

Rapid viability analysis for metapopulations in dynamic habitat networks

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For land-use planning, numerically fast and easily applicable tools are urgently needed that allow us to assess how landscape structure and dynamics affect biodiversity. To date, such tools exist only for static landscapes. We provide an analytical formula for the mean lifetime of species in fragmented and dynamic habitat networks where habitat patches may be destroyed and created elsewhere. The formula is able to consider both patch size heterogeneity and dynamics additionally to patch number and connectivity. It is validated through comparison with a dynamic and spatially explicit simulation model. It can be used for the optimization of spatio-temporal land-use patterns in real landscapes and for advancing our general understanding of key processes affecting the survival of species in fragmented heterogeneous dynamic landscapes.

Keywords: dynamic landscapes; habitat network; habitat turnover; mean lifetime; metapopulation; viability

1. INTRODUCTION

Landscapes and ecosystems are dynamic owing to various ecological and economic drivers. For instance, flooding of wetlands leads to a continuous sequence of habitat creation and destruction, or economic development leads to the destruction of habitats in some places while habitats are restored in others. Climate change is likely to alter these dynamics in the future with substantial impacts on biodiversity (e.g. Thuiller 2007; Buisson *et al.* 2008).

Managing land for conservation in dynamic landscapes is currently a hot topic in the conservation literature (Pressey *et al.* 2007). A major challenge in this context is the assessment of species viability in dynamic habitat networks. Relatively complex numerical (e.g. DeWoody *et al.* 2005; Ross *et al.* 2008) and simulation models (e.g. Johst *et al.* 2002; Wintle *et al.* 2005; Hodgson *et al.* 2009) have been developed to analyse the survival of fragmented populations (so-called metapopulations: Hanski 1999b) in dynamic habitat networks. As time and effort required for the parameterization and analysis of these models is large, they have limitations with respect to both general theoretical analysis and application in conservation management. For exploring general concepts and for devising specific management plans, more rapid approaches are urgently needed.

A promising alternative to numerical and simulation models is analytical formulae that effectively integrate the synergistic effects of network structure and dynamics. On the one hand, these formulae explicitly reveal general relationships between spatial and temporal components of metapopulation survival, furthering our theoretical understanding of metapopulation viability in dynamic landscapes. On the other hand, they are urgently

needed for conservation planning and the cost-effective allocation of conservation resources (e.g. Nicholson *et al.* 2006; Nelson *et al.* 2008).

Only few analytical approaches have been developed for metapopulation viability analysis in dynamic and spatially heterogeneous habitat networks (e.g. Gyllenberg & Hanski 1997; Hanski 1999a; Johnson 2000; Keymer *et al.* 2000; Amarasekare & Possingham 2001; Hastings 2003; DeWoody *et al.* 2005). To our knowledge, all of them focus on occupancy thresholds that tell us under which conditions the mean occupancy (mean number of occupied patches) in a metapopulation is non-zero. As these thresholds ignore variations in occupancy through time, they underestimate the true extinction risk and can lead to false conservation management recommendations (Frank 2005). Another practical disadvantage of considering occupancy thresholds is that they distinguish only between zero and non-zero mean patch occupancy associated with metapopulation extinction and survival, respectively. Any further differentiation among different levels of non-zero mean occupancy and thus different levels of metapopulation viability is not possible. Such differentiation, however, is indispensable for optimizing landscapes which involves a weighting of the improvements in species viability and the associated (finite, often even marginal) financial costs (e.g. Naidoo *et al.* 2006; Nelson *et al.* 2008). Cornell & Ovaskainen (2008) developed an analytical expression for the mean patch occupancy in dynamic landscapes which allows such differentiation. Their expression has the advantage that patches can be destroyed and created in a spatially correlated manner. However, the patch size heterogeneity characteristic for many real landscapes is not included.

An alternative measure of metapopulation viability is the expected lifetime, or mean time to extinction of a metapopulation (Grimm & Wissel 2004). Analytical formulae for calculating this mean metapopulation lifetime (MMLT) in static habitat networks have been developed

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by Frank & Wissel (2002) and Drechsler (2009). We take the formula for the MMLT by Drechsler (2009), and derive new estimates for its parameters that extend the applicability of the formula to dynamic networks where habitat patches may be destroyed through natural or anthropogenic influences and new habitat patches may be created elsewhere.

Assuming a balance between patch destruction and patch creation (e.g. Hanski 1999a; Keymer *et al.* 2000; Briers & Warren 2000; Amarasekare & Possingham 2001; Wahlberg *et al.* 2002; Biedermann 2004), we can describe the network dynamics by effective parameters that enter the formula for dynamic habitat networks. In particular, we take into account that patches may differ in size and/or quality independent of their dynamics. Metapopulation extinction times in static habitat networks are known to be exponentially distributed so that the magnitude of their mean determines the entire distribution of extinction times (Grimm & Wissel 2004). We show that the same is true for dynamic networks.

Below, we present the modelling approach and the derived formula, a numerical validation of the formula and examples that demonstrate its parameterization and application. Our formula does not explicitly account for non-stationary and spatially correlated dynamics of patch destruction and creation. However, we hypothesize that it is still applicable to this kind of network dynamics if the degree of temporal variation and spatial correlation of patch creation and destruction is within certain limits. An objective of the numerical validation is to identify these limits.

