

# Eco-evolutionary dynamics, density-dependent dispersal, and collective behaviour: implications for salmon metapopulation robustness

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The spatial dispersal of individuals plays an important role in the dynamics of populations, and is central to metapopulation theory. Dispersal provides connections within metapopulations, promoting demographic and evolutionary rescue, but may also introduce maladapted individuals, potentially lowering the fitness of recipient populations through introgression of heritable traits. To explore this dual nature of dispersal, we modify a well-established eco-evolutionary model of two locally adapted populations and their associated mean trait values, to examine recruiting salmon populations that are connected by density-dependent dispersal, consistent with collective migratory behaviour that promotes navigation. When the strength of collective behaviour is weak such that straying is effectively constant, we show that a low level of straying is associated with the highest gains in metapopulation robustness and that high straying serves to erode robustness. Moreover we find that as the strength of collective behaviour increases, metapopulation robustness is enhanced, but this relationship depends on the rate at which individuals stray. Specifically, strong collective behaviour increases the presence of hidden low-density basins of attraction, which may serve to trap disturbed populations, and this is exacerbated by increased habitat heterogeneity. Taken as a whole, our findings suggest that density-dependent straying and collective migratory behaviour may help enable metapopulations such as in salmon thrive in dynamic landscapes. Given the pervasive eco-evolutionary impacts of dispersal on metapopulations, these findings have important ramifications for the conservation of salmon metapopulations facing both natural and anthropogenic contemporary 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 low density-dependent straying when the strength of collective behaviour is intermediate allows linked populations to both be robust to disturbance and maintain local adaptations to their respective habitats.

## 1. INTRODUCTION

Intraspecific diversity can increase the resilience and stability of species or metapopulations [1]. This diversity-stability linkage can arise when there are asynchronous population dynamics within the metapopulation. Such asynchrony will increase the potential for demographic rescue [2, 3] and also decrease the variability of processes that integrate across the metapopulation [4]. For example, different responses to climate variability within populations of a rare plant reduced fluctuations in abundance [5]. This statistical buffer has traditionally been quantified as the Portfolio Effect (PE), which is the ratio of the population’s coefficient of variation (CV) to the CV of the aggregated metapopulation [6]. Larger portfolio effects are expected to increase the robustness of metapopulations to external disturbances, and by extension promote persistence [6]. In contrast, homogenization of populations leading to greater synchronization and weakened PE may be a harbinger of metapopulation collapse and extinction [7].

Permanent movement of individuals among local populations (i.e. dispersal) can have a large influence on metapopulation persistence [8]. 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 [9, 10]. Dispersal also enables demographic rescue, when depressed or extirpated populations are recolonized by immigrants from the rest of the metapopulation. On the other hand, high rates of dispersal may synchronize the dynamics of populations and subsequently increase the risk of extinction of the entire metapopulation [3, 11]. Additionally, dispersal may also introduce maladapted individuals into habitats that are host to different environmental conditions, possibly lowering the mean fitness of the recipient population [12, 13]. More broadly, dispersal can provide a mechanism by which phenotypes are sorted in space rather than time and facilitates the spread of potentially maladaptive genes [14]. 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 [15–18]. Migratory populations that return to breeding sites for reproduction can be linked to each other by some proportion of the population that disperses into the ‘wrong’ site. Recently, the role of social interactions to lead to collective navigation has been hypothesized as a mechanism shaping the success of philopatric migrations [19–21]. The collective navigation hypothesis posits that 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 [19, 21, 22]. Thus, dispersal rates can be higher at lower population abundances [23], which can in turn profoundly influence the eco-evolutionary dynamics of metapopulations.

The eco-evolutionary impacts of dispersal likely have implications for conservation and management in key taxa such as in migratory salmon [24–26]. 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 [17, 27, 28], while some individuals disperse (termed ‘straying’ and used synonymously with dispersal hereafter) to non-natal sites to spawn [29, 30]. Straying provides a mechanism for the colonization of new or connected habitats following glacial retreat or large-scale geomorphic landscape change [30]. Salmon appear to operate as metapopulations, where populations are in part reproductively isolated in discrete habitat patches, but linked by some level of straying [31, 32]. Although extensive work has been done to document the extent of straying from donor populations into recipient populations [17, 18], only recently have the abiotic, biotic, and anthropogenic influences of straying behaviours been investigated

systemically [33–35]. 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 [21, 36]. Straying can introduce new maladaptive genotypes into the recipient population, while the ensuing genetic homogenization could synchronize population dynamics and erode portfolio effects [7, 37, 38]. Given that locally distinct populations are often linked by straying, there is an opportunity and need to understand the fundamental and applied consequences of straying on metapopulation persistence, conservation, and management.

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 build upon an established 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 [12]. Specifically we compared (a) density-independent (constant) straying with (b) density-dependent straying as a function of the rate at which individuals stray and the strength of collective behaviour across (c) increasing environmental heterogeneity, by assessing two measures of metapopulation robustness: the portfolio effect and the time required for recovery 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 rescue, both of which are facilitated by straying and potentially moderated by the effects of collective navigation.

## 2. MODEL DESCRIPTION & ANALYSIS

### (a) Metapopulation framework

We follow the basic framework described by Ronce and Kirkpatrick [12], where dispersal connects two populations  $i$  and  $j$  that inhabit two distinct habitats, each with densities  $N_i$  and  $N_j$  and trait values  $x_i$  and  $x_j$ . In our version of the model,  $i$  and  $j$  are locally adapted to site-specific conditions such that 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 ( $x = \theta$ ). Moreover, we assumed that  $x_{i,j}$  are normally distributed with means  $\mu_{i,j}$  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 the optimal value at that site. Mean trait values for both populations are dynamic variables and change over time in response to differences in recruitment as individuals mix between sites. Trait means for each population are thus 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 [12, 39, 40]. This is broadly consistent with empirical patterns observed in pacific salmon dynamics [41]. The two populations occur in spatially separate sites that are close enough that a proportion of the population  $m$  strays into the wrong 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, then the trait means in each respective location will be pulled away from their optima, and recruitment rates will decline. As  $m \rightarrow 0.5$ , the populations are perfectly mixed.

We used the discrete Ricker framework described by Shelton and Mangel [42] as the basis for our two-site metapopulation model, with the added effect that the size of the local population  $N_i$  is altered by mixing  $mN_j$  individuals from the remote population. Moreover, we assume that there is no demographic overlap between generations, consistent

with the life history of many populations of pink salmon (*O. gorbuscha*) who all mature at two years of age and die after one reproductive season. 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 determined by the mean of the trait mix  $R_i(\omega_i\mu_i(t) + (1 - \omega_i)\mu_j(t), \theta_i)$ , where

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

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

$$N_i(t + 1) = R_i(\omega_i\mu_i(t) + (1 - \omega_i)\mu_j(t), \theta_i) \cdot ((1 - m)N_i + mN_j) e^{-\beta((1-m)N_i(t) + mN_j(t))}, \quad (2)$$

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

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

where  $g(x_i)$  is the Gaussian probability density function for the trait  $x_i$ . The mismatch between the mean of the local trait mix  $\omega_i\mu_i(t) + (1 - \omega_i)\mu_j(t)$  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 variability. 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. 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 lifetime fitness than individuals that do not stray, although it is unknown at what life stage this selection occurs [36].

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. 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 distribution, 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  $E\{X_i\} = \omega_i\mu_i + (1 - \omega_i)\mu_j$ , 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 [43]. 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 [12, 40, 44–46]. These simplifications are the same as those introduced by Ronce and Kirkpatrick, and were shown to have negligible impacts on dynamics [12].

Following Lande [40], and given our assumption of trait distribution normality, the mean trait value thus changes through time according to the difference equation

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

with  $\mu' = \omega_i \mu_i(t) + (1 - \omega_i) \mu_j(t)$ . Although trait heritability among salmonids is variable, most life-history traits have an  $h^2 < 0.5$  [47], and for all additional analyses we have conservatively set  $h^2 = 0.2$ . Together, equations 2 and 4 for two linked populations  $i$  and  $j$  define the 4-dimensional system of difference equations that describe the eco-evolutionary dynamics of the metapopulation.

