Long-Term Persistence of Species and the SLOSS Problem

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The single large or several small (SLOSS) problem has been addressed in a large number of empirical and theoretical studies, but no coherent conclusion has yet been reached. Here I study the SLOSS problem in the context of metapopulation dynamics. I assume that there is a fixed total amount A_0 of habitat available, and I derive formulas for the optimal number n and area A of habitat patches, where $n = A_0/A$. I consider optimality in two ways. First, I attempt to maximize the time to metapopulation extinction, which is a relevant measure for metapopulation viability for rare and threatened species. Second, I attempt to maximize the metapopulation capacity of the habitat patch network, which corresponds both with maximizing the distance to the deterministic extinction threshold and with maximizing the fraction of occupied patches. I show that in the typical case, a small number of large patches maximizes the metapopulation capacity, while an intermediate number of habitat patches maximizes the time to extinction. The main conclusion stemming from the analysis is that the optimal number of patches is largely affected by the relationship between habitat patch area and rates of immigration, emigration and local extinction. Here this relationship is summarized by a single factor ζ, termed the patch area scaling factor.

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Introduction

The acronym SLOSS stands for the phrase single large or several small, referring to the question of whether it would be beneficial for the conservation of species to divide a given total amount of habitat into one large or several small habitat patches. The SLOSS problem has been addressed in a large number of empirical and theoretical studies. However, the objectives, methods and interpretations of these studies have been so distinctive that no coherent conclusion has yet appeared.

Throughout this paper, I will denote by SL and SS the "single large" and "several small"

strategies, respectively. More precisely, SL stands for a strategy where a few (if not just one) large patches are preferred, and SS for a strategy in which a large number of small patches is preferred. I will denote by IN the intermediate strategy, where a compromise between the SL and SS ends of the continuum is optimal.

I will address the SLOSS problem in the context of single-species metapopulation dynamics, assuming that the long-term persistence of the species is based on recolonizations of empty habitat patches by migrants from extant populations. I will seek for the optimal number of habitat patches with two specific objectives in mind. First, I attempt to maximize the time to metapopulation extinction, which is an adequate

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objective for the conservation of rare species. Second, I attempt to maximize the metapopulation capacity of the habitat patch network. As shown by Hanski & Ovaskainen (2000), metapopulation capacity sets the deterministic threshold condition for persistence, and thus maximizing metapopulation capacity is equivalent with minimizing the risk of deterministic extinction. In addition, maximizing metapopulation capacity corresponds with maximizing the average fraction of occupied patches (Hanski & Ovaskainen, 2000), and it relates thus to maximizing the abundance of the species.

I start by discussing the existing SLOSS literature according to the objective assigned for the SLOSS problem. A sample of the literature is summarized in Table 1.

1. *Maximize the number of species that will eventually survive*: From the conservational point

TABLE 1

Sample of the SLOSS literature according to the objective assigned for the SLOSS problem: (1) *maximize the number of species that will eventually survive*, (2) *maximize the number of currently occurring species*, (3) *maximize time to extinction*, (4) *maximize metapopulation capacity.*

Type of study	Objective	Conclusion	Reference
Biogeographical theory, birds in islands	1	SL	Diamond (1975)
Biogeographical theory	1	SL	May (1975)
Biogeographical theory	1	SL	Wilson & Willis (1975)
Biogeographical theory	1	SL	Diamond & May (1976)
Arthropods in experimental islands	2	SS	Simberloff & Abele (1976)
Higher plants in quarry reserves	2	SS	Higgs & Usher (1980)
Birds in islands	2	IN	Gilpin & Diamond (1980)
Literature study	2	SS	Simberloff & Abele (1982)
Vascular plants in deciduous woods	2	SS	Järvinen (1982)
Mammals in islands	2	SL	Patterson & Atmar (1986)
Birds in islands	2	SL	Patterson (1987)
32 data sets of different taxa	2	SS	Quinn & Harrison (1988)
Vascular plants in islands	2	SL	Deshaye & Morriset (1989)
Vascular plants in woodlots	2	SS	Dzwonko & Loster (1989)
Vascular plants in woodlots	2	SS	Zacharias & Brandes (1990)
Birds in woodlots	2	SL	Blake (1991)
27 data sets of different taxa	2	SLOSS	Wright & Reeves (1992)
Vascular plants in deciduous woods	2	SS	Sætersdal (1994)
10 data sets of different taxa	2	IN	Lomolino (1994)
Butterflies in forest fragments	2	SS	Baz & Garcia-Boyero (1996)
Small mammals in mountaintop "islands"	2	SS	Skaggs & Boecklen (1996)
148 data sets of different taxa	2	SS	Boecklen (1997)
Vascular plants in mires	2	SS	Virolainen *et al.* (1998)
Vascular plants in woodlots	2	SS	Honney *et al.* (1999)
Analytical model	3	SL	Wright & Hubbell (1983)
Analytical model	3	SL or IN	Quinn & Hastings (1987)
Stochastic simulation model	3	SL	Burkey (1989)
Experiment with *Drosophila* flies	3	SL	Forney & Gilpin (1989)
Analytical model and five data sets	3	SL	Burkey (1995)
Experiment with bacteria and protozoa	3	SL	Burkey (1997)
Stochastic simulation model	3	SLOSS	Pelletier (2000)
Analytical model	3	SL	Etienne & Heesterbeek (2000)
Analytical model	3	IN	Present study
Analytical model	4	IN	Etienne & Heesterbeek (2000)
Analytical model	4	SL	Present study

*The abbreviations SL and SS stand for the "single large" and "several small" strategies, respectively, and the abbreviation IN stands for an intermediate strategy.

of view, the most natural definition of the SLOSS problem is to ask which kind of network would ensure the long-term persistence of the largest number of species. In spite of its fundamental importance, this question has been addressed almost solely in the beginning of the SLOSS debate. In their seminal works, Diamond (1975), May (1975) and Wilson & Willis (1975) approached this question through the theory of island biogeography (MacArthur & Wilson, 1967), the species–area curve and exponentially distributed relaxation times. The authors gave support for the SL strategy, reasoning that many species that would have a good chance of surviving in a single large reserve would have their survival chances reduced if the same area were apportioned among several smaller reserves. These studies did not account for metapopulation dynamics, i.e. that a network of habitat patches may buffer the species against extinction by allowing for recolonizations of empty habitat patches by migrants from extant populations.

