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Consequences of cyclic vegetation management for arthropod survival: Simulation experiments

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Summary

Many rare arthropod species occupy open grasslands. Mowing or grazing is needed to preserve the habitat for these species. Alternatively the vegetation cover in parts of the managed area can be periodically destroyed by ploughing or rototilling. Such treatment results in a dynamic mosaic of habitat patches in different stages of succession. This mosaic may serve as a habitat for many species. However, the interplay between the frequency of rototilling, the spatial structure of the landscape and life history attributes of the animal species will determine the success of such cyclic management strategies. We used a spatially implicit individual-based metapopulation model to examine optimal spatio-temporal management strategies. The model explicitly incorporates succession, population dynamics and dispersal between habitat patches.

Optimal management patterns strongly depend on the species' properties. Our simulation experiments show that in general the more fertile species with strong intraspecific competition are most robust against the large fluctuations of habitat quality resulting from cyclic management. However, the best management strategies found in our experiments cover the requirements of up to 70% of the species tested. Frequent management of relatively small sub-areas minimizes local fluctiations of patch capacity. Though reducing effective patch capacity by more than 50% these strategies may support the survival of the majority of species.

Zusammenfassung

Viele Arthropodenarten beanspruchen offene Weidestandorte, die durch Mähen oder Beweidung gepflegt werden. Alternativ hierzu lassen sich solche Flächen offen halten, indem sukzessiv Teile der Flächen gepflügt oder gegrubbert werden. So entsteht ein Mosaik von Flächen in unterschiedlichen Sukzessionsstadien. Dabei

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bestimmt neben der räumlichen Anordnung der Flächen und den Eigenschaften der zu schützenden Art auch die Frequenz des Eingriffs den Erfolg einer solchen zyklischen Pflege. Wir haben ein räumlich implizites individuen-basierten Metapopulations-Modell eingesetzt, um raum-zeitlich optimale Managementstrategien abzuleiten. Im Modell werden Sukzession, Populationsdynamik und die Ausbreitung zwischen Habitat-Patches berücksichtigt.

Optimale Strategien hängen sehr stark von den Eigenschaften der zu schützenden Arten ab. Unsere Simulationsexperimente zeigen, dass im Allgemeinen Arten hoher Fertilität und starker intraspezifischer Konkurrenz unempfindlicher sind gegenüber den Auswirkungen zyklischer Pflegemaßnahmen. Dennoch erfüllen die besten Strategien, die wir in unseren Simulationen finden konnten, die Ansprüche von bis zu 70% der getesteten Arten. Häufiges Grubbern kleiner Teilflächen minimiert die mit zyklischer Pflege verbundenen Schwankungen der Habitatqualität. Obwohl solche Pflege die mittlere Habitatqualität um mehr als 50% vermindert, kann durch sie eine Vielzahl von Arten erhalten werden.

Introduction

With the ongoing industrialization of agriculture, many traditional forms of land use have become more and more unprofitable. During the last decades therefore, many areas subject to these forms of land use have been abandoned and left to natural succession (Van Dijk, 1991). Unfortunately, these areas frequently offer specific habitats which support a high variety of specialist species (Steffan-Dewenter & Tscharntke, 2002). In order to conserve them, it is necessary to artificially stop or regularly reset natural succession in these areas (Morris, 2000; Poschlod & WallisDeVries, 2002; WallisDeVries, Poschlod, & Willems, 2002). Most current methods (mowing, grazing) are aimed at preserving a more or less static equilibrium state capable of sustaining certain target species. Additionally most of these methods are relatively expensive (Dolek & Geyer, 2002; Poschlod & WallisDeVries, 2002). It may be assumed that a more dynamic mix of successional states could increase the number of species supported for a lower price. Thus, there are strong economic as well as ecological incentives to test alternative approaches.

One kind of alternative method recently investigated consists in completely destroying the vegetation cover in parts of the managed area. If this treatment is applied periodically to different parts of an area, it results in a dynamic mosaic of habitat patches in different stages of succession. It is assumed that this heterogeneous mosaic will be able to serve as a habitat for many species (Steffan-Dewenter & Tscharntke, 2002).

There are several investigations (Kahmen, Poschlod, & Schreiber, 2002; Moog, Poschlod, Kahmen, & Schreiber, 2002; Morris, 2000) testing the long-term success of different management methods empirically. These studies, however, have to be pursued for rather extended periods of time in order to obtain reliable results. Besides these studies, simulation models may offer a promising way to evaluate different treatments and their consequences. In the context of ephemeral habitat patches, some attempts have been made to assess the extinction probability of metapopulations with dynamic patches. Most of these models only deal with patches switching between the states inhabitable and uninhabitable (Amarasekare & Possingham, 2001; Biedermann, 2004; Brachet et al., 1999; Hastings, 2003; Johnson 2000a, b; Keymer, Marquet, Velasco-Hernandez, & Levin, 2000) or good, poor and uninhabitable (Wiegand, Moloney, Naves, & Knauer, 1999). Others do allow for a higher number of different quality states but neglect the interactions between population dynamics of the animals and changes in habitat quality (Boughton & Malvadkar, 2002; Gyllenberg & Hanski, 1997). Johst, Brandl, and Eber (2002) investigated the impact of population dynamics and changing patch quality on the extinction risk of a metapopulation. Their scenario of patch extinction with subsequent sigmoid recovery shows some similarities with management scenarios where whole habitat patches are treated at a time.

