

Why are metapopulations so rare?

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Abstract. Roughly 40 years after its introduction, the metapopulation concept is central to population ecology. The notion that local populations and their dynamics may be coupled by dispersal is without any doubt of great importance for our understanding of population-level processes.

A metapopulation describes a set of subpopulations linked by (rare) dispersal events in a dynamic equilibrium of extinctions and recolonizations. In the large body of literature that has accumulated, the term “metapopulation” is often used in a very broad sense; most of the time it simply implies spatial heterogeneity. A number of reviews have recently addressed this problem and have pointed out that, despite the large and still growing popularity of the metapopulation concept, there are only very few empirical examples that conform with the strict classical metapopulation (CM) definition.

In order to understand this discrepancy between theory and observation, we use an individual-based modeling approach that allows us to pinpoint the environmental conditions and the life-history attributes required for the emergence of a CM structure. We find that CM dynamics are restricted to a specific parameter range at the border between spatially structured but completely occupied and globally extinct populations. Considering general life-history attributes, our simulations suggest that CMs are more likely to occur in arthropod species than in (large) vertebrates.

Since the specific type of spatial population structure determines conservation concepts, our findings have important implications for conservation biology. Our model suggests that most spatially structured populations are panmictic, patchy, or of mainland–island type, which makes efforts spent on increasing connectivity (e.g., corridors) questionable. If one does observe a true CM structure, this means that the focal metapopulation is on the brink of extinction and that drastic conservation measures are needed.

Key words: dispersal evolution; fixation index; habitat fragmentation; life-history; metapopulation; occupancy; spatially structured population; turnover.

INTRODUCTION

The number of scientific articles, edited volumes, and books on metapopulation biology has steadily increased over the last decades, which indicates a large and persistent interest in this topic (Hanski and Gaggiotti 2004). A search for the key word “metapopulation” in the database “ISI Web of Knowledge” reveals over 13 000 papers since the 1980s. Since the mid 2000s a steady stream of ~400 articles related to metapopulation biology is published every year.

This interest is not purely academic. A central topic in metapopulation biology is the study of extinctions and recolonizations. Therefore, it is of no surprise that the metapopulation concept has frequently been applied in conservation biology (see e.g., Alvarez-Buylla et al. 1996, Hanski et al. 1996, Kuussaari et al. 2009). Yet in a

large number of publications, the term “metapopulation” is loosely defined and used in an unspecific way. It appears problematic to use a concept that originates from theoretical work in applied research fields such as conservation biology without being stringent about definitions (Elmhagen and Angerbjörn 2001).

The term “metapopulation” was coined by Richard Levins in the early 1970s. With his studies on optimal pest control (Levins 1969) and on between-population selection (Levins 1970), he introduced the idea of a “population of populations.” Note that similar ideas were applied by MacArthur and Wilson (1967) to develop their theory of island biogeography (Hanski 2010). Even earlier descriptions of spatial population structure and fragmentation can be found in Andrewartha and Birch (1954) and Curtis (1956). In general, a metapopulation describes a set of subpopulations linked by (rare) dispersal events in a dynamic equilibrium of extinctions and recolonizations (Hanski and Gilpin 1991, Hanski 1999). Yet not all spatially structured populations (SSP) are classical metapopulations (CM)

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sensu stricto. In contrast to mainland–island systems (Harrison 1991), a CM is thought to have subpopulations of roughly similar size. These subpopulations should be coupled by just enough migration to avoid complete isolation on the one hand, but on the other hand not too much migration, which would lead to a single panmictic population. Of course, CMs built of identical patches in terms of population size and mainland–island systems are only two extreme examples of SSPs. Yet note that the resulting (evolutionary) dynamics may be completely different (e.g., Poethke et al. 2011).

Following Hanski et al. (1995), four conditions have to be fulfilled by a CM: (1) each discrete habitat patch must be able to support a breeding population; (2) in contrast to mainland–island metapopulations, any subpopulation must be prone to extinction; (3) recolonization has to be possible; (4) subpopulation dynamics are asynchronous in order to avoid the extinction of the entire metapopulation. Following this definition, CMs can be clearly distinguished from other SSPs like mainland–island, source–sink, patchy, and nonequilibrium metapopulations (Harrison 1991). Mainland–island metapopulations imply that some habitat patches are orders of magnitude larger than others. Usually, large mainland populations serve as source populations from which the smaller populations may be recolonized (Morrison 1998). Note that in contrast to source–sink systems (Pulliam 1988), habitat quality is assumed to be similar in all patches. True sink populations are characterized by a significantly reduced fitness of the focal species that would not allow the persistence of the populations on its own (for an example see Gaona et al. [1998]). A patchy population can be thought of as a set of habitat patches linked by such high levels of dispersal that local extinctions are prevented (by a rescue effect) and no genetic structure can be found (for an example see Sweanor et al. [2000]); such a population is panmictic. Finally, nonequilibrium metapopulations may be declining or expanding with respectively more or less frequent extinctions than recolonizations.

Evidence of proper CMs in the field remains scarce. In general, recent reviews find few examples for CMs (Elmhagen and Angerbjörn 2001, Baguette 2004, Driscoll 2007; but see Hanski [2004]). Most of these examples come from range margins. It has even been suggested that the observed turnover has nothing to do with classical metapopulation dynamics (Baguette 2004; but see Hanski [2004]): marginal populations often have higher extinction than colonization rates but are sustained by migrants from core areas (Holt and Keitt 2000, Holt et al. 2005).

