

# Eco-evolutionary dynamics and collective dispersal: implications for salmon metapopulation robustness

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The spatial dispersal of individuals is known to play an important role in the dynamics of populations, and is central to metapopulation theory. At the same time, local adaptation to environmental conditions creates a geographic mosaic of evolutionary forces, where the combined drivers of selection and gene flow interact. Although the dispersal of individuals from donor to recipient populations provides connections within the metapopulation, promoting demographic and evolutionary rescue, it may also introduce maladapted individuals into habitats host to different environmental conditions, potentially lowering the fitness of the recipient population. Thus, dispersal plays a dual role in both promoting and inhibiting local adaptation. Here we explore a model of the eco-evolutionary dynamics between two populations connected by dispersal, where the productivity of each is defined by a trait complex that is subject to local selection. Although general in nature, our model is inspired by salmon metapopulations, where dispersal between populations is defined in terms of the straying rate, which has been shown to be density-dependent, and recently proposed to be shaped by social interactions consistent with collective movement. The results of our model reveal that increased straying between evolving populations leads to alternative stable states, which has large and nonlinear effects on two measures of metapopulation robustness: the portfolio effect and the time to recovery following an induced disturbance. We show that intermediate levels of straying result in large gains in robustness, and that increased habitat heterogeneity promotes robustness when straying rates are low, and erodes robustness when straying rates are high. Finally, we show that density-dependent straying promotes robustness, particularly when the aggregate biomass is low and straying is correspondingly high, which has important ramifications for the conservation of salmon metapopulations facing both natural and anthropogenic disturbances.

Salmon metapopulations, Straying, Dispersal, Eco-evolutionary dynamics, Alternative stable states

**Media Summary** Many migratory species, such as salmon, are remarkable in finding their way home. This homing has allowed fine-scale adaptations to the environments in which they evolve. But some individuals do not find their way home and instead stray to other locations, especially when there are fewer individuals to help with collective decision-making. With an eco-evolutionary model, we discovered that an intermediate and density-dependent straying rate allows linked populations to be robust to disturbance but maintain local adaptations.

## 1. INTRODUCTION

Intraspecific diversity can increase the resilience and stability of species or metapopulations. This diversity-stability linkage occurs when there are asynchronous population dynamics, where the changes in population size varies temporally across the metapopulation. This asynchrony will increase the potential for demographic rescue [1, 2] and also decrease the variability of processes that integrate across the metapopulation [3]. For example, different responses to climate variability within populations of a rare plant reduced fluctuations in abundance [4]. This statistical buffer has traditionally been quantified as the Portfolio Effect (PE), which is the ratio of the population CV to the CV of the aggregated metapopulation [5]. Strengthened portfolio effects are expected to increase the robustness of metapopulations to external disturbances, and by extension promote persistence [5]. In contrast, homogenization of populations leading to greater synchronization and weakened PE may be a harbinger of metapopulation collapse and extinction.

Movement of individuals among local populations (i.e. dispersal) can have a large influence on metapopulation persistence [6]. Dispersal facilitates evolutionary rescue, whereby immigration of individuals with heritable adaptive traits can rescue small populations from local extinction in the context of maladaptive environmental change [7, 8]. On the other hand, high rates of dispersal may synchronize populations and actually increase the risk of extinction of the entire metapopulation [2]. Dispersal will also influence the evolutionary dynamics of the metapopulation. Although the dispersal of individuals into sites hosting other populations provides connections within the larger metapopulation, potentially promoting demographic and evolutionary rescue, it may also introduce maladapted individuals into habitats that are host to different environmental conditions, possibly lowering the mean fitness of the recipient population [9]. More broadly, dispersal can provide a mechanism by which phenotypes are sorted in space rather than time and facilitates the spread of maladaptive genes [10]. Dispersal in this case may lead to genetic homogenization that erodes the asynchrony underpinning portfolio effects and metapopulation persistence.

There is growing appreciation that a combination of abiotic, biotic, and anthropogenic factors can control the rate of dispersal among populations [11–13]. Migratory populations that return to breeding sites for reproduction are linked to each other by some proportion of the population that permanently disperses into the ‘wrong’ site. Recently, the role of social interactions and collective navigation has been hypothesized [14–16, this volume]. The rate at which individuals disperse may be linked to errors made at an individual-level that are themselves diminished by migrating in groups and pooling individual choices [14, 15, 17]. The potential influence of collective dispersal on the dynamics of individual populations and the metapopulation as a whole is a topic of considerable interest that has tangible conservation implications [18–20].

The eco-evolutionary impacts of dispersal likely have important implications for conservation and management in key taxa such as in migratory salmon. While anadromous salmonid fishes (genera *Oncorhynchus* and *Salmo*) are renown for returning to their natal spawning habitats with high accuracy and precision after years at sea [12, 21, 22], there are generally some individuals that ‘stray’ (synonymously used hereafter to refer to dispersal) to non-natal sites to spawn [23, 24]. Salmon may operate as metapopulations, where populations are genetically distinct but linked by some level of straying [25, 26]. Although extensive work has been done to document the extent of straying from donor populations into recipient populations [12, 13], only recently have the abiotic, biotic, and anthropogenic influences of straying behaviors been investigated systemically [27–29]. Straying among salmon may be influenced by environmental factors such as water temperature, human activities such as hatchery practices, and population density as predicted

by the collective navigation hypothesis [30, 31]. Straying can introduce new maladaptive genotypes into the recipient population, while the ensuing genetic homogenization could synchronize population dynamics and erode portfolio effects [32–34]. Thus, there is an opportunity and need to consider the eco-evolutionary consequences of straying for metapopulations in species of conservation and management concern such as salmon.

Here we seek to explore how collective density-dependent straying influences the stability and robustness of metapopulations through ecological and evolutionary processes. To address this question we constructed a eco-evolutionary model of two populations occupying different sites that are linked by straying individuals, each with an associated trait distribution subject to natural selection determined by local conditions. Specifically we compared (a) different rates of straying and (b) the influence of collective movement, across (c) increasing environmental heterogeneity, by assessing two measures of metapopulation robustness: the portfolio effect and the time required for a population(s) to recover following an induced disturbance. This model enables us to explore the tradeoff between the potentially detrimental erosion of local adaptation vs. the positive effects of demographic and evolutionary rescue, both of which are facilitated by straying.

## 2. MODEL DESCRIPTION & ANALYSIS

### (a) Metapopulation framework

We follow the basic framework provided by Ronce and Kirkpatrick [35], where dispersal connects two populations  $N_i$  and  $N_j$  that inhabit two distinct habitats, each with trait values  $x_i$  and  $x_j$  determining phenotype. In our version of the model, there is an optimum trait value  $\theta_i$  and  $\theta_j$  associated with each habitat, where recruitment is maximized if the trait value of the local population equals the optimum, such that  $x = \theta$ . Moreover, we assumed that  $x_{i,j}$  are normally distributed with means  $\mu_i$  and  $\mu_j$  and have the same standard deviation  $\sigma$ . As such, the recruitment rate  $R_i[\mu_i(t), \theta_i]$  for both populations is determined by the mean trait value of the local population relative to optimal value at that site. Trait means for each population are subject to selection, the strength of which is proportional to the difference between the trait mean and the local trait optimum at a given point in time [35–37].

The two populations occur in spatially separate sites that are close enough that a proportion of the population  $m$  strays into the other site. If there is no straying between these populations, then the mean trait evolves towards the optimal value for each site  $\mu_i \rightarrow \theta_i$ , and the recruitment rate for each population is maximized. If there is straying between populations at rate  $m$ , then the traits in each respective location will be pulled away from the optimum, and recruitment rates will be lowered. As  $m \rightarrow 0.5$ , the populations are perfectly mixed, effectively acting as a single panmictic population.