Often, the processes of patch creation or patch destruction are induced and/or accompanied by succession in the patches so that habitat quality does not switch between habitable and uninhabitable but continuously changes with time (e.g. Wu & Levin 1994; Stelter *et al.* 1997; Johnson 2000; Johst *et al.* 2002; Hastings 2003; Wintle *et al.* 2005; Matlack 2005; Hodgson *et al.* 2009). We provide and demonstrate a practical approach for considering succession in a convenient manner and incorporating it into our model framework.

2. MATERIAL AND METHODS

(a) Predicting the MMLT in static networks

Consider a metapopulation on a static habitat network of N habitat patches ($i = 1, \dots, N$) with patch sizes A_i and inter-patch distances r_{ij} ($i, j = 1, \dots, N$). The extinction rate e_i and the colonization rate c_i of a local population on patch i may depend on patch size A_i . A standard model for c_i and e_i has been provided by Hanski (1999b):

$$e_i = \varepsilon A_i^{-\eta} \quad (2.1)$$

and

$$c_i = m A_i^b, \quad (2.2)$$

where ε , η , m and b are species-specific constants (for empirical examples, see below and Hanski (1999b) as well as Nicholson *et al.* (2006)). In the present notation, c_i measures the rate by which individuals emigrate from patch i , divided by the number of individuals required to colonize an empty patch. Under infinite dispersal range and infinite number of patches ('Levins limit': Levins (1969) c_i represents the rate by which a local population colonizes another patch. If the patch sizes A_i differ, so do the colonization and extinction

rates c_i and e_i . An appropriate measure of patch size heterogeneity is the ratio Q of the maximum and minimum local extinction rates $e_i^{(\max)}$ and $e_i^{(\min)}$, which via equation (2.1) are associated with the smallest and largest patches in the network, respectively.

Based on Frank & Wissel (2002) and Drechsler (2009), we calculate the MMLT as:

$$T = \frac{1}{\bar{e}} \sum_{i=1}^N \sum_{k=i}^N \frac{1}{k} \frac{(N-i)!}{(N-k)!} \frac{1}{(N-1)^{k-i}} q^{k-i}, \quad (2.3)$$

where \bar{e} is the geometric mean over the local extinction rates e_i :

$$\bar{e} = \prod_{i=1}^N (e_i)^{1/N}, \quad (2.4)$$

and q is the so-called aggregated colonization-extinction ratio, which represents a spatially aggregated ratio of the colonization and extinction rates:

$$q \approx \frac{\bar{c}}{\bar{e}} H. \quad (2.5)$$

In equation (2.5), \bar{c} is a power mean with

$$\bar{c} = \left(\frac{1}{N} \sum_{i=1}^N c_i^{\eta/b} \right)^{b/\eta}, \quad (2.6)$$

and

$$H = \prod_{i=1}^N \left(\frac{1}{N-1} \sum_{\substack{j=1 \\ j \neq i}}^N \exp(-r_{ij}/d) \right)^{1/N} \\ \approx \min \left\{ \frac{10^{-R/(15d)}}{(R/d)^2} \frac{3(R/d)^{1.65}}{(R/d)^{1.65} + 5}, 1 \right\} \quad (2.7)$$

is a connectivity measure which considers that the mean dispersal distance d of individuals is finite and can be much smaller than R . Parameter R represents the spatial extent of the network. With Δx and Δy measuring the distances between the most eastern and most western, respectively, the most northern and most southern patches, R is calculated as

$$R = \sqrt{\Delta x \Delta y / \pi}, \quad (2.8)$$

so that we denote R as 'network radius'. Quantity H in equation (2.7) which depends only on the ratio of network radius and species mean dispersal distance can be regarded as a measure of spatial connectivity. The approximation on the right-hand side of equation (2.7) represents a slight refinement of the approximation provided by Drechsler (2009). If d becomes large compared with the network size R , the connectivity measure H reaches 1, reproducing the Levins limit (Levins 1969).

Equation (2.3) (taken from Drechsler 2009) is the central formula that describes the MMLT. It is dependent on four key macroscopic parameters: the number (N) of habitable patches, the mean colonization rate (\bar{c}) and the mean extinction rate (\bar{e}), and the ratio (R/d) of the average network radius and the species' mean dispersal distance. Equation (2.3) has previously been applied to static networks, which may be uncharacteristic of many real metapopulations. Our major advance in this paper is to relax the assumption that networks are static and to provide statistical estimates of the mentioned key macroscopic parameters in dynamic networks. This

Table 1. The ranges of all model parameters used in figure 1. (The geometric mean local extinction rate was set to $\bar{e} = 0.05$ —an arbitrary choice, as \bar{e} simply determines the time scale of the metapopulation and network dynamics. Rate λ is fixed via equation (2.10) by choosing N_{dyn}/N and μ .)