The most prominent metapopulation is certainly the Glanville fritillary *Melitaea cinxia* (Hanski et al. 1994), which has inspired a large number of researchers. However, it appears to be the only unequivocal example. Other populations that have been invoked as CMs remain controversial, e.g., the cranberry fritillary

Boloria aquilonaris (Mousson et al. 1999), which shows a declining nonequilibrium structure in one landscape and an occupancy of nearly 100% in an other (discussed in Baguette 2004), or the American pika *Ochotona princeps* (Peacock and Smith 1997, Smith and Gilpin 1997, Moilanen et al. 1998), where the occupancy pattern employed to identify the focal population as a metapopulation could be reproduced in simulations using a completely different mechanism (spatially correlated extinctions) (see Clinchy et al. 2002).

Hence, true CMs seem to be rare in nature (Harrison and Hastings 1996, Harrison and Taylor 1997, Driscoll 2008, Driscoll et al. 2010), a fact that should lead to reflections about the relevance of the metapopulation concept, especially in such applied areas as conservation biology. Note that similar empirical results, indicating that metapopulations are rare, also exist for plant species (Quintana-Ascencio and Menges 1996).

Here, we provide a possible explanation for this discrepancy between theory and nature. We use an individual-based modeling approach, which allows us to pinpoint the environmental conditions and the life-history attributes required for the emergence of a CM structure. Following the CM definition laid out previously (Hanski et al. 1995) and by many others (e.g., Reich and Grimm 1996, Hanski 1999, Grimm et al. 2003, Baguette 2004, Driscoll 2007), it is clear that indices like turnover (i.e., the relative frequency of extinction and recolonization events), patch occupancy, and the genetic divergence of subpopulations (i.e., the fixation index F_{ST}) should allow us to distinguish CMs from other types of SSPs. Qualitatively this can quite easily be done. However, since CMs are a general concept, an exact quantitative definition of such indices is not possible. Specific values are very difficult to assign, and will always depend on the ecological system of interest. Nevertheless, we propose some very broad and conservative criteria based on a number of relevant publications.

1) Since local population dynamics are asynchronous, a metapopulation can be seen as a network of occupied and empty patches (e.g., Baguette 2004). As a consequence, occupancy should clearly be below 100%. It is often found to be below 90%. Studies using occupancy as an index for CM structure found occupancies to lie roughly between 5% and 85% (Hanski et al. 1994, Pajunen and Pajunen 2003, Baguette 2004, Risk et al. 2011, among many others).

2) Since CMs are characterized by a dynamic equilibrium of extinction and recolonization processes, turnover has to be significant (e.g., Hanski et al. 2004). This could be interpreted as $>5\%$. Analyses of CMs yielded turnover values between $\sim 10\%$ and 40% (Hanski et al. 1994, 2004, Risk et al. 2011, among many others).

Besides these demographic measures CM structure can be assessed using population genetics. Such genetic measures are often used to analyze whether dispersal events are too rare or too common for a CM (see

Driscoll 2007). (3) A simple measure of genetic structure is Wright's fixation index F_{ST} , the standardized genetic variance among populations (Hastings and Harrison 1994, Pannell and Charlesworth 2000). The fixation index should have intermediate values since CMs are not panmictic populations (if there is no genetic structure F_{ST} is zero). Nevertheless, subpopulations are thought to be linked by (rare) dispersal events (for complete isolation, F_{ST} is one). F_{ST} mostly takes values above 0.1. The observed values scatter roughly between 0.1 and 0.7 (Kankare et al. 2005, Walser and Haag 2012, among many others). Note that Wright (1951) states that populations become substantially differentiated for $F_{ST} > 0.25$ (for a review see Pannell and Charlesworth 2000).

We thus adopt the following conservative criteria to define a metapopulation: occupancy should be below 90% ($O \leq 0.9$), turnover should be at least 5% ($T \geq 0.05$) and $F_{ST} \geq 0.1$. With these rules of thumb in mind we will analyze the conditions under which CMs may occur. Previous studies have investigated links between individual-based models and various metapopulation models (e.g., Keeling 2002, Ovaskainen and Hanski 2004, Hilker et al. 2006), but there is a deficiency in relating individual behavior directly to the typical metapopulation measures identified above.

It transpires that CMs satisfying these three criteria emerge only in a well-defined window of plausible individual behavior. We investigate and discuss the mechanisms responsible for this observation and conclude that only particular life-history traits allow the emergence of CMs. These traits are most probably found in arthropod species.

THE MODEL

Landscape

We use an individual-based model of an SSP of individuals with nonoverlapping generations, a modeling approach that has commonly been used, see e.g., Travis and Dytham (1999), Poethke and Hovestadt (2002), Kubisch et al. (2010), and Fronhofer et al. (2011). Importantly, the model can account for demographic and environmental stochasticity as well as for environmentally driven extinctions. As Poethke et al. (2007) point out, individual-based models include the effects of kin competition by default. The simulated world consists of discrete habitat patches with a large number of subpopulations ($n = 100$), as is usually assumed for CMs (Hanski 1999, 2004, Driscoll 2007). Each patch is characterized by a carrying capacity, which is fixed to $K = 50$ as a standard. This value ensures that subpopulations may suffer extinction and is in the range of plausible subpopulation size values observed in the field (Hanski et al. 1995). The effect of varying K is analyzed in the Appendix (Fig. A2). It will be indicated explicitly when we deviate from this standard value.

Individuals

Each individual carries different attributes that may evolve, i.e., one locus coding for emigration propensity (described in more detail later), and a neutral locus that is used for the calculation of the fixation index F_{ST} (see *Calculation of the fixation index F_{ST}*).

Since the genetic system is known to influence simulation outcomes, especially in the context of metapopulations (see e.g., Parvinen and Metz 2008, Fronhofer et al. 2011), we compare results for two different genetic systems. The system with haploid individuals, which are assumed to reproduce parthenogenetically, will be termed "females only." Note that this is a common assumption in theoretical and simulation models, and will be discussed in more detail later. This scenario resembles sexual systems with mating before dispersal, which is very often found in arthropods. In addition to this, we ran simulations with sexual reproduction and model female and male individuals that mate and produce offspring after dispersal. Note that in order to be able to compare the results of both scenarios, the carrying capacity in the "females only" case is half as large as in the sexual case, i.e., $K' = 25$ as a standard.