Simberloff & Abele (1976) conducted an experimental study in a mangrove island archipelago, and found out that an SS network contained more species than an SL network, and questioned the earlier results. Terborgh (1976) noted that the objectives of these two studies had been different: in the experiment of Simberloff & Abele (1976), there was a mainland acting as a continuous source of migrants, whereas the studies based on the theory of island biogeography had assumed that all habitat outside of the nature protection network would be lost. The debate continued, but the original question was almost forgotten. Only recently, the interest has returned to the question of maximizing the number of species that will eventually survive (Cabeza & Moilanen, 2001).

2. *Maximize the number of currently occurring species*: Like the pioneering study of Simberloff & Abele (1976), most empirical SLOSS studies have compared whether an SL or an SS habitat patch network currently contains more species, not considering whether the species will survive or not. The majority of these studies has concluded that SS is the better strategy, but there are also exceptions (Table 1). The most coherent conclusion from these studies is that

the result depends on the level of nestedness (Simberloff & Mertin, 1991; Bolger *et al.*, 1991; Wright & Reeves, 1992). A biota is said to exhibit a nested pattern if species compositions from species poor samples are largely subsets of those from species rich samples (Patterson, 1987). If the biota is highly nested, small habitat patches typically contain species that are found as a subset of species present in a large habitat patch, and consequently SL is found to be the better strategy. However, if the biota is not highly nested, SS tends to maximize the number of species.

Though comparing whether an SL or an SS network contains more species has an interest in itself, it has been criticized that the numerous studies on this topic do not really contribute to the design of nature conservation networks. Cole (1981) argued that many of the empirical studies finding the SS strategy to be better were influenced by a mainland acting as a source. If the mainland would not be protected, many of the species in the small habitat patches would be lost. It has also been questioned whether it is simply the species number that matters, or whether one should weigh the species in one way or another. For example, in a study of vascular plants in fragments of old-growth forests, Fukamachi *et al.* (1996) found that the maximum number of species was achieved by the SS strategy, but most of the rarest species were found solely in the largest forest patches.

3. *Maximize time to extinction*: Much of the theoretical SLOSS literature has focused on maximizing the persistence time of a single species. The models have been typically based on some specific type of local dynamics connected by some specific type of metapopulation dynamics. Most of these studies have concluded that the SL strategy is optimal (Table 1). It is, however, important to note that this conclusion depends critically on the underlying causes of local extinctions (see, e.g. Quinn & Hastings, 1987; Etienne & Heesterbeek, 2000). Let me illustrate by considering two extreme cases. First, if local extinctions are caused solely by demographic stochasticity, the lifetime of a local population scales exponentially with the number of individuals (Goel & Richter-Dyn, 1974) and thus (assuming constant density) exponentially

with the size of the habitat patch. Almost independent of the type of metapopulation dynamics, this assumption will favour the SL strategy. The other extreme is to assume that local extinctions are caused solely by catastrophic events, which always kill the local population independent of its size. This assumption is likely to lead to the SS strategy, as now the risk of extinction should be spread among a large set of small populations. Another important factor is the type of metapopulation dynamics assumed. If there is no migration between habitat patches, recolonizations are not possible, and practically all that matters are the lifetimes of local populations, favouring the SL strategy. The only factor that could favour the SS strategy is that a large number of patches provides a large number of independent populations, and the metapopulation is extinct only after all of the patches have become extinct. However, this advantage is likely to be negligible as compared to the advantages of the SL strategy. In contrast, if migration is included, the possibility of recolonizations may change the result completely, now in favour of the SS strategy.

For example, Quinn & Hastings (1987) assumed no migration between habitat patches. They found that if extinctions are caused by demographic stochasticity, SL is a better strategy once local populations reach a small threshold size. If local extinctions were caused by environmental stochasticity, Quinn & Hastings (1987) found that the time to extinction is maximized when the number of habitat patches equals the square root of the number of individuals potentially inhabiting them, suggesting an IN strategy. Burkey (1989) and Wright & Hubbell (1983) modelled migration between habitat patches, but assumed solely demographic stochasticity, concluding that SL is the optimal strategy.

An exception to the general pattern was given by Pelletier (2000), who concluded that SS is the optimal strategy if migration is not allowed for, even if local population dynamics are driven solely by demographic stochasticity. Pelletier (2000) derived his conclusions from a stochastic simulation model, but as he did not specify the details of the model, it is not possible to assess the reason for the unexpected result. Pelletier (2000) found that SL is the optimal strategy if migration with high mortality is assumed. This is to be expected, as in this case the loss of emigrating individuals is not compensated by immigration, and a large patch is expected to have a low per capita emigration rate. Assuming a lower mortality level, he concluded that neither of the SL nor the SS strategies is optimal, but the species persistence is maximized by a self-similar distribution of patch sizes.

Etienne & Heesterbeek (2000) based their analysis on the plausible assumption that, for a fair comparison, SL, IN and SS networks should have the same density of habitat. As Etienne & Heesterbeek (2000) restricted their analysis to nearest-neighbour dispersal, this assumption entails that larger patches have larger interpatch distances. Assuming further that dispersal success decreases exponentially with distance, Etienne & Heesterbeek (2000) concluded that close to the SL end of the continuum, the time to metapopulation extinction is roughly given by the lifetime of a local population, in which case the SL strategy is optimal. However, the verbal argument of Etienne & Heesterbeek (2000) essentially ignores the possibility that metapopulation level dynamics may compensate what is lost at the level of local population dynamics.

There appear to be no field studies that would have addressed the persistence time of a single species in the SLOSS context. In experimental laboratory studies, both Forney & Gilpin (1989) and Burkey (1997) found that the SL strategy is optimal for maximizing the time to extinction. This is consistent with the theoretical studies in the sense that the effect of environmental stochasticity is likely to be low in laboratory studies.

