

1 **Reconsidering the management paradigm of fragmented populations**

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13 14 15 **Abstract**

16 Habitat fragmentation and population declines call for informed management of many
17 endangered species. The dominant paradigm for such management focuses on avoiding deleterious
18 inbreeding effects in separated populations, by facilitating migration to maintain connectivity
19 between them, an approach epitomized by the “one migrant per generation” rule. We show that this
20 paradigm fails to take into account two important factors. First, it ignores an inherent trade-off:
21 maintaining within-population genetic diversity is at the expense of maintaining global diversity.
22 Migration increases local within-population genetic diversity, but also homogenizes the meta-
23 population, which may lead to erosion of global genetic diversity. Second, this paradigm does not
24 consider that because many fragmented species have declined in numbers only within the last
25 century, they still carry much of the high genetic diversity characteristic of the historically large
26 population. The conservation of a species’ global diversity, crucial for evolutionarily adaptation to
27 ecological challenges such as epidemics, industrial pollutants, or climate change, is paramount to a
28 species’ long-term survival. Here we discuss how consideration of these factors can inform
29 management of fragmented populations and provide a framework to assess the impact on genetic
30 diversity of different management strategies. We also propose two alternative management
31 strategies to replace the “one migrant per generation” dogma.

32
33 Genetic diversity is considered an important factor in a species’ likelihood of avoiding
34 extinction [1–3]. Genetic diversity can be quantified in different ways; two prominent measures are
35 allelic diversity, i.e. the number of alleles in a population, and heterozygosity, the probability that
36 two gametes sampled at random from a population differ at a certain locus [4]. Genetic diversity,

37 which includes alleles that are under strong selection as well as neutral and even slightly deleterious
38 alleles, encapsulates the evolutionary potential of a population. It serves as a reservoir of potential
39 adaptations to novel environmental and evolutionary challenges [5–9]. Such challenges include new
40 pathogens, climate change, or environmental stress by pollutants. In meta-populations, high
41 diversity, even if not widely distributed between populations, is important. Thus, for example,
42 differential susceptibility of different amphibian populations of the same species to the deadly
43 chytrid fungus may be partially attributable to previously-neutral genetic differences between these
44 populations [3]. Genetic diversity is also important for another reason: low heterozygosity is
45 associated with increased occurrence of deleterious phenotypes due to recessive alleles. Deleterious
46 recessive alleles are common across vertebrates' genomes, but as long as heterozygosity is high
47 they are usually found in heterozygous individuals that suffer no deleterious effects. Low
48 heterozygosity can thus lead to decreased fitness of many individuals, termed *inbreeding*
49 *depression*, which in some cases may lead to population decline or extinction [10,11].

50 Avoidance of inbreeding depression is the focus of many current management plans for
51 endangered species whose populations have been reduced and fragmented. This is often attempted
52 by facilitating connectivity between populations, by translocating individuals between sites or by
53 enabling migration along corridors. It is being considered or implemented for a broad range of
54 species such as tigers [12], rhinos [13], and others [14], and is reflected in the large investment in
55 wildlife corridors across man-made barriers such as highways [15]. Such facilitated migration
56 decreases the frequency of mating between relatives and increases heterozygosity at the local level;
57 however, it also homogenizes the genetics across the connected populations, increases the rate of
58 erosion of genetic diversity at the global scale, and decreases overall evolutionary potential ([3,16–
59 20], see Supplementary sections 1 and 2).

60 The “one migrant per generation” (OMPG) rule, the epitome of the current management
61 paradigm, was originally proposed to emphasize the role of gene flow in population differentiation,
62 as a balance between local (within-population) and global genetic variation (at the species' level)
63 [21–23]. It is often interpreted in conservation biology as the “at least OMPG rule”, i.e. a minimal
64 threshold for sufficient gene flow between populations, with many management plans striving to
65 increase inter-population connectivity as much as possible [23]. However, it has been pointed out
66 previously by Templeton and others [3,24] that using the OMPG as a threshold rather than as a
67 theoretical balancing point favors, in practice, maintenance of local heterozygosity over retention of

68 species' evolutionary potential. These two goals do not always overlap: the latter is dependent on
69 the maintenance of the species' global diversity, between as well as within populations. Moreover,
70 the OMPG rule assumes that populations are in equilibrium, and does not consider the fact that the
71 populations of species of conservation concern were, just a few decades ago, much larger than they
72 currently are (see, e.g., [23]). The consequence is that a precious legacy of the historically-large
73 populations still exists: much of the genetic variation, and especially allelic diversity, characteristic
74 of large populations, has not yet been lost (Supplementary Sections 1 and 2). The contemporary
75 subsample from those populations represents genetic diversity much greater, sometimes by orders
76 of magnitude, than would be expected from such small populations if genetic diversity had already
77 reached equilibrium. If frequent migration among the remaining populations takes place, genetic
78 diversity will rapidly decrease towards a new low-diversity equilibrium, characteristic of the current
79 small overall population size.

