations among the observations in the first year. Nevertheless, there is no guarantee that the method will fare so well in other cases. Ter Braak et al. (1998) estimated model parameters from two simulated data series using the J_i-based pseudolikelihood, and compared the estimates to the true values which generated the data. In one case (with a high turnover rate) the estimates and the true values matched, but in the other case (with a low turnover rate) they were significantly different. Gosselin (1999) showed that the quasi-stationary state calculated using the J_i-based pseudolikelihood may in some cases be far from the true quasi-stationary state. This provides sufficient reason to be careful in using the AJ method, however attractive it may be in terms of computing time.

To allow comparison of our results with Vos et al. (2000), we estimated six parameters, whereas there are two more in the model (α and b). Evidently, these could also be estimated in the same way as the other six. It is straightforward to extend our method to estimate parameters which vary randomly over time with some variance which is to be estimated simultaneously. This temporal stochasticity induces correlations among extinctions and colonizations, and has therefore been termed, perhaps somewhat confusingly, regional stochasticity (Hanski et al. 1996, Moilanen 1999). Other proposals for regional stochasticity, e.g. distance-dependent correlations between extinctions or colonizations, can in principle be analyzed in our Bayesian framework as well. In the Bayesian framework it is also possible to account for errors in the occupancy data along the lines set out by Moilanen (2002) for his own parameter estimation method. Moilanen (2002) found that such errors can substantially

influence the model parameter estimates.

With our case study we have shown how the theory can be put into practice, and particularly how the method naturally enables uncertainty analysis of model predictions. The uncertainty analysis can be extended in many ways, for example to identify the individual contributions of each uncertain parameter to the uncertainty in the model predictions (Jansen et al. 1994, Saltelli et al. 2000). Such analyses are particularly worthwhile in assessing the impact of human intervention on a metapopulation.

Acknowledgments

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Appendix A. The jumping distribution for missing data

In this appendix we describe our MH-algorithm for updating missing patch data. First we introduce some notation. While updating, the model parameters Θ are kept fixed. For notational convenience we therefore drop the dependence on Θ. Furthermore, let the proposal for patch i in year t be denoted by $X_i^*(t)$ to distinguish it from the current state $X_i(t)$. Of course non-missing data are not updated, so that for these patches the proposed state and current state are identical. By $X_{-i}(t)$ we mean the states, at time t, of all patches except patch i, and by X_{-i} we mean the states of all patches in all years, except $X_i(t)$.

Our mechanism to generate a proposal is motivated by the Gibbs sampler for updating a single patch (O'Hara et al. 2002). The proposal for a single patch must, of course, be either 1 or 0. The ratio f_i of the probabilities of these two states for patch i conditional on X_{-i} is

$$f_i = \frac{P[X_i^*(t) = 1 | X_{-i}]}{P[X_i^*(t) = 0 | X_{-i}]}. \tag{A-1}$$

By the definition of conditional probabilities this becomes

$$f_i = \frac{P[X_i^*(t) = 1, X_{-i}]}{P[X_i^*(t) = 0, X_{-i}]} \tag{A-2}$$

and using the properties of the metapopulation model expressed in (3) and (2), we can simplify this to

$$f_i = \frac{P[X_i^*(t) = 1 | X(t-1)] \; P[X(t+1) | X_i^*(t) = 1, X_{-i}(t)]}{P[X_i^*(t) = 0 | X(t-1)] \; P[X(t+1) | X_i^*(t) = 0, X_{-i}(t)]}, \tag{A-3}$$

so that we in fact, condition only on the two adjacent years $t-1$ and $t+1$.

Because the numerator and the dominator in (A-1) must sum to 1, we get

$$p_i = P[X_i^*(t) = 1 | X_{-i}] = \frac{f_i}{1 + f_i}. \tag{A-4}$$

Proposing $X_i^*(t) = 1$ with probability p_i (and leaving the other patches unchanged) yields a Gibbs sampler, because (A-4) is a full conditional distribution, and the acceptance ratio is equal to 1.

The Gibbs proposal is costly to compute because each probability in (A-3) involving $X(t+1)$ is already a product of N probabilities (see equation (2)). The proposal can be simplified considerably by keeping $X_i^*(t)$ at its current state $X_i(t)$ when calculating the transition probabilities for $X_j(t+1)$ for $j \neq i$ in the numerator and denominator of (A-3). Then

$2(N-1)$ probabilities cancel out and we obtain, instead of (A-3),

$$\widetilde{f_i} = \frac{P[X_i^*(t)=1|X(t-1)]\ P[X_i(t+1)|X_i^*(t)=1, X_{-i}(t)]}{P[X_i^*(t)=0|X(t-1)]\ P[X_i(t+1)|X_i^*(t)=0, X_{-i}(t)]}, \tag{A-5}$$

and, instead of (A-4),

$$\widetilde{p_i} = \frac{\widetilde{f_i}}{1+\widetilde{f_i}}. \tag{A-6}$$

In our MH-algorithm, we calculate (A-6) for each missing patch in year t and then propose, for each patch i independently, $X_i^*(t)=1$ with probability $\widetilde{p_i}$. The jumping probability from $X(t)$ to $X^*(t)$ at step u is thus

$$J_u[(X^*(t)|X(t)] = \prod_i \widetilde{p_i}^{X_i^*(t)}(1-\widetilde{p_i})^{(1-X_i^*(t))}. \tag{A-7}$$