Another area of investigation which shows some relations to our problem is the influence of coloured noise on population dynamics. Many studies examine the effects of correlated environmental stochasticity on persistence times (Petchey, Gonzalez, & Wilson, 1997; Wichmann, Johst, Moloney, Wissel, & Jeltsch, 2003). The extinction risk of populations under this kind of influence is determined by correlation length and life history

(Cuddington & Yodzis, 1999; Heino & Sabadell, 2003; Johst & Wissel, 1996; Laakso, Kaitala, & Ranta, 2004). These models account for temporal correlation of environmental changes but assume these changes to occur stochastically, whereas management regimes usually will be executed deterministically, or deal only with single isolated populations.

In our investigation, we studied the consequences of habitat quality dynamics arising from the regular treatment of small sub-areas of habitat patches in a metapopulation context. Contrary to the studies mentioned above, we therefore created a metapopulation model which explicitly includes deterministic changes in habitat quality as resulting from cyclic management. We restricted our simulation experiments to species specialized on early successional states (like many grasshoppers or butterflies). First, we investigated which treatment pattern generally will be able to protect these species. Second, we were interested in the question whether life history properties of species should influence the choice of optimal management strategies. Based on a deeper understanding of the mechanisms governing the interactions of patch quality dynamics with the life history of a species, we thus wanted to derive practical recommendations for the application of management measures.

Methods

Our model is a spatially implicit individual-based metapopulation model based on local logistic growth (Maynard Smith & Slatkin, 1973) and global dispersal between habitat patches. Since this type of model has been used several times before in conservation biology and theoretical ecology (e.g. Johst et al., 2002; Poethke, Hovestadt, & Mitesser, 2003), we will only present a short description at this point.

The landscape modelled consists of $n = 100$ discrete habitat patches surrounded by an uninhabitable matrix. During each time step (representing one year), individuals undergo the processes of migration, reproduction and death. Migration is implemented by allowing each individual to emigrate to another randomly chosen patch with a fixed probability d. There is a certain chance μ that an individual dies during migration. During reproduction each female produces a number of offspring which are placed in the same patch. The number of offspring is drawn from a Poisson distribution with mean λ_{eff}. As shown in Eq. (1), λ_{eff} is a function of the environmental stochasticity factor Φ (drawn from a log-normal distribution with mean λ and variance σ), reproduction rate λ, strength of competition β and density N/K (with population size N and capacity K):

$$\lambda_{\mathrm{eff}} = \Phi(\lambda, \sigma) a(N, K) \frac{1}{1 + (\lambda - 1)(N/K)^{\beta}}, \tag{1}$$

where a denotes the Allee effect, i.e. the decrease in reproduction rate at very low densities (e.g. caused by reduced mating success or increased predation pressure), and is defined as

$$a(N, K) = 1 - \frac{1}{2}^{\alpha(N/K)}, \tag{2}$$

following Gros (2003) and McCarthy (1997) with α regulating its strength. As we assume non-overlapping generations all individuals die after reproduction.

The behaviour of this version of the model is determined by six parameters α, β, λ, σ, d and μ. A combination of all parameters regulating the *local* population dynamics will be called life history $h{:}(= \alpha, \beta, \lambda, \sigma)$. In order to avoid confusion with management strategies, we will subsequently also use species as a synonym for an instance of h (although this does not comprise a species in the classical sense).

Succession

We modelled the patch dynamics caused by the interaction of management and succession by letting the habitat quality ($q(t)$) change over time. Habitat quality determines the local carrying capacity $K(t) = q(t)K_{\mathrm{max}}$. Reproduction rate λ is influenced only indirectly (Eq. (1)). Since there is no generally accepted formalization of the dependence of habitat quality on succession time (Johnson, 2000a), we use the standard formula for the log-normal probability distribution as a simple phenomenological model:

$$q(t) = \frac{1}{s\sqrt{2\pi}} \mathrm{e}^{-(\ln(t) - \ln(m))^2/2s^2}, \tag{3}$$

with t and m given in years. This model shows the typical hump-shaped curve often used to illustrate the concept of the temporal niche: Directly after management has taken place, habitat quality is reduced to zero ($t = 0$). Subsequently it increases until it reaches a maximum of $q(m) = 1$ at $t = m$, the species specific optimum. Afterwards it decreases asymptotically to zero again. The width of the temporal niche of a species is determined by the parameter s.

Management

Management in our model is defined as a spatio-temporal pattern of disturbances of patches or parts of patches. The disturbance of an area hereby simply results in its successional state (t) being reset to zero.