| | |
|--|--|
| $N \in \{10, 20, \dots, 100\}$ | patch number |
| $\gamma \in \{4, 8, 12\}$ | $\gamma = m(\bar{e}/\varepsilon)^{-b/\eta}/\bar{e}$ is the geometric mean over the patch-specific colonization–extinction ratios c_i/e_i and through equations (2.1) and (2.2) related to the average patch size |
| $Q = \frac{e_i^{(\max)}}{e_i^{(\min)}} \in [1, 3]$ | degree of patch size heterogeneity, where $e_i^{(\max)}$ and $e_i^{(\min)}$ represent the local extinction rates of the smallest and largest patches, respectively |
| $b/\eta \in \{0.25, 0.5, 1.0, 1.5, 2.0\}$ | scaling exponent: typical values of b range from 0.5 (emigration proportional to patch perimeter) to 1.0 (emigration proportional to patch area). η typically ranges from 0.5–2 (Lande 1993) |
| $d/R \in \{0.1, 0.5, 1\}$ | species mean dispersal distance (relative to the network radius R) |
| $\mu/\bar{e} \in \{0.2, 0.4, \dots, 2.0\}$ | ratio of patch destruction and local extinction rates |
| $N_{\text{dyn}}/N \in \{0.5, 0.75, 1\}$ | ratio of the number of habitable patches to the total number of patches |
| $w \in [0, 2]$ | range of temporal variation of the patch destruction and creation rates, measured relative to their respective long-term means |
| $\rho/R \in [0, 0.2]$ | spatial correlation length of patch destruction and creation (relative to the network radius R) |

facilitates the application of equation (2.3) to a broader class of more realistic metapopulation models in which patches may be created and destroyed and in which habitat quality of a patch may vary over time.

(b) Predicting the MMLT in dynamic networks

In this section, we extend the work of Frank & Wissel (2002) and Drechsler (2009) that applies only to static networks, and include network dynamics. We distinguish between two types of network dynamics. In the first type, habitat patches randomly disappear at a rate μ and new patches are randomly recreated elsewhere (e.g. Wu & Levin 1994; Stelter *et al.* 1997; Amarasekare & Possingham 2001; Wahlberg *et al.* 2002; Biedermann 2004). As we consider patch size heterogeneity, recreated patches can have sizes different from those of the destructed ones. Assuming a balance of habitat destruction and creation, the stationary (expected) number of patches is denoted as N_{dyn} . Patch destruction (μ) effectively increases the local extinction rates e_i ($i = 1, \dots, N$) to

$$e_i^{(\text{dyn})} = e_i + \mu \quad (2.9)$$

(e.g. Keymer *et al.* 2000; DeWoody *et al.* 2005). To calculate the MMLT for this type of dynamic network, e_i of equation (2.1) needs to be replaced by $e_i^{(\text{dyn})}$ and all occurrences of N in equations (2.3)–(2.7) need to be replaced by N_{dyn} . Parameter R in equation (2.8) represents half of the average diameter of the region within which new patches are created.

In the second type of dynamic networks, there are N patches with fixed locations and sizes. An uninhabitable patch randomly becomes habitable at a rate λ and a habitable patch becomes uninhabitable at a rate μ (e.g. Briers & Warren 2000; Ellner & Fussmann 2003). The expected number of habitable patches then is

$$N_{\text{dyn}} = \text{round}\left(\frac{\lambda}{\lambda + \mu} N\right) \quad (2.10)$$

(Keymer *et al.* 2000; DeWoody *et al.* 2005), where function $\text{round}(\cdot)$ rounds its argument to the next nearest integer number. As for the previous type of network, the MMLT is determined by replacing e_i by $e_i^{(\text{dyn})}$ of equation (2.9) and all occurrences of N in equations (2.3)–(2.7) by N_{dyn} .

In addition, in this type of network dynamics, it may be that dispersers do not only immigrate into habitable patches but also into uninhabitable ones. In that case, only a fraction $(N_{\text{dyn}} - 1)/(N - 1)$ of the dispersers contributes to the metapopulation dynamics and \bar{e} in equation (2.6) needs to be replaced by $\bar{e}(N_{\text{dyn}} - 1)/(N - 1)$.

(c) Verification of the formula for dynamic networks

To test the validity of the analytical formula (equations (2.3)–(2.10)) for dynamic networks, we compared its output with that of a spatially explicit stochastic computer simulation where the creation and destruction of habitat patches as well as the extinction of local populations and the colonization of empty patches is simulated as Markov processes (see appendix A in the electronic supplementary material). We varied all model parameters systematically within specified ranges (table 1) and for each parameter combination plotted, the predicted MMLT against that obtained from the simulation model.

