



Effects of subpopulation extinction on effective size (N_e) of metapopulations

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Abstract

Population extinction is ubiquitous in all taxa. Such extirpations can reduce intraspecific diversity, but the extent to which genetic diversity of surviving populations are affected remains largely unclear. A key concept in this context is the effective population size (N_e), which quantifies the rate at which genetic diversity within populations is lost. N_e was developed for single, isolated populations while many natural populations are instead connected to other populations via gene flow. Recent analytical approaches and software permit modelling of N_e of interconnected populations (metapopulations). Here, we apply such tools to investigate how extinction of subpopulations affects N_e of the metapopulation (N_{eMeta}) and of separate surviving subpopulations (N_{eRx}) under different rates and patterns of genetic exchange between subpopulations. We assess extinction effects before and at migration-drift equilibrium. We find that the effect of extinction on N_{eMeta} increases with reduced connectivity, suggesting that stepping stone models of migration are more impacted than island-migration models when the same number of subpopulations are lost. Furthermore, in stepping stone models, after extinction and before a new equilibrium has been reached, N_{eRx} can vary drastically among surviving subpopulations and depends on their initial spatial position relative to extinct ones. Our results demonstrate that extinctions can have far more complex effects on the retention of intraspecific diversity than typically recognized. Metapopulation dynamics need heightened consideration in sustainable management and conservation, e.g., in monitoring genetic diversity, and are relevant to a wide range of species in the ongoing extinction crisis.

Keywords Inbreeding effective population size · Eigenvalue effective size · Realized effective size · Substructured populations · Conservation genetics

Introduction

Genetic diversity within species naturally fluctuates over time as subpopulations over the distribution range go extinct while other areas of the range are recolonized via immigration (Wilcox and Murphy 1985; Whitlock and Barton 1997). Currently, however, human pressure is a major contributor to population extirpation in most taxa, often hindering recolonization (Ceballos and Ehrlich 2002; Thomas et al.

2004; Wake and Vredenburg 2008; Ceballos et al. 2017; Díaz et al. 2019). Habitat change and fragmentation, for example, result in population loss in many species (Frankel and Soulé 1981; Wilcox and Murphy 1985; Templeton et al. 1990; Kaye et al. 2019). Over-harvesting is another source of population extinction (Laikre et al. 2005; Allendorf et al. 2008). Loss of populations reduces intraspecific diversity and scientists warn for burgeoning threats to intraspecific diversity (Díaz et al. 2019).

The genetically effective population size (N_e) is a fundamental parameter in conservation as it measures the rate at which genetic diversity within populations is lost. Important conservation genetic guidelines have been based on N_e , including the “50/500” rule which posits that an N_e above 50 is required for short term conservation in order to avoid excessive inbreeding and above 500 to sustain enough variation for long-term viability and adaptive potential (Franklin 1980; Frankham 1995; Allendorf and Ryman 2002;

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Jamieson and Allendorf 2012). Some scientists propose that $N_e \geq 1000$ might be necessary for securing adaptive capacity (Frankham et al. 2014; Pérez-Pereira et al. 2022; Frankham 2022). N_e is of current focus in conservation policy with the $N_e \geq 500$ limiting value as a “Headline Indicator” within the Convention on Biological Diversity’s (CBD) post-2020 Global Biodiversity Framework (CBD 2022), as suggested by conservation genetic research (Hoban et al. 2020, 2021a,b, 2022; Laikre et al. 2020, 2021; Andersson et al. 2022; Kershaw et al. 2022).

N_e was developed for single, isolated populations (Wright 1931). In reality, most populations are only partially isolated and typically constitute parts of population systems connected by migration, so-called metapopulations (Hastings and Harrison 1994). Levels of population connectivity drastically affect N_e of the metapopulation as a whole as well as of separate subpopulations and thus the conservation genetic situation (Laikre et al. 2016).

Here, we study the effect of permanent subpopulation extinction on the metapopulation N_e as well as on the N_e of individual surviving subpopulations. We focus on highly substructured populations, i.e. on metapopulations where gene flow among subpopulations is relatively limited and subpopulations are genetically distinct. In general, species with such structure, e.g., those with subpopulations inhabiting closely located islands or interconnected lakes, or whose populations are distributed along a coast, are expected to be particularly vulnerable to subpopulation extinctions (Wilcox and Murphy 1985). Examples include ring species such as the willow warbler (*Phylloscopus trochilus*; Bensch et al. 2009), red drum (*Sciaenops ocellatus*; Gold et al. 2001), and many salmonid fishes (Gustafson et al. 2007; WWF 2011; Palmé et al. 2012). In particular, salmonid fishes show marked genetic substructuring with genetically distinct local populations, and subpopulation extinctions are well documented (Laikre et al. 2005; Katz et al. 2013). For instance, the Atlantic salmon (*Salmo salar*) of the Baltic Sea has been identified by the Swedish Agency for Marine and Water Management as a species of particular importance to monitor for genetic diversity and such work is initiated using effective population size as a key indicator (Andersson et al. 2022). This species historically inhabited approximately 100 rivers around the Baltic Sea, of which around 30 natural populations remain—an extermination mostly due to hydroelectric power plant constructions (Palmé et al. 2012). Understanding how such extinctions affect the metapopulation’s and surviving populations’ potential to retain genetic diversity is vital for management and conservation, and is the focus of the present paper.

Theoretical background to N_e of metapopulations

N_e was initially defined for a single, isolated population as the size of an ideal population exhibiting the same rate of decline of genetic variation and accumulation of inbreeding as the non-ideal population under study (Wright 1931). In contrast to an isolated population where genetic variation is affected by genetic drift alone (assuming no mutation or selection), genetic variation within metapopulations is also affected by migration. Over time, equilibrium between influx of genetic variation via migration between subpopulations, and loss of variation due to drift within subpopulations, will be established, and the rate of change in diversity across populations will be the same (Hössjer et al. 2016). Since many human activities are evolutionarily recent, impacted populations are often in their initial phases of diversity loss. It is therefore important to consider N_e dynamics during departures from migration-drift equilibrium.

Considerable research has been devoted to modelling N_e in metapopulations. Most studies use Wright’s classical island model, although departures have been analyzed e.g., hierarchical island models, stepping stone models of migration, spatial substructuring with arbitrary population sizes, and unequal migration rates (Kimura and Weiss 1964; Maruyama 1970; Nagylaki 1980; Whitlock and Barton 1997; Nunney 1999; Wang and Caballero 1999; Tufto and Hindar 2003). Studies of departures from migration-drift equilibrium exist, although these do not include extinction (Whitlock and McCauley 1990; Chesson et al. 1993; Wang 1997a, b). Among papers that treat more general substructured populations, some focus on extinction and colonization (Slatkin 1977; Maruyama and Kimura 1980; Ewens 1989; Whitlock and McCauley 1990; Gilpin 1991; Hedrick and Gilpin 1997). Most of these studies assume an island model, with exception for Maruyama and Kimura (1980) and Whitlock and Barton (1997). However, all previous work assumes equilibrium between extinction and colonization. A general conclusion from these studies on the effect of subdivision on effective size is that metapopulation effective size (N_{eMeta} ; Table 1) does not equal the sum of the subpopulation effective sizes (Waples 2010).

