Research article

The viability of metapopulations: individual dispersal behaviour matters

Simone K. Heinz[1,2,*], Christian Wissel[1] and Karin Frank[1]

[1]*UFZ – Centre for Environmental Research Leipzig Halle, Department of Ecological Modelling, P.O. Box 500136, D-04301 Leipzig, Germany;* [2]*Department of Biology, University of Bergen, Thormøhlensgt. 55, 5200 Bergen, Norway;* *Author for correspondence (e-mail: simone.heinz@bio.uib.no)*

Abstract

Metapopulation models are frequently used for analysing species–landscape interactions and their effect on structure and dynamic of populations in fragmented landscapes. They especially support a better understanding of the viability of metapopulations. In such models, the processes determining metapopulation viability are often modelled in a simple way. Animals' dispersal between habitat fragments is mostly taken into account by using a simple dispersal function that assumes the underlying process of dispersal to be random movement. Species-specific dispersal behaviour such as a systematic search for habitat patches is likely to influence the viability of a metapopulation. Using a model for metapopulation viability analysis, we investigate whether such specific dispersal behaviour affects the predictions of ranking orders among alternative landscape configurations rated regarding their ability to carry viable metapopulations. To incorporate dispersal behaviour in the model, we use a submodel for the colonisation rates which allows different movement patterns to be considered (uncorrelated random walk, correlated random walk with various degrees of correlation, and loops). For each movement pattern, the landscape order is determined by comparing the resulting mean metapopulation lifetime T_m of different landscape configurations. Results show that landscape orders can change considerably between different movement patterns. We analyse whether and under what circumstances dispersal behaviour influences the ranking orders of landscapes. We find that the 'competition between patches for migrants' – i.e. the fact that dispersers immigrating into one patch are not longer available as colonisers for other patches – is an important factor driving the change in landscape ranks. The implications of our results for metapopulation modelling, planning and conservation are discussed.

Introduction

Assessing fragmented landscapes regarding their ability to maintain viable metapopulations is complex (Hanski and Ovaskainen 2000; Etienne and Heesterbeck 2001; Frank and Wissel 2002). Metapopulation models are increasingly used to address this task (review by Verboom et al. 1993; Hanski 1999). Models can hardly give exact quantitative predictions, but by comparing alternative landscape configurations they can give qualitative assessments of which configuration would be the most favourable for metapopulation viability. Such an analysis can give ranking orders of landscapes that can be used as aids for decision support in landscape planning and conservation practice (Lindenmayer and Possingham 1996; Drechsler 2000; Possingham et al. 2000).

In order to avoid too much model complexity, the processes that determine metapopulation viability are often modelled in a simple way. Animals' dispersal between habitat fragments is mostly taken into account by using a simple exponential dispersal function that assumes the underlying process of dispersal to be random movement (Fahrig 1992; Adler and Nuernberger 1994; Hanski 1994; Vos et al. 2001; Frank and Wissel 2002). Species-specific dispersal behaviour, such as the orientation of animals along landscape structures (Merriam 1991; Haddad 1999), the ability to move straight to another patch due to a large perceptual range (Zollner and Lima 1997, 1999), or the systematic search for patches with a specific movement pattern (Conradt et al. 2000, 2001) can therefore be considered only roughly. Such more complex dispersal behaviours can affect dispersal success and exchange rates between patches (Cain 1985; Zollner and Lima 1999; King and With 2002; Conradt et al. 2003, Heinz et al. 2005) and can therefore influence the viability of a metapopulation considered. However, it is not yet clear whether and how the dispersal behaviour affects the prediction of ranking orders resulting from comparing different landscape configurations regarding their effect on metapopulation viability. Is it possible that a landscape is assessed as the more favourable of two landscapes assuming one type of underlying dispersal behaviour, but as the less favourable if the underlying dispersal behaviour is different?

This paper addresses these questions by comparing metapopulation viability in different landscape configurations, where different underlying dispersal behaviours are taken into account. This is done by using a model for metapopulation viability analysis devised by Frank and Wissel (1998). Metapopulation viability is measured in terms of the mean lifetime T_m (also called intrinsic mean time to extinction (Grimm and Wissel 2004)). Landscape ranks are determined by comparing the T_m-values for the different landscape configurations considered. To incorporate dispersal behaviour in the model, we use a submodel for the colonisation rates which utilises a previously published simple formula for the accessibility of patches (Heinz et al. 2005) and allows different movement patterns to be considered. We focus on simple movement patterns, such as random walk and correlated random walk, as well as a more complex pattern observed in nature – the loop-like movement pattern found for a variety of animals (Hoffmann 1983; Müller and Wehner 1994; Durier and Rivault 1999; Conradt et al. 2000, 2001). We analyse whether and under what circumstances dispersal behaviour influences the ranking orders of landscapes. We discuss implications for metapopulation modelling, planning and conservation.

Methods

The metapopulation model

The viability analysis in this study is based on the patch-based, stochastic metapopulation model by Frank and Wissel (1998, 2002); see also Ovaskainen (2002). This model is a time-continuous Markov chain model that considers finite metapopulations with N patches. Each patch is assumed to be either occupied ($x_i = 1$) or empty ($x_i = 0$). The state of the whole metapopulation ($x_1,...,x_N$) is given by a vector of the states x_i of the individual patches. Changes in this state can be the result of extinction or recolonisation processes: The subpopulation in a currently occupied patch i will go extinct with rate ex_i, while it will colonise an (empty or occupied) patch j with rate b_{ij}. A currently empty patch i will become recolonised with rate $\sum_{j:xj=1} b_{ji}$ where the sum is taken over all patches j currently occupied.