80 This can be illustrated by considering the diversity at a single genetic locus in a certain species.
81 Assume that 200 years ago this species' total population was large, say, 1,000,000 individuals.
82 Assuming the species' population had been fully connected for a long time and was at equilibrium,
83 the expected level of heterozygosity would have been 0.97 and approximately 400 different alleles
84 for this genetic locus would have been expected to be found in the population (the details and
85 calculation of this example are in Supplementary 5). Imagine that following hunting and
86 fragmentation, the species' global population (*meta-population*) was very recently reduced to 1000
87 individuals, fragmented into multiple small populations. Because individuals survived the
88 population crash at random, much of the original genetic diversity would still be represented in the
89 smaller contemporary meta-population: heterozygosity would still be expected to be 0.97, and
90 approximately 150 alleles would still be expected in the meta-population, representing the legacy of
91 the previous genetic diversity. If frequent facilitated migration between the remaining fragments is
92 carried out, effectively uniting them to form a single population, most alleles would be lost over
93 time. A population's equilibrium genetic diversity is dependent on its size, and so drift would
94 rapidly eliminate almost all the diversity: the expected equilibrium heterozygosity for a population
95 of 1000 individuals is 0.04, and the expected allelic diversity at equilibrium is below 2.
96 Alternatively, if no migration is carried out, drift would rapidly lead to the fixation of a single allele
97 in each population fragment. However, the changes in allele frequencies due to drift are random and
98 thus many more of the alleles that existed in the original meta-population would avoid overall

99 extinction by stochastically fixing in at least one of the population fragments. If, for example, the
100 species is fragmented to 10 populations, 9 different alleles would be expected to still be represented
101 at equilibrium (see calculation in supplementary 5), and global expected heterozygosity would
102 remain very high: 0.87.

103 The tension between maintenance of local and global genetic diversity has been pointed out in
104 many studies and relies on well-known theory of population genetics [3,5,16–18,23,24]; however,
105 this has had limited influence on the current paradigm for management of fragmented species. In
106 order to increase the likelihood of fragmented species' long-term survival, management must
107 consider protection of both local and global genetic diversity. Management should also take into
108 account the meta-population structure of fragmented species and build upon the legacy of precious
109 genetic diversity that can be preserved for the species' future benefit. In what follows, we present a
110 computational framework, in terms of the number of population fragments maintained and the rate
111 of migration between them, that shows the impact of alternative management plans on genetic
112 diversity as measured by local and global heterozygosity. This framework includes parameters that
113 apply to the endangered species, and is implemented as an interactive tool, available online, for
114 evaluating alternative management scenarios. Further, we propose two simple qualitative
115 management strategies for when and how to carry out migration between populations, facilitating
116 genetic rescue among populations as needed. Finally, we discuss the possible consequences of
117 recurring genetic rescue and the choice of minimal population sizes that would prevent fixation of
118 deleterious alleles of large effect size.

119 120 **Modeling the influence of migration on genetic diversity**

121
122 At the core of our proposed paradigm is the assumption that global genetic diversity is key to
123 long-term survival of species, in agreement with Aldo Leopold's suggestion that keeping as many
124 of the parts as possible is necessary for "intelligent tinkering" ([25]). To achieve this goal, we use a
125 simple mathematical derivation that computes the changes over time of mean heterozygosity, the
126 most common measure of genetic diversity used in conservation [11,26], in the meta-population and
127 within populations. We can explore scenarios that differ in the size and number of populations and
128 in the rate of migration between them (the model is presented in Supplementary 2; we use
129 'heterozygosity' as defined above, known also as 'expected heterozygosity' [4]). Because many
130 species are characterized by a 'historical legacy' of high genetic diversity compared to the

131 equilibrium state for the current meta-population size, and because much of the diversity that needs
132 to be protected is selectively neutral or near-neutral, especially in currently small populations, our
133 model focuses on the impact of random drift on neutral genetic diversity under different
134 management scenarios.