**(b) Density-dependent straying** There is mounting evidence that straying is density-dependent, consistent with predictions of the collective navigation hypothesis [21, 23]. Specifically, straying 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. Following Berdahl et al. [19], 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, determining to what extent collective behaviour, 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 behaviour on modifying straying – thus leading to collective navigation – are strong. Henceforth, we refer to  $C$  as determining the strength of collective behaviour: as  $C \rightarrow \infty$ , the effect of collective behaviour becomes weaker, such that the size of the population has no impact on straying, and  $m(t) \rightarrow m_0$ . In contrast, if  $C \ll \infty$ , the effect of collective behaviour is strong, and smaller populations reduce  $m(t)$ . Although the strength of collective behaviour depends both on  $C$  as well as the probability that an individual strays  $m_0$ , for a specific value of  $m_0$ , a lower  $C$  reduces straying for smaller population sizes, increasing the strength of collective behaviour. We acknowledge that the strength of collective behaviour is not exclusively determined by  $C$ , but suggest that it is an effective proxy for the role of collective navigation in this model.

**(c) Measuring metapopulation robustness** We evaluated two complementary measures of metapopulation robustness by quantifying *i*) the average-CV portfolio effect (PE) [32, 48] and *ii*) 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 [49]. 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  $N_T = \sum_i N_i$  [50], such that

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

where in this case the number of populations is limited to  $X = 2$  and the expectations  $E(\cdot)$  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 [32, 51, 52] 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 required for the system (measured as the aggregate steady-state biomass  $N_T^*$ ) to recover 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 relationship between the rate of return following a small pulse perturbation and the magnitude of the leading eigenvalue of the Jacobian matrix [53], 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  $N_T(t) < E(N_T^*) \pm \text{SD}(N_T^*)$  for  $t \in (t_r, T)$ , where  $\text{SD}(\cdot)$  is standard deviation (illustrated in figure S1). If the system recovers to a different basin of attraction after the perturbation is applied, recovery time is calculated with respect to the newly acquired steady state.

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

At low values of density-dependent straying or collective navigation, the system approaches a fixed point at which both populations persist at equal population size, but as we increase straying, other fixed points are created in which the population sizes are asymmetric (figure 1, inset). The system’s underlying symmetry implies that for every asymmetric fixed point there must be another ‘mirror-image’ fixed point in which we find the same population sizes, but where the identities of the populations are reversed. Asymmetric fixed points appear in bifurcations as a critical value of the straying parameter is crossed. As the noise in the system is negligible for the purposes of the bifurcation diagram we can use concepts of deterministic bifurcation theory. Based on the Jacobian eigenvalues we conjecture

that these bifurcations are fold bifurcations. In a generic fold bifurcation of maps, two new fixed points are created, one of which is unstable, while the other is stable. In the present case, two of these bifurcations occur at the same time, one which creates fixed points where the first population is dominant in the stable fixed point, whereas the second bifurcation creates the mirror-image fixed points where the second population is dominant.

In the asymmetric states the dominant population is well-adapted and has a high rate of recruitment. The (small) fraction of this population that strays to the subordinate site constitutes a considerable inflow of individuals, such that the population in the subordinate site is not as well adapted. This in turn reduces reproduction and stabilizes the asymmetry. In a regime found at low straying rates (regime I) both the symmetric and the asymmetric states are stable fixed points of the system (figure 1, purple points). Which of these fixed points is approached depends on the initial conditions.

As we increase straying, the asymmetric states eventually collide with the stable symmetric state. A subcritical pitchfork bifurcation occurs in which the unstable asymmetric states vanishes and the symmetric state is destabilized. After this bifurcation the stable asymmetric states are the only attractors. We find a wide regime (regime II) where the system will always approach an asymmetric state where one population is suppressed. However, if the straying is increased further the imbalance in population sizes becomes harder to maintain. Eventually we reach a critical point where the stable asymmetric fixed points become symmetric and collide with the unstable symmetric fixed point. The system undergoes a supercritical pitchfork bifurcation, in which the stable asymmetric fixed points vanish while the unstable symmetric fixed point is stabilized. After this bifurcation the symmetric fixed point is the only attractor in the system. Importantly, we find that increasing the asymmetry in the vital rates of populations between sites does not significantly alter the presence or position of these different regimes (figure S2).

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

Straying has a large effect on metapopulation robustness, measured by the portfolio effect and the time to recovery following the three types of induced disturbance: near-collapse of both populations, the extinction of the dominant population, and the extinction of the subordinate population (figure 2). Importantly, the presence of alternative stable state regimes I and II both have a direct impact on robustness as a function of straying  $m$ . We observe that as straying increases, the portfolio effect increases sharply as regime I or II is entered, and then declines gradually (figure 2a). Thus, low levels of straying (2-10% of the population) are associated with the strongest portfolio effects.

Different types of disturbance lead to different relationships between straying and portfolio effects. When either population suffers extinction, the PE is shown to increase with lower straying; in the case of near-collapse of both populations, PE increases when straying is higher (figure 2a). This difference is due to the hidden basin of attraction at low population densities that only plays a role when a disturbance impacts a single population. In other words, disturbance to a single population can push that population into a low-density alternative state, which in turn contributes to higher PE. The increase in PE for the synchronous near-collapse scenario occurs at higher values of  $m$  when the system enters regime II, where there exists only an asymmetric dominant (high-density) and subordinate (low-density) state. The PE spikes again when straying is very high and the system leaves regime II, entering a symmetric low-density state.

Similar patterns are observed with respect to the recovery time as straying is increased (figure 2b). For lower  $m$ , recovery of single extinctions is impacted by the appearance of low-density basins of attraction in regime I,

whereas recovery following near-collapse is not. For intermediate values of  $m$  (regime II), the time to recovery is only diminished when the subordinate population becomes extinct, whereas the time to recovery following near-collapse and the extinction of the dominant population are similar and grow until Regime II is exited at high  $m$ . In the case where the subordinate population is extirpated, the most rapid recovery rate occurs when straying is low ( $m = 0.08$ ). In contrast, when the dominant population goes extinct, the most rapid recovery is associated with minimal straying. It should be noted that when there is no straying ( $m = 0$ ), recovery time is infinite and these values are not shown. The relationship between straying and recovery time in the case of synchronous population disturbance is generally positive.

Collectively, these patterns in recovery time and PE are influenced by the different alternative stable states regimes. As the alternative stable state regime is approached with increasing  $m$ , both measures of robustness increase 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 [54] and has been suggested to serve as an early warning indicator for approaching phase transitions [54–58]. At this point, PE peaks along with recovery time, suggesting the former is not a good indicator of robustness very close to the bifurcation. Because these large increases in robustness pertain to a very small range of  $m$ , we do not consider them to be biologically relevant, and are primarily useful in this context for observing transitions between dynamic regimes. In general, high PE corresponds with shorter recovery times, and low PE corresponds with longer recovery times (figure S3). Together, these results suggest that under the assumption of constant (and symmetric) dispersal, robustness depends strongly on the magnitude of straying as well as the type of disturbance experienced by the metapopulation. We next examine how density-dependent straying challenges these expectations.

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

When collective behaviour is very strong, (small values of  $C$ ), small increases in population density beget large reductions in straying. These reductions can be large enough that the system avoids the alternative stable state regime altogether (figure 3, left inset). Conversely, when collective behaviour is very weak, such that  $C$  is very high, there is effectively no reduction in straying with increased group size, and the dynamics are those expected if straying were constant (figure 3, right inset). However, when collective behaviour is of intermediate strength ( $10^2 \lesssim C \lesssim 10^3$ ), 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 straying is low, and magnified when individual straying is high (figure 3, main). In other words, when collective behaviour is of intermediate strength – the more realistic range for species that navigate via collective decision-making – increased individual straying exaggerates the differences between the stable state densities, effectively pushing the subordinate population closer to extinction.