We used the discrete Ricker framework described by Shelton and Mangel [38] as the basis for our two-site metapopulation model, with the added effect of the local population  $N_i$  mixing with a proportion  $m$  of individuals from a remote population  $N_j$ , and where there is no demographic overlap between generations. In this sense, both populations serve simultaneously as donor and recipient populations. Because total recruitment will be determined by both locals (with a mean trait value closer to the site optimum) and strays (with mean trait values farther from the local optimum), the recruitment of the aggregate is given by  $R_i[\omega_i \mu_i(t) + (1 - \omega_i) \mu_j(t), \theta_i]$  (Eq. ??). This mix of individuals is subject to identical compensatory effects, which is determined by the parameter  $\beta$ . Taken together, the difference equation that determines changes in population size from time  $t$  to  $t + 1$  is

$$N_i(t+1) = R_i[\omega_i\mu_i(t) + (1-\omega_i)\mu_j(t), \theta_i] \times ((1-m)N_i + mN_j) e^{-\beta((1-m)N_i(t) + mN_j(t))}, \quad (1)$$

where

$$\omega_i = \frac{(1-m)N_i(t)}{(1-m)N_i(t) + mN_j(t)}, \quad (2)$$

and the equation for  $N_j$  mirrors that for  $N_i$ .

The recruitment of the population as a function of the mean trait value at time  $t$  and the local trait optimum is

$$\begin{aligned} R_i[\omega_i\mu_i(t) + (1-\omega_i)\mu_j(t), \theta_i] &= \\ \int_{-\infty}^{\infty} r_{\max} \exp\left\{-\frac{(x_i - \theta_i)^2}{2\tau^2}\right\} \text{pr}(x_i, \omega_i\mu_i(t) + (1-\omega_i)\mu_j(t), \sigma^2) dx_i + \tilde{P}_i \\ &= \frac{r_{\max}\tau}{\sqrt{\sigma^2 + \tau^2}} \exp\left\{-\frac{(\theta_i - (\omega_i\mu_i(t) + (1-\omega_i)\mu_j(t)))^2}{2(\sigma^2 + \tau^2)}\right\} + \tilde{P}_i. \end{aligned} \quad (3)$$

where the mismatch between the local trait mean  $\mu_i(t)$  and the local optimum  $\theta_i$  scales the recruitment rate for the population, and  $\tilde{P}_i \sim \text{Normal}(0, 0.01)$  introduces a small amount of demographic error. The parameter  $\tau$  is the strength of selection, and controls the sensitivity of recruitment to changes in the mean trait value away from the optimum (the strength of selection increases with smaller values of  $\tau$ ), which we set as  $\tau = 1$  here and throughout. Because straying individuals are emigrating from a population with a mean trait value farther from the local optimum, their rate of recruitment is diminished. Recent studies of wild sockeye salmon have indeed found that straying individuals have lower life-time fitness than individuals that do not stray, although it is unknown at what life-stage this selection occurs [30].

Because individuals from the local population are mixed with individuals from the remote population via straying and subsequent reproduction, the resulting trait distribution is a complex mixture of trait distributions (see Supplemental Materials: Appendix I for the derivation, Fig. ??). We make two simplifying assumptions. First, we approximate the distribution resulting from the mix of remote and local individuals prior to reproduction as a Gaussian, where  $X_i = x_i$  with probability  $g(x_i)$ . The expectation of the actual trait distribution as well as the Gaussian approximation are the same, such that  $E\{g(x_i)\} = \omega_i\mu_i + (1-\omega_i)\mu_j$ , with weights corresponding to the proportion of the mixed population that are local individuals,  $\omega_i$ , and straying individuals,  $1-\omega_i$ . Thus, strays can successfully reproduce and introduce their genotypes into the recipient population, which is supported by observations in wild populations [39]. Second, we assumed that changes in trait variance through time are minimal, such that  $\sigma^2$  is constant over time, which is a common simplification in eco-evolutionary models of population dynamics [35, 37, 40–42]. These simplifications are the same as those introduced by Ronce and Kirkpatrick, and were shown to have negligible impacts on dynamics [35].

Following Lande [37], and given our assumption of trait distribution normality, the mean trait value thus changes through time according to the difference equation

$$\begin{aligned}\mu_i(t+1) &= \omega_i \mu_i(t) + (1 - \omega_i) \mu_j(t) + h^2 \sigma^2 \frac{\partial}{\partial \mu'} \ln(R_i[\mu', \theta_i]), \\ &= \omega_i \mu_i(t) + (1 - \omega_i) \mu_j(t) + h^2 \sigma^2 \left( \frac{\theta_i - \omega_i \mu_i - (1 - \omega_i) \mu_j}{\sigma^2 + \tau^2} \right),\end{aligned}\tag{4}$$

given  $\mu' = \omega_i \mu_i(t) + (1 - \omega_i) \mu_j(t)$ .

**(b) Density-dependent straying** We have so far assumed that the proportion of strays leaving and entering a population is constant, however there is mounting evidence that at least in some species (including salmon) straying is density-dependent, a signature of collective navigation [31, 43]. Specifically, the rate at which individuals stray has been linked directly to a collective decision-making phenomenon, where greater numbers of individuals tend to decrease the rate at which individuals err, reducing the overall proportion of a population that strays. According to Berdahl et al. [15], given the probability that an individual strays is  $m_0$ , the proportion of the local population  $N_i(t)$  that strays is

$$m(t) = m_0 \left( 1 - \frac{N_i(t)}{C + N_i(t)} \right),\tag{5}$$

where  $C$  is a half-saturation constant, and determines to what extent collective behavior, as a function of group size, diminishes straying. If  $C$  is small, relatively small groups of organisms ‘correct’ for even high individual error rates, suppressing straying between sites. In the context of our model, small values of  $C$  indicate that the effects of collective behavior on modifying straying are strong. As  $C \rightarrow \infty$ , groups of any size have no impact on straying, such that  $m(t) \rightarrow m_0$ , and the model reverts to that of constant straying. When  $C \ll \infty$  and the population density is high,  $m(t) \rightarrow 0$ , whereas if the population is small, individuals operate without regard to the collective, such that  $m(t) \rightarrow m_0$ , such that in all cases,  $m(t) < m_0$ .

**(c) Measuring metapopulation robustness** We evaluated metapopulation robustness by measuring the average-CV portfolio effect (PE) [26, 44] as well as the recovery time, which is the time required for the system to return to a steady-state following an induced disturbance to one or both populations [45]. Throughout, we refer to an increase in portfolio effects and/or reduction in recovery time as promoting metapopulation robustness.

The average-CV portfolio effect is, as the name implies, the average CV across each population  $N_i$  divided by the CV of the aggregate  $N_T = \sum_i N_i$  [46], such that

$$\langle \text{PE} \rangle = \frac{1}{X} \sum_{i=1}^X \frac{\sqrt{\text{VAR}(N_i^*)}}{\text{E}(N_i^*)} \cdot \frac{\text{E}(N_T^*)}{\sqrt{\text{VAR}(N_T^*)}},\tag{6}$$

where in this case the number of populations is limited to  $X = 2$  and the expectations  $\text{E}(\cdot)$  and variances  $\text{VAR}(\cdot)$  are evaluated at the steady-state. The steady-state condition is denoted by ‘\*’. As the CV of  $N_T^*$  decreases relative to that of the constituent populations,  $\langle \text{PE} \rangle > 1$ , and the metapopulation is presumed to be more stable because the aggregate has functioned to dampen population-level variance. Moreover, portfolio effects greater than unity correspond to less synchronization [26, 47, 48] and thus a greater potential for demographic rescue among populations, buffering the system as a whole against extinction.