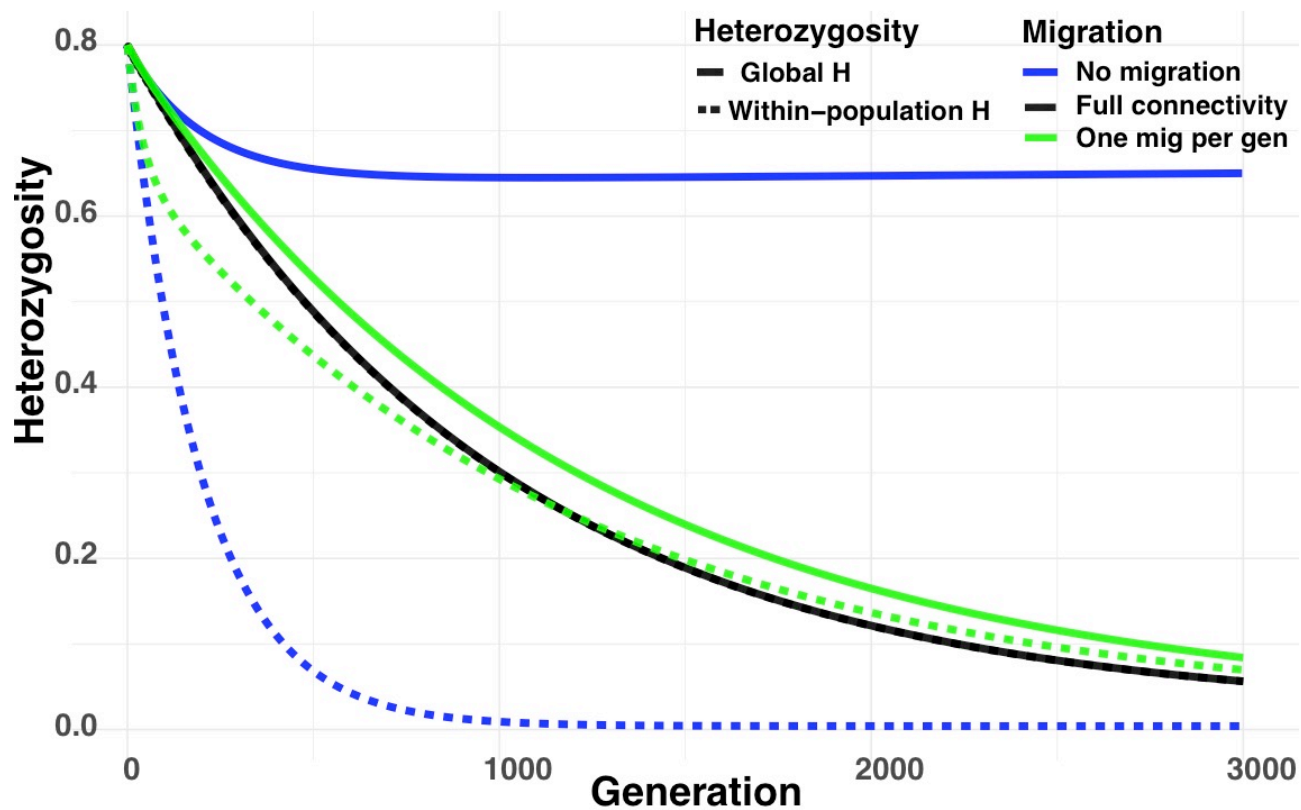
135 Figure 1 depicts the dynamics of genetic diversity, measured as heterozygosity, under one
136 management scheme in which fragments are fully connected via migration and another with no
137 migration at all, and compares them to the dynamics under an OMPG management scheme. It
138 illustrates what is expected to happen to global heterozygosity and to within-population
139 heterozygosity under each. The no-migration scheme is expected to preserve global heterozygosity
140 at much higher levels than both of the other schemes. The OMPG scheme, although commonly
141 thought to retain local genetic uniqueness of populations (e.g., [23]), genetically homogenizes the
142 separate populations at a rate similar to the fully-connected management scheme, and drives loss of
143 global diversity at a similar expected rate. However, it maintains higher local diversity within
144 populations than the no-migration scheme. Figure 1 demonstrates the tradeoff between retaining
145 local and global diversity. We suggest that management plans should not follow a specific one-rate-
146 fits-all migration rule, such as OMPG, but should aim to balance global and local diversity: Global
147 genetic diversity should be maintained at the highest levels possible, retaining as much as possible
148 of the remaining historical genetic variation. At the same time local genetic diversity must be
149 maintained at a level that is necessary to avoid population-level inbreeding depression. Our model,
150 also implemented as an online tool, allows the exploration of the effect on local and global
151 heterozygosity to be expected with different migration rates and numbers of populations.