Density-dependent straying directly alters the dynamic regimes of the model, and this has a large effect on metapopulation robustness. When the effects of collective behaviour are weak (high  $C$ ) the portfolio effects and recovery times conform to those examined in the case of constant straying (figures 2). When the effects of collective behaviour are very strong (low  $C$ ), we observe that recovery times are shorter in the case of near-collapse (figure 4b). Recovery times also tend to be shorter when a single population goes extinct except for at very low  $m_0$ , in which case the



time to recovery is much longer (figure 4c,d). As before, when the strength of collective behaviour is intermediate ( $10^2 \lesssim C \lesssim 10^3$ ), the relationships are more complex. With intermediate  $C$  there is a general increase in robustness if straying is low-intermediate (higher portfolio effect, shorter recovery time), followed by an erosion in robustness as straying becomes high. In this parameter space, collective navigation results in the low-density population straying more, losing well-adapted local individuals, while still receiving some maladapted strays from the larger population, thereby increasing the likelihood of stochastic extinction.

Sharp changes in metapopulation robustness are due to changes in alternative stable state regimes I and II as the strength of collective behaviour increases (lower  $C$ , figure 5b). When collective behaviour is weak (large  $C$ ), alternative stable states tend to occur at low-intermediate values of individual straying  $m_0$ . As collective behaviour is strengthened (smaller  $C$ ), Regime II is avoided at lower values of  $m_0$  and expands for higher values of  $m_0$ . When the effects of collective behaviour are very strong, Regime II then collapses (black region in figure 5b) and gives way to regime I, which plays a larger role over a larger range of  $m_0$  when  $C$  is low (gray region in figure 5b). Importantly, when the strength of collective behaviour is intermediate, both regimes I and II are relevant at low-intermediate  $m_0$ .

### (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. However, if straying is density-dependent, the strength of collective behaviour has a large influence on the occurrence of both alternative stable state regimes I and II. When heterogeneity is low and the effects of collective behaviour are weak such that straying is constant (high  $C$ ), regime II occurs for small-intermediate  $m_0$ , and regime I does not play a role (figure 5a). The absence of regime I implies that there are no hidden stable state configurations that might trap a disturbed population in an asymmetric low-density state. As the strength of collective behaviour increases, regime I appears at a cusp and becomes increasingly dominant with greater individual straying. For sites distributed across more heterogeneous habitats, the alternative stable state regimes I and II expand (figure 5b,c). Regime II dominates all but very high individual straying when the effects of collective behaviour are weak (high  $C$ ), and very low individual straying when the effects of collective behaviour are strong (low  $C$ ). Moreover, in highly heterogeneous habitats, if the effects of collective behaviour are strong and straying is low (low  $m_0$  and  $C$  values), regime I, which harbors low-density basins of attraction, cannot be avoided.

Until now, we have treated straying and habitat heterogeneity as independent parameters, however they could 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 [36, 59], 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 6, inset). Accordingly,  $m_0$  is greater for lower  $\Delta\theta$ , such that there is less straying between dissimilar sites and more straying between similar sites. Under these conditions we find that regime II appears for very low  $m_0$ , and regime I appears for higher  $m_0$  (figure 6), which is opposite the case where  $m_0$  and  $\Delta\theta$  are independent. As the straying rate increases and  $\Delta\theta$  decreases, a single (symmetric) stable state emerges as the fold bifurcation is crossed, which is opposite the pattern observed when straying is independent of habitat heterogeneity.

#### 4. DISCUSSION

In this paper we show that density-dependent straying between populations consistent with collective navigation, coupled with localized selection against immigrant phenotypes has large, nonlinear impacts on metapopulation robustness. Building upon the dynamical framework introduced by Ronce and Kirkpatrick [12], we assess robustness by measuring 1) the average-CV portfolio effect [4, 50], 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 [49]. These statistical and mechanistic descriptors of metapopulation dynamics and robustness are tightly coupled (figure S3), which is not uncommon for diverse metrics of stability [60]. We introduce density-dependent straying by assuming that larger group sizes lower population-level straying from the baseline probability than an individual errs  $m_0$ , with the strength of this effect determined by  $C$  in equation 5 (lower values of  $C$  indicate that the effects of collective behaviour are strong). Generally, we find that when the effects of collective behaviour are strong and collective navigation is likely, metapopulation robustness is enhanced. However, empirical observations of natural populations suggest that the effects of collective behaviour are intermediate (e.g.  $10^2 \lesssim C \lesssim 10^3$ ) [19, 23]. In this case, we find that the robustness of the metapopulation is increased only if the probability that individuals stray is low, and is substantially eroded if the probability that individuals err is high.

Metapopulation robustness was found to depend strongly on the magnitude of straying between sites. We generally found that metapopulation robustness was highest (as indicated by higher PE and lower recovery times) when straying was at a low-intermediate level. A central dynamic of the model is that straying can lead to the emergence of asymmetric alternative stable states, or *migrational meltdown* [12], pushing one of the populations to a dominant, well-adapted, high density, state, and one to a subordinate, maladapted, low density, state. Although there are subtle differences in our model and the general framework presented by Ronce and Kirkpatrick [12], the general dynamic features are the same if we assume that dispersal is symmetric between sites and density-independent (which occurs when  $C \rightarrow \infty$ ). The dynamic regimes that emerge from the eco-evolutionary model – in particular the occurrence of alternative stable state regimes I and II (figure 1) – have large effects on both the portfolio effect and the recovery time following an induced disturbance (figure 4). In general, we find that intermediate straying increases the PE and lowers the time to recovery, particularly in the case of the extinction of the subordinate (low-density) population. In this case, elevated PE occurs when the system enters either regime I or II (depending on the initial conditions), where one population assumes a subordinate low-density state. Given that the time to recovery following near-collapse of both populations increases with straying (figure 4b), it would suggest that all but the lowest values of density-independent straying erode robustness, regardless of the increase in PE observed at more intermediate values.

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. Here we explore the implications of this collective navigation on metapopulations. 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 behaviour are very strong (low  $C$ ), metapopulation robustness is increased, due primarily to the avoidance of alternative stable state regime II (figures 4,5b). This means that - despite potentially

high individual error rates - group formation minimizes straying. This occurs when groups of  $\leq 100$  individuals significantly minimizes straying, which is likely unrealistic. Moreover, when the effects of collective behaviour are strong, regime II gives way to the dominance of regime I, which harbors low-density basins of attraction (dashed lines in figure 1) that can effectively trap disturbed populations in a subordinate stable state, not unlike the Allee effects observed in the collective migration model explored by Berdahl et al. [19].

Our second important finding reveals that when the effects of collective behaviour are intermediate, metapopulation robustness is impacted in three ways, depending on the magnitude of individual straying. Here, the system is generally in alternative stable state regime I or II except for perhaps unrealistically low levels of individual straying (figure 5b). If individual straying is high ( $m_0 > 0.25$ ), 1) there is a magnified difference between the numerical densities of the subordinate and dominant populations, effectively pushing the subordinate population to lower steady state densities (figure 3), 2) the portfolio effect is low, such that the coefficient of variance for the aggregate metapopulation biomass is on-par with the coefficient of variance of its constituent populations, and 3) more time is generally required for the population(s) to recover following an induced disturbance, and this is particularly true for the recovery of the system following near-collapse of both populations (figure 4b). Together, this suggests that when the effects of collective behaviour are intermediate, and straying is high, there is an overall reduction in metapopulation robustness, thereby reducing persistence.