A more direct way to measure system robustness is to measure the time that the system (measured as the aggregate steady-state biomass  $N_T^*$ ) takes to return to a steady-state following an induced disturbance: systems that recover quickly (shorter recovery times) are more robust than those that recover more slowly (longer recovery times). Although there is a direct eigenvalue relationship between the rate of return following a small pulse perturbation [49], because we aimed to 1) assess the effects of a large perturbation far from the stable state, and 2) estimate the time required for all transient effects to decay following this perturbation (including dampened oscillations), we used a simulation-based numerical procedure. Recovery time was calculated by initiating a disturbance at  $t = t_d$ , and monitoring  $N_T(t_d + t)$  as  $t \rightarrow T$ , where  $T$  is large. The aggregate was deemed recovered at  $t_r$ , such that recovery time was calculated as  $t_r - t_d$ , and recovery at  $t = t_r$  was determined by the initial  $t$  where  $N_T(t) < N_T^* \pm \text{SD}(N_T^*)$  for  $t \in (t_r, T)$ , where  $\text{SD}(\cdot)$  is standard deviation (illustrated in figure S1).

Numerically estimating the time that it takes for a perturbed system to recover also permits a more nuanced perspective of metapopulation robustness. For example, if populations settle to alternative stable states, comparing recovery times after a disturbance applied to individual populations allows for an assessment of which component of the metapopulation has a longer-lasting influence on the system's recovery. We measured recovery time following three types of induced disturbance: (i) extinction of the low-density population; (ii) extinction of the high-density population (scenarios *i* and *ii* are equivalent if populations have the same density); (iii) near-collapse of both populations where just 1.0% of each survives.

### 3. RESULTS

#### (a) Nonlinear effects of straying on metapopulation robustness

Regardless of density dependence, straying lowers steady state densities for both populations by (i) the donor population losing locally-adapted individuals to the recipient population and (ii) the introduction of maladapted individuals to the recipient population from the donor population (Fig. 1). This prediction is in accordance with observations from natural populations [13]. The decline in steady-state densities is not gradual: as straying increases, the system crosses a pitchfork bifurcation (PB) [50] whereby the single steady-state for the metapopulation bifurcates into two basins of attraction: one at high biomass, and one at low biomass density (figure 1a, 2a). Accordingly, if straying is high enough, the populations assume asymmetric densities, referred to by Ronce and Kirkpatrick as *migrational meltdown* [35]. Mean trait values for both populations bifurcate similarly (figure 1b), where the trait optimum for the dominant population skews both dominant and subordinate trait means. If straying is increased enough, the alternative fixed points revert to a single fixed point, and the populations assume symmetric, low biomass densities. Notably, if straying is subsequently reduced *after* it has increased (such that hysteresis effects are observed), the system passes the PB without change to the dynamics until it crosses a second bifurcation (a fold bifurcation; FB) at lower values of  $m$  (figure 1). Thus, the eco-evolutionary model is characterized by two separate dynamic regimes that can lead to alternative stable states: regime I, where two (asymmetric) alternative stable states (dominant and subordinate) are separated by an unstable steady state, and regime II, where the default state is a symmetric stable state at intermediate biomass densities, but that harbours a high- and low-density basin of attraction.

Trait heritability  $h^2$  has a large effect on the degree to which straying affects both the aggregate population steady-

state density ( $N_T^*$ ; figure 2a) as well as the difference between steady-state densities (the distance between alternative stable states:  $\Delta N^* = |N_1^* - N_2^*|$ ; figure 2b). Increased trait heritability is observed to prevent the development of the alternative stable state regime, thereby maintaining greater densities in  $N_T^*$ , and a relatively uniform PE across increased straying ratios. Lower trait heritability ( $h^2 < 0.8$ ) introduces alternative stable state regimes, and the pitchfork bifurcation that marks the onset of this regime occurs for lower straying rates for traits with lower  $h^2$  (Fig 2a,b). This indicates that weaker coupling between ecological and evolutionary dynamics in addition to increased straying promotes the appearance of alternative stable states. Although trait heritability among salmonids is variable, most life-history traits have an  $h^2 < 0.5$  [51], and for all additional analyses we have set  $h^2 = 0.2$ .

As the alternative stable state regime is approached with increasing  $m$ , the portfolio effect increases sharply due to an amplification in variance within both populations. This amplification in variance is the product of *critical slowing down*, which occurs near some bifurcations [52] and has been suggested to serve as an early warning indicator for approaching phase transitions [52–56]. For larger values of  $m$  (to the right of the PB in Fig 2a-c), where alternative stable states occur, the portfolio effect declines steadily as the CV of  $N_T^*$  decreases. The decline over  $m$  is more gradual if trait heritability is low, and steeper if trait heritability is high, suggesting that the benefits provided by a higher PE are greater for traits that have a low  $h^2$  and when the straying ratio is near the pitchfork bifurcation in regime I.

As the portfolio effect is highly sensitive to straying between populations, so is the time required for the system to recover to a steady state following a large disturbance. We find that the average-CV portfolio effect is negatively correlated with recovery time (figure 2d), indicating that both measures are valuable indicators of metapopulation robustness, and where recovery time is measured for *i*) near-collapse of both populations, *ii*) extinction of the dominant population, and *iii*) extinction of the subordinate population. We find that if straying is low, recovery following near-collapse requires the most time (figure S3a). However, as straying increases and the system enters the alternative stable state regime, the extinction of the dominant population has a recovery time on-par with recovery following near-collapse, due to greater straying from a population hosting a mean trait value farther from the optimum of the recovering population. If straying continues to increase, the time required to recover from any of the disturbance scenarios grows due to the increasingly negative effects of demographic mixing on the rate of recruitment. Near the onset of the pitchfork bifurcation, recovery time increases explosively, however this is – as the name implies – characteristic of slow dynamics occurring near critical transitions [52, 57]. Given the small parameter range where this effect occurs, we do not consider slow dynamics very close to the critical transition to be ecologically significant.

#### (b) The effects of collective navigation and density-dependent straying

If we assume that the rate of straying is density-dependent, the probability that an individual errs  $m_0$  in part determines the magnitude of straying within the population (Eq. 5), such that  $m(t)$  becomes lower as  $N(t)$  increases, which we assume here to be the consequence of collective decision-making behaviors [15]. The parameter  $C$  in Eq. 5 determines to what extent straying is reduced as group size increases, where low values correspond to the effects of strong collective behavior, and high values correspond to the effects of weak collective behavior [15]. To enable comparisons between models with constant and density-dependent straying, we examine constant  $m$  with respect to both the individual straying probability  $m_0$  as well as the value of straying observed at the steady state  $m^*$ . In the alternative stable state regime, the dispersing populations are characterized by alternative  $m^*$  values, corresponding to dominant and subordinate densities.

When collective behavior is very strong, such that  $C$  is very low, small increases in population density begit large reductions in straying. These reductions can be large enough such that the system avoids the alternative stable state regime altogether (figure 3, left inset). Conversely, when collective behavior is very weak, such that  $C$  is very high, there is effectively no reduction in straying with increased group size, and the dynamics conform to those of the constant straying model (figure 3, right inset). However, when collective behavior is of intermediate strength ( $10^{1.5} \lesssim C \lesssim 10^3$ ), the dynamics are altered in two important ways. First, in the alternative stable state regime, the low density subordinate population has correspondingly higher  $m^*$ , whereas the high density dominant population has correspondingly lower  $m^*$  (figure 3, center inset). Second, the alternative stable state regime results in a  $\Delta N^*$  that is reduced when individual error rates are low, and magnified when individual error rates are high (figure 3, main). In other words, when collective behavior is of intermediate strength, a higher individual rate of error exaggerates the differences between the steady state densities, effectively pushing the subordinate population closer to extinction.

In both the constant- and dynamic straying model, there are two regimes that give rise to alternative stable states: one that is produced by a pitchfork bifurcation (regime I), and one that is produced by a fold bifurcation (regime II; figure 4). When the strength of collective behavior is intermediate, the cause of the exaggerated difference in steady state densities at high individual straying rates is due to an increase in the dominance of regime I over a greater range of  $m_0$  (figure 4). If the effects of collective behavior are very strong, regime I vanishes, and the populations generally assume symmetric densities. However, while regime I vanishes, the alternative stable state regime created by the fold bifurcation expands (regime II; figure 4). In regime II there are two possible steady state configurations: 1) the steady states of both populations can either have symmetric densities, or 2) one or both populations can revert to asymmetric dominant/subordinate states as in regime I. In this case, populations will attain asymmetric densities if  $m_0$  is first increased and subsequently decreased (introducing a hysteresis effect), or if a sufficiently large perturbation directs one of the populations towards the dominant or subordinate basins of attraction.