4. *Maximize metapopulation capacity*: Hanski & Ovaskainen (2000) considered a deterministic metapopulation model with variation in patch areas and connectivities. They concluded that metapopulation persistence is possible only if the metapopulation capacity of the landscape is greater than the ratio of extinction and colonization rate parameters, that is, if $\lambda_M > \delta$ holds, where λ_M is the metapopulation capacity of the landscape and $\delta = e/c$ is a species parameter determined by the extinction and colonization

rate parameters e and c, respectively. Metapopulation capacity is a landscape index, which characterizes the ability of a habitat patch network to support a viable metapopulation of the focal species. The metapopulation capacity of a particular landscape depends on the spatial scale at which the focal species migrates, but is independent of the extinction and colonization rate parameters of the species. As a first approximation, it may be considered to measure the amount of habitat available, but in addition it takes into account the actual spatial configuration of the habitat patch network. Metapopulation capacity increases with increasing number of habitat patches, with increasing sizes of habitat patches, and with decreasing inter-patch distances. A related and widely used concept in epidemiology is the basic reproductive ratio R_0, which has been called the "colonization potential" in metapopulation theory (Etienne & Heesterbeek, 2000), and is given by $R_0 = \lambda_M/\delta$. R_0 gives the expected number of colonizations that a single occupied habitat patch will generate during its lifetime in an initially empty network, the threshold condition for persistence being given by $R_0 > 1$.

Maximizing the metapopulation capacity λ_M is equivalent to maximizing the species abundance (in the sense of a weighted fraction of occupied patches p^* at equilibrium), as the two quantities are related as $p^* = 1 - \delta/\lambda_M$ (Hanski & Ovaskainen, 2000; Ovaskainen et al., 2002). As will be shown below, maximizing the metapopulation capacity λ_M (or equivalently R_0) differs from maximizing the time to extinction in the sense that the deterministic approach excludes the possibility of extinction due to extinction–colonization stochasticity in the patch occupancy level. The only study that has so far addressed the SLOSS problem with the objective of maximizing metapopulation capacity concluded that an IN strategy would be optimal (Etienne & Heesterbeek, 2000). This conclusion depends strongly on the assumptions that dispersal is restricted to nearest neighbours, and that dispersal success decreases exponentially with distance.

The above classification of the objectives assigned to the SLOSS problem is by no means exhaustive. For example, a possible objective

could be to maintain genetic variation, both over the entire species range, and, if inbreeding depression is important, within local populations. However, it should be clear already by the above discussion that the SLOSS debate is far from being solved, but has rather become increasingly confused. Table 1 illustrates that practically any possible combination of reasoning and conclusion has been used during the 25 years of the SLOSS debate. It is no wonder that Soulé & Simberloff (1986) suggested that the SLOSS issue should be buried as being not useful in designing nature reserves. Their idea was that decisions on reserve area should be based on the minimum area needed to sustain a viable population, habitat diversity, and auto-ecological data. Worthen (1996) also emphasized the need for species- and site-specific information, arguing that "no single index should be expected to distill the informational content of an entire community, let alone predict how it will react to habitat reduction or fragmentation".

In spite of the above pessimism, with which I largely agree, I will use here a single-species metapopulation model to address the SLOSS problem. The main reason for this exercise is not to provide an extra combination of reasoning and conclusion, but rather to draw attention on some key factors that are relevant to the SLOSS framework. My main conclusion is that the optimal solution to the SLOSS problem is determined by the *patch area scaling factor* ζ, which integrates the effect of patch area on metapopulation dynamics. Somewhat less importantly, my "solution" to the SLOSS problem will be that the IN strategy is optimal for maximizing the time to extinction, while the SL strategy is optimal for maximizing the metapopulation capacity.

In the metapopulation context, the SLOSS problem is basically an attempt to find the optimal compromise between the advantages of the SL and SS ends of the continuum. The advantages of the SL end are found at the local scale. The survival chance of a local population, and the number of individuals emigrating out and immigrating in are typically expected to increase with increasing patch size. The two former effects are mostly due to increasing population size with patch area. The advantages

of the SS end are due to the fact that "all eggs are not in the same basket", the extinction risk being spread among a larger set of patches. This advantage is especially strong if local dynamics are assumed to be independent of each other, as in this case the extinction time grows exponentially with the number of habitat patches (Andersson & Djehiche, 1998; Ovaskainen, 2001). Although I will follow this assumption, I note that this is not always the case, as for instance, regional stochasticity may result in a spatially correlated extinction risk, which may greatly increase the risk of metapopulation extinction (Hanski, 1999; Ovaskainen, 2002).

The present work stems from the analysis of Hanski (1996), who assumed that the extinction risk E of a local population depends on patch area A as $E = e/A^{\zeta_{ex}}$, where e is a parameter and ζ_{ex} describes how extinction risk depends on patch area. Hanski (1996) measured the performance of a metapopulation by the average fraction of occupied patches, and used stochastic simulations to illustrate that the optimal size of habitat patches increases with increasing scaling parameter ζ_{ex}. However, it is not only the extinction risk that scales with patch area, but also the processes of immigration and emigration (for empirical examples, see e.g. Moilanen et al., 1998; Hanski et al., 2000; Ovaskainen, 2002). I will extend the result of Hanski (1996) by showing that the optimal size of habitat patches depends on the patch area scaling factor $\zeta = \zeta_{im} + \zeta_{em} + \zeta_{ex}$, where the three terms indicate how the key metapopulation processes, namely immigration, emigration, and extinction of local populations, scale with patch area.

I will start by formulating a metapopulation model (the spatially realistic Levins model), which I will then use to address the SLOSS problem. Finally, I will attempt to estimate the realistic range of the patch area scaling factor ζ from the available data.

The Model

I assume that there is a fixed total amount A_0 of habitat available, and I attempt to derive a formula for the optimal number n and area A of habitat patches, where $n = A_0/A$. I consider "optimality" in two ways: in the sense of maximal metapopulation capacity and in the sense of maximal time to metapopulation extinction.