By interchanging the role of $X^*(t)$ and $X(t)$ in (A-5) - (A-7), we also obtain $J_u[(X(t)|X^*(t)]$ so that with

$$f = \frac{P[X^*(t)|X(t-1)]\ P[X(t+1)|X^*(t)]}{P[X(t)|X(t-1)]\ P[X(t+1)|X(t)]} \tag{A-8}$$

the acceptance ratio r is

$$r = f\frac{J_u[X(t)|X^*(t)]}{J_u[X^*(t)|X(t)]}. \tag{A-9}$$

Updating missing values in the last year (T) is not covered by the foregoing, but it can be done by Gibbs sampling, because $P[X_i(T)|X(T-1), X_{-i}(T)] = P[X_i(T)|X(T-1)]$ which can be calculated explicitly.
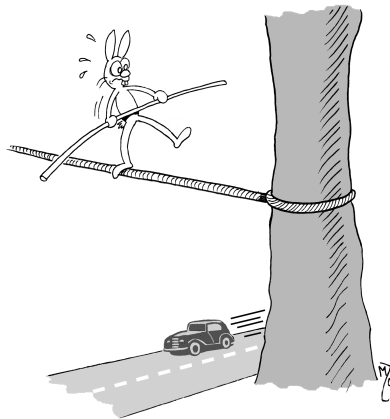
It is instructive to see which proposals are generated when E_i and C_i would be constant over time (i.e. when the connectivity of a patch remains the same over time). If $X_i(t-1)=0$ and $X_i(t+1)=0$, then $\widetilde{f_i} = C_iE_i/(1-C_i)^2$ which will be a small value if C_i and/or E_i are small, so that $\widetilde{p_i}$ is also close to 0, so that with only a small probability a 1 is proposed in year 1. Similar considerations show that if $X_i(t-1)=1$ and $X_i(t+1)=1$, $\widetilde{p_i}$ is close to 1 so that with a large probability a 1 is proposed in year 1. If $X_i(t-1) \neq X_i(t+1)$, $\widetilde{f_i} = (1-E_i)/(1-C_i)$ so that if C_i and E_i are equal or both small, $\widetilde{p_i}$ is about one half. All of these proposals make intuitive sense.

In the tree frog case study, our proposal mechanism accepted more than half of the proposals for a year. In simulated data, with lower turnover rates, acceptance probabilities of over 0.9 were observed. Our algorithm is expected to outperform the Gibbs sampler when many or all patches in a particular year have missing data, as is the case in our pre-years. However, if there is only one patch missing in a particular year, the Gibbs sampler is the most efficient and in that case we use it in our computer software. In the case study with its 202 patches and 25 pre-years, our MH-algorithm was about 10 times faster than an efficient implementation of the Gibbs sampler.

Samenvatting (Summary in Dutch)

Nederland is vol! Vol met huizen, fabrieken, wegen, spoorrails, weilanden, noem maar op. De kleine stukjes grond die we nog natuur noemen, liggen versnipperd over de Nederlandse bodem. Populaties van dieren en planten die op die stukjes grond, hun habitat, leven, zijn meestal maar klein omdat de hoeveelheid voedsel, ruimte, licht etc. beperkt zijn. Daardoor lopen deze populaties een relatief groot risico om uit te sterven, bijvoorbeeld door een toevallig tegenvallend geboortecijfer, of een strenge winter. Tussen stukjes habitat (die ik met "plekken" zal aanduiden) die met elkaar in verbinding staan, kunnen individuen heen en weer bewegen; bij planten kan men denken aan zaden of stuifmeel die worden getransporteerd door wind of dieren. Zo kunnen deze individuen vanuit de ene populatie in een andere, onbezette, plek een nieuwe populatie stichten. Als het aantal populaties dat in een bepaalde periode uitsterft (extincties) niet groter is dan het aantal gestichte populaties (kolonisaties), kan de dier- of plantensoort voortbestaan in de regio, ofschoon ze dus lokaal wel uitsterft. Het geheel van alle populaties in het netwerk tezamen heet een metapopulatie. De metapopulatie heeft dus normaliter een veel langere levensduur dan een enkele lokale populatie.

Kolonisten trotseren gevaren om de metapopulatie in balans te houden.

Omdat verbindingen tussen plekken zo'n cruciale rol spelen voor de metapopulatie, ligt het voor de hand om in het kader van het natuurbeheer van metapopulaties corridors zoals ecoducten, faunatunnels en houtwallen aan te leggen. Met name ecoducten, ook wel wild-

viaducten genoemd, zijn in het oog springende, dure bouwwerken die de negatieve, versnip-
perende, effecten van de aanleg van wegen (bijvoorbeeld de A50 door de Veluwe) teniet
moeten doen. Afgezien van de vraag of dat volledig lukt, kan men de vraag stellen wat
de meest geschikte plek in het totale netwerk is voor een corridor. En of er niet andere
maatregelen zijn die veel effectiever zijn, bijvoorbeeld het vergroten van de kwaliteit van het
leefgebied van lokale populaties, of het aanleggen van nieuwe natuurreservaten elders in de
regio. Deze vragen vormden de belangrijkste aanleiding voor dit proefschrift.