Any offspring inherits all alleles from the parent in the "females only" simulations, or one randomly chosen allele per locus from each of its parents in the sexual scenarios. Alleles may mutate with a fixed probability ($m = 10^{-4}$). When a mutation occurs at the dispersal locus, a random number drawn from a Gaussian distribution with mean 0 and standard deviation $\Delta m = 0.2$ is added to the actual value. For the (neutral) discrete locus, a random integer number is drawn from the interval [1, 100]. Dispersal alleles are initialized following a uniform distribution between 0 and 1, and the neutral alleles are initialized with random integers drawn from the interval between 1 and 100.

In summary, we use a genetic algorithm (GA) to calculate evolutionarily stable (ES) emigration rates. This method was pioneered by Fraser (1957) and is widely used in ecological modeling. (For a review on individual-based models in ecology and evolution see DeAngelis and Mooij [2005].) Evolutionary stable dispersal strategies have been analyzed and discussed at length elsewhere (for reviews see Bowler and Benton 2005, Ronce 2007) and are not the focus of this article. Our approach guarantees that the emigration rate is optimal for any given combination of parameters (results are shown in the Appendix: Fig. A5).

Local population dynamics

Local population dynamics follow the logistic growth model for discrete generations provided by Hassell (1975). Newborn individuals survive to maturity with a certain probability $s_{i,t}$:

$$s_{i,t} = \frac{1}{(1 + a \cdot N_{i,t})^\beta} \quad (1)$$

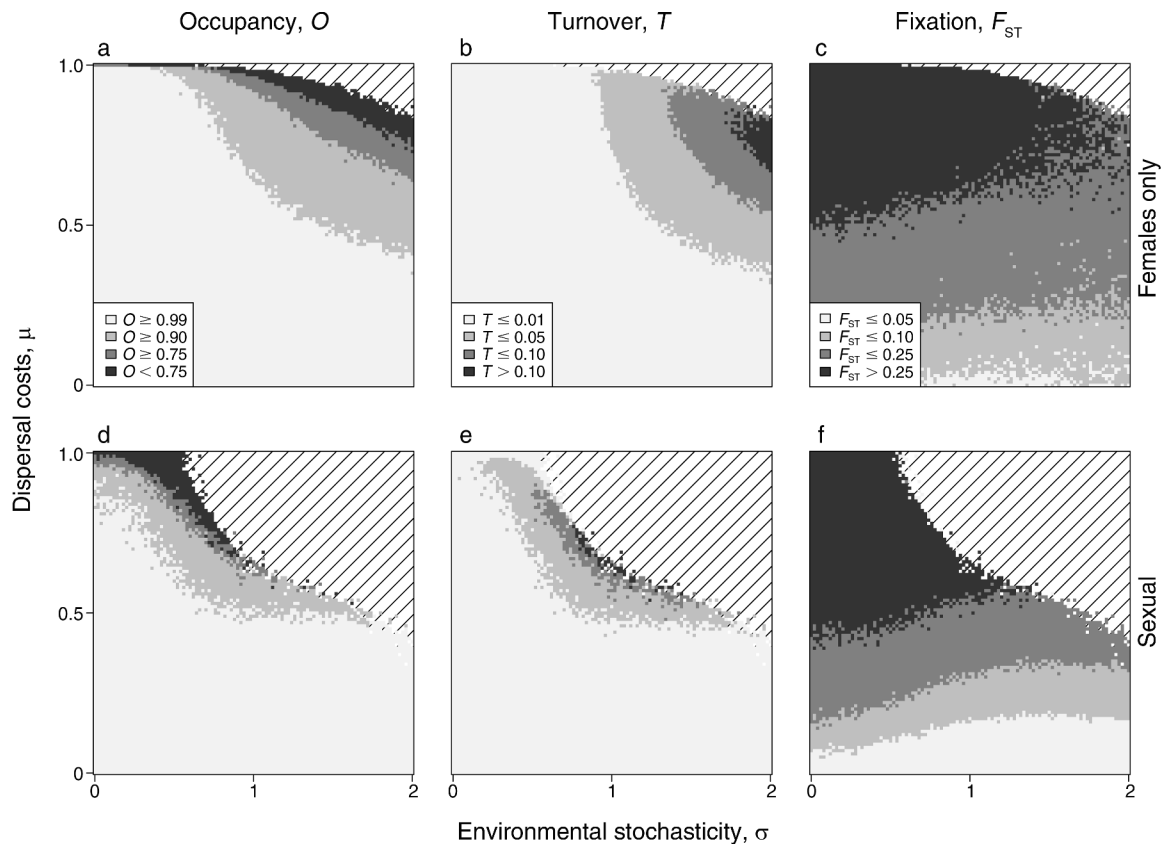


FIG. 1. Influence of dispersal costs (μ), environmental fluctuations (σ), and reproduction mode (“females only” vs. sexual) on occupancy [O ; panels (a) and (d)], turnover [T ; panels (b) and (e)], and genetic structure [F_{ST} ; panels (c) and (f)]; for asexually [top row; panels (a)–(c)] and sexually reproducing populations [bottom row; panels (d)–(f)]. Hatched areas indicate extinct populations. Constant parameters: $\lambda = 2$; $K' = 25$ [panels (a)–(c)]; $K = 50$ [panels (d)–(f)]; $\varepsilon = 0$.

where $a = (\lambda^{\beta-1} - 1)/K_i$ and $N_{i,t}$ represents the population size in patch i at time t , and K the carrying capacity of that patch. The variable a is known as the susceptibility to crowding; λ represents the mean number of offspring per generation (rate of population increase) and is set to $\lambda = 2$ as a standard. This value is quite representative for a large number of species ranging from arthropods (e.g., Hassell et al. 1976) to mammals (e.g., Ericsson et al. 2001). Characteristically, arthropods show a higher variation in breeding success than mammals, which is represented by the parameter σ (see the following paragraphs). The effect of varying λ is analyzed in the Appendix: Fig. A3. The parameter β determines the strength of density regulation. The effect of varying β is analyzed in the Appendix: Fig. A4). Note that $\beta = 1$ indicates contest competition, values >1 scramble-like competition, and values <1 undercompensation, i.e., weak density regulation (Hassell 1975).