We started with a fairly simple management scenario, assuming that each patch is subdivided into num areas which experience succession and disturbance independently of each other. Each patch will be treated deterministically every *delay* years. Management only affects the *oldest* sub-area of a patch so that each sub-area will be treated every $delay \times num$ years. Thus each patch consists of several sub-areas in different states of succession. We initialized all patches with the equilibrium age distribution of sub-areas with the age offset distributed equally over all possible values.

The capacity of a sub-area (K_i) is determined by its age (t_i), the number of sub-areas of the patch (num) and maximum patch capacity ($K_{\max}$):

$$K_i = q(t_i)\frac{K_{\max}}{num}. \tag{4}$$

The overall capacity of a patch (K_{tot}) is then defined as the sum of capacities of the sub-areas:

$$K_{\text{tot}} = \sum_{i=1}^{\text{num}} K_i. \tag{5}$$

Experiments

We investigated the management needs of different species by varying both management parameters (*delay* and *num*) for several life history strategies (see Table 1). The range of values for the life history parameters of typical dry grassland arthropod species could be derived from the results presented by Heidenreich (2000). The succession parameters m and s were equivalently adjusted to describe the temporal niche of these species (S. Hein, pers. comm.).

Table 1. Parameter values

Parameter	Values
α	0.001, 0.01, 0.1, 0.2, 0.5
β	0.5, 1, 2, 4, 8
σ	0, 1, 2, 3
λ	1.3, 1.5, 2, 4, 8
delay	1, 2, 3, 4, 5, 6, 7, 8
num	1, 2, 3, 4, 5, 6, 7, 8
m	3
s	0.4
d	0.1
μ	0.1
Number of patches	100

All combinations were used.

In pre-investigations, we found that under these circumstances management strategies which produce the highest survival rates lie within the same well defined area ($1 \leqslant num \leqslant 8$ and $1 \leqslant delay \leqslant 8$). Therefore, we restricted our experiments to this range of management parameters. A summary of all parameter values used in the simulation experiments can be seen in Table 1.

Analysis

As an indicator for the extinction risk of populations the minimum viable population size (MVP; Gilpin & Soulé, 1986), i.e. the minimum number of individuals needed to guarantee long term survival of the population, is widely applied (Benton, 2003). In this context typically an extinction risk of 0.1 or lower after 50 or 100 years is seen as a minimum requirement for survival. Like Fahrig (2001) we used the minimum patch capacity for survival as a simple replacement of the mvp. The sensitivity of a life history mvp(h) therefore is defined to be the level of capacity $K_{\max}$ which results in a survival chance of the metapopulation of 0.9 after 100 years.

We determined mvp(h) by means of a simple iterative search. Starting with $K_{\max,\text{start}} = 5$ we doubled patch capacity until extinction risk for 100 replicate runs fell below 0.1 at $K_{\max,\,\text{end}}$. Then we approximated the target mvp(h) $\left(\widehat{K_{\max}}\right)$ by applying a binary search algorithm to the interval $[\frac{1}{2}K_{\max,\text{end}}; 2K_{\max,\text{end}}]$. Again 100 replicate runs were used for the calculation of extinction risk. As a side effect of this method, we obtained a rough estimate of the dependence of extinction risk on habitat size for each species.

Since we cannot expect species with different life histories to show equal mvp(h) values even under the same conditions, we had to find a way to separate the effect of management on survival chance from the species specific "base" extinction chance under optimal conditions ($\text{mvp}(h) =$ the $\text{mvp}_{\text{opt}}(h)$). We therefore determined the mvp_{opt} (h) for all life histories in an "optimal" scenario without any succession or management, i.e. with a constant $K_{\text{tot}} = K_{\max}$. Then we calculated the mvp for scenarios with management ($\text{mvp}_{\text{man}}(h, delay, num)$). The normalized mvp:

$$\text{mvp}_{\text{rel}}(h,\ delay,\ num) = \frac{\text{mvp}_{\text{man}}(h,\ delay,\ num)}{\text{mvp}_{\text{opt}}(h)} \tag{6}$$

is then used to describe the impact of a management scenario (*delay, num*) on a life history *h*.

In order to constrain the run time of the simulations, we set an upper limit of 10,240 for patch capacity $K_{\max}$ during the search phase. Life histories that show an extinction risk above 0.1 for $K_{\max} = 10,240$ under "optimal" management were excluded from further analyses. We had to set the same limit for the runs with cyclic management. Since life histories with a high "base sensitivity" (high mvp_{opt}) have a higher chance to reach this upper limit for some management scenarios than those with a low mvp_{opt}, we had to adjust the data sample used for analysis to avoid an mvp-specific bias in mvp_{rel}. Therefore, we left out the worst strategies for each species until we reached a standard sample size of 12 viable management strategies (see section "Analysis") for each species. Since we are only interested in the best performing strategies for each species this should not influence the results of our analysis.