Experimenten lijken de beste manier om deze vragen te beantwoorden. Men neme een
versnipperd landschap en kijke welke van de mogelijke maatregelen het beste resultaat geeft.
Helaas is zo'n manipulatie ethisch niet verantwoord, noch praktisch uitvoerbaar. Maar zelfs
als dat wel het geval was, is het resultaat ervan nauwelijks te extrapoleren naar andere situ-
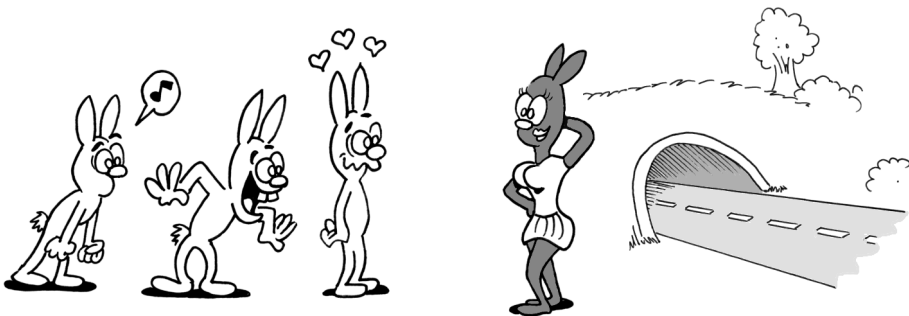aties. Voor zowel de maatschappij als de wetenschap is het daarom van weinig waarde.

Een andere weg is die van wiskundige modellen. In een wiskundig model kan men de
gezamenlijke werking van de belangrijk geachte processen bestuderen. Voor metapopulaties
zijn dat in ieder geval de processen van extinctie en kolonisatie. Met het model, een vereen-
voudigde weergave - wellicht zelfs karikatuur - van de werkelijkheid, kan men ook ex-
perimenteren door het wiskundig te analyseren, of door het simpelweg op een computer te
simuleren. Ethische bezwaren zijn er niet, en de uitvoerbaarheid is "slechts" gelimiteerd door
de kennis van de relevante biologische processen, het wiskundig vernuft en het geheugen en
de snelheid van de computer. Hoewel er kritische kanttekeningen te plaatsen zijn bij de
extrapolatie naar de realiteit, zijn modellen, vanwege hun algemene karakter, voor de weten-
schapper zeer interessant. De primaire waarde van modellen is dan ook heuristisch: het
verschaffen van inzicht in het krachtenspel van de belangrijkste betrokken processen.

In de inleiding van dit proefschrift vat ik alle hoofdstukken samen (zoals hier maar dan
in wetenschappelijk Engels), neem ik ze nog eens kritisch onder de loep en weid ik uit over
mogelijke verdere ontwikkelingen. Alvorens antwoorden op de bovengenoemde vragen met
behulp van modellen te zoeken, probeer ik in de eerste twee delen van dit proefschrift nieuwe
inzichten te krijgen in de metapopulatietheorie. In hoofdstuk 1 (tevens deel 1 van het proef-
schrift) bestudeer ik (als ik "ik" zeg, bedoel ik natuurlijk ook mijn co-auteurs indien van
toepassing!) een typisch academische vraag: gegegeven een hoeveelheid habitat, is het dan
beter voor de metapopulatie deze hoeveelheid in enkele grote of veel kleine plekken te verde-
len? Een grote plek biedt het voordeel dat de kans op lokale extinctie klein is, terwijl een
groot aantal plekken kolonisaties waarschijnlijker maken. Welke van de twee voordelen is
het belangrijkst, of ligt de waarheid in het midden?

De vraag is als zodanig nog niet volledig geformuleerd, omdat nog niet duidelijk is hoe
de plekken ten opzichte van elkaar liggen. In hoofdstuk 1 kies ik ervoor om ze zodanig
te situeren dat de hoeveelheid habitat per oppervlakte-eenheid voor beide gevallen (enkele
grote en vele kleine) even groot is. Dit betekent dat de enkele grote verder van elkaar af
liggen dan de vele kleine; in het eerste geval is kolonisatie dus nog extra moeilijk, omdat
individuen een langere afstand moeten afleggen met alle risico's van dien. Verder is het
van belang wat men onder "beter voor de metapopulatie" verstaat. Ik hanteer twee maten

hiervoor: de tijd tot extinctie van de metapopulatie en een variant op het reproductiegetal R_0. De tijd tot metapopulatie-extinctie is een maat die aangeeft hoe lang een metapopulatie kan overleven. R_0 is de verwachte hoeveelheid nieuwe populaties gesticht door een enkele populatie omringd door alleen onbezette plekken, zolang als de populatie bestaat. Als R_0 groter dan 1 is, kan het aantal populaties groeien. Het getal geeft daarmee aan hoe goed een metapopulatie zich kan herstellen van bijvoorbeeld een strenge winter waarin veel populaties uitgestorven zijn. Het blijkt nu dat met de metapopulatie-extinctietijd als maat een enkele grote plek de beste configuratie is, terwijl met R_0 als maat de beste configuratie vrijwel altijd ergens tussen een enkele grote en heel veel kleine in ligt. Waar precies hangt af van de waarden van de parameters in het model (zoals bijvoorbeeld de gemiddelde afstand die individuen kunnen afleggen), maar is eigenlijk niet zo belangrijk, omdat het hier toch om een heel hypothetisch geval gaat.

Vrijwel iedere theorie heeft zijn lichtend voorbeeld. Voor de metapopulatietheorie is dat het model van Richard Levins, dat centraal staat in deel 2 van dit proefschrift. Levins toonde in 1969 met een heel eenvoudig, maar nog immer bestudeerd, model aan dat het aantal door populaties bezette plekken afhangt van het quotiënt van de extinctie- en kolonisatiesnelheden. Aan ieder model liggen diverse veronderstellingen ten grondslag en het Levins-model is geen uitzondering. Deze veronderstellingen zijn niet altijd even helder geformuleerd. In hoofdstuk 2 behandel ik de veronderstellingen zoals ze in de wetenschappelijke literatuur meestal geformuleerd worden. Ik laat eerst zien dat één daarvan - alle lokale populaties hebben dezelfde grootte - te strikt geformuleerd is. Met een minder strikte veronderstelling - alle populaties hebben dezelfde *kansverdeling* van de grootte - is het Levins-model ook nog op te stellen.