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157 **Figure 1: Expected global and local heterozygosity under different regular migration schemes.**

158 A species whose historical meta-population size was $N_e = 100,000$, and was reduced to 5
159 fragmented populations, each characterized by $N_e = 100$. Maintenance of full connectivity (black)
160 leads to an identical decrease in global and local heterozygosity. Complete avoidance of migration
161 leads to retention of much of the original genetic diversity, reflected in high global heterozygosity
162 (solid blue), but also to rapid decline in heterozygosity within local populations (dashed blue).
163 Migration at a rate of one migrant per generation leads to coupled decline of global and local
164 heterozygosity (solid and dashed green, respectively), that diverges only slightly from that under a
165 scheme of full connectivity. Assumed rate of mutation is 10^{-5} , similar to rates found in
166 microsatellites among vertebrates. Examples for dynamics in populations with different parameters
167 are found in supplementary 1. Results are numerical calculations based on equations 3 and 6 in
168 Supplementary Section 2, and were produced using our computational tool, available at
169 <https://ryantaylor.shinyapps.io/gmfp/>.

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172 **Proposed management schemes**

173 The management paradigm we propose does not include pre-defined regular rates of assisted
174 migration between populations. Instead, we suggest that migration should be facilitated only if
175 population-level inbreeding depression becomes imminent. The impact of inbreeding and the level
176 of heterozygosity at which it becomes a problem are unclear, particularly in light of cases in which
177 populations persist despite having been founded by very few individuals or having undergone
178 severe bottlenecks (e.g. [27,28]). Among studies that show inbreeding effects in the wild, the vast
179 majority show decreased fitness of inbred individuals but do not address whether inbreeding has an
180 impact at the population level (e.g. [29,30]). However, the population, not the individual, is what
181 matters for species' conservation; the reason for preventing inbreeding should be to avoid local
182 population declines in a way that could lead to local extinction and the concomitant loss of
183 population-specific genetic diversity (see discussion in supplementary 2). We suggest that
184 management should avoid regular migration of individuals among populations; instead, we suggest
185 that managers should 'play the (genetic) cards' sparingly, and make use of inter-population genetic
186 diversity in order to prevent local extinctions only when necessary. We propose that the way to do
187 this is by employing 'genetic rescue' ([31,32]) – migration of individuals from one population to
188 another – only if the receiving population shows signs of decrease in population size that are
189 suspected to be related to lack of genetic diversity (*scheme 1*). Figure 2 illustrates recurring
190 application of genetic rescue into our model (see also Supplementary 2). We find that even under a
191 broad range of conservative assumptions, this scheme is superior to regular migration of individuals
192 between populations in the spirit of the OMPG rule. It leads to a slower rate of loss of global
193 heterozygosity (Figure 2, solid orange curve), while maintaining viable local populations.
194 Supplementary 1 discusses which populations to use as sources for migrants in genetic rescue.