Objectives

To the best of our knowledge, no previous research has addressed how permanent loss of subpopulations (without recolonization) affects a structured population’s (total/global) effective size, neither before nor after equilibrium has been obtained following the extinction event. In order to fill this gap, we study the effect of extinction on the rate

Table 1 Description of symbols used in the present study

Symbol	Definition/description
t	Time measured in generations
M	Migration rate expressed as the number of immigrants per generation from one or more particular subpopulations; migration is stochastic, and M reflects the binomial average
s	Number of subpopulations included in a metapopulation
x	An arbitrary subpopulation that is part of a metapopulation
f	Coefficient of inbreeding
Δf	Increase of inbreeding from generation t to $t + 1$
Δh	Decrease of heterozygosity from generation t to $t + 1$
N_e	Inbreeding effective size. Note that the present paper deals exclusively with inbreeding effective size (the diploid version; Hössjer et al. 2015); thus, we drop the index “ T ” from N_{eT}
N_{ex}	Inbreeding effective size of subpopulation x (in the absence of immigration; cf. Equation 23 in Hössjer et al. 2015). When referring to specific subpopulations in our models (Fig. 1) we use N_{e1} to refer to effective size of subpopulation 1 in the absence of migration, N_{e2} for subpopulation 2, etc
N_{eR}	Realized (inbreeding) effective size in general; reflects the change of inbreeding under both drift and immigration
N_{eRx}	Realized effective size of subpopulation x . In this context realized implies the increase of inbreeding that is caused both by genetic drift and migration. We use N_{eR1} to refer to the realized effective of subpopulation 1, N_{eR2} for subpopulation 2, etc
N_{eMeta}	Total (global) inbreeding effective size of the metapopulation as a whole. This quantity reflects the change of f_{Meta} from generation t to $t + 1$. It can be viewed as a weighted average of N_{eRx} over all subpopulations, or as the realized effective size of the metapopulation as a whole, and it will eventually approach N_{eE}
N_{eE}	Eigenvalue effective size (of the metapopulation as a whole) at migration-drift equilibrium. At equilibrium, $N_{eMeta} = N_{eE}$. In metapopulations where each subpopulation both receives immigrants from, and sends emigrants to, at least one other subpopulation, the rate of inbreeding will eventually be the same ($1/(2N_{eE})$) in all subpopulations
N_c	Census population size
N_{cx}	Census size for subpopulation x
G_{ST}	Coefficient of genetic differentiation among subpopulations in a particular metapopulation and a multi-locus extension of F_{ST} (Allendorf et al. 2007, p. 158). We employ the term G_{ST} for stringency with previous publications using GESP

of inbreeding and genetic variability loss in the metapopulation as a whole (quantified as metapopulation effective size; N_{eMeta}) as well as within local subpopulations (realized effective sizes; N_{eRx} , Table 1), at and during departures from migration-drift equilibrium. We focus on permanent extinction of populations that are interconnected by relatively limited gene flow, and where a large proportion of the populations go extinct. As described above such cases are of general relevance considering the ongoing population extinction crisis (Ceballos et al. 2017).

Of the large number of models possible, we deliberately restrict our analyses to simple, principal deviations from standard models of migration (island and stepping stone, incl. linear stepping stone that has previously not been analytically studied in the context of subpopulation extinction) to identify general effects of subpopulation loss in metapopulations. The following questions are addressed:

- (i) To what extent is the effect of subpopulation extinction on N_{eMeta} dependent upon migration pattern and rate among subpopulations?
- (ii) How is N_{eMeta} affected by the extinction of subpopulations before and after equilibrium has been reached?

- (iii) How are remaining subpopulations' effective sizes (N_{eRx}) affected by extinction before equilibrium has been reached?

Materials and methods

Theoretical modelling of N_{eMeta}

We use the mathematical framework of Hössjer et al. (2014, 2015, 2016) that allows modelling the expected change of heterozygosity and effective size of arbitrary metapopulations. Parts of this framework are programmed into the software Genetic Exploration of Substructured Populations (GESP; Olsson et al. 2017), which is applied in the present work. The abbreviations detailed in this section are also presented in Table 1. We consider a diploid organism without selfing where mating occurs after migration. Migration is stochastic and rates expressed as the number of immigrants per generation (M). Immigrants are drawn by binomial sampling from the gene pool of the donor subpopulation (Hössjer et al. 2014, 2015). The forces of selection and mutation are ignored.

We deal exclusively with inbreeding effective size (N_{eI} , the “diploid” version of Hössjer et al. 2015). N_{eI} quantifies the rate at which inbreeding (f) increases and heterozygosity (h) decreases (Wright 1931, 1938). We quantify expected rates of decrease of heterozygosity (Δh) and the corresponding increase of inbreeding (Δf) in terms of N_{eI} . At a given generation (t) this inbreeding effective size is defined as $N_{eI} = 1/(2\Delta f)$, where $\Delta f = (f_{t+1} - f_t)/(1 - f_t)$, and f_t is the inbreeding coefficient at generation t . The increase of inbreeding corresponds to a similar decrease of heterozygosity with $\Delta h = (h_t - h_{t+1})/h_t$. From now on we drop the index “I” and emphasize that we use the abbreviation N_e for N_{eI} .

In contrast to an isolated population where Δf is affected by genetic drift alone (assuming no mutation or selection), the heterozygosity of a local subpopulation in a metapopulation is also affected by migration. Following the nomenclature of Laikre et al. (2016) and Ryman et al. (2019) we refer to the corresponding quantity $1/(2\Delta f)$ as the *realized effective size* (N_{eR} ; Table 1). N_{eR} of a separate subpopulation is denoted N_{eRx} where “x” describes the identity of the particular subpopulation. N_{eR} of the global population is denoted N_{eMeta} (without an “R” subscript because it is assumed to be isolated and lacks immigration from other sources). N_{eMeta} is in turn denoted N_{eE} once the metapopulation has reached migration-drift equilibrium (Ryman et al. 2019).

No initial inbreeding or kinship is assumed in any of our models. Constant population sizes are assumed and we make the simplifying assumption that local census and effective population sizes are equal ($N_{cx} = N_{ex}$). We do however include cases where subpopulations have different sizes relative to each other. N_{eMeta} is then computed by weighting each subpopulation according to its local effective size in isolation (N_{ex} ; Hössjer et al. 2015).

We stress that N_e is defined exclusively for populations where genetic variation remains and where heterozygosity either decreases or remains constant (when $N_e = \infty$). N_e for populations without genetic variation, or in which inbreeding decreases, is undefined. Migration can lead to decreased levels of inbreeding, resulting in undefined N_{eR} in recipient subpopulations and sometimes even to undefined N_{eMeta} (Hössjer et al. 2016; Laikre et al. 2016). Further, for a “metapopulation” where subpopulations are completely isolated from each other with no exchange of migrants ($M = 0$; i.e., per definition not a true metapopulation), equilibrium N_{eMeta} will be $N_{eE} = \infty$. The reason for $N_{eE} = \infty$ is that the subpopulations will eventually become fixed for different alleles, and identity by descent of alleles of different subpopulations will not increase but remain the same generation after generation in the system as a whole. Thus, metapopulation— N_e is irrelevant for systems without migration between subpopulations, and as M approaches zero and the system is

close to migration–drift equilibrium, N_{eMeta} will approach its undefined state.

Metapopulation models

The framework applied here (Hössjer et al. 2014, 2015, 2016; Olsson et al. 2017) allows modelling a large variety of metapopulations. Our analyses are restricted to a few cases, focusing on standard models of migration; the island (Wright 1931; Crow and Kimura 1970), the circular stepping stone (Maruyama 1970; Wang and Caballero 1999), and the linear stepping stone (Kimura and Weiss 1964) models. The effects of subpopulation loss in metapopulations have not been extensively modelled under the conditions considered here (extensive, permanent population extinctions and non-equilibrium situations) and using standard models appears a reasonable first step. Additionally, the island model has frequently been used to provide conservation genetic guidelines, e.g., the one-migrant-per-generation rule (Frankel and Soulé 1981), and it is therefore of interest to compare the island model to the circular and linear stepping stone models, since they represent extremes with respect to connectivity among subpopulations. Furthermore, our models are chosen to mimic scenarios relevant to species that are characterized by relatively strong genetic substructuring and have suffered from extensive loss of subpopulations e.g., many salmonids (Palmé et al. 2012).

The studied models are depicted in Fig. 1. The number of subpopulations (s) is initially 10 and extinction removes half of the subpopulations such that $s = 5$ unless specified otherwise. We use equal subpopulation sizes of $N_{ex} = 50$ (Fig. 1a–f) as well as a scenario with one large and nine small subpopulations in which case $N_{e1-5,7-10} = 10$ and $N_{e6} = 410$ (Fig. 1g–i), and in both cases $\sum N_{cx} = \sum N_{ex} = 500$. Exchange of migrants is bidirectional, and the number of expected migrants per generation (M) is 1 or 3. $M = 1$ is chosen to reflect metapopulations interconnected with relatively limited gene flow but in agreement with the one-migrant-per-generation rule (Frankel and Soulé 1981) while $M = 3$ serves as comparison to illustrate the effects of increased connectivity on effective population size, while maintaining a restricted enough connectivity to allow marked population substructuring. It should be noted that migration patterns and rates remain the same after subpopulations are removed i.e., exchange of migrants is established among remaining populations at rates (M) equivalent to before removal (Fig. 1d–f, j–o), so as not to confound the effect of population extinction with altered migration patterns.