Although I concentrate on a spatially homogeneous case, meaning that all patches are assumed to be identical and equally connected to each other, it is instructive to start with a spatially structured model. The reason for this is two-fold. First, it is not only the patch sizes that matter in the SLOSS context, but also the interpatch distances, and the latter cannot be addressed without a spatial settings. Second, real patch networks are not homogeneous, but typically show great variations in patch size and connectivity. Although I restrict my analysis to the homogeneous case, the results may be generalized to heterogeneous patch networks (see below).

I will consider the spatially realistic Levins model (Hanski & Ovaskainen, 2000; Ovaskainen & Hanski, 2001), where the phrase "spatially realistic" means that the model accounts for patch areas and locations, but ignores any further details of the spatial configuration of the habitat patch network. The model belongs to the class of patch occupancy models, in which patches are classified simply as empty or occupied. Instead of explicitly modelling local population dynamics, the extinction and colonization rates are directly connected to the spatial structure of the habitat patch network. The extinction rate E_i of an occupied patch i is assumed to be $E_i = e/A_i^{\zeta_{ex}}$, where e is a species-specific extinction rate parameter, A_i is the area of patch i, and $\zeta_{ex} \geqslant 0$ describes how patch area affects the risk of extinction. The reasoning behind this assumption is that the expected population size is larger in a larger patch, and that the risk of extinction generally decreases with population size. The colonization rate C_i of an empty patch i is given by $C_i = \sum_{j \neq i} c_{ij} o_j$, where c_{ij} is the contribution that an occupied patch j makes to the colonization rate of the empty patch i, and $o_j = 1$ if patch j is occupied and $o_j = 0$ if it is empty. I assume that $c_{ij} = c A_i^{\zeta_{im}} A_j^{\zeta_{em}} f(d_{ij})$, where c is a colonization rate parameter, and $\zeta_{im} \geqslant 0$ and $\zeta_{em} \geqslant 0$ describe how patch area affects immigration and emigration, respectively. The function f describes the

dispersal kernel, i.e. the effect of the interpatch distance d_{ij} on migration success. The reasoning behind the assumptions made on the colonization rate are that only occupied patches may contribute to the colonization of an empty patch, that large occupied patches are expected to send more emigrants, and that large empty patches are expected to attract more immigrants. Although I assumed above that all the three scaling factors are positive, it might be possible that some of them are negative. For example, the per capita emigration rate may be greatly larger in small patches, which may lead to $\zeta_{em} < 0$ if the expected population size grows sufficiently slowly with patch size. The assumption that the scaling factors are positive is not needed in the analysis, and the results to be given thus hold also for negative scaling factors.

The model may be considered either in a stochastic or in a deterministic setting. The stochastic version of the model is defined as a Markov process determined by the above extinction and colonization rates, the state space consisting of all the 2^n possible combinations of empty and occupied patches. The deterministic model is defined as the mean-field approximation of the stochastic model, modelling the rate of change in the probability for patch i being occupied as

$$\frac{dp_i}{dt} = \left(\sum_{j \neq i} c_{ij} p_j\right)(1 - p_i) - E_i p_i. \qquad (1)$$

As shown by Ovaskainen & Hanski (2001), the deterministic model predicts that long-term persistence is possible only if the condition $\lambda_M > \delta$ is valid. Here λ_M is the metapopulation capacity of the landscape, which measures the capacity of the habitat patch network to support the persistence of the species. Mathematically, λ_M is given by the leading eigenvalue of the $n \times n$ nonnegative matrix M, the elements of which are defined by $m_{ij} = A_i^{\zeta_{ex}+\zeta_{im}} A_j^{\zeta_{em}} f(d_{ij})$ for $i \neq j$ and $m_{ii} = 0$. Here the factor $A_i^{\zeta_{ex}}$ is proportional to the expected lifetime of the local population in patch i and $A_i^{\zeta_{im}} A_j^{\zeta_{em}} f(d_{ij})$ is proportional to the rate at which immigrants originating from patch j succeed to colonize patch i. The threshold condition for persistence is determined by the

species parameter δ, which is defined as the ratio of the extinction and colonization rate parameters, $\delta = e/c$.

In the rest of the paper, I will restrict the analysis to the homogeneous version of the model. In this case, the extinction rate of an occupied patch reduces to $E = e/A^{\zeta_{ex}}$ and the colonization rate of an empty patch reduces to $C = ckA^{\zeta_{im}+\zeta_{em}} f(d)$, where k is the number of occupied patches. In the homogeneous model, all the n patches are assumed to be at the same distance d from each other. As this assumption is impossible already from the geometric point of view, it is important to make the reasoning behind the assumption precise. As specified above, I do not assume that dispersal is restricted to nearest neighbours only, but I assume that dispersal success reduces gradually with increasing distance. With this assumption, d should be interpreted as the effective dispersal distance between the habitat patches, characterizing typical migration distances within the patch network. Etienne & Heesterbeek (2000) assumed that the fraction of habitat is independent of the size of habitat patches, meaning that the n patches are located within a landscape of fixed size. Restricting dispersal to nearest neighbours, they argued that the interpatch distance d should increase with increasing patch area. Contrary to the study of Etienne & Heesterbeek (2000), I make here the assumption that the effective distance d is independent of the number of habitat patches. Figure 1 demonstrates that, in the present case, this assumption is roughly consistent with the assumption that the n patches are located into a total area of fixed size, illustrating an important distinction between gradually decreasing dispersal success in the present model and the nearest-neighbour dispersal in the Etienne & Heesterbeek (2000) model.