In the “females only” simulations, each individual gives birth to Λ offspring during the reproduction period. In the sexual simulations, each female mates with one randomly chosen male from the same patch (if no males are present, reproduction is not possible) and gives birth to 2Λ offspring, so that the per capita growth

rate is the same compared to the “females only” simulations. Λ itself is drawn from a Poisson distribution with patch- and time-specific mean $\bar{\lambda}_{i,t}$. The value for the latter is drawn for each patch and generation from a lognormal distribution with mean λ and standard deviation σ . The parameter σ reflects uncorrelated environmental stochasticity, i.e., environmentally caused fluctuations in offspring number. The resulting demographic stochasticity may lead to population turnover.

Turnover may also result from externally induced extinctions that are independent of population size such as floods, volcanic eruptions, or epidemics. In the simulations incorporating such external extinction risks, at the end of each generation every population in a patch goes extinct with a probability ε , independently of the actual population size.

Dispersal

After maturation, individuals emigrate with a certain (density-independent) probability d . We have tested the robustness of our model by implementing density-dependent dispersal as in Poethke and Hovestadt (2002). This did not change our results qualitatively (for the results see Appendix: Fig. A1; compare to Fig.

1). Note that the dispersal trait may evolve as outlined above. In the “females only” simulations, the emigration probability is directly coded by the single allele. For sexual reproduction the emigration probability is simply calculated as the arithmetic mean of an individual’s two dispersal alleles $a_{d,1}$ and $a_{d,2}$:

$$d = \frac{a_{d,1} + a_{d,2}}{2}. \tag{2}$$

Any emigrating individual suffers a certain dispersal mortality μ that sums up all costs that can be involved in dispersal (for a review see Bonte et al. 2012), including fertility loss through investment in dispersal ability and predation during movement (see e.g., Zera and Mole 1994, Cody and Overton 1996). Dispersal mortality or costs (μ) can also be interpreted as the degree of fragmentation of a landscape (see e.g., Kubisch et al. 2011).

If the emigrant survives, its destination patch is chosen randomly from all patches (excluding its natal one). This corresponds to global dispersal. We tested the influence of an alternative dispersal mode, i.e., nearest-neighbor dispersal, and found that our results do not change (results not shown).

Calculation of the fixation index F_{ST}

As mentioned above, besides the dispersal alleles, each individual carries one (in the sexual system two) marker allele(s) at a neutral locus, i.e., there is no selection acting on this locus. This allows us to measure genetic distance (differentiation) between the populations by calculating Wright’s fixation index F_{ST} (Wright 1950, 1951). For all alleles j within a population i , we determine the frequencies $p_{i,j}$ (i.e., their occurrence in population i divided by the total number of alleles in the population), and then calculate the average expected within-patch heterozygosity H_S (assuming random mating) over all populations as follows:

$$H_S = \frac{1}{n} \sum_{i=1}^n \left(1 - \sum_{j=1}^{n_j} p_{i,j}^2 \right) \tag{3}$$

with n being the total number of patches and n_j being the total number of integer alleles.

The expected total heterozygosity for the whole metapopulation H_T is calculated by determining the allele frequencies \bar{p}_j over all populations (i.e., their number of occurrences in the whole metapopulation divided by the total number of alleles), $H_T = 1 - \sum_{j=1}^{n_j} (\bar{p}_j)^2$. (The bar above the variables indicates the mean.) Finally, we calculate the fixation index as

$$F_{ST} = \frac{H_T - H_S}{H_T}. \tag{4}$$

In summary, F_{ST} is the “correlation of randomly chosen alleles within the same subpopulation relative to the entire population” as Holsinger and Weir (2009) put it in their review of genetics in SSPs. Thus, this measure

represents the variation of allele frequencies among populations. If F_{ST} is zero, no variation could be observed, and as a consequence the population is panmictic. If $F_{ST} = 1$ there is no resemblance among individuals from different populations, i.e., no gene flow (dispersal) occurred, and the populations are completely isolated.

Calculation of turnover rates and occupancy

To determine the turnover rate ($T_{\Delta t}$) between two generations, we quantify the number of patch extinctions ($n_{ext,\Delta t}$) and colonizations ($n_{col,\Delta t}$) from one generation to the next and divide the number of these events by the total number of patches:

$$T_{\Delta t} = \frac{n_{ext,\Delta t} + n_{col,\Delta t}}{n}. \tag{5}$$

The census is conducted after the dispersal period and thus accounts for rescue effects.

Occupancy (O) is calculated as the relative number of occupied patches.

Simulation experiments and scenarios

Our standard scenario (A) assumes asexual reproduction (“females only” scenario), equal patch sizes ($K' = 25$), and no externally induced patch extinctions ($\epsilon = 0$). (See Table 1 for more information on parameter values.) In alternative scenarios, respectively, one of these assumptions is modified and the effect analyzed: scenario B introduces sexual reproduction ($K = 50$ to keep the results comparable with scenario A), scenario C includes externally induced patch extinctions, and scenario D includes variable patch sizes.

Simulation time is set to 5000 generations. This period of time is more than sufficient for the system to reach a state of (quasi-)equilibrium. Note that a steady state is usually reached within 2000 generations. The analysis is conducted over the last 500 generations. The values for F_{ST} and turnover given are arithmetic means over that period.