Het rescue effect: immigratie heeft effect op de lokale populatie

Vervolgens laat ik zien welke invloed het aanpassen van twee andere veronderstellingen heeft op het model en de modeluitkomsten. Deze veronderstellingen zijn: 1. immigratie in reeds bezette plekken heeft geen enkel effect, en 2. potentiële kolonisten die hun populatie verlaten om hun heil elders te zoeken hebben geen voorkeur voor bezette of onbezette plekken. Wat de eerste veronderstelling betreft, het effect van immigratie in reeds bezette

plekken zou kunnen zijn dat de populatie groter en genetisch diverser (minder inteelt!) wordt en daardoor minder kans loopt volledig uit sterven. Dit wordt het "*rescue effect*" genoemd. Immigranten redden dus een lokale populatie van de ondergang. Er zijn wel modellen geformuleerd waarin dit *rescue effect* een rol speelt, maar voor zover ik weet, heeft niemand de moeite genomen om te kijken of uit modellen die deze invloed op de lokale populatie expliciet meenemen weer een simpel model als het Levins-model te destilleren is. Dat leek me een gat in de wetenschappelijke markt en het blijkt dat slechts een kleine aanpassing van het Levins-model nodig is.

Wat de tweede veronderstelling betreft, de voorkeur voor bezette of onbezette plekken kan men biologisch verklaren als aantrekking tussen soortgenoten respectievelijk het ontlopen van territoria van soortgenoten. Als men deze voorkeur in het model stopt, dan verandert het Levins-model enigszins. De aanpassingen ten gevolge van de veranderingen van de veronderstellingen hebben gevolgen voor de zogenaamde Levins-regel die uit het Levins-model volgt. Deze luidt: de benodigde hoeveelheid plekken om een metapopulatie in stand te kunnen houden is gelijk aan het aantal lege plekken van een metapopulatie die in evenwicht verkeert (d.w.z. extincties en kolonisaties wegen tegen elkaar op). Als er nu plekken verdwijnen (bijvoorbeeld door vernietiging door de mens), dan geeft de Levins-regel aan tot hoever dit mag gaan om het voortbestaan van de metapopulatie niet in gevaar te brengen: we hoeven namelijk alleen maar het aantal lege plekken te tellen om te weten hoeveel plekken er minstens over moeten blijven. Als het *rescue effect* een rol speelt of als er sprake is van een voorkeur voor bezette plekken, dan leidt het toepassen van de Levins-regel tot het uitsterven van de metapopulatie! Het minimale aantal plekken dat nodig is voor het voortbestaan van de metapopulatie, is in deze gevallen namelijk hoger dan het aantal lege plekken in evenwicht.

In hoofdstuk 3 bespreek ik nog een uitbreiding van het Levins-model, namelijk het Allee-effect, genoemd naar de bioloog Allee. Hij constateerde dat populaties beneden een bepaalde kritische omvang niet kunnen groeien, omdat de leden van de populatie geen partner kunnen vinden, of omdat een grote omvang noodzakelijk is om zich tegen roofdieren te beschermen. Denk bijvoorbeeld aan de strepen van een kudde zebra's. Als ze met veel zijn, is het voor de leeuw met honger moeilijker om uit die brij van zwart en wit een individu te pikken, maar een enkeling heeft hij zo te pakken. Maar met velen is het natuurlijk ook makkelijker om een roofdier te verjagen. In een metapopulatie kan dit Allee-effect een grote rol spelen, omdat er voortdurend nieuwe populaties gesticht worden door meestal maar een klein aantal kolonisten. Een Levins-model met Allee-effect was al eerder in 1998 besproken door een Amerikaanse, Priyanga Amarasekare, maar in dat model zitten mijns inziens een paar schoonheidsfoutjes die redelijk eenvoudig te verhelpen zijn. Hoofdstuk 3 is een reactie op het artikel van Amarasekare (waaruit overigens eens te meer blijkt dat dit proefschrift een verzameling van wetenschappelijke artikelen is) waarin ik die schoonheidsfoutjes aan de kaak stel en een alternatief voorstel dat deze foutjes niet bezit en naar mijn mening meer inzicht geeft in de werking van het Allee-effect.

In hoofdstuk 4 borduur ik voort op het Levins-model. Ik stel daarin een stochastische variant op van het (deterministische) Levins-model. Een stochastisch model gaat uit van de hypothese dat processen (in dit geval extinctie en kolonisatie) kansprocessen zijn. Het model geeft dan als resultaat de kans dat er bijvoorbeeld twee plekken bezet zijn op een bepaalde

tijdstip. Als iedere lokale populatie een keer uitsterft, dan zal de metapopulatie als geheel, ondanks de herkolonisaties, ook ooit eens uitsterven, hoewel de metapopulatie heel lang in een soort van schijnevenwicht kan verkeren. Het ligt dan voor de hand te pogen de verwachte tijd tot metapopulatie-extinctie uit te rekenen. Hoe langer die is, hoe beter, natuurlijk.