Assuming homogeneity greatly simplifies the analysis of the model, but also restricts the applicability of the results. However, as mentioned above, the results to be given here generalize to heterogeneous habitat patch networks. The reason for this is that metapopulation dynamics in a heterogeneous patch network can be approximated by metapopulation dynamics in a homogeneous patch network with
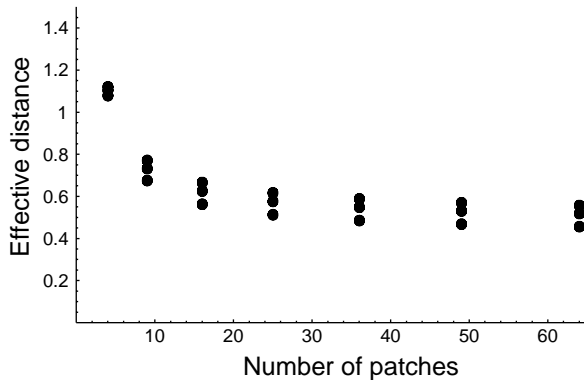
FIG. 1. Dependence of the effective interpatch distance on the number of habitat patches. An $N \times N$ patch network (with $N = 2, ..., 8$) of $n = N^2$ patches was located uniformly in the unit square. The metapopulation capacity of the habitat patch network was calculated with the spatially realistic Levins model, where the dispersal kernel was defined as $f(d) = e^{-\alpha d}$. The dots depict the effective interpatch distance, defined as the distance which gives the same metapopulation capacity for a homogeneous model with equal distances among patches. The parameter α attains the values $\alpha = 1, 2, 4$, corresponding to the dots from top to bottom. The result is independent of the parameter ζ.

appropriately transformed parameter values (Ovaskainen & Hanski, 2001, 2002; Ovaskainen, 2002).

SLOSS

For a homogeneous habitat patch network, the metapopulation capacity is given by

$$\lambda_M = (n - 1)A^{\zeta}f(d), \qquad (2)$$

where the patch area scaling factor $\zeta = \zeta_{im} + \zeta_{em} + \zeta_{ex}$ measures how strongly patch area affects metapopulation dynamics (Ovaskainen & Hanski, 2001). Approximating $n - 1$ by n and substituting $n = A_0/A$ in eqn (2), I obtain

$$\lambda_M \approx A^{\zeta-1}A_0 f(d) = n^{1-\zeta}A_0^{\zeta}f(d). \qquad (3)$$

Equation (3) suggests that if $\zeta > 1$, SL is the optimal strategy for maximizing λ_M, whereas $\zeta < 1$ would lead to the SS strategy. This is to be expected, as $\zeta > 1$ ($\zeta < 1$) indicates that the metapopulation capacity of a patch network grows with patch area faster (slower) than linearly. Equation (3) depends on the approx-

imation $(n - 1)/n \approx 1$, which is not expected to hold for very small n, as illustrated by the fact that $n = 1$ leads to $\lambda_M = 0$. Equation (3) thus actually suggests that for $\zeta > 1$ the metapopulation capacity is not maximized by a single patch, but rather by a small number of habitat patches. This is also evident in Fig. 2, where the value of λ_M attains its maximum either at $n = 2$ or at $n = 3$.

It is worth emphasizing here that the patch area scaling factor ζ integrates the effect of patch area on metapopulation dynamics. It is convenient that metapopulation capacity does not depend separately on the individual components ζ_{im}, ζ_{em} and ζ_{ex}, so that it suffices just to consider the integrated patch area scaling factor ζ.

As the time to extinction is exponentially distributed, we will lose no generality by attempting to maximize the expected time to extinction. The expected time to metapopulation extinction (using the lifetime of a local population as a time unit) behaves for $\lambda_M > \delta$ as (Andersson & Djehiche, 1998; Ovaskainen, 2001)

$$T = \sqrt{\frac{2\pi}{n}} \frac{e^{n(\hat{\delta}-1-\log\hat{\delta})}}{1 - \hat{\delta}} (1 + \mathcal{O}(1/n)), \qquad (4)$$

where $\hat{\delta} = \delta/\lambda_M$ is the scaled species parameter. As the exponential term dominates already with small n, I will simplify the analysis by attempting to maximize

$$g(n, \hat{\delta}) = n(\hat{\delta} - 1 - \log\hat{\delta}). \qquad (5)$$

If $\zeta < 1$, $\hat{\delta} - 1 - \log\hat{\delta}$ is maximized as $n \to \infty$, and thus the SS strategy is optimal. The interesting case occurs if $\zeta > 1$, as in this case there is a trade-off between maximizing the factors n and $\hat{\delta} - 1 - \log\hat{\delta}$ in eqn (5). For a given species (i.e. a given species parameter δ) and fixed amount of total habitat, n behaves [by eqn (3)] as $\hat{\delta}^{1/(\zeta-1)}$. Thus, we should maximize $h(\hat{\delta}) = (\hat{\delta} - 1 - \log\hat{\delta})\hat{\delta}^{1/(\zeta-1)}$. Setting $h'(\hat{\delta}) = 0$, it turns out that the maximum occurs when $(\hat{\delta} - 1)\zeta = \log\hat{\delta}$. This equation cannot be solved analytically, but $\hat{\delta}(\zeta) \approx 1/\zeta^2$ gives a reasonable approximation (Fig. 3). By eqn (3), the optimal
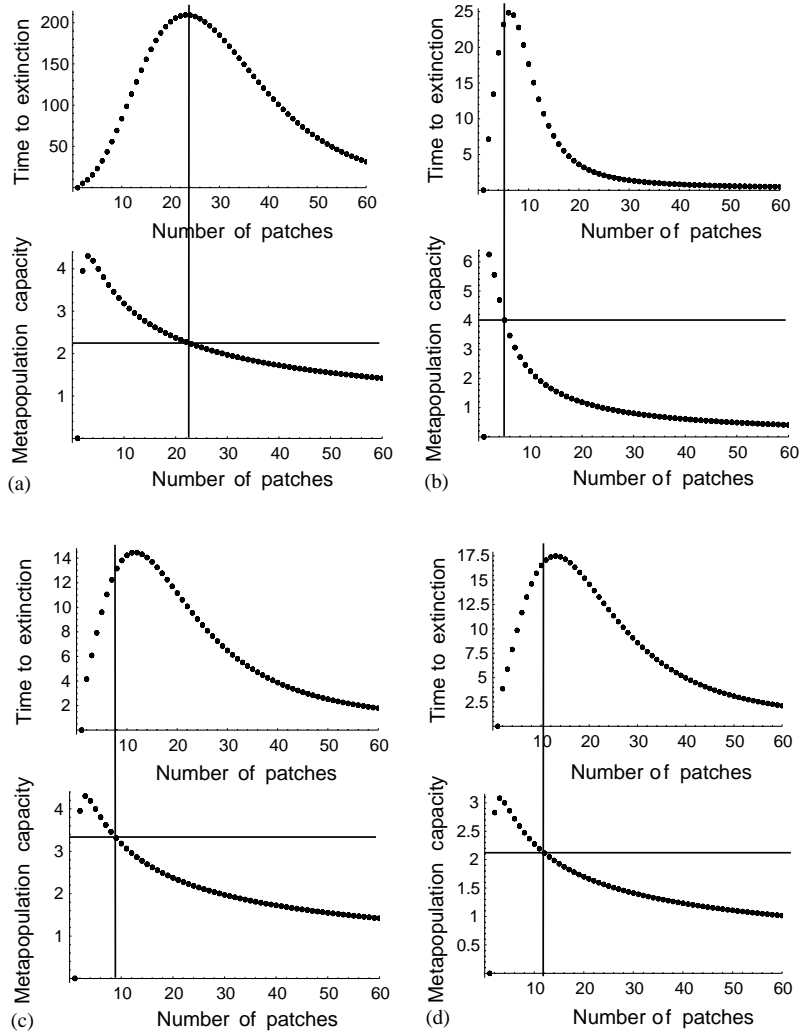
FIG. 2. Dependence of the SLOSS problem on the parameters ζ, δ and A_0. Each panel shows how the metapopulation capacity (lower figure) and the time to extinction (upper figure) depend on the number of habitat patches. Panel a is a reference case with parameters $\zeta = 1.5$, $\delta = 1$, $A_0 = 5$ and $f(d) = 1$. In each of the panels b–d, one of the parameters is changed while all the other parameters are held fixed. The changed parameters are $\zeta = 2.0$ (panel b), $\delta = 1.5$ (panel c) and $A_0 = 4$ (panel d). In each panel, the horizontal line corresponds to $\hat{\delta} = 1/\zeta^2$, the vertical line demonstrating that this roughly coincides with the maximal mean time to extinction.