Dynamic straying via collective behavior directly alters the dynamic regimes of the model, and this has an impact on measures of robustness such as the portfolio effect and recovery time. When the effects of collective behavior are weak (large  $C$ ) the portfolio effects and recovery times conform to those examined in the case of constant straying. As the effects of collective behavior are increased to intermediate values (intermediate  $C$ ), the expansion of regime I has contrasting effects on metapopulation robustness as measured by the portfolio effect and time to recovery following near-collapse of both populations (figure 5): *i*) if individual straying is low, regime I is avoided; *ii*) if individual straying is intermediate, the system enters regime I, resulting in an increase in robustness as observed by an elevated portfolio effect and suppressed recovery time; *iii*) if individual straying is high, the time to recovery becomes extreme, such that robustness is eroded. When the effects of collective behavior are unrealistically strong (low  $C$ ), the portfolio effect remains relatively constant and the recovery time increases with higher values of  $m_0$ , tracking a gradual decline in steady state densities.

As is described above, the alternative stable state regime II created by the fold bifurcation expands with lower  $C$  (figure 4). Here, the lone extinction of either population will push the system into a different configuration. Directly after extinction and as the site is being recolonized by the undisturbed population, instead of returning to its previously higher (symmetric) density that it shared with the undisturbed population, it becomes trapped in the basin of attraction defined by the subordinate state that is generally not observed barring the occurrence of hysteresis. The extinction of either population in regime II therefore has a shorter time to recovery (figure S4), but this is in part



driven by the newly acquired subordinate steady state density. Importantly, this low-density basins of attraction, which is particularly prevalent across  $m_0$  when the effects of collective behavior are strong, would not be easy to anticipate or detect prior to a large disturbance.

### (c) The role of habitat heterogeneity and changing selective landscapes

As habitat heterogeneity ( $\Delta\theta$ ) increases, even small amounts of straying can lead to the appearance of alternative stable states, and this is in direct accord with the findings of Ronce and Kirkpatrick [35]. However, if straying is density dependent, the strength of collective behavior has a large influence on the occurrence of alternative stable states defined by both regimes I and II. When habitat heterogeneity is low and the effects of collective behavior are weak (large  $C$ ), regime I occurs for small-intermediate  $m_0$ , and regime II does not play a role (figure 6a). The absence of regime II implies that there are no hidden steady state configurations that might trap a disturbed population. As the strength of collective behavior increases, regime II appears at a cusp and becomes prevalent with increased  $m_0$ .

When habitat heterogeneity is high, the proportion of  $(m_0, C)$ -space that is dominated by alternative stable state regimes expands (figure 6b,c). Only when habitat heterogeneity is intermediate does regime II play a significant role as straying is relatively constant (figure 6b). For high  $\Delta\theta$ , there is no longer any sanctum from regimes I or II except for very high individual straying. In this case, regime I dominates when the strength of collective behavior is weak. When the strength of collective behavior is strong, regime II is dominant when individual straying is low, and regime I is dominant when individual straying is high.

Until now, we have treated straying and habitat heterogeneity as independent parameters, however they may also be assumed to covary. For instance, if sites are separated by greater distance, they may be assumed to have increased habitat heterogeneity as well as less straying. Alternatively, individuals may be genetically predisposed to stray into sites that are more similar, such that higher straying can be assumed to occur between sites that are more homogeneous in aspect. We implemented this inverse relationship by setting  $m_0 = 1/(2 + \epsilon\Delta\theta)$  where  $\epsilon$  controls the degree to which an increase in  $\Delta\theta$  lowers  $m_0$  (figure 7, inset). Accordingly, that  $m_0$  is greater for lower  $\Delta\theta$ , such that there is lower straying between dissimilar sites and higher straying between similar sites. Under these conditions we find that regime I appears for very low  $m_0$ , and regime II appears for higher  $m_0$  (figure 7). As the straying rate increases and  $\Delta\theta$  decreases, a single (symmetric) steady state emerges as the fold bifurcation is crossed, which is opposite the pattern observed when straying is independent of habitat heterogeneity.

## 4. DISCUSSION

We have shown that density-dependent straying between populations consistent with collective navigation, coupled with localized selection against donor phenotypes, has a large and nonlinear impact on dynamic properties that affect metapopulation robustness. We measured robustness as: 1) the average-CV portfolio effect [3, 46], a statistical metric commonly used to assess the buffering capacity of metapopulations, and 2) the recovery time, defined here as the time required for the aggregate metapopulation biomass  $N_T^*$  to return to its steady-state following an induced disturbance, which is mechanistically linked to persistence [45]. In our eco-evolutionary model of dispersal and natural selection between two populations, we show that these statistical and mechanistic descriptors of metapopulation dynamics and robustness are tightly coupled (figure 2d), which is not uncommon for diverse metrics of stability [58]. Taken as a whole, our results point to an important role of density-dependent straying in the colonization and recovery dynamics

within metapopulations, while also underscoring the risk of straying by individuals with maladaptive traits to reduce the productivity of locally adapted stock complexes.

A central dynamic of the model is that straying can lead to the emergence of asymmetric alternative stable states, or *migrational meltdown* [35], pushing one of the populations to a dominant, high density, state, and one to a subordinate, low density, state. In regime I (figures 1a, ??), there exists only one configuration for alternative stable states: dominant and subordinate. By contrast, in regime II, there exist two configurations: a symmetric intermediate density, or the asymmetric dominant/subordinate state. These general dynamic features are exactly those observed for the eco-evolutionary model investigated by Ronce and Kirkpatrick [35], where dispersal is assumed to be symmetric between sites and constant over time. An important aspect of our eco-evolutionary model is that there are similar forces that dictate interactions within and between sites, and this naturally results in a symmetry that could limit the relevance of our findings for natural (and inherently less symmetric) systems. Although the emergence of alternative stable states via the combined effects of the fold and pitchfork bifurcations are characteristic of symmetrical systems, we find that increasing the asymmetry in the vital rates of populations between sites does not significantly alter the presence or position of alternative stable states (figure S5).

Under the assumption of constant straying, we find that an intermediate degree of straying increases metapopulation robustness, whereas low to intermediate rates of straying appear to have a beneficial effect on transient dynamics, which is measured by determining the time to recovery following an induced disturbance. When there is just enough straying to cause the system to enter regime I, the portfolio effect at first increases and the recovery time at first declines: signs of increased metapopulation robustness. In the alternative stable-state regime, a lower rate of straying inhibits admixture of maladapted individuals. Following a large disturbance, such as the near-collapse of both dominant and subordinate populations, this limited mixing increases the growth rates of both populations, permitting faster recovery times. As straying becomes very large, robustness declines, as observed by a decrease in PE (figure 2c) and increase in recovery time (figure S3a). In this case, increased straying promotes the influx of maladapted individuals into both populations, inhibiting local growth rates, lengthening recovery.

This themed issue formalizes the role of collective movement in the ecology of natural systems and illuminates a signature of collective navigation in animal populations on the move. When straying is dynamic, straying at the steady state is determined by a) the probability that individuals err  $m_0$ , and b) the influence that group size has on straying at the level of the population, which we assume here is the product of collective decision-making, determined by the parameter  $C$  (small values of  $C$  mean that the influence of collective behavior on reducing straying is large; Eq. 5). We highlight three important findings that contribute to our understanding of collective movement suggesting that density-dependent straying may play an important role in the persistence of metapopulations over evolutionary time.