When running this model, one always finds the following typical behaviour: the metapopulation either very quickly goes extinct or approaches quasi-stationarity. Quasi-stationarity means that the metapopulation shows typical fluctuations in the occupancy patterns before it goes extinct, while extinction occurs with a constant probability per time λ (e.g., Darroch and Senata 1965; Keilson 1979; Wissel and Stöcker 1991; Pollett 1997). Here, we exclusively focus on quasi-stationary metapopulations. Their viability is measured in terms of the mean lifetime $T_m = 1/\lambda$ (also called intrinsic mean time to extinction) that is given by the reciprocal value of the overall extinction rate λ. This quantity is known be an adequate currency for assessing the viability of quasi-stationary metapopulations and can be extracted from simulation data (Frank and Wissel 1998; Grimm and Wissel 2004).

Specification of the model parameters

The model allows the effect of species–landscape interactions on metapopulation viability to be analysed, provided its parameters are appropriately specified.

Extinction rate

In order to avoid an overloading of the study with too many details, we assume patches to be identical. Consequently, we work with an equal rate of local extinctions for all patches ($ex_i = ex = 0.1$).

Colonisation rate

The colonisation rate b_{ij} with which patch i colonises patch j is described as a product of three factors: (i) the mean number of emigrants E_i leaving the occupied patch i per year, (ii) the probability of an emigrant starting from patch i reaching patch j ('patch accessibility' r_{ij}), and (iii) the number of emigrants I_j needed on patch j to establish a new subpopulation with probability of success of 0.5.

The colonisation rates are therefore calculated as follows:

$$b_{ij} = E_i * r_{ij} * \frac{0.5}{I_j} \qquad (1)$$

To understand the functional structure of the submodel, note that the ratio $\frac{E_i r_{ij}}{I_j}$ gives the total number of immigrants from patch i into patch j measured in units of I_j. Each of these 'colonisation units' has a probability of success of 0.5. Hence, the overall term (1) gives the mean number of successful colonisations per time.

Since we assumed patches to be identical, we kept the number of emigrants E_i and the number of immigrants I_j equal for all patches. This enables equation (1) to be simplified to $b_{ij} = E * r_{ij} * \frac{0.5}{I}$. The values used for E and I are contained in Table 1. The patch accessibility r_{ij} allows individual movement behaviour and the competition between patches to be taken into account (see section below).

A formula for calculating patch accessibility for different underlying movement patterns. The movement behaviour of the individuals acts on the patch accessibility r_{ij}. Most metapopulation models assume a simple exponential dependence of the patch accessibilities r_{ij} on the inter-patch distances d_{ij}. Using an individual-based simulation model

Table 1. The parameters needed to calculate local extinction, correlated extinction, colonisation rates and the patch accessibility included in the colonisation rates.

Process	Parameter determining the process	
Local extinction	Rate of extinction $ex_i = ex$	0.1
Colonisation rates	$E_i = E$	10
	$I_j = I$	3
Parameter a and b for patch accessibility of different movement patterns	Uncorrelated random walk:	
	a	2.149
	b	0.076
	r^2	0.985
	Fairly correlated random walk:	
	a	0.796
	b	0.025
	r^2	0.974
	Correlated random walk:	
	a	0.580
	b	0.091
	r^2	0.906
	Loops:	
	a	5.840
	b	0.075
	r^2	0.999

for movements in patchy landscapes, Heinz et al. (2005) found a simple exponential function to be unable to describe the functional relationship between patch accessibility and the landscape structure in an adequate way. This is especially the case if other movement patterns than random walk are considered and the individuals are assumed to stay at the first patch they reach. They also revealed that, in these more complex cases, the patch accessibilities r_{ij} can be approximated by the following formula:

$$r_{ij} = W_{ij} R(d_{ij}) \qquad (2)$$

where

$$W_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_{k(\neq i)} (d_{ik})^{N-1}} \qquad (3)$$

and

$$R(d) = 1 - e^{-ae^{(-bd)}} \qquad (4)$$

The function $R(d)$ (equation (4)) gives the potential patch accessibility in a landscape with two

patches (start and target patch) only by considering the distance d between them. Its shape is determined by the individual movement pattern. For the range of movement patterns considered, negative exponential and sigmoidal shapes were found to be typical. The double-exponential structure of function $R(d)$ is flexible enough to cover both exponential and sigmoidal shapes while it is at the same time structurally simple (Heinz et al. 2005). In a landscape with more than two patches, emigrants intercepted by one patch cannot reach another one (assuming that the migrants stay on the first patch they reach (Hein et al. 2004; Heinz et al. 2005)). This induces a 'competition' between patches for emigrants. This competition is described by the weighting factor W_{ij} (equation (3)). The weighting factor is completely expressed in terms of the potential patch accessibility function $R(d)$ and a power given by the number N of patches in the landscape. This weighting factor accounts for the fact that the competition strengths of patches depend on the relationship of the potential accessibility of patch j, $R(d_{ij})$, with the potential accessibilities of all patches k, $R(d_{ik})$, in the landscape. The overall patch accessibility formula (equation (2)) is completely expressed in terms of the distances from the start-patch i to all other patches k and two function parameters, a and b, which subsume all the relevant effects of the individuals' movement behaviour.