Het Allee-effect wordt overwonnen

In hoofdstuk 4 ben ik in het bijzonder geïnteresseerd in hoe metapopulaties reageren op plotselinge veranderingen die de lokale extinctiekans, de kolonisatiekans of het aantal plekken aantasten. Men kan hierbij denken aan verstoring van lokale populaties (lawaai), aanleg van wegen en vernietiging van plekken, maar ook aan het weren van recreatie, aanleg van ecoducten en aanleg van nieuwe natuurreservaten. De metapopulatie wordt dan ruw uit haar schijnevenwicht gebracht en het duurt enige tijd voordat zich een nieuw schijnevenwicht instelt met een nieuwe verwachte metapopulatie-extinctietijd. Wat ik in hoofdstuk 4 laat zien, is dat de reactie van de metapopulatie op veranderingen in de kolonisatiekans meestal het traagst verloopt. Dit heeft onder andere als consequentie dat de fragmentatie van het landschap pas op langere termijn gevolgen heeft, maar dat het herstellen van de oorspronkelijke situatie ook pas op langere termijn effect heeft, en intussen kan de metapopulatie al uitgestorven zijn. Beter is het om het aantal plekken uit te breiden, of om de plekken te vergroten (met als gevolg een lagere extinctiekans van de erin levende populatie die dan namelijk weer kan groeien). Bedenk hier wel bij dat het model een sterk vereenvoudigde weergave van de werkelijkheid is, dus voorzichtigheid blijft geboden, zoals de ervaringen met de Levins-regel uitgewezen hebben.

Deel 3 van het proefschrift poogt de eerder opgeworpen vragen die de belangrijkste aanleiding vormden voor dit proefschrift te beantwoorden, met behulp van een model dat sterk verwant is aan het in hoofdstuk 4 geïntroduceerde stochastische model. In hoofdstuk 5 gebeurt dit in termen van extinctie- en kolonisatiekansen, in hoofdstuk 6 in termen van plekgrootte en afstanden tussen plekken. In beide gevallen bekijk ik 1000 gesimuleerde landschappen van ieder 5 plekken (in hoofdstuk 5 kijk ik ook nog naar een paar gevallen met minder en meer plekken). In hoofdstuk 5 zijn dat abstracte landschappen waarin alleen extinctie- en kolonisatiekansen bestaan. In hoofdstuk 6 beginnen de landschappen al wat

realistischere vormen aan te nemen, omdat alle plekken een bepaalde grootte en bepaalde
coördinaten toegewezen krijgen; de extinctie- en kolonisatiekansen worden gerelateerd aan
de plekgroottes en de onderlinge afstanden. Zo neem ik aan dat de extinctiekans lager is
voor grotere plekken en dat de kolonisatiekans van de ene plek naar de andere hoger is als
de onderlinge afstand kleiner is en de plekken groter zijn. Formules bepalen die relaties
exact. Voor de 1000 gesimuleerde landschappen bereken ik de metapopulatie-extinctietijd
en in hoofdstuk 6 tevens het reproductiegetal R_0 voor en na het veranderen van de configu-
ratie (in hoofdstuk 5 verander ik dus de extinctie- en kolonisatiekansen, en in hoofdstuk 6 de
plekgroottes en onderlinge afstanden).

   Uit de resultaten voor al deze landschappen probeer ik tendensen te ontdekken. De con-
clusies van hoofdstuk 5 luiden als volgt.

1. Het is voor het bevorderen van het voortbestaan van de metapopulatie in het algemeen
   beter om de extinctiekansen van de plekken te verlagen dan de kolonisatiekansen te ver-
   hogen.
2. Bij het verlagen van de extinctiekans gaat de voorkeur uit naar de populatie die al de
   laagste extinctiekans heeft.
3. Bij het verhogen van de kolonisatiekans gaat de voorkeur uit naar de kolonisatiekans
   tussen de populaties met de laagste extinctiekansen.

Deze twee laatste conclusies *suggereren* dat het het beste is om de grootste plek te vergroten
en om de effectieve afstand tussen de grootste plekken te verkleinen (door bijvoorbeeld een
ecoduct aan te leggen).

   In hoofdstuk 6, waarin deze suggesties nader onderzocht worden, blijkt dit maar ten dele
waar. Inderdaad is het verbeteren van de verbinding tussen de grootste plekken het meest te
prefereren, maar het vergroten van de grootste plek heeft alleen maar de beste papieren, als
we kijken naar relatieve vergrotingen. Met andere woorden, als we iedere plek om de beurt
met bijvoorbeeld 10% vergroten, dan heeft dat wel de grootste gevolgen bij de grootste plek,
maar als we iedere plek om de beurt met bijvoorbeeld 1 ha vergroten, dan zijn de gevolgen
het grootst bij het vergroten van de kleinste plek. Dat wil zeggen, over het algemeen. Dit
geldt lang niet altijd voor alle 1000 landschappen en het hangt sterk af van de formules
die de relaties aangeven tussen extinctie- en kolonisatiekansen enerzijds en plekgrootte en
onderlinge afstand anderzijds. Hier moet ook nog eens benadrukt worden, dat economische
afwegingen buiten beschouwing gelaten zijn. Wellicht is het veel duurder om kleine plekken
met 1 ha te vergroten dan om grote plekken nog 1 ha groter te maken. Dan zou de balans
wel weer eens in het voordeel van de grootste plek kunnen doorslaan. Dit verdient dus zeker
nader onderzoek.

   In het vierde en laatste deel van dit proefschrift gebruik ik stochastische modellen voor
voorspellingen voor twee specifieke situaties. In hoofdstuk 7 bestudeer ik het effect van het
weer in gebruik nemen van een spoorlijn in Limburg, bijgenaamd de IJzeren Rijn, op de
metapopulaties van twee amfibieën, de kamsalamander en de rugstreeppad. Dit is een klein
onderdeel van een grote studie van het onderzoeksinstituut Alterra naar het effect van de
IJzeren Rijn. In hoofdstuk 8 illustreer ik een nieuwe methode om modelparameters uit data

te schatten, de Bayesiaanse methode, aan de hand van data van de boomkikkermetapopulatie in Zeeland.