As outlined previously, we analyze the influence of relaxing our strict assumption of equal patch sizes. In the scenario with varying carrying capacities, the values for individual patches (K_i) are drawn from a uniform distribution between 5 and 45. In the mainland–island scenario the size of one habitat patch is set to $K_{mainland} = 10\,000$, while the other 99 habitat patches have a carrying capacity of $K_{island} = 10$.

RESULTS

In all simulation experiments, turnover rates (T) and the genetic structure of populations (fixation F_{ST}) increase with increasing cost of dispersal (μ), i.e., increasing habitat fragmentation. Note that, conversely, the fraction of occupied patches decreases with increasing dispersal costs (occupancy O).

The results of our simulations show that in the “females only” case (Fig. 1 a–c), relevant turnover rates

TABLE 1. Important model parameters, their meaning, and the values used for different scenarios.

Parameter	Meaning	Scenario				Parameter space explored (Appendix: Figs. A2–A4)
		A (Fig. 1 a–c)	B (Fig. 1 d–f)	C (Fig. 2)	D (Fig. 3)	
K	carrying capacity	25	50	25	[5–45] {10, 10 000}	12.5, 25, 50, 75, 100
σ	environmental stochasticity	[0–2]	[0–2]	0	[0–2]	[0–2]
ε	patch extinction probability	0	0	[0–0.25]	0	[0–0.5]
λ	fertility			2	2	1.1, 1.2, 1.3, 1.4, 1.5, 2, 3, 4
β	density regulation			1	1	0.5, 1, 2
μ	dispersal costs			[0–1]	[0–1]	[0–1]

Notes: Scenario A (“females only”) implies mating before dispersal, which is very often found in arthropods. For scenario B, sexual reproduction (equal sex ratio) is introduced. In order to keep the results comparable with scenario A, K was set to 50. This scenario includes mating after dispersal, which is often found in vertebrates. Scenario C analyzes the influence of externally induced extinctions, and scenario D relaxes our assumption of equal patch sizes (see *Methods*).

only arise for specific values of dispersal costs. For lower dispersal costs ($\mu < 0.5$) there is hardly any turnover and occupancy approaches 100%, whereas higher dispersal costs result in evolutionary suicide (Rankin and López-Sepulcre 2005, Dieckmann and Metz 2006) of the metapopulation, i.e., dispersal evolves to values too low to balance demographic extinctions with sufficient recolonization rates (see Appendix: Fig. A5 for results of evolved emigration rates).

The influence of environmental stochasticity is also depicted in Fig. 1. In general, more variable environments lead to a higher risk of global extinctions as well as to a reduced occupancy (Fig. 1a) and to more turnover (Fig. 1b).

Thus, we find a clearly defined range of values of dispersal costs and environmental stochasticity, which leads to a system behavior that agrees with the demographic CM criteria. The clear reaction of occupancy and turnover is not reflected in the genetic structure of the metapopulation (Fig. 1c). The pattern of F_{ST} is dominated by the effect of fragmentation (μ): F_{ST} continuously increases with increasing dispersal costs until it reaches a critical limit for dispersal costs above which the metapopulation cannot persist. Note that a clear spatial structure ($F_{ST} > 0.1$; Hartl and Clark 2007) can be seen already in SSPs without any turnover and full occupancy. The influence of σ on genetic structure is less pronounced (Fig. 1c).

Sexual reproduction

The introduction of sexual reproduction does not lead to qualitative changes in comparison to the “females only” case (Fig. 1 d–f). Yet, importantly, with sexually reproducing individuals, the fraction of parameter space leading to global extinction is increased, and the transition zone with intermediate occupancy and substantial turnover is considerably reduced (Fig. 1). Particularly for strong environmental fluctuations ($\sigma > 1.5$) or high dispersal costs ($\mu > 0.7$), the transition

zone becomes very narrow. Genetic structure (F_{ST} ; Fig. 1f) is less sensitive to the mode of reproduction.

Taking all parameter ranges together, the overlap of the CM criteria for sexual systems we have presented is very small. This is well depicted by the turnover rates (Fig. 1e).

Externally driven patch extinctions

In many metapopulation models, local patch extinctions are assumed to be independent of patch and population size (see *Discussion*). Such externally driven extinctions may be the result of environmental catastrophes or may be induced by the immigration of efficient predators.

Fig. 2 shows the influence of such externally driven patch extinctions (ε) on SSP structure. They increase the risk of global extinction (hatched areas in Fig. 2). Even for rather small extinction probabilities (ε), the metapopulation will go extinct if dispersal costs (μ) surpass a critical level. Occupancy is significantly reduced (Fig. 2a) and turnover rates (Fig. 2b) are considerably increased. F_{ST} values (Fig. 2c) indicate that completely isolated populations are rare. This is due to strong selection for dispersal (not shown).

In our model of discrete generations (with strict synchronization of reproduction, dispersal, and extinction events), the measurement of turnover rate critically depends on the exact moment of data collection. If turnover is evaluated immediately after externally induced patch extinctions, the turnover rate is trivially at least equal to the extinction rate. However, due to high emigration rates, a great fraction of the empty patches will be immediately recolonized (rescue effect). To account for this rescue effect, we have evaluated turnover rates after dispersal.