size and number of habitat patches are given by

$$A \approx \left[\frac{\delta}{\hat{\delta}(\zeta) A_0 f(d)} \right]^{1/(\zeta-1)},$$

$$n \approx \left[\frac{A_0^\zeta f(d) \hat{\delta}(\zeta)}{\delta} \right]^{1/(\zeta-1)}. \qquad (6)$$

Based on eqn (6), I conclude that for $\zeta > 1$:

1. The optimal size of habitat patches increases (and thus their number decreases) with

increasing patch area scaling factor ζ (Fig. 2, panels a and b). This is intuitive, as ζ describes the strength of area dependence in metapopulation dynamics. However, now the result is not as extreme as with maximizing the metapopulation capacity, where $\zeta > 1$ led to the SL strategy. When maximizing the time to metapopulation extinction, the number of habitat patches should always be kept reasonably large to gain the advantages of risk spreading, leading to an IN strategy. The expected time to metapopulation extinction is more sensitive to the number of
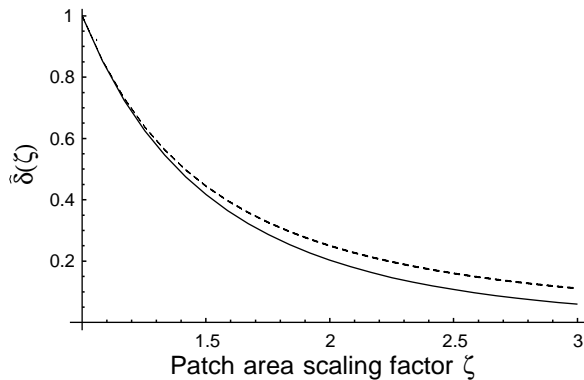
FIG. 3. The exact solution $\hat{\delta}(\zeta)$ to the equation $(\hat{\delta} - 1)\zeta = \log \hat{\delta}$ (solid line) and its approximation $\hat{\delta}(\zeta) \approx 1/\zeta^2$ (dashed line).

habitat patches if ζ is large, as demonstrated by the more narrow peak in the time to extinction curve shown in Fig. 2(b) as compared to that of Fig. 2(a).

2. The optimal size of habitat patches increases with increasing δ (Fig. 2, panels a and c). This may be interpreted as follows. Consider two species, labelled A and B, which are otherwise identical (same f and ζ), but species A has a smaller value of δ, either because it is a better colonizer than B (greater c) or because it persists better as local populations (smaller e) than species B. Thus in the same environment, the abundance of species A is greater than that of species B. With a given amount of habitat available, it would be beneficial to divide the habitat to a larger number of habitat patches for species A than for species B. This makes sense, as we note from eqn (4) that as soon as the scaled species parameter $\hat{\delta}$ is relatively small, the expected time to extinction starts to grow exponentially with the number of habitat patches.

3. The optimal size of habitat patches decreases with increasing A_0 (Fig. 2, panels a and d). This may seem counterintuitive, as one might expect that with a large amount of habitat available, it would be optimal to have a reasonable number of large habitat patches. However, as noted before, eqn (4) predicts exponential growth in time to extinction with the number of habitat patches. Although the metapopulation capacity λ_M decreases with decreasing A, λ_M is still reasonably large for small A if the total

amount of habitat is very large. This implies that the scaled species parameter $\hat{\delta}$ is reasonably small, in which case it is the number of habitat patches that really matters. On the contrary, if the total amount of habitat is small, persistence as a true metapopulation is not likely, in which case it is better to have a few patches that are as large as possible in order to enhance the survival of local populations.

Note that the above analysis is based on the assumption that the metapopulation is above the deterministic threshold, as eqn (4) is based on the assumption $\lambda_M > \delta$. If this is not the case, the metapopulation is expected to go deterministically extinct. As an example, assume that a rapid episode of habitat loss has deteriorated a landscape below the extinction threshold. In such a situation, the time to extinction calculated from the quasi-stationary distribution is not expected to be of major importance, as the quasi-stationary distribution may not be reached at all before extinction. As occupied patches will go extinct, but recolonizations are expected to be rare, it is the initial patch occupancy pattern that really matters. In such a case, large occupied patches are of major importance, as these are expected to delay the inevitable extinction as much as possible.