Results

Conforming to our expectations the differences in minimum viable population size (mvp_{opt}) between species are extremely large. Values range from as low as 10 individuals for the most robust species to several 100 individuals for the vulnerable ones. The distribution of values is extremely skewed with most values lying below 200 (Fig. 1A). Even with the threshold for patch capacity ($K_{\max}$) set to 20,240 only a few species which stay below this value show an mvp above 1000.

The shape of the relation between patch capacity ($K_{\max}$) and extinction risk is rather similar for all species (Fig. 1B). Extinction risk decreases within a narrow band around mvp_{opt}.

Following Eqs. (3), (4) and (5) patch capacity ($K_{\max}$) usually will be greater than the actual capacity under management (K_{tot}). We thus expect the increase in patch capacity (mvp_{rel}) necessary to compensate for the losses due to succession under cyclic management to be greater than 1. Indeed we find that – compared to classical management methods that try to keep the habitat in the optimal state – cyclic management generally raises the local carrying capacity (mvp_{man}) (and consequently the patch area) necessary for survival. There are only a few combinations of life history and management strategies which approximate the case with constant, optimal capacity – the lowest increase in mvp measured is 20% ($\text{mvp}_{\text{man}}/\text{mvp}_{\text{opt}} = \text{mvp}_{\text{rel}} = 1.2$) (Fig. 1A). Nevertheless, for all species there are at least some management strategies with which they perform reasonably well with typical values for mvp_{rel} lying around 2. Though vulnerable species show a general tendency to be affected by management more badly (Fig. 1A, $p<0.01$, $r^2 = 0.035$), even the most robust life histories may need an increase in patch capacity by 120% ($\text{mvp}_{\text{rel}} = 2.2$) with cyclic management.

In the next step, we analyzed the dependency of the effect of management strategies on life history properties. A multiple linear regression shows that the required increase in patch capacity (mean mvp_{rel} of the best 12 strategies for each species) increases with the strength of the Allee effect (α, Fig. 2A and the intensity of intraspecific competition (β, Fig. 2B and decreases with fertility (λ)

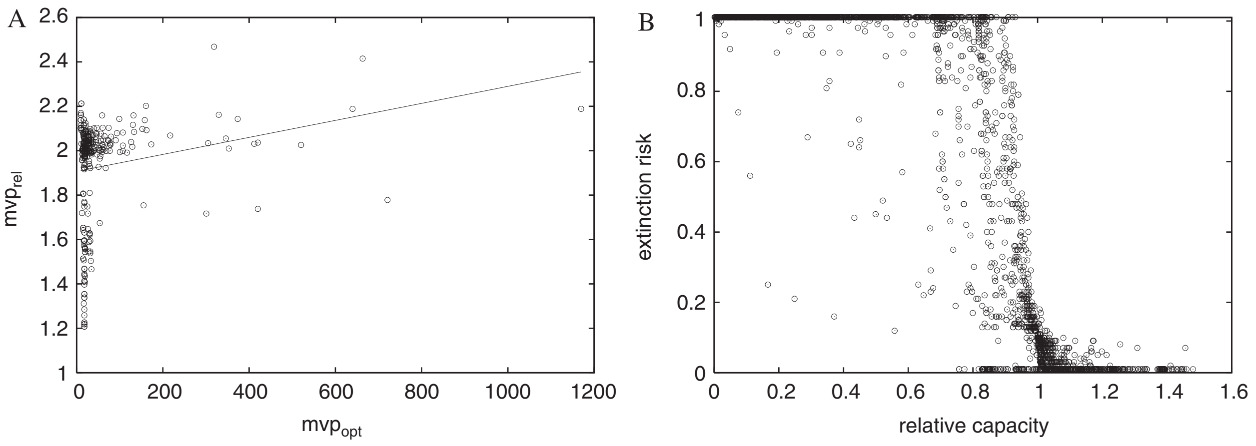

Figure 1. (A) mvp_{rel} shown against base mvp. Only the best management strategy for each species is included. The relative increase in patch capacity necessary for long term survival (mvp_{rel}) significantly increases with the minimum viable population size of the unmanaged population (mvp_{opt} ($p<0.01$)). (B) Extinction risk against relative capacity $K_{\max}/\text{mvp}_{\text{opt}}$ for all species.

($p < 0.01$). Environmental variability (σ does not have a simple linear influence on manageability (Fig. 2). But at least for moderate environmental fluctuations ($\sigma < 2.5$) the required increase in patch capacity decreases with increasing environmental variability (σ). Obviously, species suffer less from management-induced fluctuations of habitat quality when they live already under the influence of strong environmental fluctuations. These dependencies do not change when considering only the best management strategy for each species. There are, however, strong interactions between these parameters (Fig. 2). Especially β and σ seem to have strong non-linear effects on $\mathrm{mvp}_{\mathrm{rel}}$ if seen in interaction with each other (Fig. 2B).

Species clearly differ in their preferences for certain management strategies (Fig. 3). Especially the number of sub-areas optimal for a species (Fig. 3A) is sensitive to the species-specific Allee effect (α) and fertility (λ). While an increased Allee effect (increased α) increases the optimal number of sub-areas per patch, an increase in fertility (λ) reduces the number of sub-areas required for successful management. This result is in good agreement with the influence of fertility (λ) and Allee effect (α) on the optimal delay (Fig. 3B). With increasing fertility (λ) the optimal *delay* increases while it decreases with increasing Allee effect (α).