Heinz et al. (2005) compared the resulting patch accessibility of this formula with the results of their simulation model where the patch accessibility was simulated for different movement patterns in varying landscape configurations. This comparison showed that the formula has a high predictive power for a wide range of movement patterns and patchy landscapes. Therefore, we decided to use this formula as a submodel for the patch accessibilities r_{ij} as an integrative part of the submodel (1) for the colonisation rates b_{ij}. In this way, the overall metapopulation model can be kept simple, but the individuals' movement behaviour can be incorporated in an adequate way.

The movement patterns. The movement patterns investigated were uncorrelated random walk, fairly correlated random walk, strongly correlated random walk, and loops. For the loop-like pattern (Hoffmann 1983; Bell 1985; Müller and Wehner 1994; Durier and Rivault 1999; Conradt et al. 2000, 2001), the individuals move away from the start point, returning to it on a different path. The next loop is started in another direction, creating a petal-like path. The size of the loops increases with their number, and so the radius searched increases. The parameters a and b of the formula were obtained by simulating the movement patterns in random two-patch landscapes with the individual-based simulation model by Heinz et al. (2005), measuring the resulting $R(d)$ fitting equation (4) to it. The a and b values resulting for the different movement patterns considered and the corresponding r^2 values are listed in Table 1, an example of the simulated movement patterns is shown in Figure 1. For more information about the fitting procedure, see Heinz et al. (2005) for a thorough analysis of the relationship between a and b and the movement parameters see Heinz 2004.
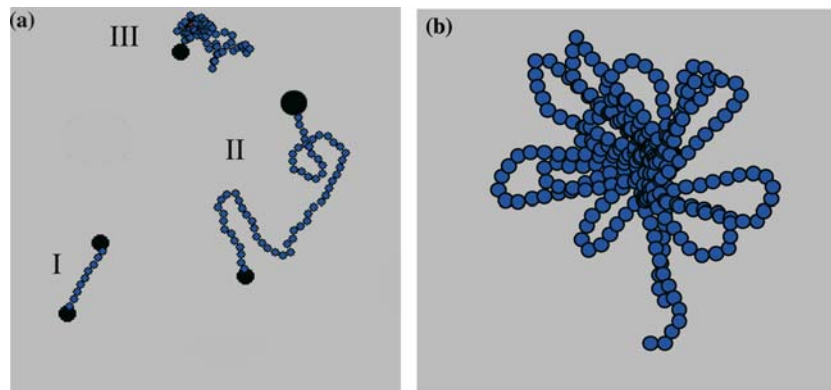

Figure 1. Examples for different movement patterns. (a) Random walk with three different degrees of correlation: strongly correlated, fairly correlated and uncorrelated. (b) Loop-like movement pattern.

Experiments

In the two first experiments (see Sections 'Does behaviour matter' and 'Why behaviour matters'), we used randomly generated landscapes. For this, the *x*- and *y*-coordinates of patches were randomly taken from 100 uniformly distributed values. In the third experiment, landscapes were generated systematically (see description in 'Gaining understanding: how competition between patches acts').

From the resulting patch positions we calculated inter-patch distances (measured between patch centres). These distances were used to calculate the patch accessibilities r_{ij} (using equations 2–4) and the corresponding colonisation rates b_{ij} (equation 1) for the movement patterns considered. The resulting matrix of colonisation rates b_{ij} was inserted in the metapopulation model and the mean lifetime T_m obtained. We started with a fully occupied metapopulation. However, since the mean lifetime T_m summarises all effects of the quasi-stationary phase, it is independent of the initial state.

Results

Does behaviour matter?

The aim of this study is to understand how the individual dispersal behaviour affects the viability of metapopulations with respect to relative ranking orders between T_m-values in varieties of alternative landscape configurations. In order to obtain an initial answer, we generate 10 random landscape configurations with 9 patches by way of an example (Figure 2). The resulting mean lifetime T_m is plotted for every landscape and every movement pattern (Figure 3). The absolute values of T_m for a particular landscape vary among the different movement patterns. This quantitative effect of behaviour is not surprising. By comparing T_m-values for the different landscapes, we find that ranking orders also differ among movement patterns. A landscape where this is particularly obvious is Landscape 9. Assuming 'Loops' and 'Fairly correlated walk' as underlying movement patterns, this landscape has a low T_m-value and hence one of the lowest ranks. Yet considering 'Uncorrelated random walk' or 'Strongly correlated random walk', Landscape 9 has the highest T_m-value of all the landscapes and the highest rank. Another

extreme example of different landscape ranks is Landscape 4. Although this landscape has a low rank for 'Loops', 'Fairly correlated random walk' and 'Uncorrelated random walk', it has a comparatively high rank for 'Strongly correlated random walk'.

The fewest differences between ranking orders can be found when 'Loops' and 'Fairly correlated random walk' are compared. Yet even here landscape orders change considerably. If we consider 'Loops' as underlying movement behaviour, the T_m-value and the rank of Landscape 2 are lower than for Landscapes 3, 5 and 7, while for 'Fairly correlated random walk' the opposite is true. Note that differences between landscapes in the absolute T_m-values are not as high as in the more drastic examples. Nevertheless, ranking orders vary.