Essentially, our formula captures network and metapopulation dynamics by appropriate averages over space and time. Large levels of variability and spatial correlations naturally constrain the applicability of this kind of approach. Therefore, we investigated how our formula performs if the heterogeneity in patch sizes (Q) increases beyond the ranges considered in table 1. Further, in the simulations we allowed for non-stationary network dynamics in the sense that patch destruction and creation rates (λ and μ) randomly vary in time and the processes of patch destruction and creation are spatially correlated (see appendix A in the electronic supplementary material). As a measure of prediction error, we plotted the standard deviation of our formula on a log scale between simulated and predicted MMLT as a function of patch size heterogeneity, the range of temporal fluctuations in the patch destruction and creation rates, and the range of spatial correlation in patch destruction and creation events. The log standard deviation was calculated by taking the logarithm (to the base of 10) of the simulated and predicted (i.e. analytically calculated) MMLT and calculating the standard deviation between these two quantities over all parameter combinations. A log scale was chosen, so a prediction of 90 years where the true MMLT is 100 years; e.g. is

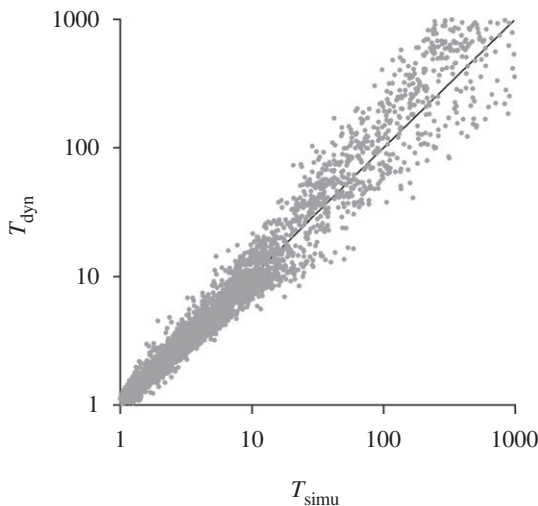


Figure 1. MMLT obtained from the formula (equations (2.3)–(2.10)) versus the expected lifetime obtained through numerical simulations (100 simulation runs per parameter combination), both plotted in units of \bar{e}^{-1} (the geometric mean of the expected lifetimes of all local populations in the absence of network dynamics: equation (2.4)). If, e.g. local populations on average survive for $\bar{e}^{-1} = 20$ years, the dots between 1 and 1000 correspond to MMLTs between 20 and 20 000 years. All parameters are systematically varied according to table 1 with $w = 0$ and $\rho = 0$.

regarded equivalent to a prediction of 900 years where the true value is 1000 years.

(d) *How to incorporate habitat succession on the patches*

So far, we have assumed that all habitable patches have a temporally constant habitat quality: when a patch is created, its habitat quality h jumps from zero to h_{\max} , remains at that level and drops to zero again as the patch is destroyed. However, the quality of a habitat patch may change in time, e.g. owing to succession so that habitat quality is a function of the patch age τ , i.e. the time after patch creation: $h = h(\tau)$. Assuming $h = h_{\max}$ throughout the lifetime of the patch obviously overestimates the patch quality. A more appropriate choice is the average habitat quality h_m . To calculate h_m , we consider that for a patch destruction rate μ , the probability that the patch has not yet been destroyed exponentially decreases with increasing patch age τ by $\exp(-\mu\tau)$. Because at small τ , the patch is most probably not yet destroyed, habitat qualities at these times contribute more to h_m than habitat qualities associated with larger ages. Denoted by $p(\mu; \tau) = \mu \exp(-\mu\tau)$, the probability of a patch not being destroyed (the normalization factor μ was included to ensure that the integral of $p(\mu, \tau)$ over time equals 1), the average habitat quality h_m is:

$$h_m = \int_{\tau=0}^{\infty} P(\mu, \tau) h(\tau) d\tau, \quad (2.11)$$

for continuous time, or for discrete time steps:

$$\begin{aligned} h_m &= \sum_{n=0}^{\infty} P(\mu, \tau_n) h(\tau_n) \\ &= \mu \Delta t \sum_{n=0}^{\infty} \exp(-\mu n \Delta t) h(n \Delta t), \end{aligned} \quad (2.12)$$

where Δt is the length of the time step.

To calculate the MMLT in a dynamic network shaped by succession, it has to be specified how the local extinction rate e_i and the colonization rate c_i depend on habitat quality. A plausible model would be to replace patch size A_i in equations (2.1) and (2.2) by the product of patch size and expected habitat quality, $h_m A_i$. Clearly, there are other ways to modelling local extinction and colonization rates than equations (2.1) and (2.2) (see the empirical example in §3). The general principle, however, remains the same: we consider succession through an averaged patch quality that takes the probability of observing a patch of a particular age into account.

3. RESULTS

(a) *Verification of the formula for dynamic networks*

For stationary network dynamics with patch destruction rates of up to twice the average local extinction rate, no spatial correlation, and heterogeneity in local extinction rates e_i of up to a factor of $Q = 3$, we observed good agreement between formula and simulation model (figure 1). The standard deviation of the lifetimes on a log scale is 0.14 (an interpretation of this number is given in §4). Smaller errors are obtained for networks with short dispersal ranges, low ratios of colonization and extinction rates (c_i/e_i), and low patch size heterogeneity. The validation results are independent of whether patches are recreated where they had been destroyed, or elsewhere within the spatial range ($\Delta x, \Delta y$) defined after equation (2.8).

Figure 2 shows the effect of patch size heterogeneity and non-stationary network dynamics on the precision of the formula. Patch size heterogeneity beyond about $Q = 3$ measurably increases the error of the approximation formula (figure 2a). While temporal variability in the patch destruction and creation rates (w) only moderately increases the error of our approximation formula (figure 2b), a spatial correlation ρ of patch destruction and creation that extends over more than about 25 per cent of the network radius (R) can lead to substantial error (figure 2c).