The effect of extinction is studied at migration-drift equilibrium, as reflected by N_{eE} , and before equilibrium by considering N_{eMeta} and N_{eRx} . We compare values of N_e before extinction ($s = 10$) to those after extinction ($s = 5$). The scenarios are described in further detail below.

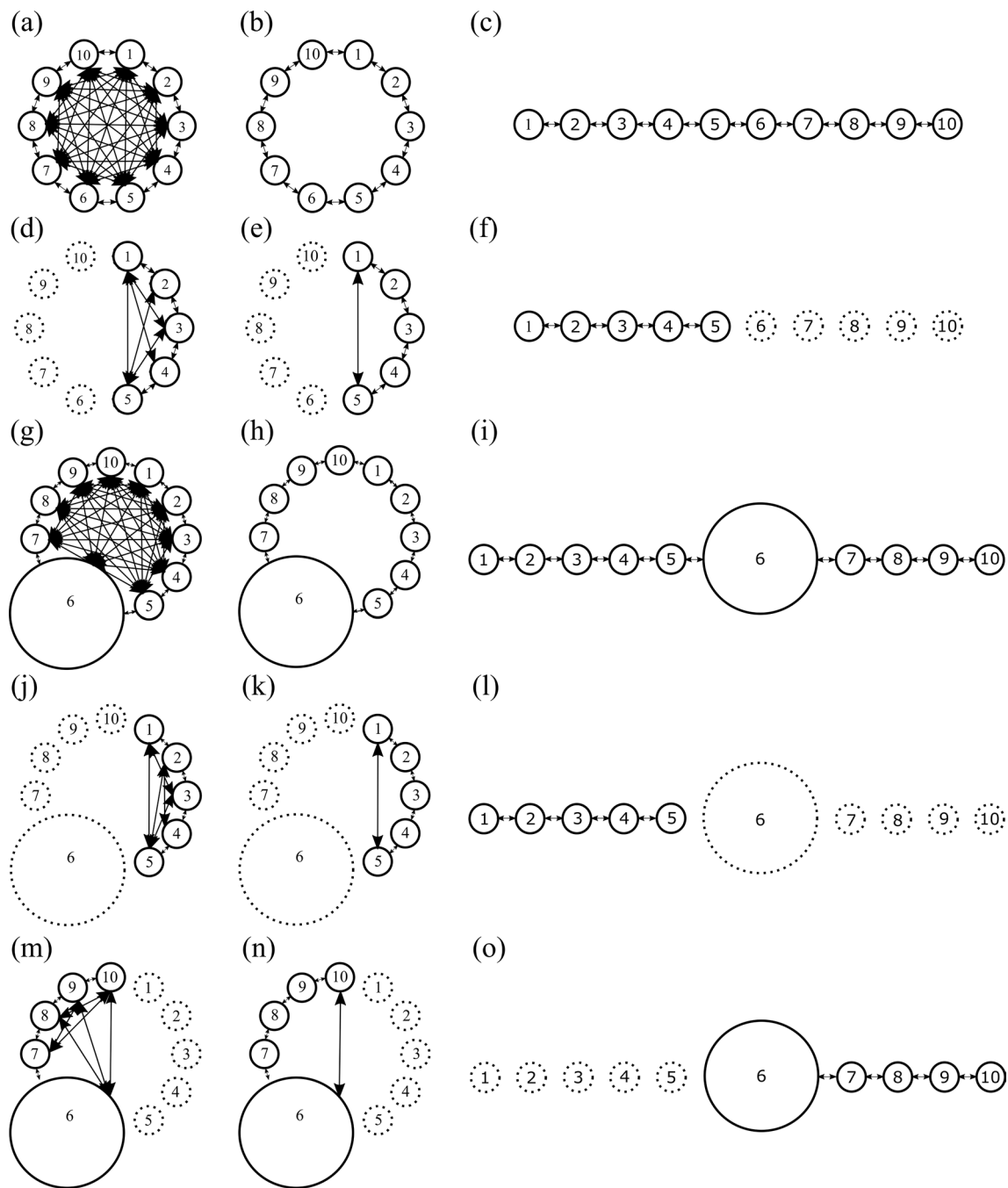


Fig. 1 Schematic illustration of the general migration models analyzed in this study. Arrows indicate two-way migration between subpopulations and dotted lines represent subpopulations that go extinct. In (a–f) all the subpopulations are of the same size ($N_{ex} = 50$); in (g–o) one subpopulation (number 6) is larger than the others ($N_{e6} = 410$) which all have $N_{ex} = 10$. Five neighboring subpopulations are removed from the metapopulation, and the extinct subpop-

ulations either include (j–l) or exclude (m–o) the large one. In the island model (leftmost column) all the 10 subpopulations exchange migrants, whereas in the circular and linear stepping stone models (center and rightmost columns) exchange only occurs between next neighbors (i.e. under the linear stepping stone subpopulations 1 and 10 only exchange migrants with one neighbor)

Effects of extinction on N_{eMeta} at migration-drift equilibrium

First, we analyze the effect on N_{eE} from extinction of

subpopulations. We use metapopulations with $s = 10$ subpopulations with local effective population sizes (N_{ex}) of $N_{e1-10} = 50$ (Fig. 1a–c). We then remove 5 of the 10 subpopulations and compute N_{eE} for the new metapopulations

(Fig. 1d–f, where 1d, 1e, and 1f are obtained after subpopulation extinction in 1a, 1b, and 1c, respectively).

Since most natural populations vary in size, we also model extinction within metapopulations with unequal subpopulation sizes. For comparability to models of metapopulations with equally sized subpopulations, the sum of all initial ($t=0$) subpopulation's N_e should be 500. Thus, we model cases where one of the subpopulations is considerably larger than the others ($N_{e1-5,7-10}=10$, $N_{e6}=410$; Fig. 1g–i). We model situations where 5 out of the 10 subpopulations are removed from the system, both including and excluding the large subpopulation among the remaining subpopulations (Fig. 1j–o).

Effects of extinction on N_{eMeta} before a new migration-drift equilibrium

We consider N_e dynamics following population extinction before a new migration-drift equilibrium has been attained in order to understand such dynamics in evolutionarily recently disturbed populations. The dynamics of N_{eMeta} and N_{eRx} are assessed in generations immediately following subpopulation extinction, well before equilibrium. We do this by first running the models of Fig. 1a–c, g–i over 750 generations ($t=0$ to $t=750$, by which time most metapopulations reach equilibrium) with either equal N_{ex} ($N_{e1-10}=50$; Fig. 1a–c) or with one large and nine small subpopulations ($N_{e1-5,7-10}=10$ and $N_{e6}=410$; Fig. 1g–i) and subsequently explore the effects on N_{eMeta} of removing 5 of the 10 subpopulations at generation $t=750$ (Fig. 1d–f, j–o). We only use $M=3$ to avoid excessive computing times.

Additional analyses

We conduct extended analyses in addition to the modelling described above, focusing on effects of subpopulation extinction on G_{ST} , on N_{eE} of very large metapopulations, and on effects of altered migration pattern after extinction.

G_{ST}

We examine the effects of subpopulation extinction in the above models (Fig. 1) on between population genetic diversity, measured as the coefficient of genetic divergence (G_{ST} ; Nei 1977, here comparable to F_{ST} cf. Table 1).

A large metapopulation

We explore the effects of extinction in a very large metapopulation ($s=100$) for all three migration models and with permanent extinction of 50 and 90 percent of the populations, respectively, under equilibrium conditions. We include this analysis to relate our modelling to an empirical case;

the Atlantic salmon metapopulation in the Baltic Sea, which originally consisted of ca. 100 rivers with genetically distinct subpopulations from which only ca. 10–30 percent currently remain as wild, self-sustaining populations (Palmé et al. 2012). Because we do not have data to conduct a fully realistic modelling of the Baltic salmon (we do not have data on N_{ex} per river prior and after the extinction event) we use a simplified model to get a first idea of the effects of such subpopulation loss on metapopulation effective size (to avoid cluttering, these results are described in Supplementary Information (Appendix S1, S2)).