Empirical observations of straying support low-intermediate levels of individual error rates in most species [16, 17]. If  $m_0$  is low ( $m_0 < 0.25$ ), 1) alternative stable state regime II tends to be avoided for a larger range of  $m_0$  (figures 3, 5b), 2) the portfolio effect is exaggerated, meaning that the variance of the combined metapopulation has dampened variance relative to its constituent populations (figure 4a), and 3) the time required for the population(s) to recover following an induced disturbance is lower (figure 4b). Interestingly, the largest portfolio effects are observed when straying is just large enough to enter regime II, where one population assumes a subordinate state, and the differences between the subordinate and dominant population densities is largest. This does not appear, in fact, to be a robust condition because the system relies to a large extent on the dominant population as the source, whereas the subordinate population assumes the role of a sink. However, recovery time was measured with respect to the aggregate biomass of the metapopulation ( $N_T = N_i + N_j$ ), and despite the source-sink dynamics that emerge in regime II, the aggregate biomass of the system recovers more quickly in this region following the near-collapse of both populations (figure 2b). From this perspective, the existence of asymmetric dominant/subordinate alternative stable states could be considered to be more robust with respect to the recovery time of the total biomass, or less robust because one population is always at greater risk of stochastic extinction.

Third, we find that greater habitat heterogeneity increases the role of alternative stable state regimes, particularly when the effects of collective behaviour are strong (high  $\Delta\theta$ , low  $C$ ; figure 5c), and this increases the potential complexity of metapopulation dynamics. 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 [34]. 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 stable states associated with regime II becomes unavoidable, particularly for  $0.1 \leq m_0 \leq 0.4$ , and regime I is minimized (figure 5). 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 interactions between 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 [61]. Straying of domesticated hatchery-produced fish from release sites and spawning in the wild reduces the productivity of wild populations through competition and outbreeding depression [62, 63].

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 [41, 64, 65]. It is thus reasonable to expect a larger number of straying individuals between sites that are geographically proximate and indeed evidence corroborates this prediction [66, 67]. Alternatively, salmon that cue to specific environmental conditions may be more likely to stray into sites that are structurally and physiognamically more similar [36]. 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 6, inset). When habitat heterogeneity and straying are linked in this way, we show that very small amounts of straying gives rise to regime II, and that regime I occurs for higher values of  $m_0$  (figure 6). 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 complex eco-evolutionary consequences [68, 69], and compromise management or conservation objectives.

A general message from our theoretical framework is that the emergence of alternative eco-evolutionary states depends jointly on the strength of collective behaviour and level of individual straying, and that this has large implications for metapopulation robustness. Although robustness is in many cases aided by increasing the strength of collective behaviour, the greater role of both alternative stable state regimes I and II portends additional complexity in eco-evolutionary dynamics, and this could serve to hinder effective management. Moreover, this increased complexity at empirically observed levels of straying [16] and at realistic (intermediate) ranges of the strength of collective behaviour, is only magnified with increasing habitat heterogeneity and when heterogeneity itself is linked to individual straying. An additional component that we have not explored here, but that may be particularly relevant to consider, are the effects of including additional sites within the metapopulation network, as well as the patterns of dispersal that connect these sites. The structure of dispersal has been shown to have a large influence on population dynamics [52, 70–72], and to what extent density-dependent straying influences the eco-evolutionary dynamics of populations in large spatially-structure networks is of considerable interest. We are hopeful that these predictions will inspire future theoretical and empirical studies that aim to expand upon the relationships that we have explored.

A particularly salient finding of our work was that density-dependent straying may serve to promote or inhibit population robustness, depending on the strength of the collective behaviour, and the underlying magnitude of straying. When the strength of collective behaviour is at plausible intermediate levels, a moderate level of straying increased population robustness by reducing the time to recovery following metapopulation collapse (figure 4b). Salmon have evolved within the context of dynamic geomorphic landscapes where habitat quantity and quality shifts as a mosaic through time [73]. Our results provide evidence supporting the hypothesis described in Berdahl et al. [23] that collective behaviour may support rapid habitat colonization following natural disturbance such as volcanic eruptions [74], reconnected habitats following restoration [69, 75], or in the context of glacial retreat and climate

warming [76]. Moreover, our results are consistent with the role of collective behaviour in facilitating reproductive isolation and local adaptation to site-specific selection in populations that recover following disturbance to the extent that straying decreases as population sizes increase. Additionally, collective behaviour may be beneficial in facilitating navigation through increasingly modified and fragmented habitats [21]. On the other hand, collective behaviour coupled with high straying may push populations to extirpation. Thus, collective behaviour could provide both resilience to salmon metapopulations but also vulnerabilities.

Our study broadly indicates that management activities that alter patterns of straying could have profound implications for metapopulation robustness and adaptive potential. High rates of straying are predicted to decrease metapopulation robustness, and there are a series of common practices in salmon management that may be elevating straying rates [24, 77]. For example, transporting young salmon downstream to increase survival during outmigration may disrupt the processes involved with critical periods of imprinting prior to or during downstream migration by sea-going individuals and increase straying by adults later in life. Our results support the conservation concern that large-scale releases of salmon produced in hatcheries that stray could decrease robustness of salmon metapopulations through the erosion of portfolio effects and increase in recovery times. Moreover, hatchery environments are associated with marked changes in fish social behaviour that may increase collective dynamics of migrating groups [78], consistent with the findings of Jonsson and Jonsson [28] who report stronger associations between straying and abundance in escaped aquaculture produced Atlantic salmon than their wild counterparts. Thus, management activities that have the unintended consequence of altering straying may compromise recovery efforts.

Beyond salmon, density-dependent dispersal, whether it is caused by collective decision-making or other factors, 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 navigation at the population level, are two important components of dynamic dispersal [19]. 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 behaviour mitigates the potentially negative impacts of so-called *migrational meltdown* [12]. Thus, preserving the biological processes that facilitate collective behaviour of migratory species may be an important conservation target in its own right, echoing the sentiments of Hardesty-Moore et al. [20]. We suggest that increased understanding of the proximate and ultimate factors governing dispersal among local populations within metapopulations, across heterogeneous environments, in tandem with the mosaic of selective forces acting on those environments, may be key to promoting persistence in the wild [79].

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**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/jdyekel/SalmonStrays>

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- [1] Gibert JP, 2016 The effect of phenotypic variation on metapopulation persistence. *Population Ecology* **58**, 345–355
  - [2] Brown JH, Kodric-Brown A, 1977 Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**, 445–449
  - [3] Earn DJD, Levin SA, Rohani P, 2000 Coherence and conservation. *Science* **290**, 1360–1364
  - [4] Schindler DE, Armstrong JB, Reed TE, 2015 The portfolio concept in ecology and evolution. *Front. Ecol. Environ.* **13**, 257–263
  - [5] Abbott RE, Doak DF, Peterson ML, 2017 Portfolio effects, climate change, and the persistence of small populations: analyses on the rare plant *Saussurea weberi*. *Ecology* **98**, 1071–1081
  - [6] Thibaut LM, Connolly SR, 2013 Understanding diversity-stability relationships: towards a unified model of portfolio effects. *Ecol. Lett.* **16**, 140–150
  - [7] Carlson SM, Satterthwaite WH, 2011 Weakened portfolio effect in a collapsed salmon population complex. *Can. J. Fish. Aquat. Sci.* **68**, 1579–1589
  - [8] Milner-Gulland EJ, Fryxell JM, Sinclair ARE, 2011 *Animal Migration*. Oxford: Oxford University Press
  - [9] Bell G, Gonzalez A, 2011 Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science* **332**, 1327–1330
  - [10] Carlson SM, Cunningham CJ, Westley PAH, 2014 Evolutionary rescue in a changing world. *Trends Ecol. Evol.* **29**, 521–530
  - [11] Satterthwaite WH, Carlson SM, Bradbury I, 2015 Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex. *Can. J. Fish. Aquat. Sci.* **72**, 1860–1875
  - [12] Ronce O, Kirkpatrick M, 2001 When sources become sinks: migrational meltdown in heterogeneous habitats. *Evolution* **55**, 1520
  - [13] Muhlfeld CC, Kovach RP, Jones LA, Al-Chokhachy R, Boyer MC, Leary RF, Lowe WH, Luikart G, Allendorf FW, 2014 Invasive hybridization in a threatened species is accelerated by climate change. *Nature Climate Change* **4**, 620–624
  - [14] Lowe WH, Muhlfeld CC, Allendorf FW, 2015 Spatial sorting promotes the spread of maladaptive hybridization. *Trends Ecol. Evol.* **30**, 456–462
  - [15] Travis MJJ, *et al.*, 2013 Dispersal and species' responses to climate change. *Oikos* **122**, 1532–1540
  - [16] Westley PAH, Quinn TP, Dittman AH, 2013 Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations. *Can. J. Fish. Aquat. Sci.* **70**, 735–746
  - [17] Keefer ML, Caudill CC, 2014 Homing and straying by anadromous salmonids: a review of mechanisms and rates. *Rev Fish Biol Fisher* **24**, 333–368
  - [18] Bett NN, Hinch SG, Burnett NJ, Donaldson MR, Naman SM, 2017 Causes and consequences of straying into small populations of Pacific salmon. *Fisheries* **42**, 220–230
  - [19] Berdahl A, 2016 Collective behavior as a driver of critical transitions in migratory populations. *Movement Ecology* **4**, 1–12