Variable patch sizes

In all simulation experiments presented up to this point, we have assumed an SSP of equally large patches

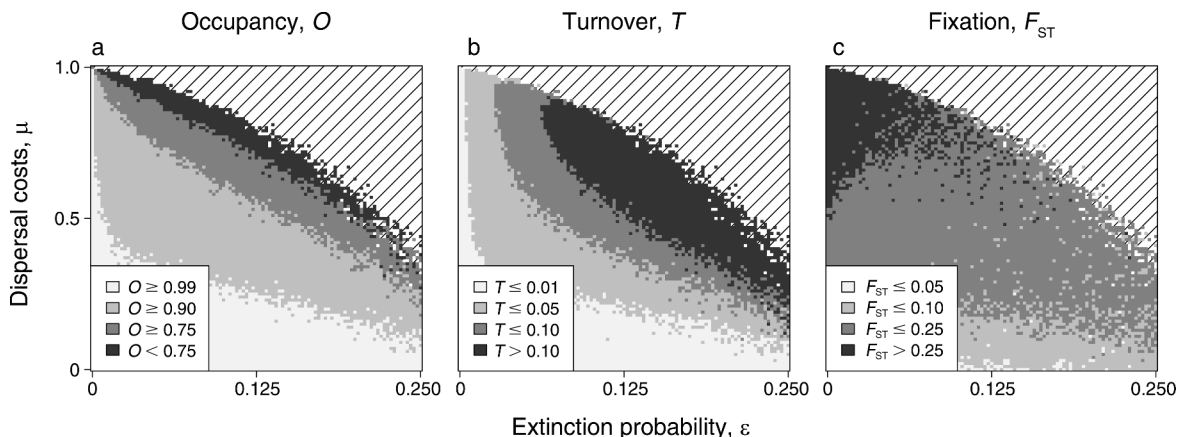


FIG. 2. Influence of dispersal costs (μ) and the frequency of externally induced extinctions (ϵ) on occupancy [O , panel (a)], turnover [T , panel (b)], and genetic structure [F_{ST} , panel (c)] for “females only” populations. Hatched areas indicate extinct populations. Constant parameters: $\lambda = 2$, $K' = 25$, $\sigma = 0$.

($K = \text{constant} = 50$). This is a rather restrictive and unrealistic assumption. If we assume habitat patches of different sizes (Fig. 3), we find that with increasingly variable carrying capacities, the area of parameter space allowing intermediate occupancy (Fig. 3a) and signifi-

cant turnover becomes larger (Fig. 3b). Note that the panmictic area ($F_{ST} < 0.05$) nearly disappears when patch sizes vary substantially (Fig. 3c).

Mainland–island populations are an extreme case of variability in patch size (Figs. 3d–f). The SSP almost

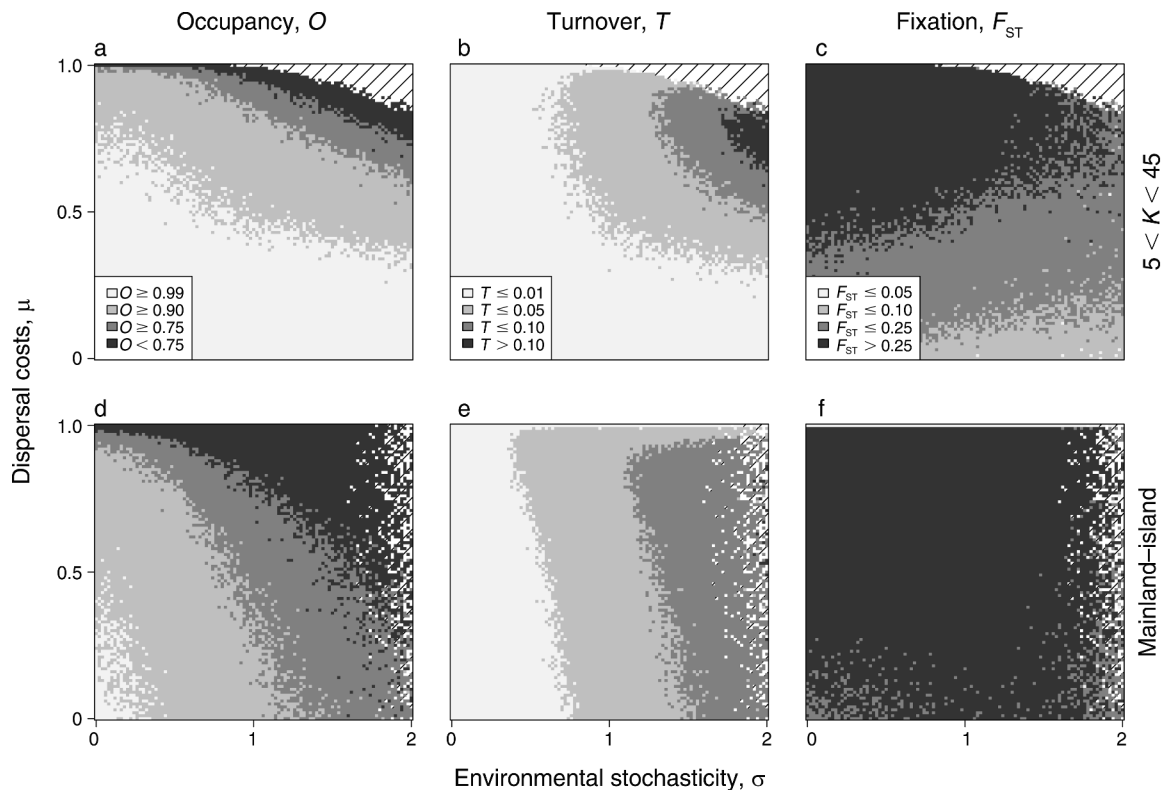


FIG. 3. Influence of dispersal costs and environmental stochasticity on occupancy [O , panels (a) and (d)], turnover [T , panels (b) and (e)], and genetic structure [F_{ST} , panels (c) and (f)] for “females only” populations in an environment with varying carrying capacities. For the upper panels (a–c), variable K is between 5 and 45; for the lower panels (d–f), there is a mainland–island scenario with one large patch at $K_{\text{mainland}} = 10\,000$ and the other 99 patches at $K_{\text{island}} = 10$. Hatched areas indicate extinct populations. Constant parameters: $\lambda = 2$, $\epsilon = 0$.