(b) *Theoretical application and biological insights*

The derived formula (equations (2.3)–(2.10)) allows users to rapidly calculate MMLTs for a variety of different landscapes and species attributes. Such broad and differentiated analyses are indispensable for advanced biological insights. We demonstrate this on the example of trade-offs between different landscape parameters. Knowledge of such trade-offs is of high relevance for conservation planning and the optimization of landscapes (Nicholson *et al.* 2006; Nelson *et al.* 2008), because they tell how much change in one landscape parameter (such as mean patch size, patch size heterogeneity, connectivity, patch dynamics, etc.) must be compensated by changing another one in order to maintain the same MMLT. Figure 3a illustrates that increasing patch size heterogeneity or decreasing patch turnover (μ) increases the MMLT. As a consequence, an increase in patch turnover can be compensated for by a sufficient increase in patch size heterogeneity. The numerical simplicity of the formula allows calculation of this trade-off rapidly (more than 30 times faster than with a simulation model) and

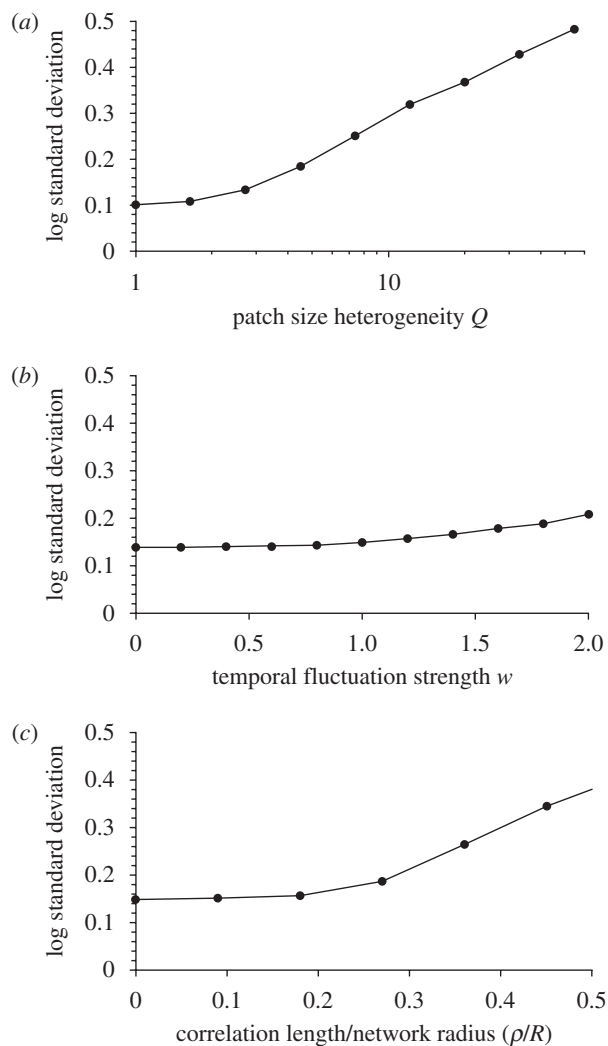


Figure 2. Log standard deviation of the formula (standard deviation of the predicted MMLT on log scale) as a function of (a) the patch size heterogeneity Q , (b) the temporal variation w of the patch creation and destruction rates (relative to their means), and (c) the length of the spatial correlation ρ of patch destruction and creation relative to the network radius R . Other parameters as in figure 1.

in a systematic manner. Figure 3b presents such a systematic analysis. It shows that patch size heterogeneity Q needs to be increased by about three units to compensate for an increase in patch destruction μ by $0.1\bar{e}$ (to recall, \bar{e} is the geometric mean of the local extinction rates: equation (2.4)).

Figure 3a provides yet further biological insights. It shows that the capacity of habitat networks to buffer landscape dynamics depends on the patch size heterogeneity. Metapopulations in networks with patch size heterogeneity ($Q > 1$) turn out to be less robust to patch turnover (μ) than metapopulations in homogeneous networks ($Q = 1$), because at $Q > 1$ the MMLT decreases more strongly with increasing patch turnover (μ) than at $Q = 1$. For instance, an increase of the patch destruction rate μ from $0.2\bar{e}$ to $0.4\bar{e}$ reduces T_{dyn} by a factor of about 3 at $Q = 1$, and by a factor of 40 at $Q = 7$.

Another option to compensate for patch destruction is to create more patches by increasing the patch creation rate λ (figure 3c). However, the systematic analysis (figure 3d) reveals that the effectiveness of this measure

is limited, particularly if the patch destruction rate is high. At small patch destruction rates, an increase in the patch destruction rate μ by $0.5\bar{e}$ can be compensated by an increase in the patch creation rate by about $0.2\bar{e}$, while at large patch destruction rates the patch creation rate would have to be increased by \bar{e} or more.