Although these results are merely based on few examples, they bring an important problem to light: They indicate that individual dispersal behaviour can markedly influence relative results on T_m for varieties of different landscapes. The latter result has serious implications for theory and conservation (see Discussion) since relative results such as ranking orders and trends are important aids for decision-making. Therefore, there is an urgent need to fully understand the effect of behaviour on the ranking orders between different landscapes.

Why behaviour matters

Below, we intend to derive a hypothesis concerning why individual dispersal behaviour changes landscape ranks. With our settings ($ex_i = ex$, $b_{ij} = \frac{0.5E}{T} r_{ij}$), T_m is exclusively influenced by landscape structure and individual behaviour via patch accessibility r_{ij}. Equation (2) says that r_{ij} consists of two components: the potential patch accessibility $R(d_{ij})$ (equation (4)) and the weighting factor W_{ij} (equation (3)) accounting for the competition between patches for migrants (see Section 'A formula for calculating patch accessibility for different underlying movement patterns'). Both components can be responsible for the change in the landscape rank.

To test whether the competition between patches causes a change in landscape ranks, we repeat the same experiment as before using the 10 landscapes of the first experiment (Figure 2),
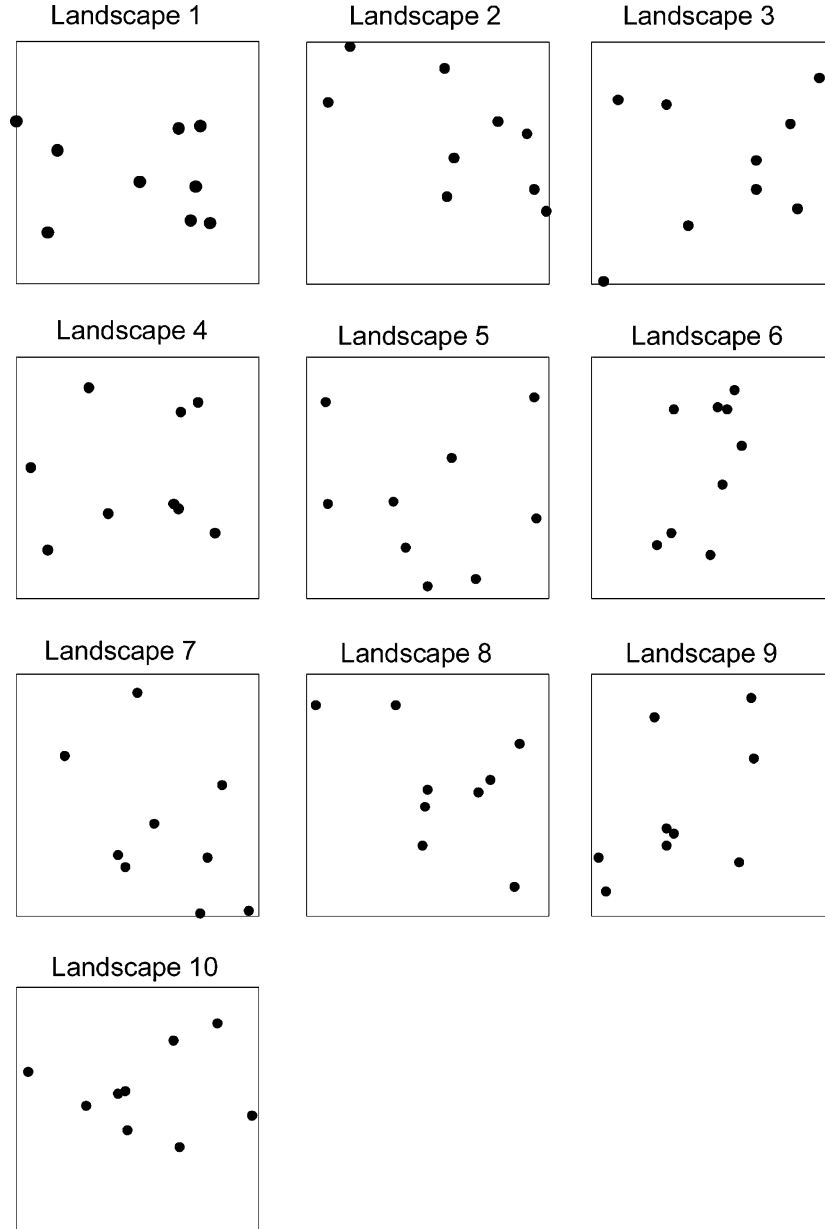
Figure 2. The 10 randomly generated landscapes used for the analysis.

but modifying formula (2) for patch accessibility such that the competition between patches is ignored, i.e., $r_{ij} = R(d_{ij})$ as is the case in many metapopulation models (Fahrig 1992; Adler and Nuernberger 1994; Vos et al. 2001). We therefore calculate the patch accessibility r_{ij} by using the potential accessibility function (equation (4)).