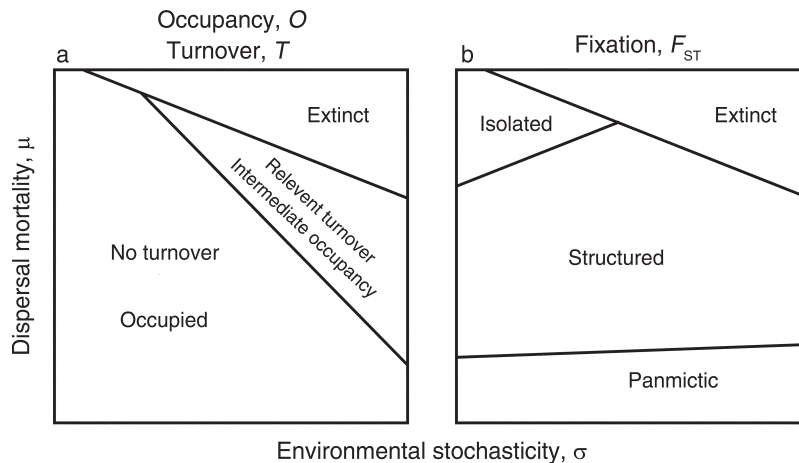


FIG. 4. Schematic representation of the influence of dispersal mortality (μ) and environmental stochasticity (σ) on occupancy, turnover [O and T , panel (a)] and genetic structuring [F_{ST} , panel (b)]. As becomes clear from our results, occupancy and turnover react similarly to dispersal mortality and environmental stochasticity. Classical metapopulations can only be found in a well-defined band in parameter space which is characterized by intermediate occupancy, relevant turnover, and spatial structure.

never goes completely extinct, since the mainland is far too large to be affected by demographic and environmental stochasticity. There are critical parameter combinations, however, where only very few of the small (island) patches are occupied (large values of μ). In this region of parameter space, the SSP tends to become highly genetically structured (Fig. 3f; $F_{ST} > 0.25$) as its structure is determined by founder effects. Note that this is not the case in sexual systems, since the mate-finding Allee effect lowers the rate of successful recolonization, which leads to substantially lower F_{ST} values.

DISCUSSION

Our simulations represent a systematic exploration of conditions that favor the emergence of significant turnover, which is the most critical attribute of classical metapopulation dynamics. We analyze two more measures often used to classify metapopulations: occupancy and genetic structure F_{ST} . The results of our simulation experiments clearly show that only specific environmental conditions and life-history attributes promote the emergence of CM dynamics as defined in the *Introduction*. Fig. 4 schematically illustrates this point and recapitulates our results. Note that our results are not strongly affected by the exact minimum values assumed for occupancy, turnover, and F_{ST} (see *Introduction*), since the transition zones are very abrupt (Figs. 1–3). In summary, it is not surprising that CMs are only rarely found in nature (Harrison and Taylor 1997, Elmhagen and Angerbjörn 2001, Bague 2004, Driscoll 2007). Typical requirements for the emergence of CMs are reduced dispersal and a substantially variable environment.

The general tendency of F_{ST} values observed above can be readily explained by the influence of environmental fluctuations (σ) and dispersal costs (μ) on the

evolving emigration rate (see Appendix: Fig. A5). For a given value of dispersal costs, increasing environmental fluctuations lead to higher interpatch variance of population size and consequently to increased emigration rates (Cadet et al. 2003, Poethke et al. 2007), which in turn result in reduced genetic spatial structure (smaller F_{ST}). If dispersal is costly (high dispersal costs μ), selection favors lower emigration tendencies, and, as a result, the genetic structure of the metapopulation is increased. Clearly, an interaction of both selective forces (high μ and σ) implies a high net loss of individuals from the metapopulation due to high dispersal mortality (at high dispersal rates). This ultimately leads to an increased global extinction risk. The parameters dispersal costs (μ) and environmental stochasticity (σ) can also be interpreted as proxies for colonization and (population size dependent) extinction probability, respectively. Higher values of dispersal costs lead to a lower colonization probability, because fewer individuals emigrate to begin with and more migrants die en route. Increasing the environmental stochasticity (σ) leads to more stochasticity in population size and consequently increases the rate of patch extinctions.

We have also tested the influence of further assumptions of dispersal behavior: nearest-neighbour dispersal (NND; not shown here) and density-dependent emigration (DDE; Appendix: Fig. A1). Both factors have no qualitative influence on the results. However, DDE generally increases the persistence of metapopulations under high environmental fluctuations, i.e., the area with complete population extinction is reduced (compare Fig. 1 and Appendix: Fig. A1).

Moreover, the influence of fertility (λ) and carrying capacity (K) has been tested thoroughly (see Appendix: Figs. A2 and A3). Generally, varying carrying capacity and fertility only shifts the position of the transition zone in parameter space but does not lead to important

qualitative changes. Clearly, larger values of fertility (λ) or carrying capacity (K) stabilize the system, so that turnover is reduced and ultimately tends toward zero. The same pattern is true for the strength of density regulation (β ; Appendix: Fig. A4).

Our analysis of the influence of the genetic system shows that a characteristic pattern of “females only” simulations is a highly reduced extinction risk of the metapopulation (Fig. 1). Although a “females only” scenario seems to be very artificial, it may be seen as equivalent to sexual systems with mating before dispersal, i.e., where only fertilized females disperse, as in many insects. This explains the reduced extinction risk, which is due to a higher colonization efficiency in comparison to sexual systems, because the latter implicitly includes a mate-finding Allee effect (Courchamp et al. 2008). Generally, mating before dispersal can be expected when migrants are likely to immigrate into empty habitat patches.