Altered migration after extinction

We also examine the effect of altering migration rates and patterns after extinction for the circular stepping stone model. In the following cases models are the same as previously (i.e. Fig. 1b), with $s=10$ and $M=3$ before extinction and an extinction of five subpopulations. Changes occur after the extinction event at $t=750$. First, we examine the effects of reducing migration after extinction, so that $M=0.6$ and $M=2.5$ after extinction. Secondly, we reconsider which particular subpopulations that go extinct. Instead of five consecutive populations, we model the loss of every other subpopulation (subpopulations 2, 4, 6, 8, and 10). Here, $M=0.6$, $M=2.5$, and $M=3$ after extinction. Lastly, we previously assumed the relatively unlikely scenario that remaining subpopulations form a new circle of migration (cf. Fig. 1c). We now reduce migration between subpopulation 1 and 5 to $M=0$ (i.e. the model becomes a linear stepping stone), $M=0.6$, and $M=2.5$, respectively.

Results

Some of our results concerning effective population size dynamics of substructured populations under migration-drift equilibrium are anticipated for population geneticists, but may not be apparent to conservation geneticists in general. We present these findings first.

Effects of extinction on N_e at migration-drift equilibrium

The effective population size of the metapopulation, N_{eMeta} , equals N_{eE} at migration-drift equilibrium (Fig. 2). We summarize key findings of N_{eE} , some of which have been only partially described before (Maruyama and Kimura 1980; Whitlock and Barton 1997; Hössjer 2015):

1. N_{eE} is larger for a linear than for a circular stepping stone model, while the island model attains the lowest N_{eE} .
2. N_{eE} is greater when $M=1$ than when $M=3$.

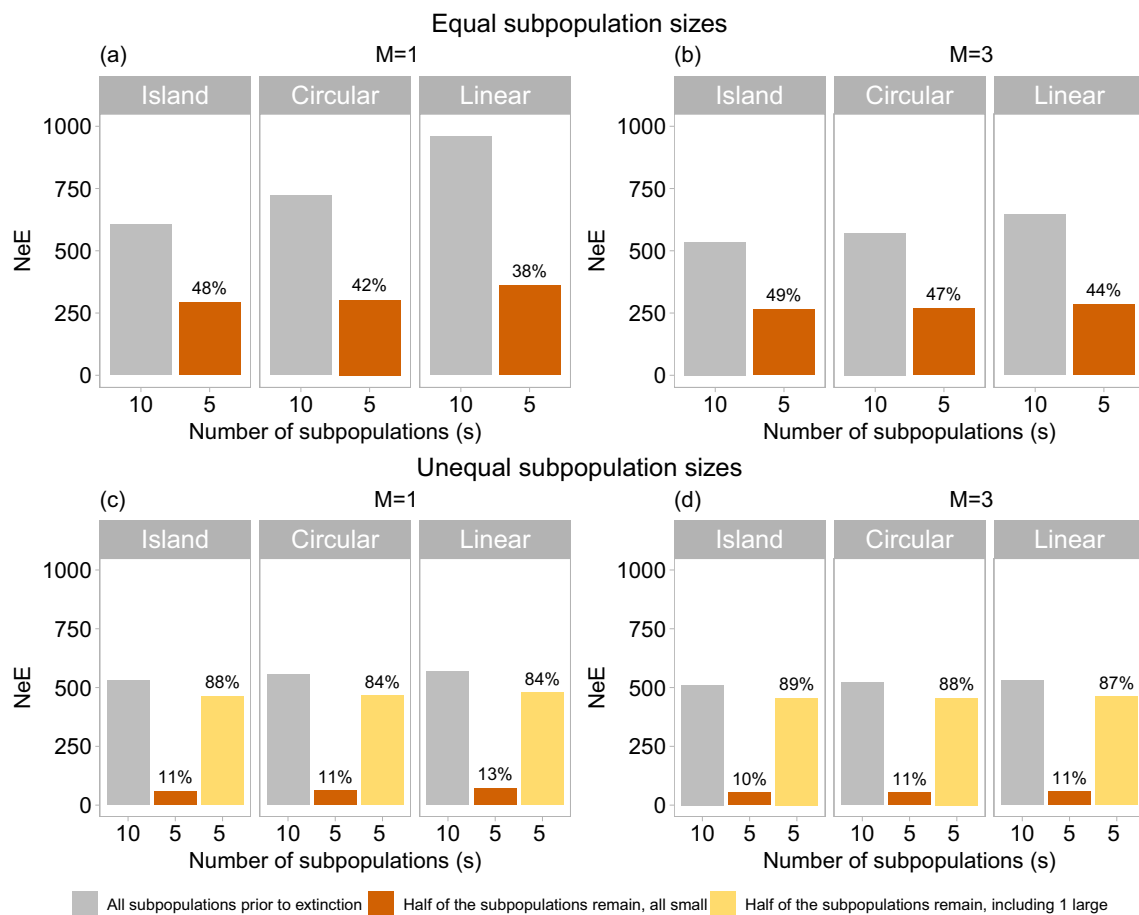


Fig. 2 Equilibrium effect of subpopulation extinction on eigenvalue effective size (N_{eE}) under different migration models (island, circular and linear stepping stone models) and migration rates ($M=1$ or $M=3$). The original metapopulation consists of $s=10$ subpopulations and five of them go extinct. **a, b** *Equal subpopulation sizes*, i.e. all subpopulations are of size $N_{ex}=50$; grey and red bars denote N_{eE} before ($s=10$) and after ($s=5$) extinction. Percentages indicate the

proportional N_{eE} relative to the value before the extinction event. **c, d** *Unequal subpopulation sizes*, i.e. subpopulation 6 (cf. Fig. 1g–o) is of size $N_{e6}=410$ and the others $N_{ex}=10$, and the large one is either goes extinct (red) or survives (yellow). Grey bars and percentages as before. See Appendix 1 for extinction in metapopulations with $s=100$ and Table 2, for the exact values of N_{eE}

- N_{eE} exceeds the sum of local subpopulation sizes (N_{eRx}) in all migration models and migration rates, before as well as after extinction. With more connectivity (migration pattern and rate), N_{eE} approaches the sum of subpopulation sizes.
- The relative reduction of N_{eE} following subpopulation extinction of half of the subpopulations is greatest within the linear stepping stone model, smallest in the island model, and greater when $M=1$ than when $M=3$.

The results listed above hold true whether subpopulation sizes are equal or differ (Table 2, Fig. 2). They also hold for the case of a large metapopulation containing $s=100$ subpopulations (Appendix S1). We note that N_{eE} increases as M decreases but proportionally more so for the stepping stone models than the island (Table 2, Fig. 2; as noted above $N_{eE}=\infty$ when $M=0$), and especially for large

metapopulations (Appendix S1). We also find that when one subpopulation is very large, N_{eE} is lower than when all subpopulations are of the same size.

When subpopulations are of equal size and $s=10$, the relative reduction of N_{eE} following subpopulation extinction of half of the subpopulations exceeds 50% in all migration models (Table 2, Fig. 2). When instead subpopulation sizes differ ($s=10$), the effect of losing five subpopulations depends on whether the large population is retained or not. More than 80% of N_{eE} remains when the large population survives but only ca. 11% if the large population goes extinct—irrespective of migration model.