(c) Example for the parameterization of the formula for a static network

Drechsler *et al.* (2003) consider a metapopulation of butterflies, *Melitaea cinxia*, inhabiting a static network of $N = 48$ habitat patches on the Finnish Åland Islands. The estimation of the parameters of equations (2.1) and (2.2) is provided by Drechsler *et al.* (2003); the mean dispersal distance estimated by the authors is $d = 2.5$ km. Below, we focus on the remaining step: the calculation of the connectivity H (equation (2.7)). According to fig. 1 of Drechsler *et al.* (2003), the 48 patches are spread over an area with east–west and north–south dimension of about $\Delta x = \Delta y = 6$ km. With equation (2.8), we obtain a network radius of about $R = 3.4$ km and with equation (2.7), a connectivity of about $H = 0.3$.

(d) Example of the parameterization of the formula for a dynamic network in the presence of succession

Stelter *et al.* (1997) consider a metapopulation of plant hoppers, *Bryodemus tuberculata*, inhabiting a dynamic network of vegetated gravel banks with identical sizes in the River Isar, Germany. We focus here on the establishment of the colonization and extinction rates, c and e , which depend on the network dynamics. Floods destroy local populations and recreate bare gravel banks at a frequency μ . After creation of a gravel bank, it takes 3 years for vegetation to establish and for the gravel bank to become habitable. In the model of Stelter *et al.* (1997), this is modelled by a jump in the local carrying capacity for the plant hoppers (only females are considered in the model) from zero to $K_{\text{max}} = 50$. Owing to succession, the quality of the vegetation declines with time, associated with a decline of the local carrying capacity by 1 per year. This continues for 45 years after which the local carrying capacity assumes a value of $K_{\text{min}} = 5$, where it remains constant until the gravel bank is washed away. Mathematically, the dynamics of the carrying capacity of gravel banks are described by

$$K(\tau_n) = \begin{cases} 0 & 0 \leq n \leq 3 \\ 53 - n & 3 \leq n \leq 48 \\ 5 & n \geq 48 \end{cases} \quad (3.1)$$

(with time step length $\Delta t = 1$ year). Inserting equation (3.1) into equation (2.12) (identifying $K(\tau_n)$ with $h(\tau_n)$) delivers the expected carrying capacity as a function of μ : $K_m(\mu)$ (figure 4). It is small for very frequent floods, because in the first 3 years the patch is inhabitable, and small for very infrequent floods, because the carrying capacity declines with increasing patch age (equation (3.1)). Stelter *et al.* (1997) assume that local extinction is caused by two processes: environmental stochasticity and demographic stochasticity lead to local extinction with annual probabilities of 0.1 and $1/K$, respectively.