Finally we looked for those management strategies that perform well for all or at least most species at the same time. For each species, we therefore chose either the best strategy or all strategies with an increase in patch capacity ($\mathrm{mvp}_{\mathrm{rel}}$) below a certain threshold. For each management strategy, we then counted the number of species included.

If only taking the best strategy for each species into account, no management scenario can protect all 500 species tested. The highest proportion of species covered will be 70% with $num = 5$ and $delay = 1$ (Fig. 4A). With an increase of patch area by 200% ($\mathrm{mvp}_{\mathrm{rel}} = 3$, Fig. 4B) the range of adequate strategies as well as the number of species that can be protected increases and for $\mathrm{mvp}_{\mathrm{rel}} = 4$ there are

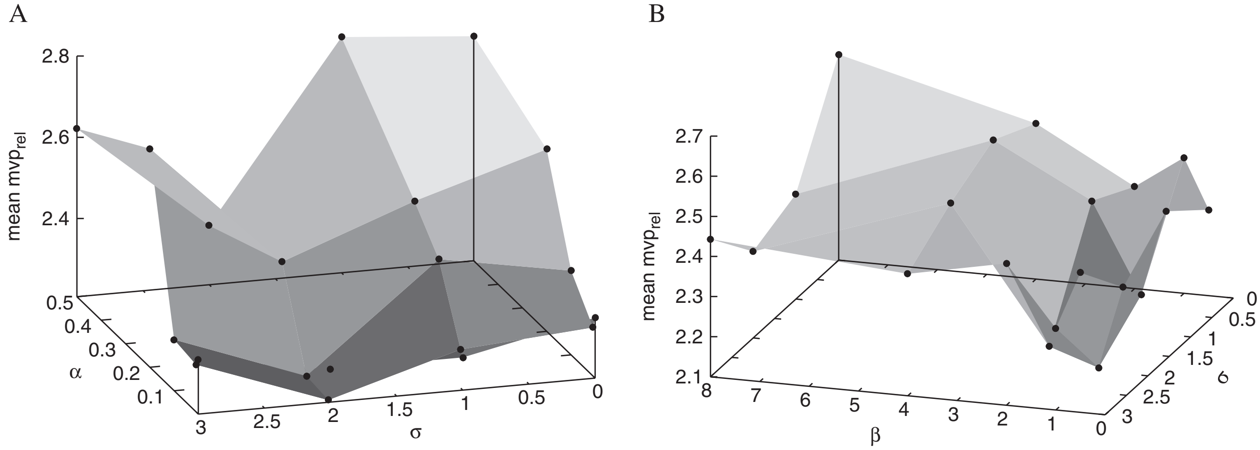

Figure 2. Mean $\mathrm{mvp}_{\mathrm{rel}}$ (of the best 12 strategies of each species) over (A) α and σ and (B) β and σ.

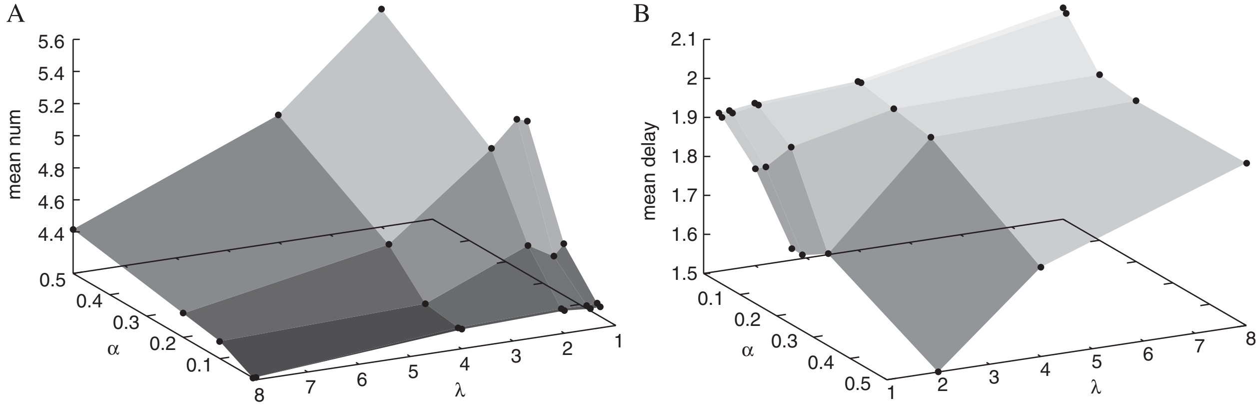

Figure 3. Mean num (A) and mean delay (B) of the best 12 management strategies for different values of α and λ. Note that for technical reasons axes differ in direction between (A) and (B).