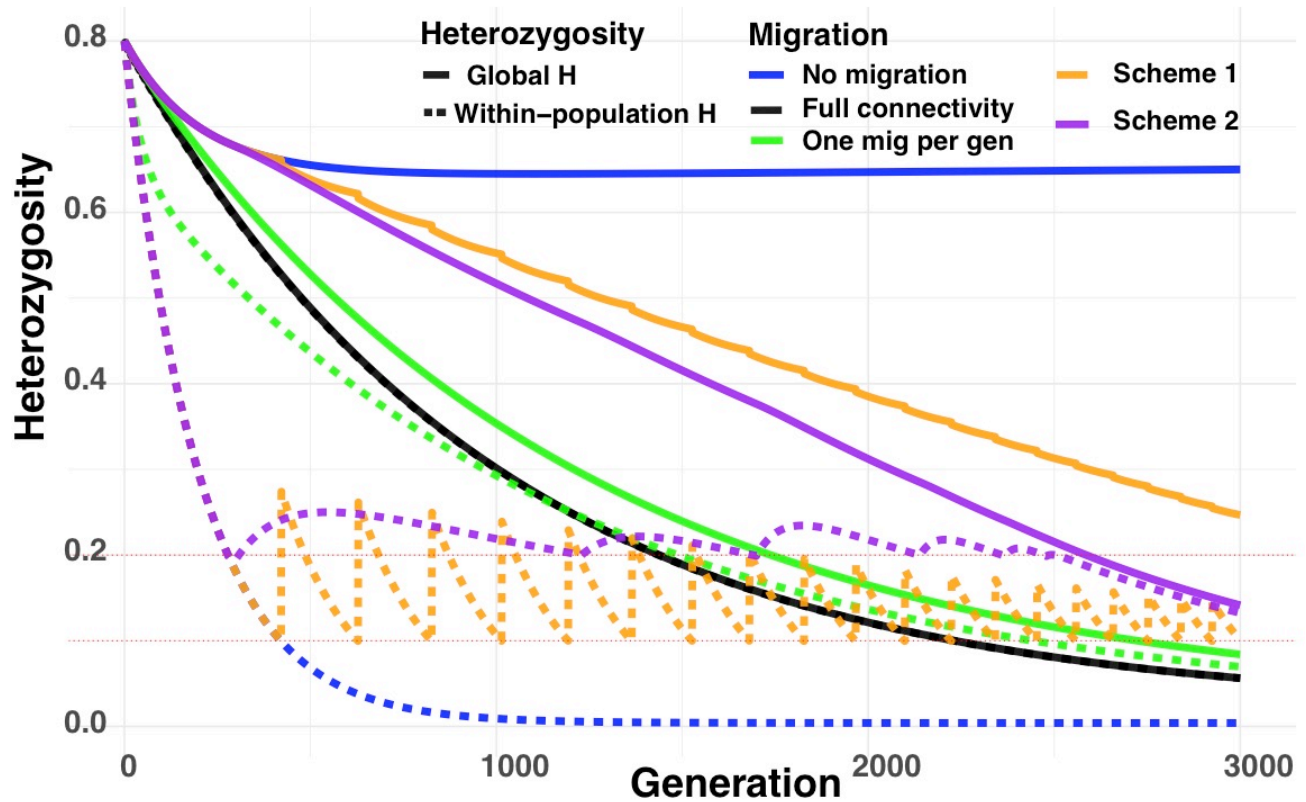
195 Although evidence suggests that genetic rescue can be very rapid, there may be species in which
196 demographic dynamics make this less likely to succeed or too risky due, for example, to stochastic
197 fluctuations in population sizes. There are also populations whose close monitoring is impossible,
198 and for these population decline may go unnoticed until very late. For such cases, we propose an
199 alternative management scheme (*scheme 2*), which can be viewed as an informed version of the
200 OMPG (details in supplementary 1). In scheme 2, managers define the critical level of
201 heterozygosity that they believe must be avoided in order to prevent population-level inbreeding
202 depression. Initially, no migration is carried out, thus preventing unnecessary loss of global

203 diversity. When a population's heterozygosity nears the chosen threshold, migration at a low rate is
204 facilitated, maintaining heterozygosity above the threshold. This rate of migration is updated every
205 few decades to maintain the population above the critical heterozygosity threshold for as long as
206 possible. This scheme outperforms all schemes of regular migration between populations, both in
207 the length of time that it allows avoidance of the critical threshold of heterozygosity in each
208 population (Figure 2, dashed purple), and in the global diversity that is retained (Figure 2, solid
209 purple; also Supplementary 1).

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215 **Figure 2: Proposed management schemes and comparison to the OMPG.** The primary scheme
 216 (scheme 1) includes no migration, except when a population begins to decline, in which case
 217 genetic rescue via migrants from another population is facilitated. Using a derivation based on the
 218 pseudo-hitchhiking model [33] (Supplementary Section 2), we assume that genetic rescue leads to
 219 replacement of the variant found at each genomic site in a certain fraction of the individuals in the
 220 rescued population, $R=0.2$ in this illustration, by the allele for that site that was carried by the
 221 rescuing individual. The figure depicts the expected global and local heterozygosity (solid and
 222 dashed orange, respectively) assuming for this illustration that such rescues need to be implemented
 223 whenever local heterozygosity reaches $H=0.1$ (merely for the sake of illustration, since rescues are
 224 not expected to be required in a regular manner, and are not expected to be directly related to
 225 heterozygosity). The alternative scheme we propose (scheme 2, purple) is the facilitation of minimal
 226 migration while avoiding a pre-defined level of heterozygosity that is deemed critical with respect
 227 to the risk of inbreeding depression (here, $H_{critical}=0.2$): no migration until this threshold is reached,
 228 followed by a shift to a regular rate of migration which is updated every few decades as necessary