The resulting mean lifetimes T_m of all landscape configurations and movement patterns for the competition-free case are shown in Figure 4. As before, the absolute T_m-values for a particular landscape are affected by a change in the movement patterns. The ranking orders in the T_m-values between the different landscapes, however, are
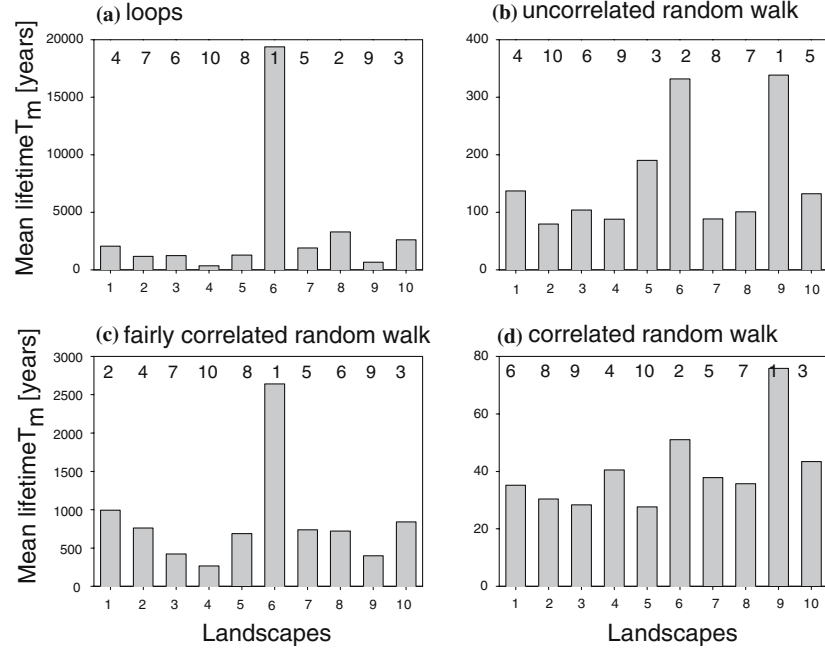
Figure 3. The mean metapopulation lifetime T_m for metapopulations in 10 different randomly generated landscape configurations calculated assuming different underlying individual dispersal behaviours: (a) loop-like behaviour, (b) uncorrelated random walk, (c) fairly correlated random walk, (d) correlated random walk. The numbers on the top indicate the landscape ranks.

almost the same for all underlying dispersal behaviours. A change occurs only between patch 1 and 8 which have almost similar T_m-values, but all the other ranks stay the same. Without competition between patches, dispersal behaviour seems to have almost no effect on the landscape ranks. This gives rise to the hypothesis that the competition effect is responsible for the change in ranking orders.

Gaining understanding: how competition between patches acts

To systematically gain a mechanistic understanding of the effect of landscape structure and individual behaviour on metapopulation viability and the role of the competition effect in this context, we perform an experiment with a hypothetical landscape consisting of five patches. We change the position of just one patch (Figure 5a) by gradually moving patch 1 towards patch 2. The corresponding patch accessibilities r_{ij} are calculated in two different ways: (i) without competition between patches using equation (4) and (ii) with competition using equation (2).

In Figure 5b, c, the resulting mean lifetime T_m of the simulation experiment is plotted against the distance d_{12}. Since the T_m-values drastically differ for the same landscape but different movement patterns (we found 50,000 years ('Loops') and 250 years ('Strongly correlated random walk') in the initial landscape), we normalised T_m, i.e. we measured T_m as a percentage of the maximum T_m-value found in the variety of landscapes considered for a given movement pattern.

In the case without competition between patches (Figure 5a), T_m increases with decreasing distance d_{12} between patches 1 and 2, regardless of the movement behaviour. Therefore, the ranking orders of the landscapes are the same for all the movement patterns considered. This effect can be explained as follows. Metapopulation theory shows that metapopulation viability is not only dependent on the number of individuals arriving at a patch (with our settings depending on the total incoming patch accessibilities $\sum_{j(\neq i)} r_{ji}$), but also on the number of individuals a patch contributes to other patches (depending on the total outgoing accessibilities $\sum_{j(\neq i)} r_{ij}$) (Hanski and Ovaskainen 2000; Frank and Wissel 2002). Shifting patch 1
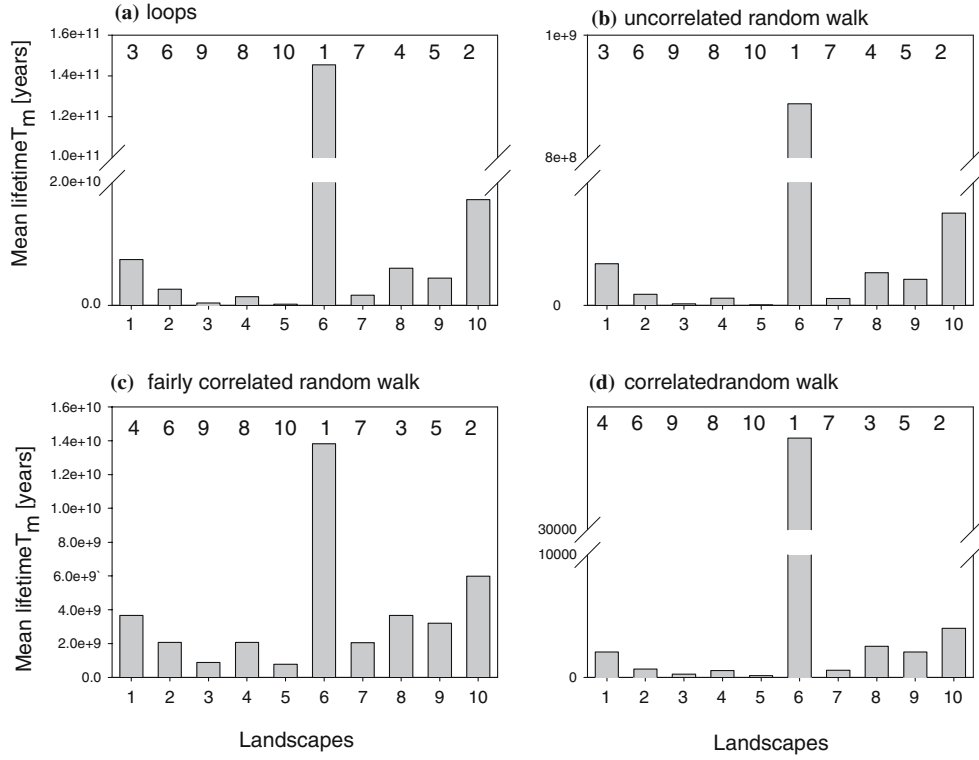
Figure 4. The mean metapopulation lifetime T_m for metapopulations in 10 different randomly generated landscape configurations calculated with equation (3) only, ignoring the competition between patches. Different underlying individual dispersal behaviours were assumed: (a) loop-like behaviour, (b) uncorrelated random walk, (c) fairly correlated random walk, (d) correlated random walk. The numbers on the top indicate the landscape ranks.