- [20] Hardesty-Moore M, *et al.*, 2017 Migration in the Anthropocene. *Philos. T. Roy. Soc. B* **This volume**
- [21] Berdahl A, Kao A, Flack J, Westley PAH, Codling E, Couzin ID, Dell AI, Biro D, 2018 Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Philos. T. Roy. Soc. B* **This volume**
- [22] Simons AM, 2004 Many wrongs: The advantage of group navigation. *Trends Ecol. Evol.* **19**, 453–455
- [23] Berdahl A, Westley PAH, Levin SA, Couzin ID, Quinn TP, 2014 A collective navigation hypothesis for homeward migration in anadromous salmonids. *Fish Fish.* **17**, 525–542
- [24] Brenner RE, Moffitt SD, Grant WS, 2012 Straying of hatchery salmon in Prince William Sound, Alaska. *Environ Biol Fish* **94**, 179–195
- [25] Johnson RC, Weber PK, Wikert JD, Workman ML, MacFarlane RB, Grove MJ, Schmitt AK, 2012 Managed metapopulations: do salmon hatchery ‘sources’ lead to in-river ‘sinks’ in conservation? *PLoS ONE* **7**, e28880–11
- [26] Fullerton AH, Lindley ST, Pess GR, Feist BE, Steel EA, McElhany P, 2011 Human influence on the spatial structure of threatened Pacific salmon metapopulations. *Conserv Biol* **25**, 932–944
- [27] Quinn TP, 2011 *The Behavior and Ecology of Pacific Salmon and Trout*. Vancouver: UBC Press
- [28] Jonsson B, Jonsson N, 2011 *Ecology of Atlantic Salmon and Brown Trout*. Dordrecht: Springer Netherlands
- [29] Quinn TP, 1993 A review of homing and straying of wild and hatchery-produced salmon. *Fish Res* **18**, 29–44
- [30] Hendry AP, Bohlin T, Jonsson B, Berg OK, 2004 The evolution of philopatry and dispersal: homing versus straying in salmonids. In AP Hendry, SC Stearns, eds., *Evolution Illuminated*. Oxford: Oxford University Press on Demand
- [31] Schtickzelle N, Quinn TP, 2007 A metapopulation perspective for salmon and other anadromous fish. *Fish Fish.* **8**, 297–314
- [32] Anderson SC, Moore JW, McClure MM, Dulvy NK, Cooper AB, 2015 Portfolio conservation of metapopulations under climate change. *Ecol. Appl.* **25**, 559–572
- [33] Keefer ML, Caudill CC, Peery CA, Lee SR, 2008 Transporting juvenile salmonids around dams impairs adult migration. *Ecol. Appl.* **18**, 1888–1900
- [34] Westley PAH, Dittman AH, Ward EJ, Quinn TP, 2015 Signals of climate, conspecific density, and watershed features in patterns of homing and dispersal by Pacific salmon. *Ecology* **96**, 2823–2833
- [35] Bond MH, Westley PAH, Dittman AH, Holecek D, Marsh T, Quinn TP, 2016 Combined effects of barge transportation, river environment, and rearing location on straying and migration of adult snake river fall-run Chinook salmon. *T Am Fish Soc* **146**, 60–73
- [36] Peterson DA, Hilborn R, Hauser L, 2014 Local adaptation limits lifetime reproductive success of dispersers in a wild salmon metapopulation. *Nat Commun* **5**, 3696
- [37] Moore JW, McClure M, Rogers LA, Schindler DE, 2010 Synchronization and portfolio performance of threatened salmon. *Conserv. Lett.* **3**, 340–348
- [38] Braun DC, Moore JW, Candy J, Bailey RE, 2016 Population diversity in salmon: linkages among response, genetic and life history diversity. *Ecography* **39**, 317–328
- [39] Simpson GG, 1953 *The Major Features of Evolution*. New York: Simon and Schuster
- [40] Lande R, 1976 Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30**, 314–334
- [41] Reisenbichler RR, 1988 Relation between Distance Transferred from Natal Stream and Recovery Rate for Hatchery Coho Salmon. *N. Am. J. Fish. Manage.* **8**, 172–174
- [42] Shelton AO, Mangel M, 2011 Fluctuations of fish populations and the magnifying effects of fishing. *Proc. Natl. Acad. Sci. USA* **108**, 7075–7080
- [43] Jasper JR, Habicht C, Moffitt S, Brenner R, Marsh J, Lewis B, Fox EC, Grauvogel Z, Olive SDR, Grant WS, 2013 Source-sink estimates of genetic introgression show influence of hatchery strays on wild chum salmon populations in Prince William Sound, Alaska. *PLoS ONE* **8**, e81916
- [44] Schreiber SJ, Bürger R, Bolnick DI, 2011 The community effects of phenotypic and genetic variation within a predator

population. *Ecology* **92**, 1582–1593

[45] Gibert JP, Brassil CE, 2014 Individual phenotypic variation reduces interaction strengths in a consumer–resource system. *Ecol Evol* **4**, 3703–3713

[46] Gibert JP, DeLong JP, 2015 Individual variation decreases interference competition but increases species persistence. *Adv Ecol Res* **52**, 45–64

[47] Carlson SM, Seamons TR, 2008 A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. *Evol Appl* **1**, 222–238

[48] Schindler DE, Armstrong JB, Reed TE, 2015 The portfolio concept in ecology and evolution. *Front. Ecol. Environ.* **13**, 257–263

[49] Ovaskainen O, Hanski I, 2002 Transient dynamics in metapopulation response to perturbation. *Theor Popul Biol* **61**, 285–295

[50] Anderson SC, Cooper AB, Dulvy NK, 2013 Ecological prophets: quantifying metapopulation portfolio effects. *Methods Ecol Evol* **4**, 971–981

[51] Loreau M, de Mazancourt C, 2008 Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat.* **172**, E48–E66

[52] Yeakel JD, Moore JW, Guimarães Jr PR, de Aguiar MAM, 2014 Synchronisation and stability in river metapopulation networks. *Ecol. Lett.* **17**, 273–283

[53] Guckenheimer J, Holmes P, 1983 *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields*. New York: Springer

[54] Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G, 2009 Early-warning signals for critical transitions. *Nature* **461**, 53–59

[55] Lade SJ, Gross T, 2012 Early warning signals for critical transitions: A generalized modeling approach. *PLoS Comp. Biol.* **8**, e1002360

[56] Boettiger C, Ross N, Hastings A, 2013 Early warning signals: the charted and uncharted territories. *Theor. Ecol.* **6**, 255–264

[57] Dakos V, Bascompte J, 2014 Critical slowing down as early warning for the onset of collapse in mutualistic communities. *Proc. Natl. Acad. Sci. USA* **111**, 17546–17551

[58] Krkošek M, Drake JM, 2014 On signals of phase transitions in salmon population dynamics. *Proc. Roy. Soc. B* **281**, 20133221

[59] Lin J, Quinn TP, Hilborn R, Hauser L, 2008 Fine-scale differentiation between sockeye salmon ecotypes and the effect of phenotype on straying. *Heredity* **101**, 341–350

[60] Donohue I, Petchey OL, Montoya JM, Jackson AL, McNally L, Viana M, Healy K, Lurgi M, O’Connor NE, Emmerson MC, 2013 On the dimensionality of ecological stability. *Ecol. Lett.* **16**, 421–429