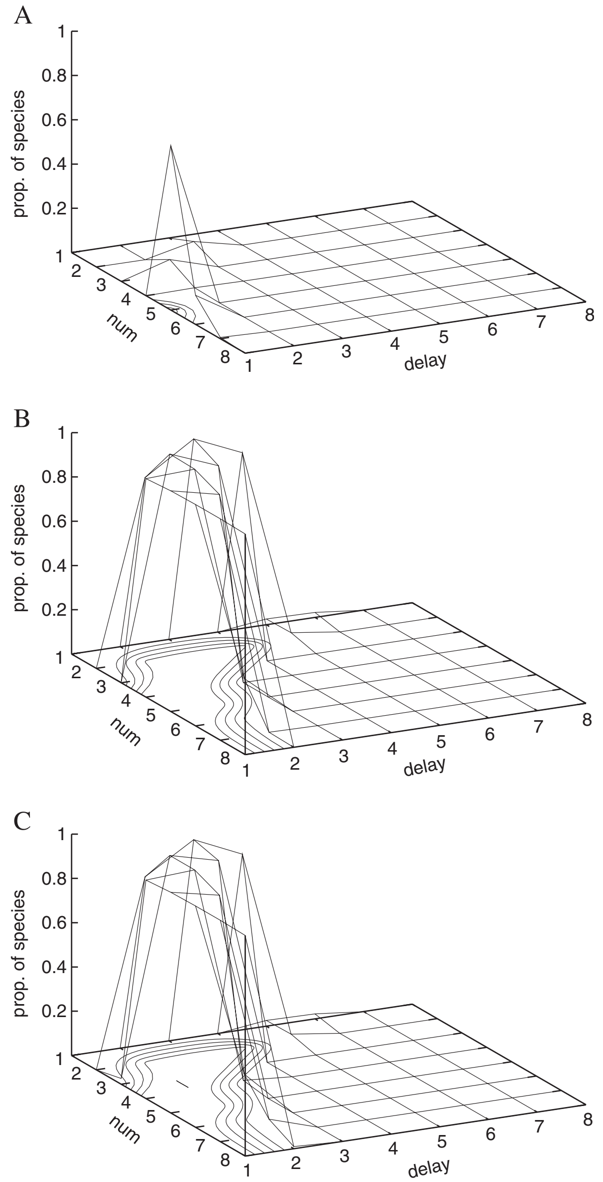

Figure 4. Proportion of good strategies for all management scenarios. (A) For each management strategy the proportion of species which perform best with this strategy is shown. (B) The proportion of species with an $\mathrm{mvp}_{\mathrm{rel}}$ of 3 or lower for the specific combination of *delay* and *num* is shown instead. (C) The same as in (B). but with a threshold of 4 for $\mathrm{mvp}_{\mathrm{rel}}$.

already three different strategies that can successfully protect all species (Fig. 4C). It is necessary to include less optimal strategies, i.e. increase the allowed maximum value of $\mathrm{mvp}_{\mathrm{rel}}$ or to abandon the idea of protecting all species at the same time to get a reasonable number of valid management scenarios (Fig. 5).

Good strategies mostly lie in the area of frequent management in many small sub-areas. This is more or less independent of the species and the maximum allowed $\mathrm{mvp}_{\mathrm{rel}}$ (Fig. 4). Especially for no sub-division of patches (number of areas being (1) there are no successful management strategies.

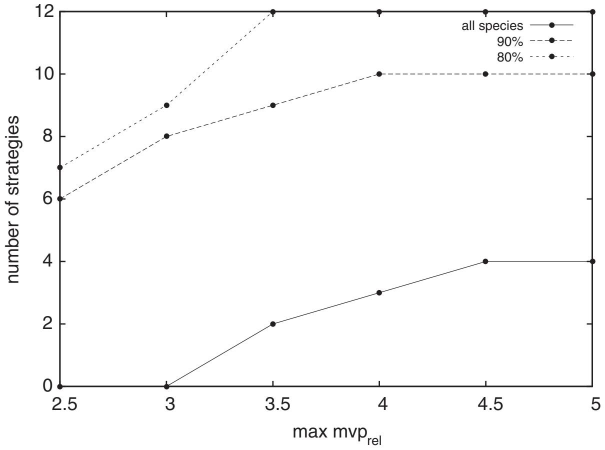

Figure 5. Number of valid strategies depending on different constraints. Lines in the graph show the number of valid management strategies depending on the maximum value of $\mathrm{mvp}_{\mathrm{rel}}$ allowed. Each line corresponds to a different percentage of species below the respective value of $\mathrm{mvp}_{\mathrm{rel}}$.

This distribution can be directly related to the influence of the respective management regimes on local patch capacities K_{tot} and, more specifically, to the strength of fluctuation in patch capacity over time. Good strategies are constrained to an area with high temporal mean of patch capacity K_{tot} (Fig. 6A). But they are also constrained to an area where management prevents too small values of local patch capacity (high minimum of K_{tot}; Fig. 6B). In Fig. 7, relative $\mathrm{mvp}_{\mathrm{rel}}$ is shown against min $K_{\mathrm{tot}}\bar{K}_{\mathrm{tot}}$. In order to filter out differences between species, $\mathrm{mvp}_{\mathrm{rel}}$ values were normalized with the best $\mathrm{mvp}_{\mathrm{rel}}$ of each species. Indeed we can see that nearly all species prefer high values of min K_{tot} and $\bar{K}_{\mathrm{tot}}$. Interestingly this relationship weakens for life histories with strong density dependence together with a high growth rate (crosses in Fig. 7).