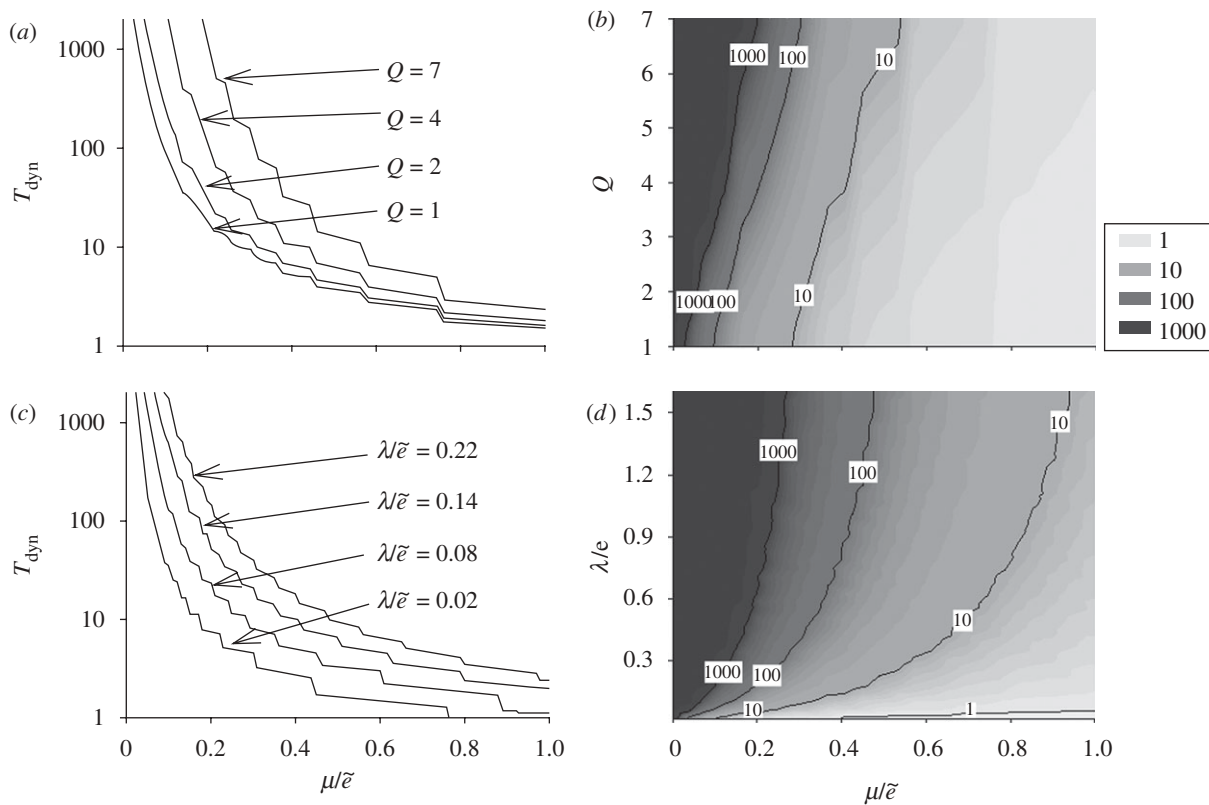


Figure 3. (a) MMLT (equation (2.3)) in units of \bar{e}^{-1} (equation (2.4)) as a function of the patch destruction rate μ (in units of \bar{e}) for four levels of patch size heterogeneity Q . (b) MMLT (indicated by greys) as a function of the patch destruction rate μ (in units of \bar{e}) and patch size heterogeneity Q . The solid lines mark so-called iso-MMLT lines, where all points (combinations of Q and μ) lead to the same MMLT. (c) MMLT in units of \bar{e}^{-1} as a function of the patch destruction rate μ (in units of \bar{e}) for four levels of the patch creation rate λ (in units of \bar{e}). (d) MMLT (indicated by greys) as a function of the patch destruction rate μ and the patch creation rate λ (both in units of \bar{e}). The model parameters are $N = 30$, $d = 0.25$, $b/\eta = 2$, $\bar{c}/\bar{e} = 12$, $\bar{e} = 0.05$ and $\lambda/\bar{e} = 0.1$ (for a, b) and $Q = 3$ (for c, d). The steplike run of the curves is owing to the rounding of the patch number in equation (2.10).

The (annual) local extinction rate is therefore

$$e(\mu) = 1 - (1 - 0.1) \left(1 - \frac{1}{K_m(\mu)} \right) \\ = 1 - 0.9 \left(1 - \frac{1}{K_m(\mu)} \right). \quad (3.2)$$

The annual probability of a female plant hopper leaving a gravel bank is 0.1. Each female immigrating into an empty gravel bar is assumed to establish a local population, leading to a colonization rate (cf. equation (2.2)) of

$$c = 0.1 K_m(\mu). \quad (3.3)$$

Inserting K_m of equation (3.1) into equations (3.2) and (3.3) yields the colonization and extinction rates c and e (identical for all patches, as these have identical sizes) as functions of the patch destruction rate μ . These two parameters include the indirect effects of the flood dynamics and, like the expected carrying capacity, are ‘optimal’ (i.e. c maximal and e minimal) for flood rates around $\mu = 0.1$. The additional direct effect, the destruction of local populations owing to patch destruction at rate μ , is considered through the dynamic local extinction rate e_{dyn} which is obtained by adding μ to e (equation (2.9)). Inclusion of this direct and adverse effect shifts the optimal flood rate from 0.1 (associated with the minimum of e) to a smaller value around 0.02 (figure 4, short

dashed line). The flood rate that maximizes the ratio of colonization and dynamic extinction rates, c/e_{dyn} , is a compromise between maximizing c and minimizing e_{dyn} and is located around a value of 0.05.

As mentioned above, Stelter *et al.* (1997) assume that floods destroy and create gravel banks at the same time and with the same numbers so that the total number of gravel banks in the system is constant at $N_{\text{dyn}} = 30$ and independent of the flooding frequency. The patch destruction rate that maximizes the ratio c/e_{dyn} therefore maximizes the lifetime of the metapopulation. In the simulation model analysis of Stelter *et al.* (1997), the patch destruction rate is given by the product Flood \times Wash, where Flood is the flood rate and Wash the proportion of gravel banks affected by a flood. The authors set Wash = 0.25, meaning that in each flood one-fourth of all gravel banks is affected, and find that the mean lifetime of the *Bryodemys* metapopulation is maximized by Flood = 0.2, ..., 0.3. So, the optimal patch destruction rate is $(0.2, \dots, 0.3) \times 0.25$, which agrees very well with our approximation.

4. DISCUSSION

We provide a formula for the expected lifetime of a metapopulation in a dynamic habitat network with heterogeneous patch sizes. The validity of the formula over large parameter ranges confirms our initial

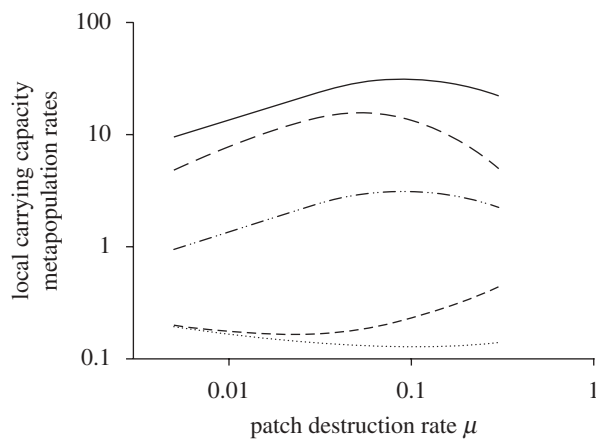


Figure 4. Parameters of the metapopulation dynamics as functions of the patch destruction rate μ for the metapopulation of Stelter *et al.* (1997). Solid line, expected patch carrying capacity K_m ; dotted line, the static local extinction rate e (but considering the indirect effect of patch destruction on the average patch carrying capacity); short-dashed line, the dynamic local extinction rate $e_{\text{dyn}} = e + \mu$ (considering direct and indirect effects of patch destruction); dash-dotted line, the colonization rate c ; long-dashed line, the ratio c/e_{dyn} .

hypothesis that the lifetime of a metapopulation in a dynamic habitat network can be estimated by casting the stationary properties of network dynamics into effective parameters and inserting these appropriately into a static metapopulation formula.