229 (rates chosen for this illustration are, respectively: no migration, one migrant per 20 generations,
230 one per 10 generations, one per 6 generations, one per 4 generations, and one per 2 generations;
231 details of this illustration, and illustrations for other parameter values, are in supplementary 1). The
232 population sizes are as in Figure 1; the plots for the regular migration schemes, identical to those
233 shown in Figure 1, are presented for comparison (black, green, blue). Scheme 1 allows maximal
234 retention of global diversity for the longest period of time, avoiding $H=0.2$ for thousands of
235 generations longer than does OMPG, while maintaining viable local populations. Scheme 2 allows
236 the retention of less global diversity than scheme 1, but may be more appropriate in some cases (see
237 text), and also far outperforms OMPG both in maintenance of global diversity and in the duration
238 for which it allows the avoidance of the critical threshold of local heterozygosity (purple and green
239 curves; avoidance of the threshold for hundreds of generations longer than the OMPG). The figure
240 was produced using our online tool and can be further explored at:
241 <https://ryantaylor.shinyapps.io/gmfp/>.

242
243 A potential challenge in maintaining small populations is the avoidance of fixation of
244 deleterious mutations: efficiency of purifying selection against deleterious mutations is dependent
245 on population size. The detailed dynamics of such purging in small populations are debated ([34–
246 36]), and the relative importance of deleterious mutations in the conservation context is unclear. We
247 propose that an advisable precaution is to determine the size of the managed populations in a way
248 that is conservative in its likelihood of preventing fixation of deleterious mutations of large effect.
249 Using standard assumptions and denoting this effect size by s and the *effective population size* by
250 N_e , deleterious mutations that satisfy $N_e \cdot s \gg 1$ have a negligible probability of fixing. For
251 example, if each population had $N_e=40$ or more, then $N_e \cdot s > 2$ for deleterious mutations that
252 reduce fitness by 5%, thus effectively preventing their fixation (see supplementary 4 for details and
253 discussion of relation between N_e and census population size). Accordingly, where local populations
254 are very small, we advise the creation of a regional structure, such that each *region* consists of a
255 number of populations that together meet the requirement for the minimal N_e and constitutes a
256 management unit. Within each region, migration of individuals should be facilitated such that the
257 populations will be effectively fully connected or nearly so. Among regions, migration will be
258 facilitated only when genetic rescue is required.
259

260 **Summary**

261 The paradigm shift we propose for management of fragmented species, with the goal of
262 increasing the likelihood of long-term species' survival, is based on a simple model of the dynamics
263 of genetic variation. We challenge the currently-prevalent paradigm, which is focused on increasing
264 inter-population connectivity and does not consider the historical legacy of high genetic diversity, a
265 valuable asset for species long-term survival. It is based on models that do not directly address
266 genetic diversity and the risk of inbreeding depression, but focus on population divergence, a
267 measure that is frequently irrelevant to this risk.

268 Beyond the scope of the genetic diversity model that we focus on here lie a number of additional
269 important genetics-related arguments against facilitated migration between populations that we do
270 not discuss. These include the risks of outbreeding depression and the loss of local adaptations.
271 Consideration of these factors lends further support to the approach we are suggesting.

272 Our focus here has been on genetic diversity, which is only one factor among many in species'
273 conservation. Our study does not address demographic or ecological considerations, which may
274 often pose a greater risk for species' survival in the short term (e.g., [37,38]). Such considerations
275 include the risk of Allee effects, risk of extinction due to stochastic fluctuations in population sizes,
276 and risk of spreading disease and parasites between populations by migration. Finally, removing
277 direct threats to the species' existence such as hunting and road kill, and maintaining or restoring
278 ecosystem and habitat integrity and resilience, are additional crucial steps.

279 As conservation efforts are forced to shift towards management of discrete protected areas and
280 their resident populations, informed strategies should be adopted that both maintain high global
281 genetic diversity and avoid local population extinctions. Our paradigm suggests that to do so
282 successfully, populations should be closely monitored but that active maintenance of connectivity
283 be reduced to the bare minimum necessary, recognizing that the one migrant per generation rule
284 may be, in many cases, one migrant too many.

285

286 **Software**

287 We offer an online tool for the assessment of different migration rates on global and local
288 heterozygosity, as shown in Figure 1 and 2. The code and link can be found at
289 <https://github.com/rwtaylor/GMFP>.

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297 298 References

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