[61] Christie MR, Marine ML, French RA, Blouin MS, 2012 Genetic adaptation to captivity can occur in a single generation. *Proc. Natl. Acad. Sci. USA* **109**, 238–242

[62] Chilcote MW, 2003 Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* **60**, 1057–1067

[63] Araki H, Cooper B, Blouin MS, 2007 Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* **318**, 100–103

[64] Fraser DJ, Weir LK, Bernatchez L, Hansen MM, Taylor EB, 2011 Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. *Heredity* **106**, 404–420

[65] Westley PAH, Corinne M Conway, Fleming IA, 2012 Phenotypic divergence of exotic fish populations is shaped by spatial proximity and habitat differences across an invaded landscape. *Evol. Ecol. Res.* **14**, 147–167



- [66] Candy JR, Beacham TD, 2000 Patterns of homing and straying in southern British Columbia coded-wire tagged Chinook salmon (*Oncorhynchus tshawytscha*) populations. *Fish Res* **47**, 41–56
- [67] Schick RS, Lindley ST, 2007 Directed connectivity among fish populations in a riverine network. *J. Appl. Ecol.* **44**, 1116–1126
- [68] Anderson JH, Faulds PL, Atlas WI, Quinn TP, 2013 Reproductive success of captively bred and naturally spawned Chinook salmon colonizing newly accessible habitat. *Evol Appl* **6**, 165–179
- [69] Pess GR, Quinn TP, Gephard SR, Saunders R, 2014 Re-colonization of Atlantic and Pacific rivers by anadromous fishes: linkages between life history and the benefits of barrier removal. *Rev Fish Biol Fisher* **24**, 881–900
- [70] Heino M, Kaitala V, Ranta E, Lindstrom J, 1997 Synchronous dynamics and rates of extinction in spatially structured populations. *Proc. Roy. Soc. B* **264**, 481–486
- [71] Carrara F, Rinaldo A, Giometto A, Altermatt F, 2014 Complex Interaction of Dendritic Connectivity and Hierarchical Patch Size on Biodiversity in River-Like Landscapes. *Am. Nat.* **183**, 13–25
- [72] Gilarranz LJ, Rayfield B, Liñán-Cembrano G, Bascompte J, Gonzalez A, 2017 Effects of network modularity on the spread of perturbation impact in experimental metapopulations. *Science* **357**, 199–201
- [73] Stanford JA, Lorang MS, Hauer FR, 2017 The shifting habitat mosaic of river ecosystems. *Verh. Internat. Verein. Limnol.* **29**, 123–136
- [74] Leider SA, 1989 Increased straying by adult steelhead trout, *Salmo gairdneri*, following the 1980 eruption of Mount St. Helens. *Environ Biol Fish* **24**, 219–229
- [75] Pess GR, Hilborn R, Kloehn K, Quinn TP, 2012 The influence of population dynamics and environmental conditions on pink salmon (*Oncorhynchus gorbuscha*) recolonization after barrier removal in the Fraser River, British Columbia, Canada. *Can. J. Fish. Aquat. Sci.* **69**, 970–982
- [76] Milner AM, Robertson AL, Monaghan KA, Veal AJ, Flory EA, 2008 Colonization and development of an Alaskan stream community over 28 years. *Front. Ecol. Environ.* **6**, 413–419
- [77] Ford MJ, 2002 Selection in captivity during supportive breeding may reduce fitness in the wild. *Conserv Biol* **16**, 815–825
- [78] Ruzzante DE, 1994 Domestication effects on aggressive and schooling behavior in fish. *Aquaculture* **120**, 1–24
- [79] Westley PAH, Berdahl A, Torney CJ, Biro D, 2018 Emerging study of collective movement ecology. *Philos. T. Roy. Soc. B* **This volume**

Parameter	Definition	Value/Range
$N_i(t), N_T(t)$	Individual, aggregate population over time	dyn.
$x_i$	Trait value for an individual in population $i$	dyn.
$\mu_i(t)$	Mean of $x$ for population $i$ over time	dyn.
$m; m(t)$	Constant, density-dependent straying	$(0, 0.5)$ ; dyn.
$m_0$	Individual straying probability	$(0, 0.5)$
$C$	Strength of collective behaviour (low=strong)	$(10^1, 10^5)$
$r_{\max}$	Maximum recruitment rate	2.0
$\beta$	Strength of density dependence	$10^{-3}$
$\theta_i$	Optimal trait value for habitat $i$	5.0
$\sigma^2$	Genetic variance of trait $x$	1.0
$\tau$	Strength of selection	1.0
$h^2$	Heritability	0.2
$\Delta\theta$	Habitat heterogeneity	2.0
$\epsilon$	Sensitivity of $m_0$ to changes in $\Delta\theta$	20.0
PE	Portfolio Effect	$\geq 1$
$T$	Terminal simulation time	$10^5$

Table I: Table of parameters, definitions, and assigned values or ranges.

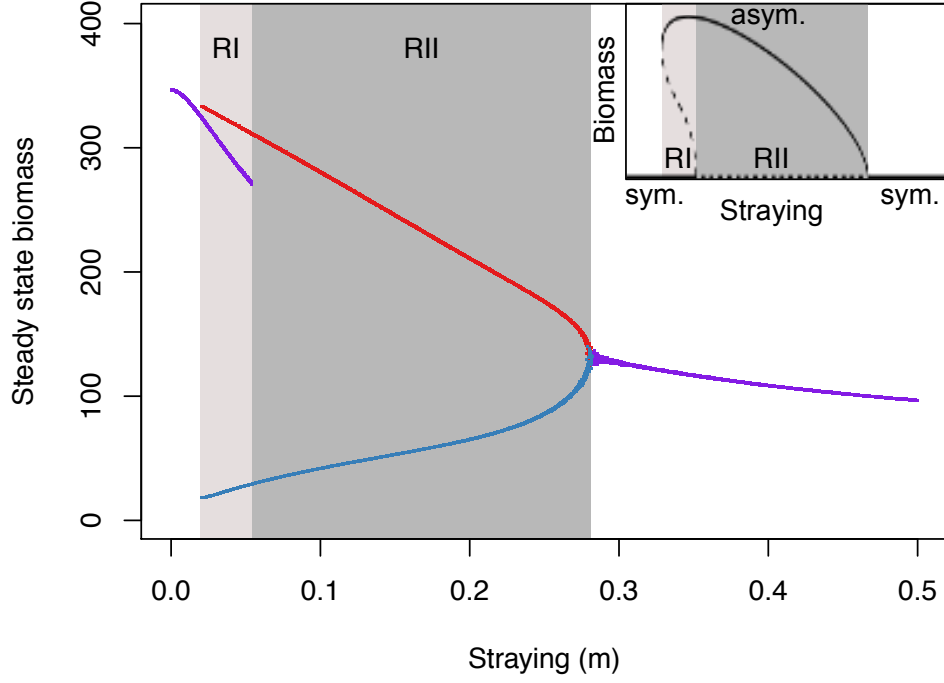


Figure 1: The steady-state densities of  $N_i$  and  $N_j$  vs. straying  $m$  for the constant straying model. Alternative stable states exist for regimes I and II, labeled RI and RII, respectively. In regime I the system can approach qualitatively different states: a symmetric, intermediate state (purple points), and asymmetric dominant/subordinate states (red and blue points, respectively). In regime II only one type of attractor exists: an asymmetric dominant/subordinate state (red and blue points, respectively), and its mirror image where identities of dominant and subordinate are exchanged. Inset: A qualitative sketch of the bifurcation diagram, showing the stable (solid lines) and unstable (dashed line) fixed points in regime I (light gray area) and II (dark gray area). The symmetric condition (sym.) is the horizontal line at the base of the inset, whereas the asymmetric condition (asym.) is represented by the curved line.