Time to migration-drift equilibrium

We define the time required for the entire metapopulation to reach equilibrium as the first generation at which N_{eMeta}

Table 2 Effect of subpopulation extinction on eigenvalue effective size (N_{eE}) under different migration models (island, circular and linear stepping stone models) and when subpopulation sizes are equal ($N_{ex} = 50$) and unequal ($N_{e6} = 410$ and the other $N_{ex} = 10$)

Number of subpopulations	Subpopulation size	N_{eE} (Island)	N_{eE} (Circular)	N_{eE} (Linear)
<i>M</i> = 1				
Before extinction (<i>s</i> = 10)	Equal	605	722	959
	Unequal, 1 large	531	555	569
After extinction (<i>s</i> = 5)	Equal	292	303	360
	Unequal, large subpopulation survives	463	465	478
	Unequal, large subpopulation goes extinct	59	61	72
<i>M</i> = 3				
Before extinction (<i>s</i> = 10)	Equal	535	572	646
	Unequal, 1 large	511	521	530
After extinction (<i>s</i> = 5)	Equal	264	268	285
	Unequal, large subpopulation survives	456	456	462
	Unequal, large subpopulation goes extinct	53	53	57

Migration rate is *M* = 1 and *M* = 3, respectively

Table 3 Approximate number of generations (*t*) required for N_{eMeta} and all N_{eRx} to reach equilibrium (N_{eE}), respectively, in metapopulations before (*s* = 10) and after extinction (*s* = 5), for different migration models when subpopulations are of equal (Fig. 1a–f) and unequal sizes (Fig. 1g–o)

Subpopulation size	Migration model	<i>t</i> to equilibrium before extinction	<i>t</i> to equilibrium after extinction
Equal	Island	63	1
	Circular stepping stone	360	156
	Linear stepping stone	750	543
Unequal, large subpopulation goes extinct	Island	83	5
	Circular stepping stone	186	29
	Linear stepping stone	351	78
Unequal, large subpopulation survives	Island	83	87
	Circular stepping stone	186	123
	Linear stepping stone	351	273

The number of migrants per generation is *M* = 3. *t* required to reach equilibrium is the first generation when N_{eMeta} and all N_{eRx} differ from N_{eE} by at most 0.1%

and all N_{eRx} differ from N_{eE} by at most 0.1%. We find, when considering our metapopulations with *M* = 3, that the time to equilibrium is longest for the linear stepping stone (750 generations) and shortest for the island model (63 generations; Table 3). Under the island model, metapopulations with unequal subpopulation sizes take longer to reach equilibrium than models with equally sized subpopulations, while the opposite is true for the linear and circular stepping stone models (Table 3).

After extinction, between one and 550 generations are required for the new equilibrium to be attained (Table 3). In metapopulations with unequally sized subpopulations, time to equilibrium under all three models of migration is longer when the large subpopulation remains than when it has gone extinct (Table 3).

Effects of extinction before a new migration-drift equilibrium

The effect of subpopulation extinction on N_{eRx} and N_{eMeta} , before the metapopulation has reached a new equilibrium, is radically different than when equilibrium has been attained. We find that subpopulations can experience inflated or reduced rates of inbreeding, depending on their location within the metapopulation and initial proximity to extinct subpopulations. Detailed results are described below.

Equal subpopulation sizes (models of Fig. 1a–f)

Extinction under an island model is reflected in an immediate change of N_{eMeta} and N_{eRx} , while for the stepping stone

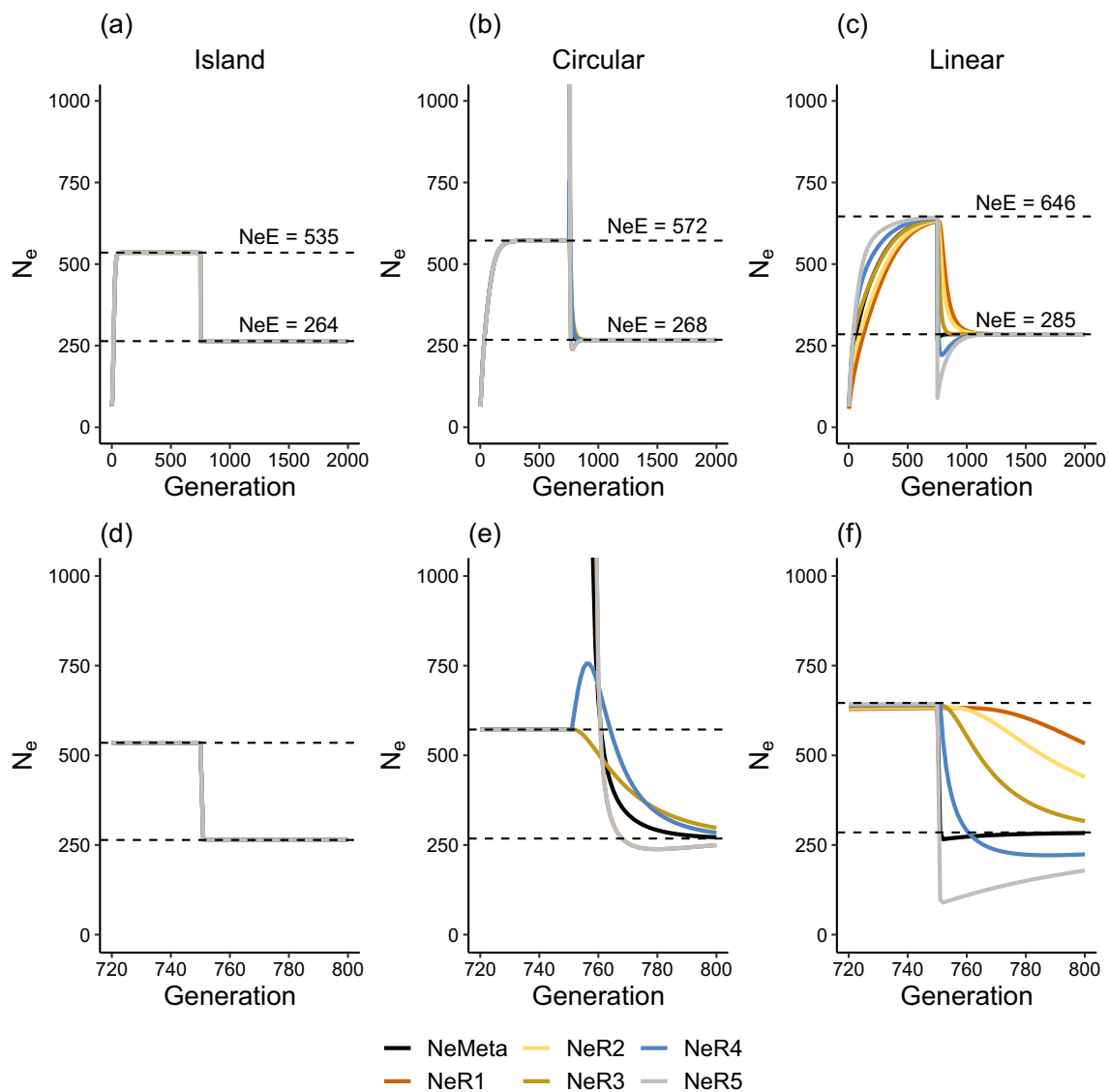


Fig. 3 Effect of subpopulation extinction on metapopulation effective size (N_{eMeta}) and realized effective size (N_{eRx}) before a new equilibrium has been reached for scenarios of Fig. 1d–f. The initial number of subpopulations is $s=10$ with local subpopulation effective size $N_{ex}=50$, and migration rate $M=3$. At generation $t=750$ the number

of populations is reduced to $s=5$. Eigenvalue effective sizes (N_{eE}) are included before ($s=10$) and after extinction ($s=5$), respectively. **a, b, c** Top panels show generation $t=0$ to $t=2000$, whereas **d, e, f** bottom panels depict a close-up of generation $t=720$ to $t=800$. See Appendix S3, sheet B, for the exact values of N_e

models, the situation is more complicated (Fig. 3). In particular, the effects of extinction on N_{eRx} vary, and depend on the subpopulation’s location in the metapopulation and initial proximity to extinct subpopulations.

The circular stepping stone metapopulation is modelled such that remaining subpopulations form a new circle of migration after extinction. As a consequence, inbreeding rates initially decrease in subpopulations 1, 2, 4, and 5, which is reflected in inflated N_{eR1} , N_{eR2} , N_{eR4} , and N_{eR5} for some generations before their descent to the new equilibrium (Fig. 3b, e). This is most pronounced within subpopulations 1 and 5, where inbreeding initially decreases as they come

into direct migratory contact, resulting in undefined N_{eR1} and N_{eR5} for eight generations (Fig. 3b, e). For subpopulation 3, now in the middle of the new circle, N_{eR3} decreases immediately after extinction. As a consequence of inflated N_{eRx} in subpopulations 1, 2, 4, and 5, N_{eMeta} becomes undefined over some generations after the extinction before attaining the new value of $N_{eE}=268$ at $t=818$ (Table 2, Fig. 3b, cf. Appendix S3, sheet B). It is not until generation $t=906$ that the entire metapopulation has reached equilibrium and $N_{eRx}=N_{eMeta}=N_{eE}=268$ (Table 3, Fig. 3b, e). Note that $N_{eR1}=N_{eR5}$ and $N_{eR2}=N_{eR4}$ after extinction and before the new equilibrium.