Voor het in hergebruik nemen van de IJzeren Rijn zijn verschillende scenario's voorgesteld, inclusief andere trajecten. Doel is te weten te komen welk scenario de minst ernstige gevolgen voor de beide amfibieën heeft. Een model kan daarbij helpen. Een model moet echter geparametriseerd worden; in dit geval betekent dat dat ik waarden moest weten voor de extinctie- en kolonisatiekansen. Omdat er nauwelijks data beschikbaar zijn in deze situatie, moest ik terugvallen op expertkennis. De schattingen die hieruit volgen, zijn natuurlijk vergeven van onzekerheden. Daarom gebruik ik in hoofdstuk 7 een onzekerheidsanalyse van de modelvoorspellingen, die niet alleen aangeeft hoe groot de onzekerheid is in het effect op de metapopulatie, maar ook informatie geeft over de belangrijkste bronnen van onzekerheid. Een inherente bron van onzekerheid in een stochastisch model is dit stochastische karakter zelf. Onzekerheid over de toekomstige omstandigheden (bijvoorbeeld het weer, bosbrand, geboorte- en sterftecijfer) waarin het systeem zich zal bevinden, zit in dit stochastische karakter besloten. Een andere bron van onzekerheid is onze beperkte kennis over hoe de lokale populaties op deze toekomstige omstandigheden zullen reageren. In het model geven de extinctie- en kolonisatiekansen aan hoe sterk ze hierop reageren, maar die kansen weten we dus niet zeker. Een derde bron van onzekerheid is onze beperkte kennis over hoe de verschillende scenario's deze extinctie- en kolonisatiekansen beïnvloeden. In de onzekerheidsanalyse blijkt dat de eerste twee bronnen *gezamenlijk* voor de grootste bijdrage aan de onzekerheid zorgen. Met gezamenlijk bedoel ik dat meer informatie (zekerheid) over slechts één van de twee bronnen meestal niet zoveel meer zekerheid oplevert voor de modelvoorspellingen; we moeten over beide bronnen meer zekerheid hebben.

De Bayesiaanse methode om informatie uit data te halen is sterk in opmars. De methode gaat uit van een vooronderstelling over de mogelijke waarden van modelparameters. Zo'n vooronderstelling zegt bijvoorbeeld dat een parameter, zoals de dispersieafstand, niet negatief kan zijn, en dat het zeer onwaarschijnlijk is dat de waarde ervan meer dan, zeg, 5 km bedraagt. Dit wordt de *prior* genoemd. Dan wordt deze vooronderstelling bijgesteld aan de hand van de beschikbare data, en hebben we een soort van naonderstelling die de *posterior* genoemd wordt. Als meer en andere data beschikbaar komen, zou deze posterior dan weer als prior voor een nieuwe analyse dienst kunnen doen. De data die geschikt zijn voor het type model dat ik gebruik, zijn gegevens over het al dan niet aanwezig zijn van een populatie in ieder van de plekken van een metapopulatie gedurende een aantal jaren. Als aanwezigheid in een plek in het ene jaar gevolgd wordt door afwezigheid in het volgende jaar, dan is er sprake van een extinctie en het omgekeerde geeft een kolonisatie aan. Er bestond al een Bayesiaanse methode om uit overgangen van het ene naar het andere jaar (de extincties en kolonisaties dus, maar ook de niet-extincties en de niet-kolonisaties) informatie te halen over de model- parameters, maar deze methode benut niet alle informatie in de data. Er zit namelijk ook veel informatie in het eerste jaar van de data; deze geeft het resultaat van de extincties en kolonisaties in de vele jaren ervoor (die we dus niet weten). De Bayesiaanse methode van hoofdstuk 8 maakt het mogelijk om te doen alsof deze jaren er wel zijn door hiervoor wat in te vullen. Helemaal willekeurig gebeurt dat natuurlijk niet, want de verzonnen jaren mogen geen informatie bevatten. Met deze truc is het nu wel mogelijk de data van het eerste jaar

volledig te benutten, en bij de voorbeelddataset van de boomkikker in Zeeland blijkt ook dat deze methode verschillen geeft met de methode waarin alleen de informatie van overgangen wordt gebruikt. Verder is de methode een stuk sneller dan de al bestaande methode. Bij rekentijden in de orde van een dag is dat natuurlijk zeer welkom.

Op de vragen die de aanleiding vormden voor dit proefschrift heb ik met dit proefschrift nieuw licht willen werpen. In het natuurbeheer zou de aandacht meer moeten verschuiven van ecoducten en de Ecologische Hoofdstructuur naar lokale kwaliteit van leefgebieden, maar dan wel die leefgebieden waarbij een kwaliteitsverbetering het grootste effect voor het metapopulatienetwerk heeft. Dat kan zowel het kleinste (lees: kwalitatief slechtste) als het grootste gebied (lees: kwalitatief beste) zijn of iets ertussenin, afhankelijk van of eenzelfde kwaliteitsverbetering voor kleine en grote gebieden evenveel (moeite) kost. Definitief uitsluitsel over wat de optimale strategie is, kan dus pas gegeven worden als duidelijk is hoe een en ander economisch uitwerkt. Met andere woorden: hoeveel kun je de kwaliteit van de lokale leefgebieden verbeteren met de miljoenen die je anders voor een ecoduct nodig hebt? Als we hierop het antwoord weten, kunnen we beoordelen of we onze euro in ecoducten of in lokale kwaliteit moeten investeren, en welk ecoduct of welke plek dan de voorkeur geniet.