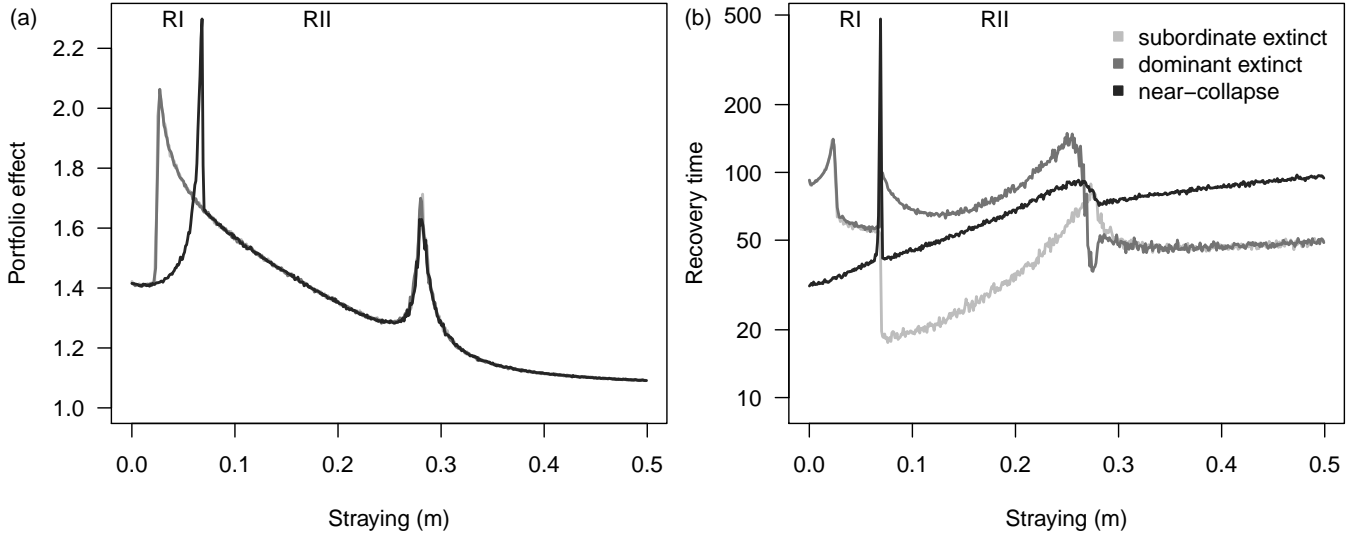


Figure 2: Measures of metapopulation robustness for the constant straying model as a function of straying  $m$ . Alternative stable state regimes I and II corresponding to those in figure 1 are labeled RI and RII, respectively. (a) Portfolio effect as a function of  $m$ . (b) Recovery time as a function of  $m$ . Measures of metapopulation robustness are shown with respect to different induced disturbances: the near-collapse of both populations (black), and the lone extinction of either the dominant (dark gray) or subordinate (light gray) population. Portfolio effects are different for the near-collapse and single extinction scenarios due to different CVs for the populations and aggregate in alternative basins of attraction that exist in regimes I and II.

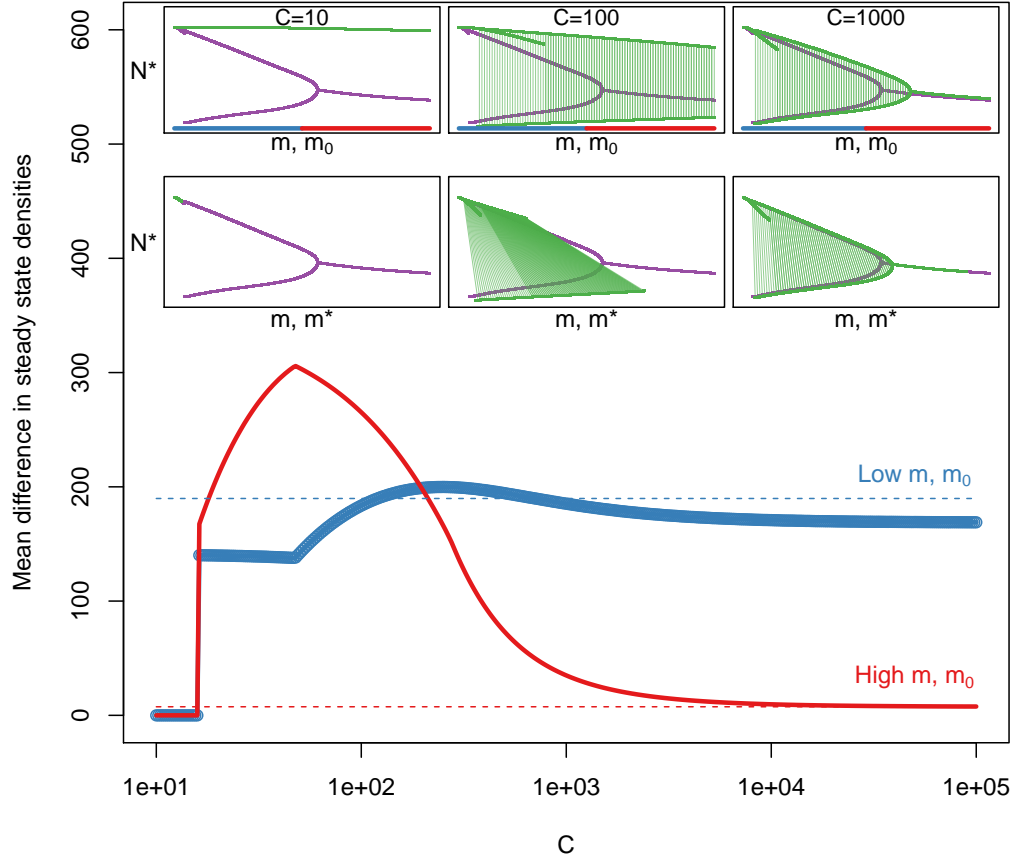


Figure 3: Comparison of steady state population densities for the constant straying model and density-dependent straying model. Inset: stable state densities for the constant straying model (purple) and density-dependent straying model (green) for different strengths of collective behaviour. Low  $C$  corresponds to strong effects of collective behaviour. The top row shows stable state densities as a function of individual straying  $m_0$ ; the bottom row shows stable state densities as a function of straying at the stable state  $m(t)^*$ . Vertical green lines link paired subordinate and dominant population densities. Main: The absolute difference in stable state densities averaged across intervals of low straying ( $0 < m, m_0 < 0.25$ ; blue) and high straying ( $0.25 < m, m_0 < 0.5$ ; red).