The linear stepping stone model barely reaches the first equilibrium by $t=750$, and there is a difference between subpopulations such that subpopulations 5 and 6 are closer to this equilibrium than the others (exemplified by N_{eR5} in Fig. 3c, f). After extinction, remaining subpopulations are decreasingly affected the further they are from extinct subpopulations: subpopulation 5, which has become the new “endpoint”, experiences a marked increase in inbreeding rate as reflected in N_{eR5} instantly dropping far below the new equilibrium value. Subpopulation 4 decreases slightly below the new N_{eE} for a few generations. Subpopulations 1–3 slowly descend towards the new N_{eE} , and remain above this value throughout their trajectory, with subpopulation 1 taking the longest to reach the new N_{eE} (at $t=1293$; Appendix S3, sheet B). The marked reduction of N_{eR5} is the main driver of reducing N_{eMeta} below the new N_{eE} , before attaining this value at $t=822$. The entire metapopulation reaches equilibrium $N_{eE}=285$ at $t=1293$ (Tables 2, 3, Fig. 3c, f).

Unequal subpopulation sizes (models of Fig. 1g–o)

When one subpopulation is very large, the effect of population extinction on N_{eMeta} and N_{eRx} largely depends on whether the large population survives or not—for all models of migration. The effects of extinction on N_{eRx} of remaining subpopulations also depend on how close they initially were to the large subpopulation.

The large subpopulation goes extinct For the island model, N_{eMeta} and N_{eRx} of all the remaining subpopulations reach the new equilibrium within only five generations after extinction (Table 3; Fig. 4a, d). In the circular stepping stone model, subpopulation 1 comes into migratory contact with subpopulation 5. As a result, inbreeding initially decreases in subpopulations 1 and 2, resulting in undefined N_{eR1} and N_{eR2} for one and two generations, respectively (Fig. 4b, e). The effect on subpopulation 5 of gaining migratory contact with subpopulation 1 (which when subpopulations are of equal size results in an increase in heterozygosity; Fig. 4b, e) is dominated by the loss of the large subpopulation 6. Inbreeding rate is extensively increased in subpopulations 4 and 5 after the extinction event, such that N_{eR4} and N_{eR5} drop to values below the new N_{eE} . Decreased inbreeding in subpopulations 1 and 2 result in initially undefined N_{eMeta} for three generations before N_{eMeta} asymptotically approaches the new equilibrium value ($N_{eE}=53$) at $t=767$ (Table 2, Fig. 4b, Appendix S3, sheet C). Equilibrium is attained by all populations within the metapopulation at $t=779$ (Table 3).

Under the linear stepping stone model, subpopulations 1, 2, and 3 decline toward the new $N_{eE}=57$, while N_{eR4} and N_{eR5} are initially reduced below this value (Table 2, Fig. 4c, f). The further away from the large, now extinct, subpopulation that surviving populations are located, the less rapid and

pronounced is the decline of their respective N_{eRx} (Fig. 4d–f, cf. Appendix S3, sheet C). N_{eMeta} remains above the new N_{eE} throughout its trajectory and attains the new N_{eE} value at $t=769$. The entire metapopulation reaches equilibrium at $t=828$ (Table 3).

The large subpopulation survives As expected, extinction of the five small subpopulations has a less drastic effect on N_{eMeta} and remaining N_{eRx} than when the large subpopulation goes extinct. N_{eMeta} and some N_{eRx} are initially undefined under the island and circular stepping stone models, but not under the linear one. The large subpopulation is the first to reach the new N_{eE} value, under all models of migration (Appendix S4).

G_{ST}

The amount of genetic variation due to divergence between populations (G_{ST}) is affected by subpopulation extinction in ways similar to N_{eMeta} . At migration-drift equilibrium, G_{ST} increases with increased isolation among subpopulations: G_{ST} is greatest within the linear stepping stone model and smallest in the island model, and G_{ST} when $M=1$ exceeds that of $M=3$ (Appendix 2). The effect of subpopulation extinction on G_{ST} is more dramatic for stepping stone models than within an island model—especially before the system has reached its new equilibrium, in which case stepping stone models experience a ca. 50% reduction of G_{ST} , whereas the island model exhibits a proportional loss of ca. 30% (Appendix S2, see Appendix S3, sheet F for exact values). In contrast to N_{eMeta} , the effect of subpopulation loss on G_{ST} when subpopulations have unequal sizes is similar to situations when subpopulations are of the same size [note that by the original definition of G_{ST} , subpopulations are weighted equally regardless of their size (Nei 1973)].

A large metapopulation

The effect of extinction on N_{eE} in a large metapopulations ($s=100$) compared to a small one ($s=10$) depends on migration model (Fig. S1). For the island model, the proportional decrease in N_{eE} due to extinction of half of the subpopulations is greater when $s=10$ than when $s=100$ while the reverse is true for stepping stone patterns of migration (cf. Fig. 2 and Fig. S1).

Altered migration after extinction

The effect of extinction with altered migration after extinction is illustrated in a circular stepping stone model where $s=5$ out of $s=10$ populations go extinct. Initially, $M=3$. When comparing the scenario of maintained migration after extinction (Fig. 3b) to models with reduced migration