Conclusies gebaseerd op dit proefschrift of een economische extensie daarvan bieden geen garantie op een optimale toepassing in reële situaties waarin andere factoren dan gemodelleerd in dit proefschrift van belang zijn. Enkele van deze factoren zijn interacties tussen dier- en/of plantensoorten, de aanwezigheid van besmettelijke ziekten, en correlaties tussen extincties (het tegelijkertijd uitsterven van populaties door een gemeenschappelijke oorzaak, bijvoorbeeld een strenge winter). De rol van de wetenschapper is dus nog niet uitgespeeld.

Dankwoord

Allereerst wil ik iedereen bedanken die tenminste de samenvatting van dit proefschrift heeft doorgelezen. Want voor hen heb ik dit boekje geschreven. En voor mijzelf. Wetenschap bedrijven is tenslotte egotripperij.

Dat neemt niet weg dat gezamenlijk wetenschap bedrijven heel prettig is. Daarvoor ben ik mijn co-auteurs van de hoofdstukken in dit proefschrift zeer erkentelijk. Cajo, Claire, Hans, Kees, Lia, Marjolein en Michiel, ik heb met veel plezier met jullie samengewerkt en veel van jullie geleerd. Cajo, als we het alleen hadden moeten doen, was het waarschijnlijk nooit gelukt; bedankt voor je niet aflatende ijver. Claire, ik weet nog steeds niet veel over padden en salamanders, maar ik weet nu wel wie ik erover moet raadplegen! Kees, bedankt voor de e-maildiscussies en de leuke anekdotes tussendoor. Hans, jij komt later nog aan bod. Lia, bedankt voor je steun, vooral in de laatste fase en voor de vele gezellige bijeenkomsten. Marjolein, jij hebt me aan het denken gezet, een prestatie op zich. Michiel, er is geen onzekerheid over jouw kennis; dank je dat je steeds bereid was deze met me te delen.

Ik ben ook de co-auteurs van de stukken die niet in dit proefschrift zijn gekomen, veel dank verschuldigd. Breg, Jim, Petra en nogmaals Lia, we hebben aangetoond dat gezelligheid en wetenschap hand in hand kunnen gaan. Breg, ik heb grote bewondering voor je enorme kennis en werklust, maar ik waardeer vooral ook je vriendschap en je steun bij de laatste lay-outloodjes, terwijl je het zelf zo druk had. Ik hoop dat we nog lang zullen samenwerken en pannenkoeken eten met Erik en Heleen. Jim, thanks for your hospitality during my visit to Logan and for introducing me to some of your colleagues. You led me into the world of Matlab and I haven't left it since. Petra, hoewel onze samenwerking beperkt was, waren je opmerkingen steeds weer nuttig. Je liet altijd een frisse wind waaien, en niet alleen op het wetenschappelijke vlak. Lia, laat ik niet vergeten je voor de heerlijke koppen soep te bedanken! Hopelijk volgen er nog veel meer.

Zonder collega's had ik dit proefschrift waarschijnlijk ook geschreven, maar was het lang niet zo leuk geweest. Ik wil toch wat namen in het bijzonder noemen: Marco, Margriet, Martin, Saskia en Wies, jullie waren altijd in voor een praatje en stonden ook klaar als ik een vraag voor mijn proefschrift had. Dat gold ook voor een collega in wat ruimere zin: Jana, jij hebt me altijd weer nieuw gedachtevoedsel gegeven en me in contact gebracht met interessante mensen. Dat heb ik altijd zeer gewaardeerd.

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dank in woorden uit te drukken. In ieder geval in mijn geval. Ik ben echter, net als jij Hans, eigenwijs en doe toch een poging. Je hebt me vooral ruimte en mogelijkheden geboden. Je hebt me altijd vertrouwen gegeven. Je hebt me mensen laten ontmoeten. En je hebt me altijd constructieve kritiek gegeven, en de puntjes op de i gezet, of juist aangegeven waar de puntjes verwijderd moesten worden. Heel veel dank daarvoor.

Als er iemand is die ervoor gezorgd heeft dat tenminste mijn samenvatting gelezen wordt, dan ben jij het wel, Mathijs. Jouw komische illustraties zijn voor mij volwaardig onderdeel van dit proefschrift. Ik ben je ook reuze dankbaar voor de snelheid waarmee je leverde, terwijl dat allerminst ten koste ging van de kwaliteit.

Denise, jouw bijdrage is uiteindelijk minder tastbaar geworden dan je had gewild, maar ik denk dat ik zonder jou nog steeds over een titel zou nadenken. Ik hoop dat het toch naar je zin geworden is.

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Ik ben vast iemand vergeten. Lees dan alsjeblieft de samenvatting, dan heb ik je hierboven toch bedankt.