The Patch Area Scaling Factor ζ

As shown by the above analysis, the optimal solution to the SLOSS problem depends on several factors, most importantly on the patch area scaling factor ζ. A qualitative change occurs at the critical value $\zeta = 1$. I will next discuss factors that affect the value of ζ, considering separately the three components ζ_{ex}, ζ_{im} and ζ_{em}.

1. *Extinction*: It is often difficult to state one clear-cut reason that dominates the extinction risk, as the risk of extinction is determined by several mechanisms, such as demographic stochasticity, environmental stochasticity, catastrophic events, predator–prey or host–parasite interactions, inbreeding depression, ephemeral nature of the habitat, or human influence of various types. The variation that is observed in the value of ζ_{ex} may be explained by differences

in the relative importance of the underlying causes that drive populations to extinction. Indeed, if the extinction risk is determined solely by demographic stochasticity, the extinction probability should decrease exponentially with population size and thus with patch area, if population density is assumed to be constant (e.g. Goel & Richter-Dyn, 1974; Lande, 1993). If the extinction risk originates solely from environmental stochasticity or by random catastrophes, the extinction probability should decrease as a power of the patch area (Lande, 1993; Foley, 1997). Thus, in sufficiently large patches, environmental stochasticity and random catastrophes pose a greater risk of extinction than demographic stochasticity, suggesting that the polynomial form $e/A^{\zeta_{ex}}$ used here is adequate. In small populations, where demographic stochasticity may be of major importance, the polynomial scaling of the extinction risk may be considered to approximate the true exponential scaling if ζ_{ex} is sufficiently high. In line with the above reasoning, Hanski (1992, 1998) has suggested that the value of ζ_{ex} may be used as a measure describing how sensitive the species is to environmental stochasticity, a small value of ζ_{ex} indicating that environmental stochasticity has a large effect on the extinction risk as compared to the effect of demographic stochasticity.

As discussed by Hanski (1992), Cook & Hanski (1995) and Hanski (1998), the parameter ζ_{ex} is among vertebrates often related to the body size of the species; for instance, smaller animals often suffer more from environmental stochasticity because of their sensitivity to temporal variation in food availability. Hanski (1992) reported the values $\zeta_{ex} = 0.46, 0.91, 2.30$ for three species of shrews, Wahlberg et al. (1996) the values $\zeta_{ex} = 0.84, 0.95, 0.96, 0.98$ for four species of butterflies, and Moilanen et al. (1998) the value $\zeta_{ex} = 1.28$ for the American pika. Cook & Hanski (1995) estimated ζ_{ex} for 49 species of birds, the minimum, median, and maximum values being 0.05, 0.75 and 2.10, respectively. However, many of these studies have ignored the effect of patch area on immigration rate, in which case the estimates given above may represent estimates for the sum $\zeta_{ex} + \zeta_{im}$, and may thus overestimate ζ_{ex}. Separ-

ating the effects of ζ_{ex} and ζ_{im}, Ovaskainen (2002) estimated the value $\zeta_{ex} = 0.32$ for a species of butterfly.

2. *Emigration*: The emigration parameter ζ_{em} describes how patch area affects the number of individuals that emigrate from an occupied habitat patch per unit time. The parameter ζ_{em} is influenced by two factors, which are the relation between population size and patch area, and the relation between per capita emigration rate and patch area. Both of these are determined by a number of factors, but it is reasonable to assume that the former increases with patch area, whereas the latter decreases with patch area. For example, in a study of a butterfly metapopulation, Hill et al. (1996) concluded that the per capita emigration rate was significantly higher in small patches, but that in absolute numbers more emigrants came from the largest patches where the source population was the largest. In a study of a field vole archipelago metapopulation, Crone et al. (2001) concluded that emigration from tiny, ephemeral skerry populations was about as important as emigration from more persistent populations on large islands. The pattern resulted from less stable vole densities on smaller islands, combined with increased emigration before local extinction. Note that although the per capita emigration rate may depend on the density of individuals, I assume here that population density depends on patch area, and thus the per capita emigration rate is a function of patch area.

As a theoretical remark, I note that the value $\zeta_{em} = 0.5$ would follow by assuming that population density is independent of patch size, and that the probability for an individual to emigrate is proportional to the ratio of boundary length and patch area. Moilanen et al. (1998) reported the value $\zeta_{em} = 0.74$ for the American pika, and Ovaskainen (2002) estimated the value $\zeta_{em} = 0.28$ for a species of butterfly.

3. *Immigration*: Much of the theoretical metapopulation literature assumes that the immigration rate is independent of patch area, corresponding to $\zeta_{im} = 0$. However, it is clear that patch area may have an effect on immigration rate. Large patches are easier to find, they are possibly more attractive for migrants, and the probability of successful colonization per

attempted colonization may be greater. Assuming that the localization of an empty patch is the main factor affecting ζ_{im}, and assuming that dispersing individuals search for patches along straight lines at the local scale around a habitat patch would lead to the scaling $\zeta_{im} = 0.5$ As species exhibit a wide variety of dispersal strategies, including the possibility of detecting habitat patches from a distance, it is clear that the scaling factor may vary greatly among species. Hanski *et al.* (2000) reported the scaling 0.26 for a species of butterfly, but they considered only whether the individuals were able to locate the habitat patch, thus neglecting whether they attempted colonization or if that attempt was successful. Ovaskainen (2002) restricted his analysis to succesful colonizations, and estimated the value $\zeta_{im} = 0.44$ for another species of butterfly.

Although current empirical knowledge about the scaling factors is admittedly very limited, the reasoning above suggests that in a "typical" metapopulation, the value of ζ would be in the range $1.0 < \zeta < 2.0$. In the context of the SLOSS problem, I thus conclude that in a "typical" case, SL is the optimal strategy to maximize the metapopulation capacity of a habitat patch network, whereas IN maximizes the expected time to metapopulation extinction.