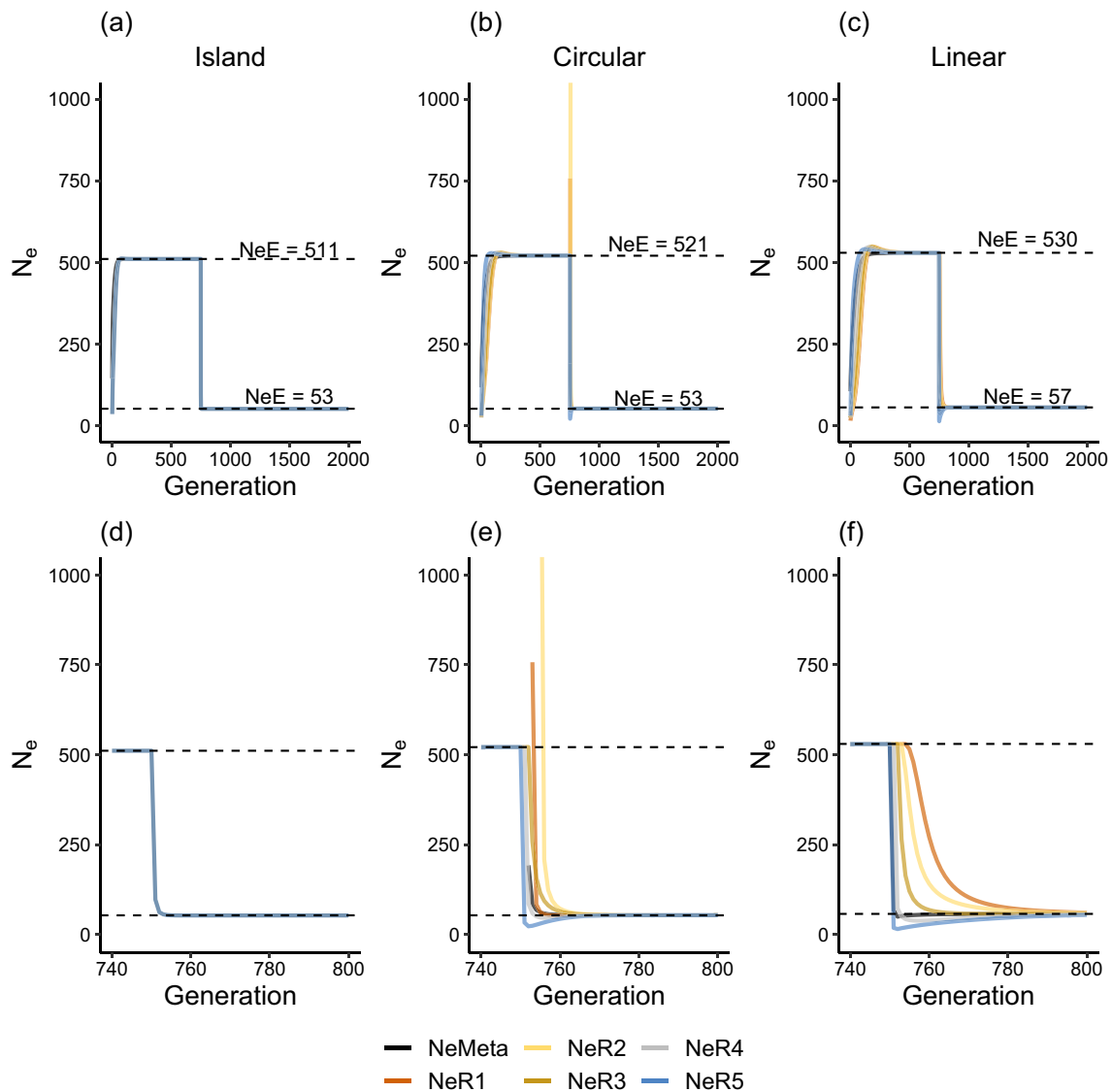


Fig. 4 Effect of subpopulation extinction on metapopulation effective size (N_{eMeta}) and realized effective size (N_{eRx}) before equilibrium has been reached for scenarios of Fig. 1j–l when subpopulation effective sizes are unequal ($N_{e1-5,7-10}=10$ and $N_{e6}=410$) and the large subpopulation is among the five to go extinct. The initial number of subpopulations is $s=10$ and at generation $t=750$ the number of popula-

tions is reduced to $s=5$. $M=3$ migrants per generation. Eigenvalue effective sizes (N_{eE}) are included before ($s=10$) and after extinction ($s=5$), respectively. **a, b, c** Top panels show from generation $t=0$ to $t=2000$, whereas **d, e, f** bottom panels depict a close-up of generation $t=720$ to $t=800$. See Appendix S3, sheet C, for the exact values of N_e

between all the subpopulations surviving extinction ($M=0.6$ and $M=2.5$), we find that reduced migration inflates N_{eE} (Fig. S6a–c). However, the transient state of N_{eMeta} and N_{eRx} before the new equilibrium has been reached is more severe when migration is reduced after extinction as compared to when migration is maintained, including greater reduction in initial N_{eMeta} and N_{eRx} values and longer time to equilibrium (Fig. S6a–c, Appendix S3, sheet G). In fact, when $M=0.6$, the system does not reach equilibrium within the 1000 generations modeled (Fig. S6a).

If migration after extinction is reduced to $M=0.6$ among the five remaining subpopulations, neither N_{eRx} nor N_{eMeta} become undefined before the new equilibrium (Fig. S6a). This is because inbreeding within subpopulations does not decrease when $M=0.6$. We identify a threshold of migration near $M=2.5$ below which N_{eRx} and N_{eMeta} do not become undefined (Fig S6b, e, i).

It does not matter for N_{eMeta} which subpopulations go extinct, as long as they are of equal size and contribute equally to the migrant pool (Fig. S6d–f, Appendix S3, sheet G). When extinction occurs in such a way that every second

subpopulation dies out, the resulting decrease in N_{eMeta} before the new equilibrium is comparable to when extinction removes five consecutive subpopulations in Fig. S6a–c. However, when every other subpopulation is removed, N_{eRx} of surviving subpopulations are equal after extinction (Fig. S6d–f).

If a new circle is not formed after extinction, i.e., if migration between subpopulations 1 and 5 is zero but maintained ($M=3$) between all other subpopulations, the pattern turns into a linear stepping stone and the new N_{eE} is inflated compared to when a circle is maintained (Fig. S6g cf. Fig. S6c). If migration between subpopulations 1 and 5 remains but is lower than among other subpopulations ($M=0.6$ between 1 and 5, but $M=3$ among subpopulations 2–4) then all N_{eRx} and N_{eMeta} decrease after the extinction (Fig. S6h). Inbreeding rates within subpopulations 1 and 5 even exceed the new equilibrium value—both drop to below 275 for ca. 100 generations following the extinction event (Figure S6h, Appendix S3, sheet G).

Discussion

This study demonstrates that the effect of subpopulation extinction on the capacity to retain genetic variation within metapopulations largely depends on the degree of migration (pattern and rate) among subpopulations, subpopulation sizes, and whether migration-drift equilibrium has been attained. The relative reduction of metapopulation effective size at equilibrium (N_{eE}) following subpopulation extinction is greatest within the linear stepping stone model and smallest in the island model, and greater when $M=1$ than when $M=3$. Similarly, under stepping stone patterns of migration, large metapopulations (more subpopulations) are proportionally more affected than small ones (cf. Fig. 2 and Fig. S1). Before the metapopulation has reached a new equilibrium, the effect of subpopulation extinction on N_{eRx} and N_{eMeta} is radically different from when equilibrium has been attained.

Further, depending on the migration pattern and rate, the number of subpopulations, and their individual N_{ex} , time to equilibrium may be so long that in practical situations it can be assumed to never occur, highlighting the importance for considering N_e dynamics during departures from equilibrium (Vachon et al. 2018). The divergent characteristics of subpopulations and metapopulations during departures from equilibrium found here were first noted by Varvio et al. (1986) but have received relatively little attention, despite implications for conservation and management (but see Lacy 1987; Mills and Allendorf 1996; Whitlock and McCauley 1999). Our study adds to the limited research aimed at describing the effects of extinction over contemporary time

with conclusions that offer a wide range of practical implications for conservation and management.

Main management implications

Previous work has shown metapopulation effective size at equilibrium (N_{eE}) to be a poor representation of inbreeding rates within the metapopulation during departures from equilibrium (N_{eMeta} ; Hössjer et al. 2016). Present results add that under non-equilibrium conditions, extinction affects rates of inbreeding in the remaining subpopulations (N_{eRx}) beyond what is reflected by N_{eMeta} —especially for systems characterized by spatial structure with genetically distinct subpopulations, e.g., stepping stone models with limited gene flow among subpopulations. In such cases, the effects of extinction on surviving subpopulations may be diverse and depend on the subpopulations' location in the metapopulation and initial proximity to the extinct subpopulations. The impact is manifested faster, and in many cases stronger, in subpopulations neighboring extinct ones. However, these populations are also the first to attain the new equilibrium value of N_{eMeta} (N_{eE}). Populations further away may be “buffered” from the effects of extinction for many generations, and will take longer to reach the new N_{eE} . In practice, this phenomenon is expected to result in difficulties to detect reductions of effective size from empirical data collected after an extinction event, meaning the genetic effects of an extinction can go unnoticed and—depending on the species—possibly for decades. This is of vital concern for management and conservation.

Our results also highlight that extinction of local subpopulations may cause conservation concern for surviving subpopulations within the metapopulation. Large subpopulations may carry an important role for a metapopulation, resulting in reduced inbreeding rates in the smaller subpopulations they are connected to. As mentioned above, the Atlantic salmon in the Baltic Sea functions as an empirical example of our study, where natural populations are extinct in ca. 70 of historically 100 rivers (Palmé et al. 2012). The Rivers Torneälven and Kalixälven in Sweden are among the largest Baltic rivers still inhabited by wild populations (Östergren et al. 2021). Our results suggest that these rivers may be crucial for the genetic variability maintained in other surviving populations in smaller Baltic rivers and for the Baltic salmon system as a whole. Recognizing these interlinked effects and maintaining connectivity in such populations needs heightened recognition.

The models used here were chosen to mimic scenarios relevant to species that are characterized by genetic substructuring and have suffered from extensive and terminal loss of subpopulations. Our results suggest that the island model gives an overly optimistic account of effects of subpopulation extinction on metapopulation effective size for systems,

e.g., stepping stone types of migration. Examples of stepping stone metapopulations include species inhabiting fragmented habitats, ring species, populations scattered along a coast, inhabiting closely located islands, or interconnected lakes, and many salmonids (Gustafson et al. 2007). Consider again the Baltic salmon. This highly substructured metapopulation is more similar to either of the stepping stone models than the island model of migration. Present results suggest that the genetic impacts on remaining subpopulations' N_{eRx} and N_{eMeta} likely exceed the proportion of extinct populations and predictions based on an island model. Thus, loss of genetic diversity within the Baltic salmon has probably been overlooked.