Curriculum vitae

Ik, Rampal Stefan Etienne, werd op 30 april 1971 geboren in het toenmalige Beatrixziekenhuis (nu verpleeghuis) te Culemborg als eerste van een tweeling. Mijn voorbereidend wetenschappelijk onderwijs had plaats op het ook in Culemborg gevestigde Koningin Wilhelmina College, en na afronding daarvan in 1989 nog een jaar op de Salisbury High School in Allentown, PA, Verenigde Staten. Bij terugkeer in Nederland in 1990 startte ik mijn natuurkundestudie aan de Universiteit Utrecht die ik begin 1996 met lof afsloot in de afstudeerrichting grondslagen van de natuurkunde met een scriptie over het kosmologische horizonprobleem. Inmiddels, in een zoektocht naar een wat meer maatschappelijk relevante studie, was ik in 1993 begonnen met de bovenbouwstudie natuurwetenschappelijke milieukunde aan de Katholieke Universiteit Nijmegen. Na onderzoek in stiltegebieden bij de Wetenschapswinkel Natuurkunde te Utrecht en aan onzekerheden in een milieumodel voor de verspreiding van (vluchtige) stoffen bij het Rijksinstituut voor Volksgezondheid en Milieu in Bilthoven mocht ik begin 1997 met lof mijn doctoraalbul in ontvangst nemen. Ik bleef nog een jaar bij de vakgroep Milieukunde in Nijmegen als toegevoegd docent werken aan het onderwijs in milieumodellen. Nog steeds geïntrigeerd door de filosofische aspecten van het natuurwetenschappelijk onderzoek (en om financiële redenen) had ik me eind 1996 ingeschreven voor de studie filosofie van de exacte natuurwetenschappen aan de Universiteit Utrecht, een aanvulling op de grondslagen van de natuurkunde, die ik in 1999, vlak voor mijn huwelijk met Heleen Laan, met lof wist te beëindigen. Intussen was ik in 1998 aangenomen als assistent-in-opleiding bij het Centrum voor Biometrie, nu Biometris, te Wageningen om het promotieonderzoek te verrichten waarvan het resultaat in de pagina's hiervoor beschreven is. Behalve aan dit onderzoek werkte ik ook, samen met Bregje Wertheim, Lia Hemerik, Petra Schneider (allen Wageningen Universiteit) en Jim Powell (Utah State University, Logan, Utah, Verenigde Staten), aan het modelleren van de populatiedynamica van fruitvliegjes, onderdeel van de promotie van Bregje Wertheim waarbij ik op 1 oktober 2001 als paranimf mocht optreden. Tijdens mijn promotieonderzoek werd ik veelvuldig in de gelegenheid gesteld mijn wetenschappelijke kennis en netwerk uit te breiden in veelal buitenlandse bezoeken aan symposia, workshops en conferenties en twee werkbezoeken (aan Jim Powell in de Verenigde Staten en aan de groepen van Ilkka Hanski en Mats Gyllenberg in Finland).

Stellingen
Propositions

1.
Het is ongepast voor jonge mensen om adagia te uiten.
It is unbecoming for young men to utter maxims.
ARISTOTELES

2.
Een metapopulatie is als een harde schijf: het is beter om uit te breiden dan om te defragmenteren.
A metapopulation is like a hard disk: it is better to expand than to defragment.
DIT PROEFSCHRIFT - THIS THESIS

3.
Stochastische modellen zeggen minstens zoveel over onze onzekerheid over een systeem als over het systeem zelf.
Stochastic models tell us at least as much about our uncertainty about a system as about the system itself.
DIT PROEFSCHRIFT - THIS THESIS

4.
Seksuele aantrekking is nadelig voor het voortbestaan.
Sexual attraction is disadvantageous for survival.
DIT PROEFSCHRIFT - THIS THESIS

5.
Wetenschap is als seks: soms komt er iets nuttigs uit, maar dat is niet de reden waarom we het doen.
Science is like sex: sometimes something useful comes out, but that is not the reason we are doing it.
RICHARD FEYNMAN

6.
Als het menselijk brein zo simpel was dat we het konden begrijpen, dan zouden wij zo simpel zijn dat we dat niet konden.
If the human brain were so simple that we could understand it, we would be so simple that we couldn't.

7.

Het is makkelijker om voor je principes op te komen dan ernaar te leven.
It is easier to fight for one's principles than to live up to them.

8.

Wie een ander het licht in de ogen misgunt, heeft zelf het licht niet gezien.
He who begrudges someone the light in the eyes, has not seen the light himself.

9.

Een gewaarschuwd mens telt tot twee.
A warned person counts till two.

10.

Als twee honden vechten om een been, loopt de derde er met een boog omheen.
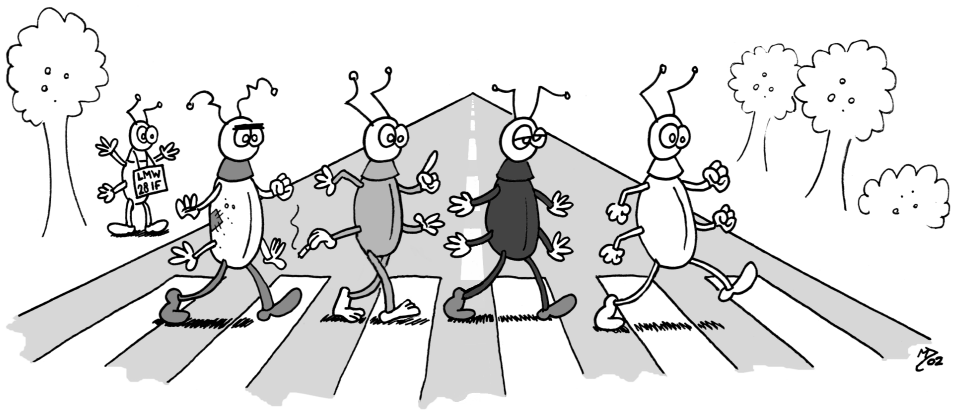*When two dogs are fighting for a bone, the third dog avoids the fighting zone*.

11.

Sinds 1 januari heeft de uitdrukking "met gelijke munt betalen" een vredelievende betekenis gekregen.
Since January 1, the Dutch proverb "paying with the same coin" has got a peaceful meaning.

Corridors raise the probability of beetle survival