First, if the effects of collective behavior are very strong, the alternative stable state regime I can be avoided altogether. This means that - despite potentially high individual error rates - group formation minimizes straying, and the pitchfork bifurcation can be avoided altogether. However, this occurs when groups of  $\leq 10^2$  individuals significantly minimizes straying, which may be unrealistic. As the heterogeneity between habitats increases, avoidance of the pitchfork bifurcation becomes impossible, and alternative stable state regime I becomes unavoidable. Second, if collective behavior is of intermediate strength, the differences between the steady state densities are exaggerated, effectively pushing the subordinate population closer to extinction (figure 3). Moreover, although robustness generally

declines with increased individual straying (quantified by a decrease in PE and an increase in recovery time), it remains elevated iff collective behavior is of intermediate strength (figure ??), but this effect is eroded as  $m_0 \rightarrow 0.5$

Third, we find that the alternative stable state regime II expands across a larger range of  $m_0$  as the effects of collective behavior grow. In regime II, alternative stable states are generally avoided, however there exist hidden low-density basins of attraction, which may trap a population in the wake of a large disturbance. We observe this by instituting the extinction of a single population. If the system is outside of regime II, the population will rebound to its previous state as it is colonized by the surviving population. If the system is within regime II, the recovering population will become trapped in the subordinate basin of attraction, and will not recover its previous density. So although strong collective behavior can provide benefits to a metapopulation by either 1) avoiding the alternative steady state regime I, or 2) increasing robustness for higher individual straying rates, there is an unavoidable cost, which lies in the expanded parameter space dominated by these hidden low-density basins of attraction.

[Beta] The dynamics of our eco-evolutionary model with either constant or density dependent straying can be divided into: a high density symmetric state, the alternative stable state regimes I and II, and a low density symmetric state. It is tempting to speculate that high density symmetric states are always more preferable, that alternative stable states are always less preferable, and that the low density symmetric state is to be avoided. Although the latter is undoubtedly true from a conservation perspective, it is less clear to what extent high density symmetric states are ‘better’ or ‘worse’ than the alternative stable states found in regimes I or II. For example, although high densities buffer populations against large disturbances, symmetric densities are by definition synchronized, which eliminates the potential for ecological rescue. By contrast, although regime I subjects one population to a subordinate state, and regime II harbours low-density basins of attraction, these dynamic features decrease synchronization and increase measures of robustness such as PE and recovery time. What can be said is that alternative stable state regimes increase the potential complexity of the system, which may introduce considerable challenges from a management perspective. Of particular concern for management is the expansion of regime II for organisms with non-negligible individual straying and that navigate by collective decision-making, due to the likely undetectable basins of attraction that lurk at low population densities.

Salmon are distributed and stray across a diverse range of habitats, and the rates of straying between geographically diverse sites can be plastic and idiosyncratic [28]. Our surrogate measure for habitat heterogeneity is the difference in trait optima between sites  $\Delta\theta$ . We show that as habitat heterogeneity increases, the occurrence of alternative steady states associated with regime I becomes unavoidable, particularly for  $0.1 \leq m_0 \leq 0.4$ , and regime II becomes minimized (figure 6). This may be particularly consequential for populations that are spatially adjacent but separated by sharp environmental boundaries, such that trait optima are divergent yet dispersal is relatively high. Such a scenario plays out repeatedly in the context of wild and hatchery-produced salmon. Although wild and hatchery populations may occur close on the landscape, and indeed often are sympatric within the same river network, the selective environments to which they are locally adapted differ dramatically [59]. Straying of domesticated hatchery-produced fish from release sites and spawning in the wild drastically reduces the productivity of wild populations through competition and outbreeding depression [60, 61].

In other cases, habitats that are closer in space can be assumed to have greater similarity in environmental conditions than those that are geographically distant, and phenotypes of more proximately located populations should be

more similar [62–64]. It is thus reasonable to expect a larger number of straying individuals between sites that are geographically proximate and indeed evidence corroborates this prediction [65, 66]. Alternatively, salmon that cue to specific environmental conditions may be more likely to stray into sites that are structurally and physiognomically more similar [30]. These considerations justify imposing a negative correlation between habitat heterogeneity and individual straying  $m_0$ : as site heterogeneity increases, so too should straying decrease (figure 7). When habitat heterogeneity and straying are linked in this way, we show that very small amounts of straying give rise to regime I, and that regime II occurs for higher values of  $m_0$  (figure 7). This pattern is opposite that observed for scenarios where habitat heterogeneity and straying are assumed to be independent, and suggests that increases in straying that are associated with growing similarities between habitats can push a metapopulation into a regime where hidden low-density basins of attraction exist. Thus, management activities that alter dispersal rates by outplanting individuals or reconnecting disconnected habitats could have unintended eco-evolutionary consequences [67, 68].

Although our study was inspired by salmon metapopulations, the results have general implications for the conservation and management of other migratory metapopulations as well. Because changes in straying can have large and nonlinear impacts on robustness, human activities that alter straying could have unintended consequences. For example, salmon produced by hatcheries often stray into proximate wild populations [18], and these recipient populations can have lower fitness due in part to the introduction of maladapted genes [69]. We show that an intermediate individual straying rate can result in faster recovery times following a large disturbance, but that this is largely determined by the strength of collective behavior. This finding suggests that salmon stocking efforts that aim to lower recovery times following dam removal could actually prolong recovery if the rate at which individuals are introduced and the suitability of those fish in that habitat (i.e. their measure of pre-adaptation) is not taken into account. Ongoing examinations of experimental restocking in the recently re-opened Elwha River (Washington State) will provide empirical insight into the potential short- and long-term consequences of facilitated recovery [70].

Density dependent straying, whether it is caused by collective decision-making or otherwise, has a large influence on the dynamics of populations in the presence of local adaptation. The rate at which individual err, and the influence of group size on straying at the population level, are two important components of dynamic straying [15]. We show that changes in these characteristics can alter the occurrence and positioning of two different alternative stable state regimes, one of which may harbor hidden low-density basins of attractions that can effectively trap populations after a large disturbance. Generally, increasing the strength of collective behavior mitigates the potentially negative impacts of what Ronce and Kirkpatrick describe as *migrational meltdown* [35]. Preserving the biological processes that facilitate this collective behavior may be an important conservation target in its own right, echoing the sentiments of Hardesty-Moore et al. [16]. We suggest that understanding the spatial complexity of metapopulations dispersing across heterogeneous environments, in tandem with the mosaic of selective forces acting on those environments, may be key to uncovering those factors that promote persistence in the wild.

**Competing interests:** The authors declare no competing interests

**Author contributions:** JDY and JWM conceived of the initial project design. JDY and JPG designed the modeling framework and conducted the analyses. JDY, JPG, PAHW, and JWM interpreted the results, and drafted and wrote the manuscript.

**Data Accessibility:** Code is made available at <https://github.com/jdyeakel/SalmonStrays>

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550 *Am Fish Soc* **17**, 1–39



Parameter	Definition	Value
$N_i(t), N_T(t)$	Individual, aggregate population over time	var.
$x_i$	Trait value for an individual in population $i$	var.
$\mu_i(t)$	Mean of $x$ for population $i$ over time	var.
$\sigma^2$	Genetic variance of trait $x$	1.0
$m, m(t)$	Constant, density-dependent straying rate	var.
$m_0$	Straying rate of an individual	var.
$R_i[\mu(t)]$	Recruitment rate of population $i$	var.
$r_{\max}$	Maximum recruitment rate	2.0
$e^{-Z}$	Survival rate	0.6
$\beta$	Strength of density dependence	$10^{-3}$
$\theta_i$	Optimal trait value for habitat $i$	5.0
$\Delta\theta$	Habitat heterogeneity	var.
$\tau$	Strength of selection	1.0
$h^2$	Heritability	var.
$C$	Half saturation constant for $m(t)$	$10^3$
PE	Portfolio Effect	var.
$T$	Terminal simulation time	$10^5$

Table I: Table of parameters, definitions, and assigned values (var. = variable).