Present results demonstrate the benefit to populations of belonging to a metapopulation, particularly when equilibrium has been attained. The rate of inbreeding will then be governed by the metapopulation, which typically implies a considerably slower rate of inbreeding than had the subpopulation been isolated (Laikre et al. 2016). In our models, although some subpopulations experience marked increase in inbreeding rate after the extinction, they remain above their size at isolation ($N_{ex} = 50$). It must be stressed, however, that after extinction and before new equilibrium, low migration rates between remaining subpopulations will inflate N_{eMeta} , while inbreeding rates within individual subpopulations may increase. Thus, rates of inbreeding can be excessively high in some subpopulations and overlooked if only N_{eMeta} is regarded, which needs to be considered in practical management (Varvio et al. 1986; Laikre et al. 2016; Ryman et al. 2019).

Population connectivity

Our results suggest that metapopulations with less connectivity retain genetic diversity more efficiently over time than those with higher degree of connectivity when undisturbed—yet, they may be proportionally more affected by subpopulation extinction. This contention is supported by the following observations. At equilibrium, stepping stone models retain comparably larger metapopulation effective size (N_{eE}) than the island model, and systems with a genetic exchange of $M = 1$ exceed those with $M = 3$ (Fig. 2). Conversely, the largest proportional reduction of N_{eMeta} following extinction occurs under linear followed by circular stepping stone cases of genetic exchange (Figs. 2, 3, 4), and when $M = 1$ rather than $M = 3$ (Fig. 2). These conclusions are in line with previous work, e.g., Whitlock and Barton (1997) who suggest that species with lower dispersal rates are expected to be most affected by extinction and recolonization processes.

Extinction is generally expected to reduce genetic diversity that exists as differences between populations (G_{ST} ; Nei 1973, 1977). We find G_{ST} to be affected by subpopulation

extinction in ways similar to N_{eMeta} . The proportional reduction of G_{ST} is greater in metapopulations with limited connectivity. Previous studies of the effect of extinction on G_{ST} have included recolonization and shown G_{ST} to depend on the mode of recolonization (Wade and McCauley 1988; Pannell and Charlesworth 1999). In reality, however, recolonization may not always follow extinction. Loss of intraspecific diversity is documented in wild populations as an effect of population extirpation e.g., following habitat fragmentation in tigers (*Panthera tigris*; Thatte et al. 2018).

In the case of the Baltic salmon, loss of genetic diversity between populations is documented and explained by genetic homogenization through introgression from large scale releases of domestic conspecifics over decades (Östergren et al. 2021; Ozerov et al. 2016; Laikre et al. 2006, 2010). Our results show that a reduction of between population genetic diversity (F_{ST} , here modelled as G_{ST}) is also expected from subpopulation extinction and that this reduction is particularly pronounced with stepping stone models of migration and limited gene flow. Our findings are relevant to preserving intraspecific variation in sustainable management and conservation, e.g., through monitoring genetic diversity between populations, as recently highlighted in conservation genetic research (Laikre et al. 2020; Hoban et al. 2020; Andersson et al. 2022) and policy (CBD 2022).

Limitations

As a first step in examining the effects of extinction on remaining subpopulations, we restrict modelled scenarios to three standard models of migration. Alternative ones of relevance for substructured metapopulations, e.g., asymmetric migration across elevated landscapes (“dendritic” model; Morrissey and de Kerckhove 2009) and source-sink dynamics, are ignored. Hierarchical models may maintain higher levels of heterozygosity within subpopulations than linear models. However, unequal contribution of subpopulations to the migrant pool is expected to reduce the metapopulation effective size below the sum of subpopulation effective sizes (Kimura and Weiss 1964; Maruyama 1970; Nagylaki 1980; Whitlock and Barton 1997; Nunney 1999; Wang and Caballero 1999). For instance, asymmetric migration may greatly reduce the overall metapopulation effective size, as previously shown for wolves (Laikre et al. 2016) and salmonids (Tufto and Hindar 2003). We find that reducing migration after extinction inflates equilibrium values of N_e (N_{eE}) compared to when migration is maintained but that the transitory state of all N_{eRx} and N_{eMeta} after extinction and before the new equilibrium is prolonged with reduced migration (Fig S6). This again emphasizes the need to consider non-equilibrium dynamics of N_e for sustainable conservation and management.

Extinction in our simplified models occurs in the middle of the metapopulation, killing off five consecutive subpopulations. While overly simple, these models do in fact reflect cases of extinction in natural metapopulations, e.g., extinction of consecutive salmon populations in rivers dammed for hydropower, where populations above the dam go extinct and those below survive, as mirrored in our linear stepping stone models, or habitat loss cutting of parts of a metapopulation, e.g., documented for mountain gorillas (Van Der Valk et al. 2018) and as exemplified by our circular stepping stone models. Also, we find that when other patterns of extinction occur (such as every other subpopulation going extinct in a circular stepping stone) the effects are the same on N_{eMeta} and surviving subpopulations providing that migration rate remains (Fig. S6d–f). Our seemingly simple models highlight the main threats to N_{eMeta} , namely, the number of subpopulations and the pattern and rate of migration that connects them.

We also assume that initial kinship and inbreeding coefficients within populations are zero. In reality many natural metapopulations likely experience repeated extinction and recolonization events, making relatedness coefficients vary over time. Previous studies demonstrate that demographic fluctuations decrease the metapopulation effective size relative to its size under panmixia (Slatkin 1977; Maruyama and Kimura 1980; Whitlock and Barton 1997). The specific effect of recolonization on N_{eMeta} depends on the mode of recolonization, and extinction and colonization rates (Slatkin 1977; Whitlock and Barton 1997). Hedrick and Gilpin (1997) model an island where subpopulations may go extinct and new ones are colonized. Interestingly, subpopulation effective sizes do not converge on the eigenvalue effective size of the metapopulation. It is thus possible that recolonization, had it occurred in our scenarios, would extend the transient state of N_{eMeta} and N_{eRx} beyond current time. The effects of extinction and colonization have to our knowledge not been described for N_{eRx} , nor have cases of natural extinction/recolonization in combination with permanent extinction, both of which warrant further study.

We have ignored the effects of selection and mutation. These forces are relevant for conservation and although their consequence for N_{eMeta} is unknown, they may be presumed to be small (Wang and Whitlock 2003).

Finally, we have focused exclusively on the inbreeding effective size (N_{eI}) since this N_e is most relevant for preserving genetic diversity (Franklin 1980). Many empirical measures of N_e use the variance effective size (N_{eV} ; Ryman et al. 2019). Theoretical expectations of N_{eV} and N_{eI} in (diploid) metapopulations include that N_{eV} within local subpopulations is smaller than the equivalent N_{eI} while metapopulation N_{eV} exceeds metapopulation N_{eI} (Hössjer et al. 2016). It is therefore possible that in our models of extinction, N_{eV} exhibits larger disparity between N_{eMeta} and N_{eRx} before

equilibrium than captured by N_{eI} . This is of particular importance for empirical assessments of N_e which is often based on estimates of N_{eV} from observed allele frequency shifts (Ryman et al. 2019; Andersson et al. 2022). Other frequently used methods focus on linkage disequilibrium N_e which also deviates from N_{eI} in substructured populations (Ryman et al. 2019).

Conclusions

To the best of our knowledge, no previous research has addressed how permanent loss of subpopulations affects the (total/global) effective size of structured populations. Here, analyses are restricted to deviations from principal assumptions (e.g., pattern and rate of migration and equilibrium states) of standard models of migration. We demonstrate that subpopulation extinction has intricate effects on rates of inbreeding in both the remaining subpopulations and the metapopulation as a whole. The magnitude of these effects depends on the pattern and rate of migration, and is enhanced in systems with weak connectivity. Moreover, the effects of subpopulation extinction before and at migration-drift equilibrium are different. Effective size dynamics among the subpopulations surviving extinction are affected both by the subpopulations that once belonged to the metapopulation and by migration between the remaining ones. The effects of subpopulation loss on remaining subpopulations' effective sizes may lag in time and are thus expected to be difficult to detect empirically. These findings highlight the need to consider metapopulation dynamics in management and conservation, e.g., in monitoring genetic diversity. Increased empirical and theoretical focus on effective size dynamics of individual subpopulations belonging to metapopulations is required to fully appreciate the effects of extinction. Extended exploration of how the genetically effective population size behaves in substructured populations and following subpopulation extinction is therefore warranted—crucial even, in light of the current extinction crisis.

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Data availability Additional data are provided as Supplementary Information.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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