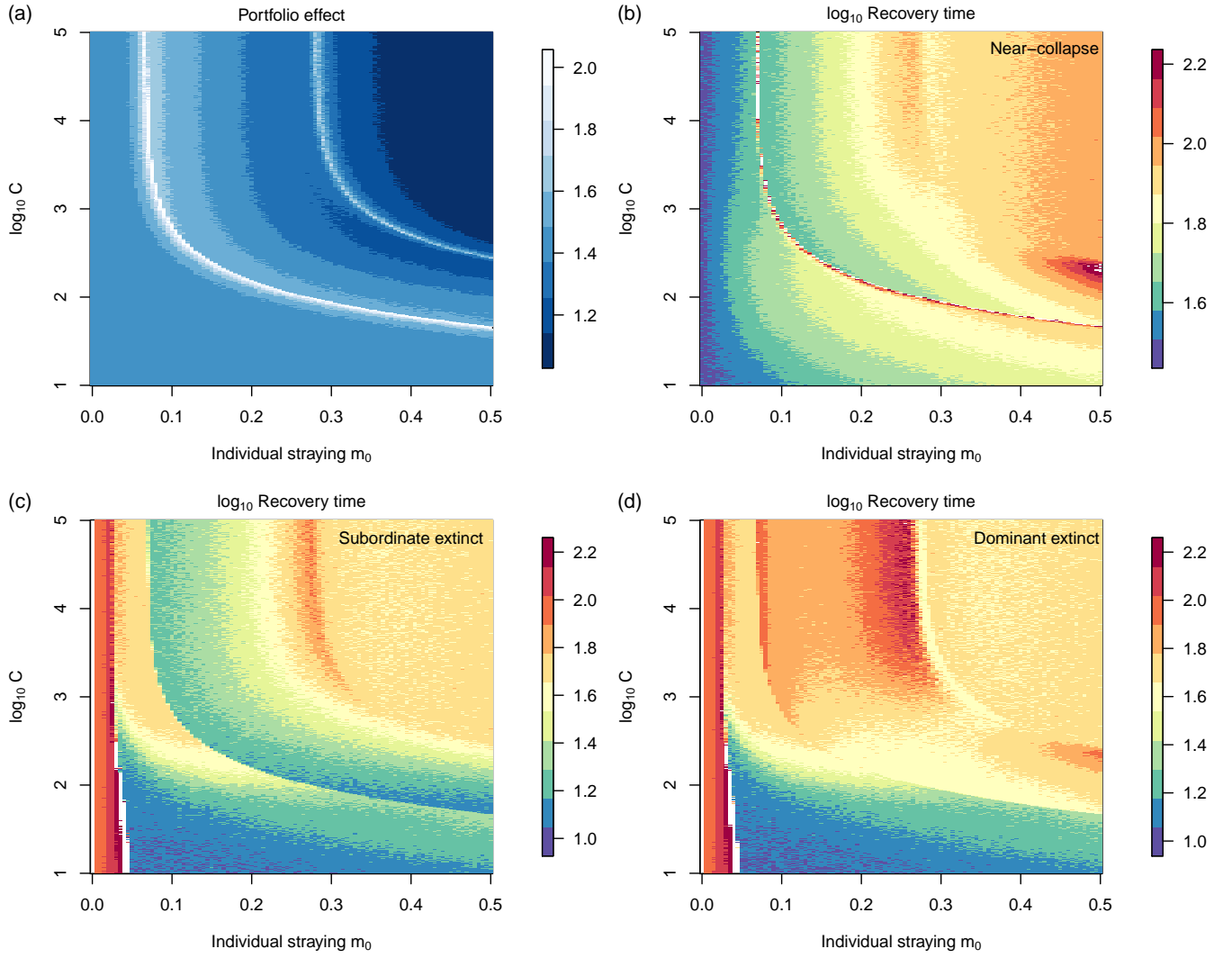


Figure 4: Measures of metapopulation robustness for the density-dependent straying model as a function of individual straying  $m_0$  and the strength of collective behaviour  $C$  (note the  $\log_{10}$  scale, including a) the Portfolio effect, b) the time to recovery following near-collapse of both populations, c) the time to recovery following the extinction of the subordinate population, and d) the time to recovery following the extinction of the dominant population.

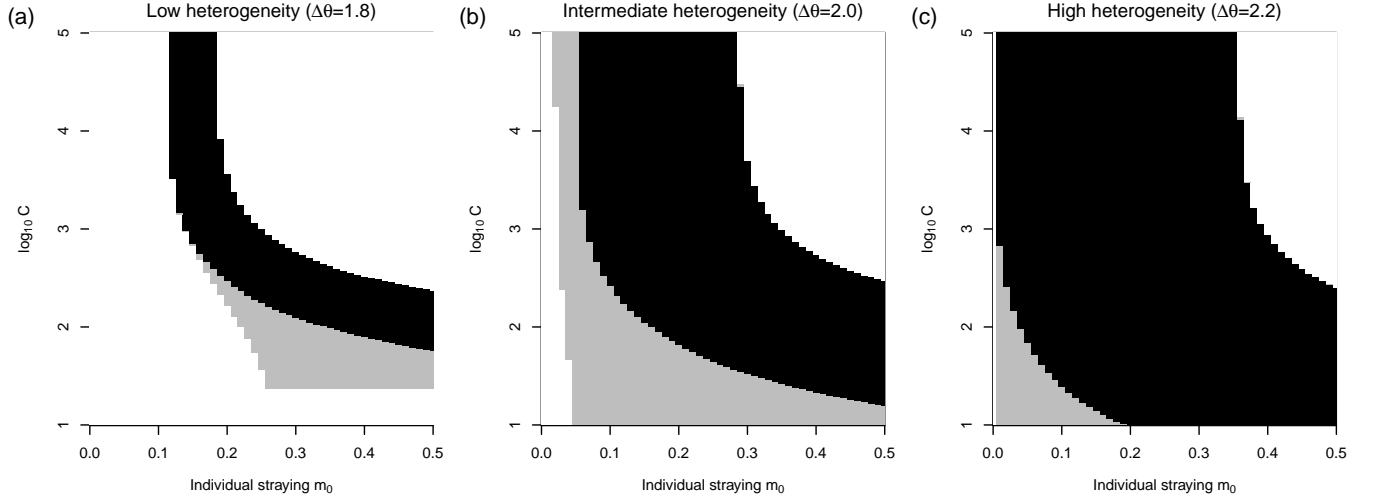


Figure 5: Alternative stable state regimes I (gray) and II (black) as a function of individual straying  $m_0$  and the strength of collective behaviour  $C$  (note the  $\log_{10}$  scale). Regime I signifies parameter space where there is either 1) an intermediate-density, symmetric, steady state, or 2) an asymmetric dominant/subordinate density. Regime II signifies parameter space where there is an asymmetric dominant/subordinate steady state density. The white space to the left (lower values of  $m_0$ ) signifies high-density, symmetric, stable states, and the white space to the right (higher values of  $m_0$ ) signifies low-density, symmetric, steady states. Relationships are shown for (a) intermediate habitat heterogeneity ( $\Delta\theta$ ), as well as (b) low habitat heterogeneity and (c) high heterogeneity.

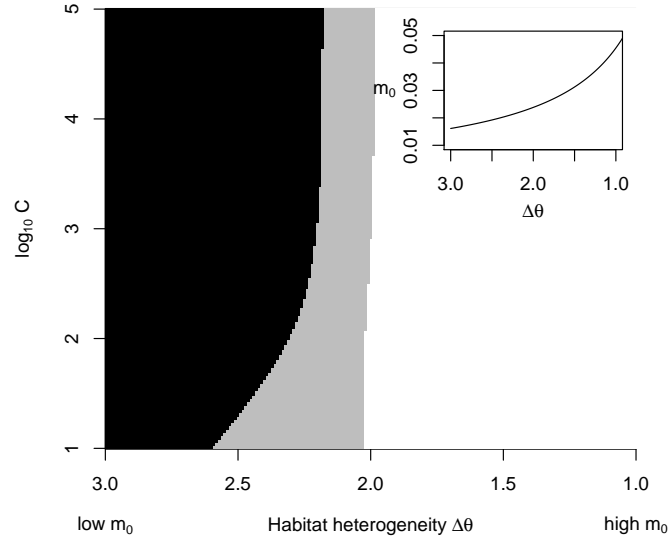


Figure 6: Alternative stable state regimes I (gray) and II (black) as a function of individual straying  $m_0$  and the strength of collective behaviour  $C$  (note the  $\log_{10}$  scale), for the case where individual straying increases with lower habitat heterogeneity (inset). Regime I signifies parameter space where there is either 1) an intermediate-density, symmetric, steady state, or 2) an asymmetric dominant/subordinate density. Regime II signifies parameter space where there is an asymmetric dominant/subordinate steady state density.

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: Steady-state densities of both populations as a function of  $m$ : 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  $r_{\max,1} = (1 + \alpha)r_{\max,2}$  and  $\beta_1 = (1 + \alpha)\beta_2$  where  $\alpha$  is increased from 0 to 0.1, thereby increasing the asymmetry in vital rates. Steady-states for populations with increasingly asymmetric values ( $\alpha \rightarrow 0.1$ ) for vital rates  $r_{\max}$  and  $\beta$  are shown in warmer tones. The lower-density values that appear between  $m = 0.06$  and  $m = 0.1$  represent populations that have been trapped in the low-density basins of attraction associated with regime I. Increasing the asymmetry in vital rates does not impact the qualitative nature of the dynamics.

Figure S3: Comparison of portfolio effects vs. recovery time following the near-collapse of both populations.