Discussion

It could be shown that for all species there are management strategies where the increase in patch capacity needed for survival under cyclic management ($\mathrm{mvp}_{\mathrm{rel}}$) stays below 2.5. If patch size is sufficient to guarantee this capacity, there are no species which cannot cope at all with the kind of patch dynamics simulated. When assessing differences between species however, one has to keep in mind that the required increase in patch capacity

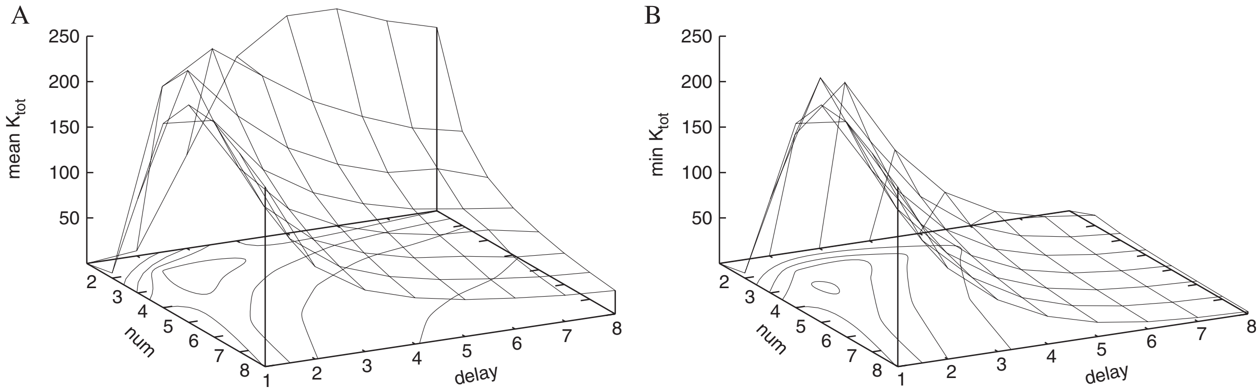

Figure 6. Mean (A) and minimum value of K_{tot} (B) for all management scenarios.

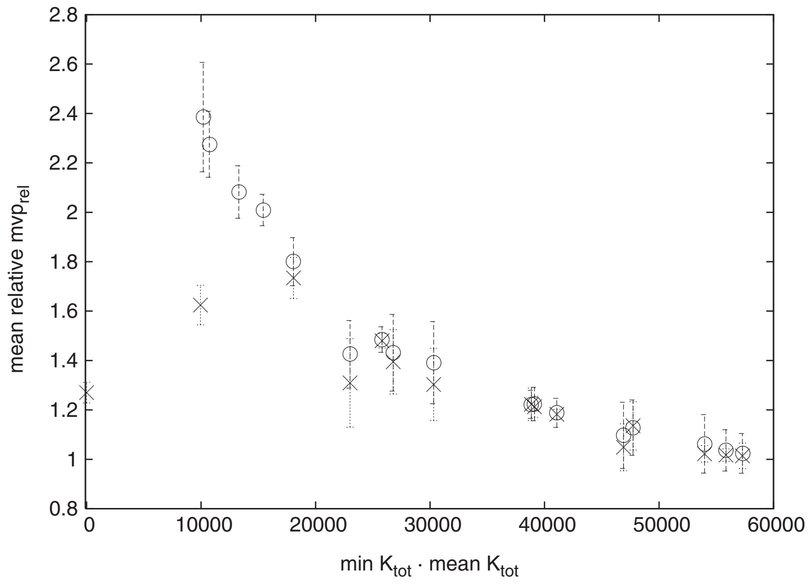

Figure 7. Normalized increase in mvp (see text) shown against minK_{tot} × meanK_{tot} for $\beta \cdot \lambda < 32$ (o) and $\beta \cdot \lambda \geqslant 32$ (x). Standard deviation is indicated by error bars.

(mvp_{rel}) does not map linearly to extinction risk. As Fig. 1B shows an increase in needed capacity by a factor of 2 could mean certain extinction for a population already endangered. If seen on the scale of extinction risk, therefore, there are relatively large differences between species (Fig. 1A).