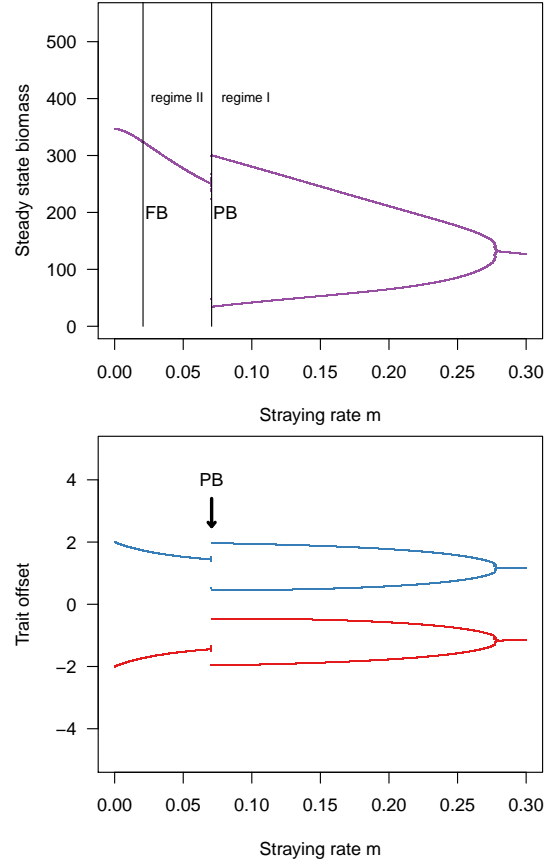


Figure 1: (a) The steady-state densities of  $N_1$  and  $N_2$  vs. the stray rate  $m$ . Which population attains the low- or high-density state is random due to small applied fluctuations in the initial conditions. (b) The steady-state trait values measured as the offset from the local optimum  $\theta_i - mu_i$ , vs. the stray rate  $m$ . DCB marks the discrete cusp bifurcation.

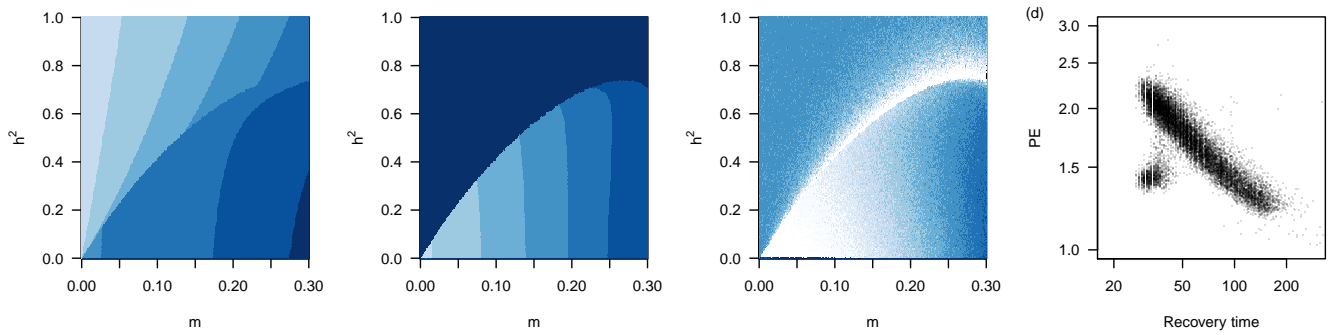


Figure 2: (a) Total means  $N_t^*$ , (b) difference in means  $\Delta N^*$ , and (c) the portfolio effect PE as a function of heritability  $h^2$  and a constant stray rate  $m$ . Light colors = high values. The black line shows the cusp bifurcation separating a single steady-state (left) from alternative stable states (right). (d) The relationship between the time to recovery following a disturbance and the portfolio effect. Portfolio effects greater than unity corresponds to less synchronization.

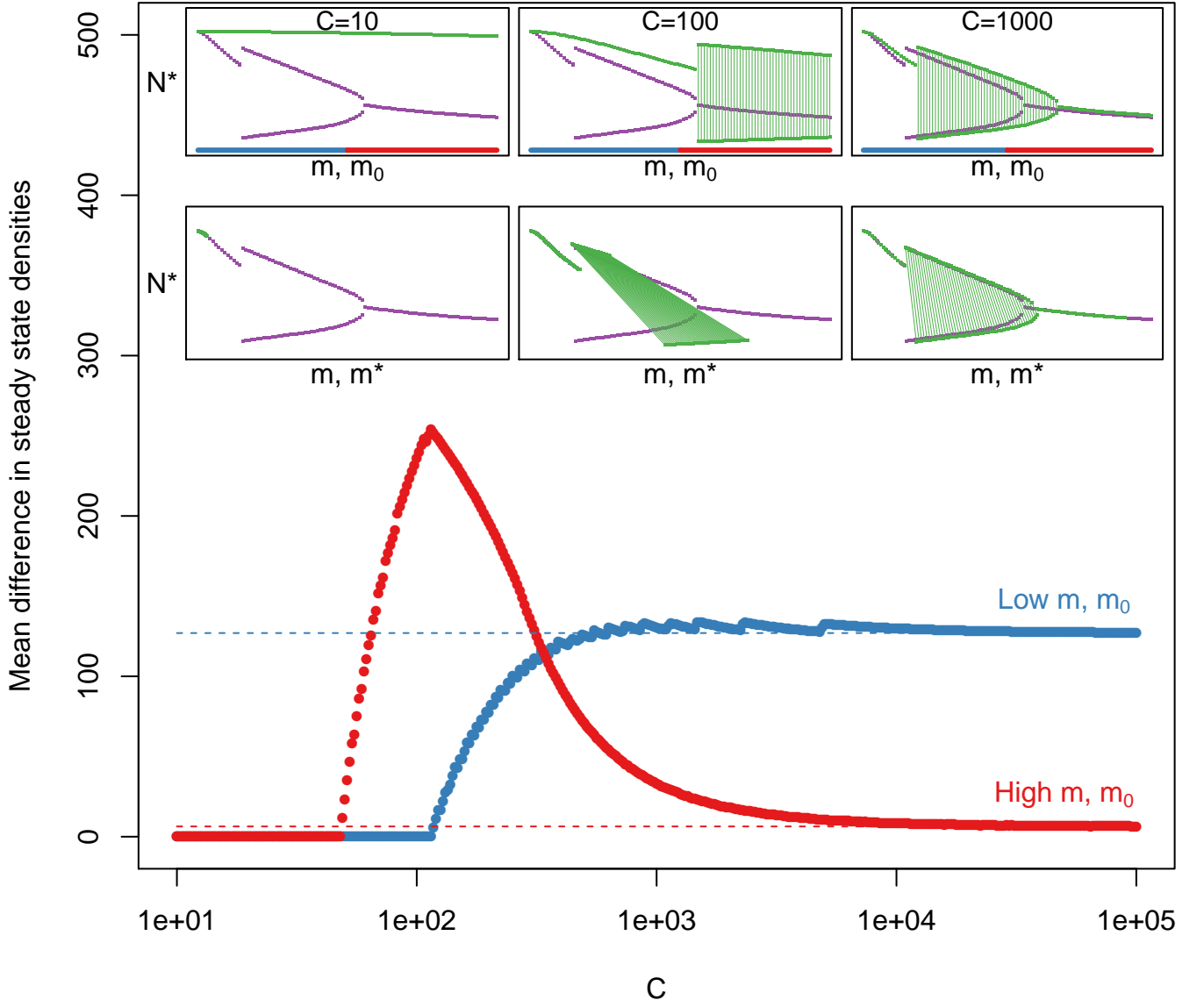


Figure 3: Inset: steady states for the constant straying model (purple) and density-dependent straying model (green) for different strengths of collective behavior. Top row shows steady state densities as a function of individual straying  $m_0$ ; bottom row shows steady state densities as a function of steady state straying  $m(t)^*$ . Main: Difference in steady states averaged across low straying values ( $0 < m, m_0 < 0.25$ ; blue) and high straying ( $0.25 < m, m_0 < 0.5$ ; red).