towards patch 2 mainly results in a decrease in the distance $d_{12} = d_{21}$ between patches 1 and 2, while all the other distances d_{ij} remain almost unchanged. In the case without competition between patches, the accessibilities of patch 1 and 2 $r_{12} = r = 21 = R(d_{12})$ increase, while all the other accessibilities r_{ij} remain almost constant. In consequence, the total incoming and outgoing accessibilities for patches 1 and 2 increase, while the others remain unchanged.

A totally different picture occurs in the case where competition between patches is included (Figure 5c). For each movement pattern, there is some optimum distance d_{12} at which T_m is highest. This optimum distance varies among the dispersal behaviours considered. The existence of different optima results in different ranking orders for different movement patterns. While the decrease in distance d_{12} may result in an increase in T_m for one movement pattern (for example for 'Strongly correlated random walk'), it may also result in a

decrease for another movement pattern (for example 'Loops').

What are the mechanisms leading to the behaviour-dependent optimum? An optimum always indicates a trade-off of some sort. Such a trade-off mechanism can actually be found and is reflected by equation (2):

(a) The decrease in the $d_{12} = d_{21}$ leads to an increase in the potential patch accessibilities $R(d_{12}) = R(d_{21})$ of the patches 1 and 2 as well as in an increasing competition strength of those two patches (W_{12} and W_{21} increase). More individuals leaving patch 1 will reach patch 2 and vice versa. This results in an increase in the overall values r_{12} and r_{21}.