These differences extend to the species' preferences for different management strategies. Although one single management strategy ($num = 5$, $delay = 1$) is adequate for roughly 70% of the species the remaining 30% vary considerably in their requirements. The reason for this is getting clearer when we look at the properties of the preferred management regimes. A good part of the differences between species can be related to their different reaction to very low minimum capacities which are created either by long delays between management events or by the management of large parts of a patch at a time (see Fig. 6B). This is supported by our findings concerning the effects of life history properties. Low minimum capacities will increase patch extinction rates creating gap effects (Boughton & Malvadkar, 2002) and therefore make the situation difficult for species with bad colonization ability (Amarasekare & Possingham, 2001). Similar to Johst et al. (2002), we were indeed able to show that life histories with a low reproduction rate (λ) and a high Allee effect (α) prefer higher numbers of sub-areas and therefore a higher minimum capacity (Fig. 3).

On the other hand, there are life histories which are not significantly affected by low minimum capacity. These are very fertile (high λ) species with intense intraspecific competition (high β and therefore high realized reproduction rates at low densities (see Eq. (1)). This indicates that another detrimental effect of a low number of areas could be sudden increases in patch capacity: Species with a low (realized) reproduction rate are not able to follow this growth in capacity and therefore effectively experience a lower mean capacity and thereby an increased extinction risk.

Contrary to Heino and Sabadell (2003), we did not find any negative effects of high competition as caused by overshooting and undershooting population dynamics. In a limited way, our system is comparable to a correlated noise scenario. A lower number of areas hereby causes weaker temporal correlations in carrying capacity $\min K_{\text{tot}} \ll \bar{K}_{\text{tot}}$. Petchey et al. (1997) found that species with a high competition parameter (β) prefer strongly correlated fluctuations while reproduction rate (λ) had no influence on the reaction to noise. Our results show the opposite effect with species with a low competition factor (β) and/or a low reproduction rate (λ) clearly not being favoured by temporally uncorrelated changes in patch capacity. A possible reason for these differences might be the lack of dampening effects of dispersal in the model by Petchey et al. (1997).

What do our results imply for the application of management measures? It is difficult to assess the *absolute* quality of a management scenario. Although we can predict which extinction risk will be the consequence of a specific patch size with a particular management strategy, the conversion of the patch capacity K in the model to real world patch sizes and vice versa can be difficult. Furthermore, the kind of successional habitat considered in this study does generally not occur as a static state and all kinds of management measures result in more or less pronounced dynamics (Moog et al., 2002). In order to compare a given "real world" scenario with cyclic management, however, it is necessary to translate this scenario into the model which can accordingly be difficult. Since species differ considerably in their reaction to different treatments (Morris, 2000) caution is required when representing a given situation in the model the same way for different species.

However, there are some general conclusions to be drawn. In comparison to the (hypothetical) homogeneous optimal state, all management strategies which lead to a habitat mosaic in different successional states cause a strong reduction of effective patch capacity. Most species will experience a decrease of 50% ($\text{mvp}_{\text{rel}} = 2$), for many species this reduction will even reach 60–75% (Fig. 5). As mentioned above, even small changes in capacity can lead to big increases in extinction risk (Fig. 1B). Thus, the aforementioned reduction in patch capacity could have dramatic consequences on already endangered populations.

Concerning the evaluation of different management patterns within the framework presented in this paper, more definitive statements can be made. Dependent on their life history properties species show quite different management requirements. Thus optimal management of *all* modelled species at the same time is impossible. The best management strategies are a compromise between the different needs of different species. As was shown they are close to the optimum only for 70% of the species, the remaining 30%, however, may – for these strategies – need more than three times the patch capacity than in an undisturbed habitat (mvp_{rel} of up to 3.5). Compared to their specific "best cyclic management" patch capacity with these compromise strategies has to be increased by 40%.

If seen from an economical perspective, infrequent management of few sub-areas would be most preferable. Unfortunately our results show that only species with high growth rates can cope with this kind of pattern. Contrary to this, management strategies which protect most or all species require annual (*delay* = 1) or bi-annual (*delay* = 2) treatment of small sub-areas as this type of management minimizes fluctuations of local capacity.

Although the results of our model could give some advice concerning optimal management, many additional factors remain to be explored. Dispersal rates may strongly influence metapopulation survival. However, apart from changing the general survival probability, dispersal with different constant rates will probably not influence the relative success of different management strategies drastically. The general inclusion of spatial effects in our model, however, could show some interactions with dispersal rates. The findings by Petchey et al. (1997) indicate that spatially correlated management (which would be economically reasonable) in connection with short-range dispersal could favour management strategies leading to less pronounced fluctuations in population size.

It can be concluded that the general concept of cyclically resetting succession and thereby conserving early successional habitats may help to support the survival of species dependent on these types of habitat. As cyclic management allows to manage only a small fraction of each patch every year (for the scenario with *num* = 5 and *delay* = 1 only 20% of a patch must be rototilled each year), it may allow to reduce the cost of management substantially. However, this will depend on the size of the managed area as well as on local conditions which determine the relative cost of mowing, grazing and rototilling. But in any case the reduced costs of management must be bought with an increase in extinction probability. Our modelling results show certain tendencies but our model is far too simple to derive explicit management directives. The application in real world management plans will demand much more information on the ecology of species. We analyzed the importance of management frequency but timing of management (relative to reproduction and dispersal of species) may have a severe influence on the modelling results, too.

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