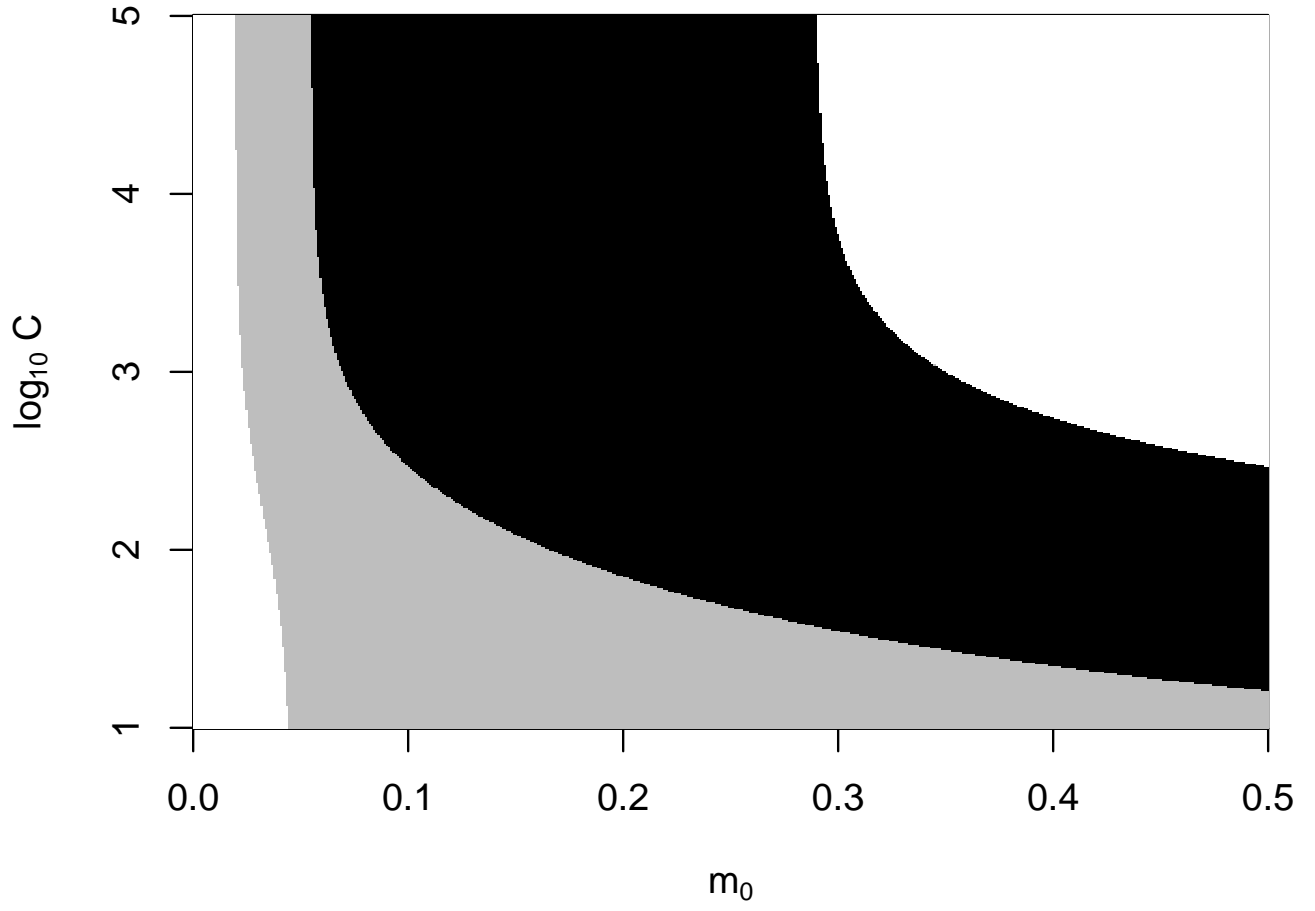


Figure 4: Regime I (black); Regime II (gray). Leftmost white is symmetric high density stable state regime; white space to left is symmetric low density stable state regime.

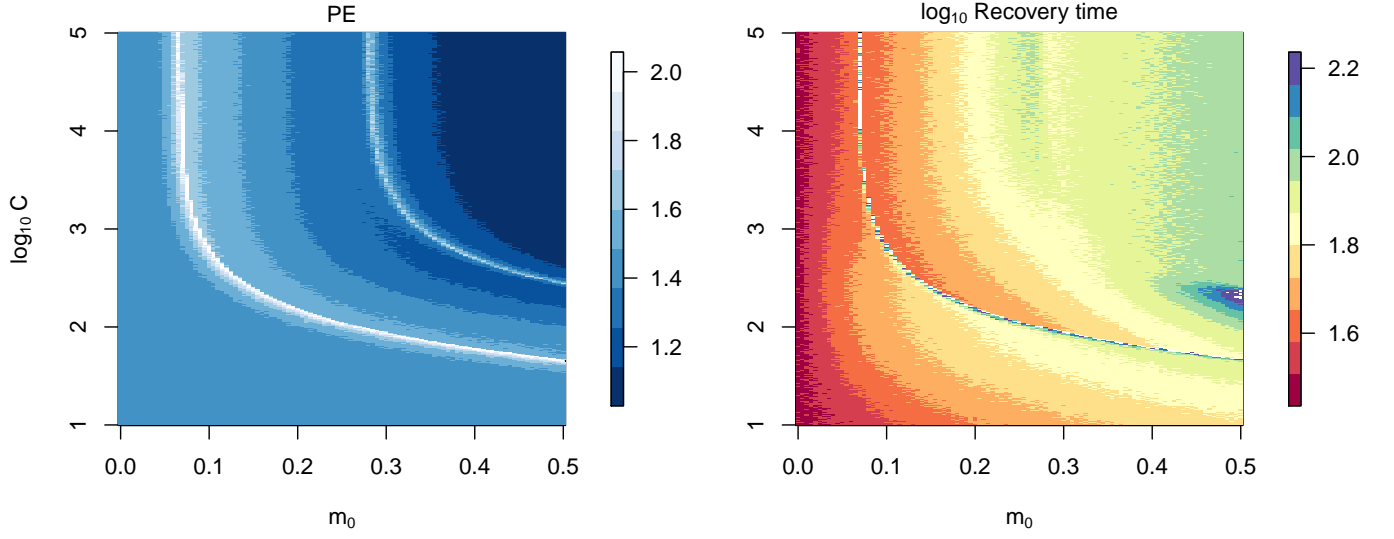


Figure 5: a) Portfolio effect b) Recovery time following near-collapse of both populations.