Previously developed formulae for heterogeneous and dynamic landscapes are based on occupancy thresholds. They ignore stochasticity and predict that below a certain level of network dynamics, a metapopulation persists indefinitely and above it goes extinct with certainty. Focusing on the MMLT, our formula provides a more differentiated view on the impact of network dynamics on metapopulation viability (e.g. figure 3*a*) and allows the rapid assessment of different spatio-temporal landscape structures and trade-offs between them in a continuous manner (e.g. figure 3*b*). Such broad and differentiated analyses are indispensable for both advanced biological insights and conservation management. Another important consequence of focusing on the MMLT is that (meta)population extinction times are generally exponentially distributed. This has been proven for static landscapes (Grimm & Wissel 2004) but we found this to be true also under the considered network dynamics (figure A1 in the electronic supplementary material). Thus, the mean of this exponential distribution, the MMLT, captures all essential information required to assess (meta)population viability (Grimm & Wissel 2004).

The way of its derivation implies that our formula can be applied only in metapopulations where the landscape dynamics are stationary. Transient dynamics where, e.g. patches are destroyed at one end of the landscape and recreated on the other (e.g. Travis 2003), or where patches are lost on net (e.g. Bascompte & Solé 1996; Casagrandi & Gatto 2002) cannot be considered with our formula. However, we found that temporal variation in the patch destruction and creation rates has relatively little influence on the precision of our formula.

Succession dynamics on the patches can be considered in a statistical manner (another example is Hastings (2003) for homogeneous successional landscapes). We propose a relatively simple approach for heterogeneous successional landscapes based on temporal averages of local patch qualities and implied local extinction and colonization rates that can be inserted into our formulae. As demonstrated in the example of a plant hopper metapopulation, the simplicity of the approach allows us to derive insights into the role of disturbance in successional landscapes that could not be obtained with the original simulation model.

Another limitation of the formula is that it assumes there is no spatial correlation in the network dynamics of patch destruction and recreation (Johst & Drechsler 2003; Vuilleumier *et al.* 2007). We found that our formula approximates the simulated MMLT with acceptable precision if the correlation length is less than about 25 per cent of the network radius. Cornell & Ovaskainen (2008) developed an analytical expression for mean patch occupancy for these cases, however, without consideration of patch size heterogeneity. Developing analytical approaches for both heterogeneous and correlated landscapes is still an unresolved challenge.

A final limitation is the degree of patch size heterogeneity, which via equations (2.1) and (2.2) reflects in heterogeneity in the extinction and colonization rates of the local populations. We found that if local extinction rates differ by more than a factor of 3, the error in the output of the formula may be judged unacceptable. The definition of unacceptable is of course subjective. In the notion of the present paper, a standard deviation between predicted and simulated MMLT on a log scale of less than 0.14 is considered acceptable. The 95% confidence interval associated with a standard deviation of 0.14 comprises true MMLTs between ± 0.28 of the predicted value on a log scale. With a predicted MMLT of 100 years, for instance, this means that the true MMLT lies between $100 \times 10^{-0.28} = 52$ and $100 \times 10^{0.28} = 190$. This error may seem substantial but in fact is not larger, or even smaller, than that produced by many other models used for (meta)population viability analysis (Drechsler *et al.* 2003; Lindenmayer *et al.* 2003; McCarthy *et al.* 2003). Like the cited authors, we suggest using our formula for comparing and ranking of conservation strategies rather than making crisp predictions of the future of a particular metapopulation.

Within the stated limits of application, the formula represents a straightforward tool for rapidly assessing metapopulation survival under a variety of spatio-temporal network structures. Thus, it is valuable for conservation management and for optimizing large spatio-temporal landscape structures with multiple species where detailed simulation models are not applicable because of long computation times (e.g. Nicholson *et al.* 2006; Nelson *et al.* 2008). Once a basic understanding has been obtained about what constitutes an optimal landscape, more sophisticated models may be employed to refine the optimum (Polasky *et al.* 2008). Our formula is also useful for general analyses of metapopulation viability in heterogeneous and dynamic landscapes to advance our theoretical understanding of population ecology in dynamic fragmented landscapes. Systematic evaluation of the formula, revealed that

metapopulations with heterogeneous patch sizes are more vulnerable to network dynamics than metapopulations with homogeneous patch sizes, and patch creation can effectively compensate for patch destruction only if the patch destruction rate is not too high. This type of comprehensive understanding of the synergistic effects of landscape structure and dynamics is crucial for both ecological theory and conservation management.

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