Discussion

I have addressed the SLOSS problem from the viewpoint of classical metapopulation dynamics. Assuming that long-term persistence of the focal species is based on compensation of local extinctions by recolonizations, I have shown that the time to extinction is maximized with the IN strategy, whereas the metapopulation capacity of a patch network is typically maximized with the SL strategy. The location of the optimum point along the SL to SS axis is largely determined by the patch area scaling factor ζ, the optimum moving towards the SL end with increasing ζ. The patch area scaling factor ζ integrates the effects of patch area on metapopulation dynamics, including the processes of immigration, emigration and local extinction.

Metapopulation capacity λ_M sets the threshold for persistence as $\lambda_M > \delta$, where δ is a species parameter. Below the threshold, the species is expected to go deterministically extinct, meaning that the drift affecting the patch occupancy state is negative. The other quantity considered in this study, time to metapopulation extinction, is a stochastic quantity, with the mean value not depending only on the drift term but also on the variance around the mean. If the number of habitat patches is large the variance is small and thus the time to extinction is smaller than in an otherwise similar situation with a small number of habitat patches. Thereby, the time to extinction, unlike metapopulation capacity, accounts also for the advantages of risk spreading, leading to a strategy towards the SS end of the SLOSS continuum.

I have considered a homogeneous metapopulation model, which assumes that all habitat patches are identical and equally connected. Most real habitat patch networks are not homogeneous. The justification for restricting the present study to the homogeneous case is that the behaviour of an appropriately weighted average of the occupancy state in a heterogenous patch network is often well approximated by a homogeneous model (Ovaskainen & Hanski, 2001, 2002; Ovaskainen, 2002). Hence, the present results generalize to heterogeneous patch networks, where the question is to optimize the average size (and thus number) of habitat patches. At the optimum, the scaled species parameter $\hat{\delta}$ satisfies approximately $\hat{\delta}(\zeta) \approx 1/\zeta^2$. Comparing the scaled species parameter (which can in an equilibrium situation be estimated from a snapshot of occupancy data; Hanski & Ovaskainen, 2000) with the patch area scaling factor gives a rough way of estimating whether the survival of the species suffers more from the smallness or from the fewness of the habitat patches. If $\hat{\delta}(\zeta) < 1/\zeta^2$, the critical factor is the number of patches, whereas for $\hat{\delta}(\zeta) > 1/\zeta^2$ the critical factor is the average patch size.

One of the main assumptions of the present model is that metapopulation processes scale as a power of patch area. While this is likely to be a reasonable assumption even for networks with considerable variation in patch areas (Hanski, 1999), it is clear that the range of patch areas

over which the assumption is valid has a limit. This is illustrated in Fig. 4, where I show the probability that a local population of a hypothetical species would go extinct in unit time. The extinction probability is shown over a wide range of patch areas as emphasized by the logarithmic scale in the *x*-axis. As ζ_{ex} measures how sensitive the extinction rate is to patch area, a deep slope in Fig. 4 corresponds to a high value of ζ_{ex}. The dashed lines classify the patch sizes to four different classes. In size class *A*, the patches are so small that they are unable to support a local population. In size class *B*, the patches are large enough to support a local population, but the expected population size is so small that demographic stochasticity is expected to be one of the main risks of extinction. In this size class, the extinction probability is very sensitive to patch area and consequently ζ_{ex} is large. In size class *C*, the patches are so large that the probability of extinction due to demographic stochasticity is negligible, and the main cause of extinction is due to environmental stochasticity. For example, several consecutive years with adverse environmental conditions may be needed to cause a local extinction. Patch size has an effect on the extinction risk, but the effect is much milder than in size class *B*, and consequently ζ_{ex} is lower. In size class *D*, the habitat patches are large enough to buffer the species against environmental stochasticity, and the extinction risk is now largely determined by catastrophes. For example, human land use practices may change in such a way that the species cannot persist anymore. In this size class, the extinction probability is almost independent of patch size, corresponding to a very low value of ζ_{ex}. The metapopulation approach taken in this paper is most appropriate for networks with patches from the intermediate size classes (*B* and *C* in Fig. 4), as in such networks local extinctions and recolonizations are expected to be a regular part of regional scale dynamics.

There are several reasons why the conclusions of the present study should be interpreted with caution even for species which persist as classical metapopulations at the spatial scale that is relevant to the problem setting. Most importantly, the model assumes that the extinction
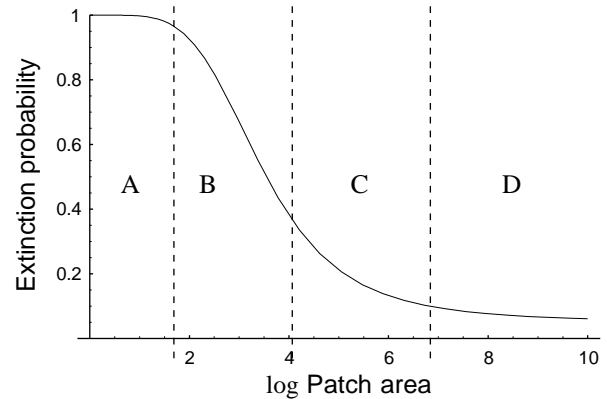

FIG. 4. A qualitative plot of the local extinction probability of a hypothetical species over a wide range of patch areas. The letters *A*, *B*, *C* and *D* refer to different size classes, for which the main risks of local extinction are different.

rates in the different habitat patches are not temporally or spatially correlated, which is a critical assumption for the exponential scaling of the mean time to extinction with respect to *n*. Interpatch correlation in extinction or colonization rates could drastically reduce the effective number of habitat patches (Ovaskainen, 2002). In such a case the extinction of the metapopulation is most likely to occur when multiple extinctions happen simultaneously (Harrison & Quinn, 1989).

Most species are not likely to follow classical metapopulation dynamics, or at least the spatial scale over which they do so is limited. Nevertheless, due to habitat loss and fragmentation, most populations are increasingly patchy at all spatial scales, and metapopulation dynamics are likely to play an increasingly important role in conservation biology (Hanski, 1999). The main contribution of the present study to the SLOSS debate is the demonstration that the effects of patch area on emigration, immigration and extinction should be considered while assessing the relative advantages of a large number of small patches vs. a small number of large patches.

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