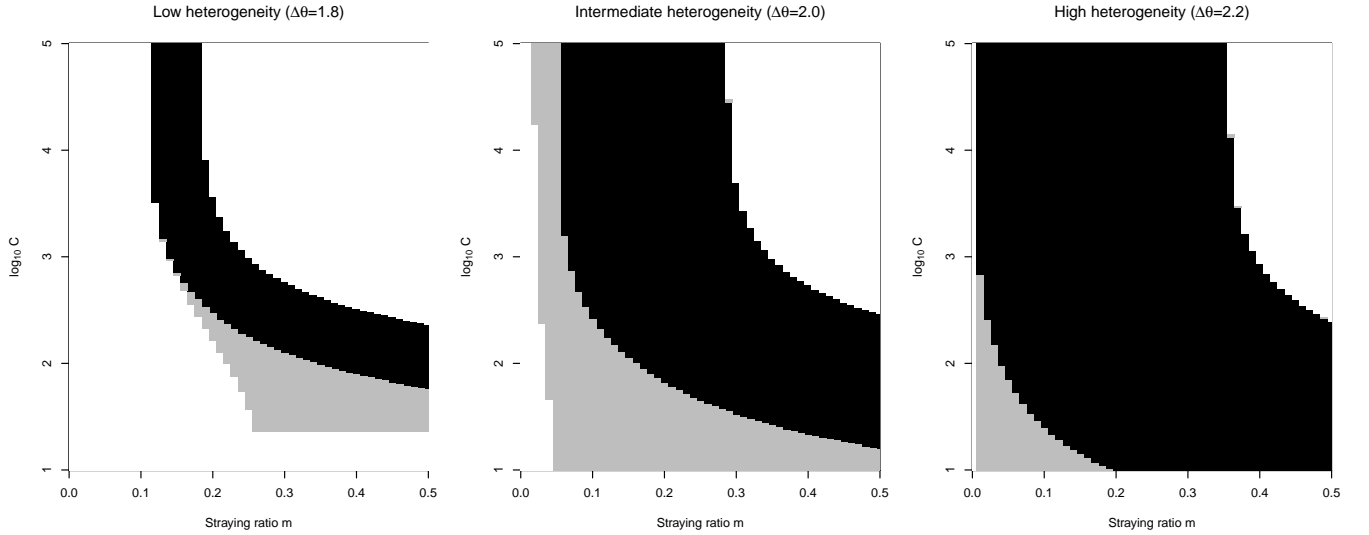


Figure 6: Each subfig: Regime I (black); Regime II (gray). Leftmost white is symmetric high density stable state regime; white space to left is symmetric low density stable state regime. The cutoff white area on rightmost fig is an artifact.

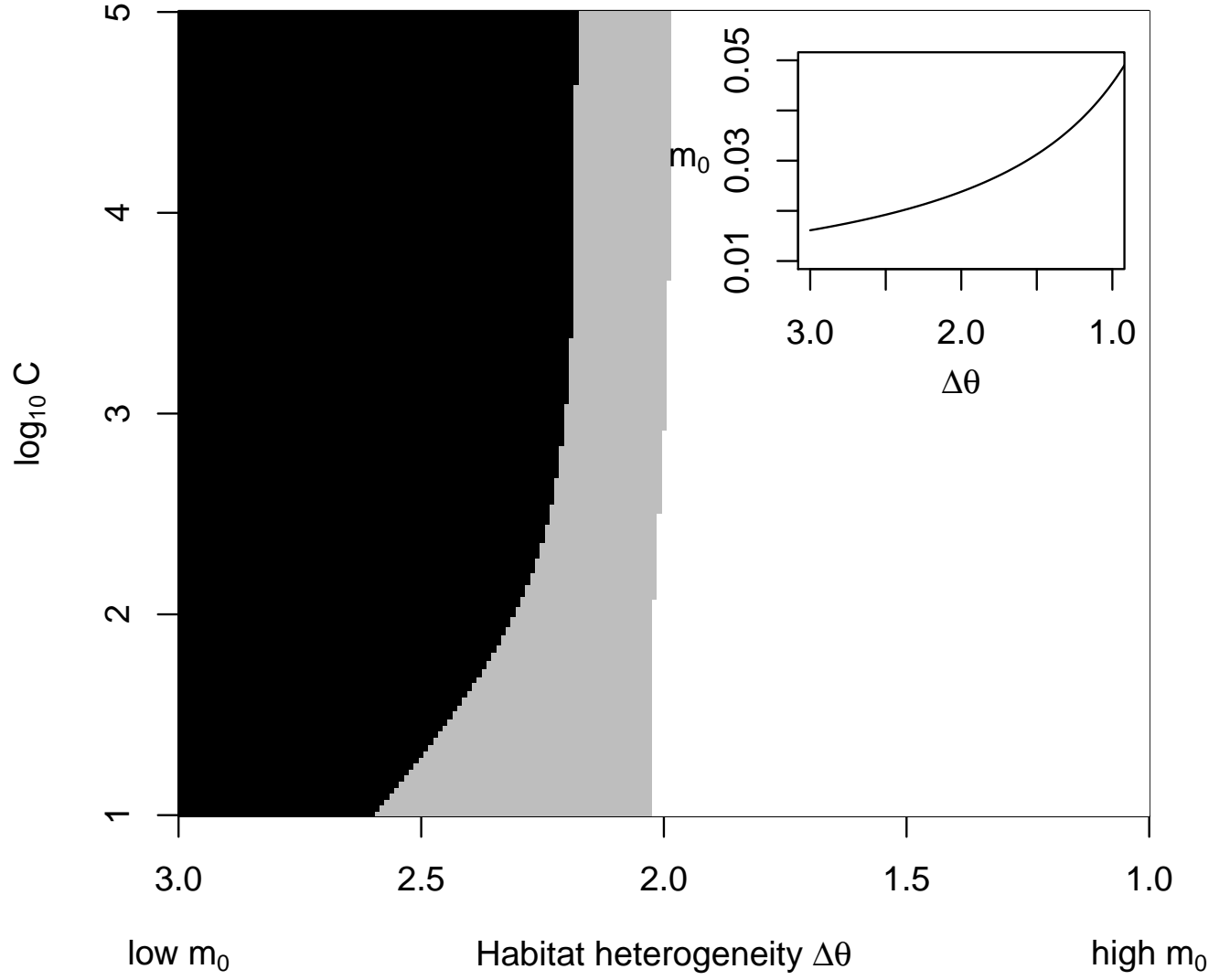


Figure 7: Inset: relationship imposed between  $m_0$  and  $\Delta\theta$ . Regime I (black); Regime II (gray). Rightmost white is symmetric (low-density) stable state.

Figure S1: Example of the numerical procedure used to estimate recovery time. After a disturbance is introduced, the recovery time is calculated by measuring the point in time where  $N_T$  (in black), which is the aggregate of both populations (blue, red) settles to within one standard deviation of the new equilibrium  $N_T^*$ .

Figure S2: The real parts of the four eigenvalues for the Jacobian matrix of the 4-dimensional system. The cusp bifurcation occurs when the dominant eigenvalue crosses the unit circle at +1.

Figure S3: Recovery time of  $N_T^*$  following the extinction of either the low-density (light gray) or high-density (gray) population, or the near-collapse of both (dark gray) assuming (a) constant straying rates  $m$  and (b) density-dependent straying rates (evaluated at the steady-state  $m^*$ ) with trait heritability  $h^2 = 0.2$ . If  $m$  is density-dependent, in the alternative stable state regime there are two straying rates observed: one each for the low- and high-density populations, respectively, which are linked by a horizontal line. DCB marks the discrete cusp bifurcation.

Figure S4: PE and recovery time after the sole extinction of the subordinate and dominate populations.

Figure S5: Steady-state densities of both populations as a function of  $m$ , where a cusp bifurcation indicates the emergence of alternative steady-states: one in a dominant state and one in a subordinate state. Steady-states for populations with symmetrical values ( $\alpha = 0$ ) in the vital rates  $r_{\max}$  and  $\beta$  are shown with cool tones. As the asymmetry among populations between sites increases ( $\alpha > 0$ ), their vital rates diverge, such that the maximal growth at sites 1 and 2 is now  $r_{\max}(1) = r_{\max}(1 + \tilde{r}v_1)$  and  $r_{\max}(2) = r_{\max}(1 + \tilde{r}v_2)$  where  $\tilde{r}v_{1,2}$  are independently drawn from  $\text{Normal}(0, \alpha)$  and  $r_{\max} = 2$ . Similarly the strength of density dependence is calculated at sites 1 and 2 as  $\beta(1) = \beta(1 + \tilde{r}v_1)$  and  $\beta(2) = \beta(1 + \tilde{r}v_2)$  where  $\tilde{r}v_{1,2}$  are independently drawn from  $\text{Normal}(0, \alpha)$  and  $\beta = 0.001$ . Steady-states for populations with increasingly asymmetric values ( $\alpha \rightarrow 0.1$ ) for vital rates  $r_{\max}$  and  $\beta$  are shown in warmer tones.