(b) The potential accessibilities $R(d_{1j})$ and $R(d_{2j})$ from patches 1 and 2 to all other patches j remain almost unchanged. The competition strength of patches j decrease, because the competition strength of patch 1 and 2 increase (W_{1j} and W_{2j} decrease). More individuals starting at patch 1 will reach
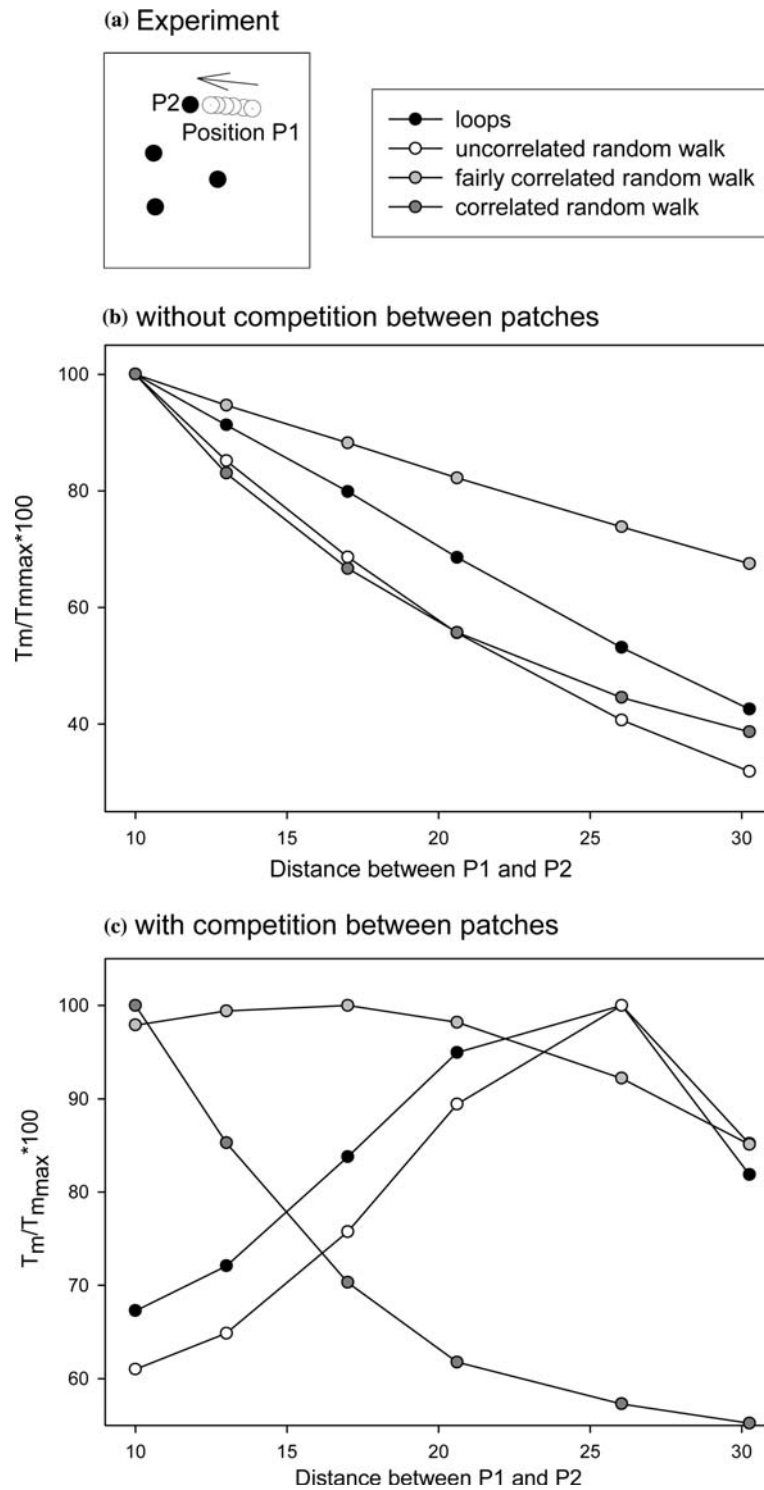
Figure 5. a) An experiment to investigate the effect of the interaction between movement behaviour and landscape systematically: the position of one patch is changed such that patch 1 is moved closer to patch 2, while the positions of all other patches are kept constant. (b) and (c) The resulting mean lifetime T_m (to allow better comparison between movement patterns, T_m is measured as a percentage of the maximum T_m-value found for a given movement pattern in the variety of landscapes of one experiment) for different landscape configurations and movement patterns, calculated (b) neglecting the competition between patches and (c) considering competition between patches.
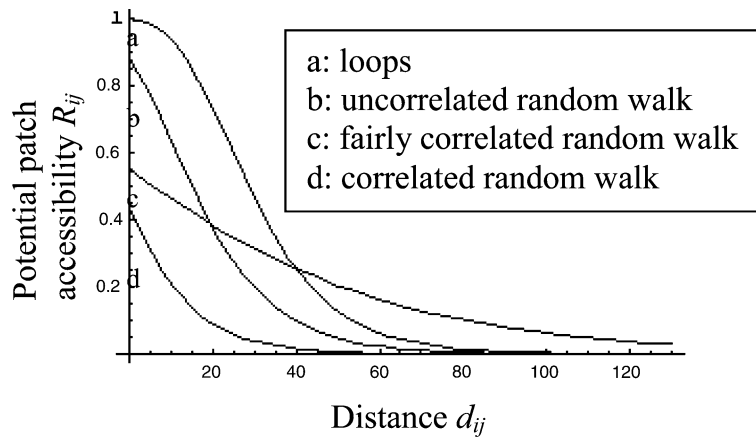
Figure 6. Relationship between the potential patch accessibility R_{ij} and the distance d_{ij}.

patch 2 and vice versa – and less will reach patch j. Therefore, the accessibilities r_{1j} and r_{2j} decline.

(c) The accessibilities r_{ij} between all other patches i and j remain almost unchanged.

The findings on the pair-wise accessibilities r_{ij} result in an increase of the total incoming and outgoing accessibilities of patches 1 and 2. For all other patches $j(\neq 1,2)$, the incoming accessibilities decrease (because of the decrease in r_{1j} and r_{2j}), while the outgoing accessibilities remain almost unchanged (because of the almost constant r_{jk}'s).

Considering competition between patches leads to a trade-off between the disadvantage and advantage of moving patch 1 closer to patch 2. The optimum distance d_{12}, where the advantage and disadvantage cancel each other out, depends on two things: the size of the increase in r_{12} and r_{21} and the size of the decrease in r_{1j} and r_{2j}. These changes are related to the change in $R(d_{12})$. Therefore, the optimum distance depends on the shapes of the R vs. d curves. These shapes and thus the optimum distance depend on the movement pattern (Figure 6). This is the reason why different movement behaviours result in different optimum distances and, hence, in different landscape ranks.

Discussion

Behaviour matters

We found that the dispersal behaviour of individuals has not only a quantitative effect on the viability of a metapopulation but also a qualitative

effect: it can influence ranking orders among alternative landscapes rated regarding the mean lifetime of the corresponding metapopulations. The 'competition' between patches for migrants resulting from the behavioural rule that individuals stay at the first patch they reach was found to be an important factor driving the shift in landscape ranks. Our analysis of the consequences of a systematic change in a hypothetical 5-patch landscape revealed the mechanism of how competition acts on the landscape ranks: if the distance between two patches is decreased while the rest of the landscape is kept constant, a trade-off results between the advantage (improved potential patch accessibility) and the disadvantage (increased competition strength to the detriment of the remaining patches) of this decrease in one inter-patch distance. Whether the advantage compensates for the disadvantage in a given landscape was found to depend on the shape of the potential accessibility function $R(d)$ and hence on the dispersal behaviour.