Externally induced extinctions increase the transition zone, i.e., the area in which CMs can be observed (Fig. 2). As mentioned above, the time of measurement is of great importance. If turnover is measured after extinctions take place, the results only reflect the external extinction rate, which is trivial. Yet an important rescue effect (Brown and Kodric-Brown 1977, Hanski 1999) changes the results substantially. This is due to high emigration rates selected under externally driven extinctions (Comins et al. 1980, Ronce et al. 2000, Poethke et al. 2003). Regarding genetic structure (Fig. 2c), the direct effect of external extinctions, which increases the transition zone, is nearly compensated by their effect on the evolving emigration propensity and the rescue effect.

Many metapopulation models assume asexual populations (“females only”; for a discussion see Rankin and Kokko [2007]) and/or externally driven extinctions (Ronce and Olivieri 1997, Travis et al. 1999, Ronce et al. 2000, Keeling 2002, Bonte et al. 2010) or implicitly include these assumptions (e.g., the Levins model). These two factors are obvious mechanisms that introduce at least massive rescue effects, and in the case of asexual reproduction, also considerable turnover and thus CM dynamics.

We believe the assumption that population extinctions occur completely independently of the state and size of local populations must be carefully justified, and therefore, not taken as a standard assumption. Clearly, external catastrophes like diseases, volcanic eruptions, or flooding may occur. Stelter et al. (1997), for example, examine a SSP of the grasshopper *Bryoderma tuberculata*, which inhabits vegetation-free gravel bars along rivers in the Alps. Here, catastrophic floods have a dual effect: on the one hand, of course, floods destroy local populations, yet on the other hand, such extinctions counteract succession. This creates suitable habitat for the species (see also Thomas 1994). Yet we think that for most species it is reasonable to assume that extinctions are related to the population’s current state. This is

reflected by our parameter for environmental fluctuations (σ ; for an in-depth discussion see Poethke et al. [2003]). In these scenarios population extinctions occur purely because of environmental and demographic stochasticity.

Introducing patch size variability leads to a large transition zone with significant turnover, intermediate occupancy, and a clear genetic spatial structure (Fig. 3). The increased probability of intrinsic local population extinction and ultimately global extinction can be explained by the fact that large differences in patch size or quality may select against dispersal (Hastings 1983). This can even lead to a decrease in successful recolonizations, subsequently to reduced incidence, and ultimately to global extinction (“Metapopulation paradox”; see Poethke et al. [2011]). In addition to this, if the SSP does not go extinct, panmictic areas disappear because metapopulation dynamics are defined by the few large patches. In the mainland–island scenario, complete extinction is very rare since the mainland is too large to be affected significantly. As outlined in the *Introduction*, the mainland–island scenario is, strictly speaking, not a classical metapopulation (Harrison and Taylor 1997, Driscoll 2007).

In our simulations we include a large variety of life-history strategies. These range from typically mammalian (e.g., mating after dispersal, only very limited effect of environmental stochasticity; see Fig. 1d–f) to characteristic insect or arthropod life-histories (e.g., mating before dispersal, high impact of environmental stochasticity; see Fig. 1a–c). In scenarios including life-history parameters typical for large mammals, the parameter space showing CM dynamics is very restricted (see Fig. 1). This finding is supported by evidence from field data, which indicates that mammalian populations do usually not exhibit CM dynamics (Elmhagen and Angerbjörn 2001, Olivier et al. 2009). In contrast to this, especially in “females only” scenarios typical for arthropod taxa, we have found significant areas in parameter space that do show CM dynamics. We therefore suggest that the CM concept is more applicable to arthropod species.

CONCLUSION

In our simulation model, CM dynamics can only be found under specific circumstances. For typical life-histories of large mammals, our model indicates the occurrence of CMs in the strict sense only very rarely. In contrast, for stereotypic insect species we do find the emergence of CM dynamics.

Heterogeneity in habitat size is an important factor increasing turnover and thus facilitating the emergence of CM dynamics. As outlined in the *Introduction*, variable patch sizes are not included in the original (Levins) CM definition. Of course, it is a matter of taste where to draw the separation line between moderate (realistic) variability and mainland–island systems.

Nevertheless, our results show that considerable variability is needed to increase turnover noticeably.

The CM concept may be applicable to populations on the brink of extinction. A classical metapopulation structure will often occur as a transient state before extinction (see e.g., the parameter combinations indicating extinct population in our model). Such populations are typically of concern for conservation biologists. Here, time to extinction is an important issue, because if the delay is long enough conservation measures may be successful. The question remains whether sensible conservation guidelines can be derived in such cases, or whether populations conforming to the CM concept may already be too far down the path toward extinction (Kuussaari et al. 2009). Many management recommendations derived from metapopulation models appear applicable to spatially structured populations as well (see Hanski et al. [2004] for a number of examples). In general, however, it is important to be aware of the specificity of CMs, since the specific spatial structure of focal populations does influence conservation decisions (Guiney et al. 2010). For instance, efforts spent on increasing patch connectivity (e.g., by constructing corridors) may be wasted when the population is actually of a mainland–island type, and the primary concern therefore should be the conservation of the mainland population. If a population is actually panmictic (patchy) rather than a CM, this would suggest focusing on different spatial scales and changing the monitoring and sampling system. Wrong assumptions about spatial population structure may thus lead to unnecessary spending of resources that would be much better invested elsewhere, and incorrect conservation concepts with potentially fatal consequences, such as loss of biodiversity. We thus advise more care when using the term “metapopulation.” Often, “spatially structured population” may be more appropriate.

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SUPPLEMENTAL MATERIAL

Appendix

Analysis of the influence of density-dependent emigration, carrying capacity (K), fertility (λ), and competition strength (density regulation, β) on our results; and evolutionarily stable emigration rates depending on environmental stochasticity (σ), dispersal costs (μ), fertility (λ), and carrying capacity (K) (*Ecological Archives* E093-173-A1).