Implication for metapopulation modelling

Most submodels for the colonisation rates b_{ij} used in metapopulation modelling do not take competition between patches for migrants into account. The most prominent example is the simple exponential function $b_{ij} = yE_i \exp(-ad_{ij})$. This function corresponds roughly to the dispersal function considered in the case of uncorrelated

random walk without competition (note that the accessibility function $r_{ij} = R(d_{ij})$ declines nearly exponentially in this case). As we have seen, competition-free colonisation models are unable to reproduce the found sensitivity of ranking orders in T_m-values of alternative landscape configurations to dispersal behaviour. This bears the risk of counter-productive conclusions about the relationship between landscape configuration and metapopulation viability.

These arguments show that it is vital to check whether the individuals' dispersal strategy induces competition between patches for migrants. If this is the case than a colonisation model is needed that takes both the competition effect and the individuals' movement behaviour in an adequate way into account.

As our results indicate, the dispersal behaviour has to be considered explicitly enough to allow an as good as possible landscape ranking. This reflects the opinion of many other authors calling for the better integration of behavioural aspects into the analyses of ecological landscapes (Lima and Zollner 1996; Roitberg and Mangel 1997; Morales and Ellner 2002). On the other hand, models need to be simple enough to be understandable and comprehensible (Gillman and Hails 1997). Modelling movement behaviour explicitly may complicate the model considerably, which is why metapopulation models usually work with formulas. The formula used here (equation (2); see also Heinz et al. (2005)) is an example of a formula that is structurally simple but allows the effect of a variety of (hypothetical and realistic) movement patterns to be described.

Our study also demonstrates the value of using functional formulas to represent processes as a basis for gaining ecological understanding. The formula for patch accessibility r_{ij} by Heinz et al. (2005) says that r_{ij} is the product of the potential accessibility R_{ij} and a competition term W_{ij}. This enabled the competition term to be switched on and off and the hypothesis that competition for migrants is responsible for the ranking effect to be tested. This would have been impossible by using the individual-based simulation model underlying the formula. Hence, using an approximation formula can even be more advantageous than directly using the output of a simulation model.

Implication for landscape management

The fact that ranking orders among alternative landscape configurations can change with the individuals' dispersal behaviour has serious consequences for landscape management. Decision-making is often based on relative results of comparisons between alternative scenarios, allowing best or worst cases to be determined. Ignoring the individuals' dispersal behaviour can lead to counter-productive conclusions. This means that all tools used for decision-support in landscape management (e.g., rules of thumb, software for viability analysis, landscape indices) have to be accordingly designed to enable planners to meet this requirement. But note that ranking orders do not take the extent of differences in mean lifetimes T_m into account. Ranking orders might change without considerable changes in absolute values, and in our study is true for some patches. Whether the extent of differences is relevant for the decision process or not depends on the management goal to be met.

The need to incorporate individual behaviour may give the impression that it is impossible to derive any rule of thumb or any other transferable statement on the effect of landscape changes on metapopulation viability which are valid for a wide range of species. But as we have seen, all the behavioural effects on relative results and ranking orders among the T_m-values of alternative landscapes are summarised in the shape of the potential accessibility function $R(d)$ (equation (4)), which is completely determined by the two function parameters a and b. These two parameters give rise to a categorisation of species in the sense that movement patterns which result in the same values a and b lead to the same ranking orders and, hence, to common recommendations for landscape management. This tallies with the results of other studies that ecologically differentiated but still simple rules of thumb need to and can be derived which are valid for whole ecological classes of species (Verboom et al. 1993; Weaver et al. 1996; Frank and Wissel 1998; Frank 2004).

One appropriate software tool for including behaviour into metapopulation viability analysis is META-X (Frank et al. 2002; Grimm et al. 2004). The speciality of this software is its open structure. Being based on the metapopulation model by Frank and Wissel (1998) also used in this paper, META-X

allows the use of any (internally implemented or externally specified) submodel for the colonisation rate. Hence, the formula for the patch accessibility (Heinz et al. 2005) can be incorporated and therewith the individuals' movement behaviour.

The formula for the patch accessibility by Heinz et al. (2005) can be interpreted as an ecologically scaled landscape index (Vos et al. 2001), since it is completely expressed in terms of distances and two parameters which summarise the effect of the individuals' behaviour. Usually these indices are used as tools for quantifying landscape structures and making predictions on landscape connectivity. This study indicates a new field of applicability of such indices: once these indices are integrated in more sophisticated analysis frameworks (here: a metapopulation model), they can become an important tool for analysing and understanding landscape effects on ecological processes 'through the eyes of the species'.

Prospects

The present study was based on two simplifying assumptions: we considered landscapes with a relatively small number (9 and 5) of patches and assumed all patches to be identical. This simplification was necessary for gaining understanding and sufficient for showing that the individuals' movement behaviour may have important quantitative and qualitative effects on metapopulation viability. Moreover, metapopulations with a small number of patches are much more relevant for conservation questions than those with a large number of patches. This study ought to be seen as a contribution toward a comprehensive understanding of the interplay between individual behaviour and landscape structure and its effect on metapopulation viability. Real landscapes are often of course more complex, differing from each other not only in one but in a whole variety of respects. These aspects may be complementary or contrary to each other, affecting the shift in landscape ranks in the same or the opposite direction. Furthermore, it is not yet clear how heterogeneous patch sizes influence the effect of dispersal behaviour on the ranking orders of landscapes. Heterogeneously sized patches may increase or reduce the effects found in this study. More research is needed to enable a systematic assessment.

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