

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

Justin D. Yeakel^{1,2,*}, Jean P. Gibert¹, Peter A. H. Westley³, & Jonathan W. Moore⁴

¹School of Natural Sciences, University of California, Merced, Merced CA, USA

²The Santa Fe Institute, Santa Fe NM, USA

³College of Fisheries and Ocean Sciences, University of Alaska, Fairbanks, Fairbanks AK, USA

⁴Earth2Oceans Research Group, Simon Fraser University, Vancouver BC, Canada

*To whom correspondence should be addressed: jdyeakel@gmail.com

Abstract

We show that taking straying into account leads to alternative stable states in population densities and trait values, which has consequences for maladaptation, intraspecific trait variability, and long-term robustness of salmon metapopulations.

I. INTRODUCTION

Intraspecific diversity can increase the resilience and stability of species or metapopulations. This diversity-stability linkage can occur when there are asynchronous population dynamics, where the changes in population vary across a 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.

It is clear that dispersal (i.e., movement with consequences for gene flow) can influence the evolutionary dynamics of the metapopulation, the interplay between selection, population dynamics, and persistence is not well understood. 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]. Third, straying will influence the evolutionary dynamics of the metapopulation. Although the dispersal of individuals into sites hosting other populations pro-

vides 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]. Further, this straying may lead to genetic homogenization that erodes the asynchrony that underpins portfolio effects and metapopulation persistence. Thus, straying can influence the resilience and robustness of metapopulations through both ecological and evolutionary processes.

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 [This issue]. The rate at which individuals stray, m , may be linked to errors made at an individual-level that are themselves diminished by migrating in groups and pooling individual choices [14–16]. 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 [17–19].

The eco-evolutionary impacts of dispersal likely has 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, 20, 21], there are generally some individuals that ‘stray’ to non-natal sites to spawn [22, 23]. Salmon may operate as metapopulations, where populations are genetically distinct but linked by some level of straying [24, 25]. Although extensive work has been done to document the extent of straying from donor populations and into recipient populations [12, 13], only recently have the abiotic, biotic, and anthropogenic influences of ‘straying’ behaviors been investigated systemically [26–28]. Straying among salmon may be influenced by environmental factors such as water temperature, human activi-

ties such as hatchery practices, and population density as predicted by the collective migration hypothesis [29]. These strays can introduce new maladaptive genotypes into the recipient population. Further, straying and genetic homogenization could synchronize population dynamics and erode portfolio effects [30–32]. Thus, there is opportunity and a 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 construct a minimal eco-evolutionary model of two populations occupying different sites that are linked by straying individuals, each of which with an associated trait distribution subject to natural selection determined by local conditions. Specifically we compare (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 multiple and potentially opposing pathways by which straying influences metapopulation robustness such as the potentially detrimental erosion of local adaptation vs. the positive effects of demographic and evolutionary rescue.

II. MODEL DESCRIPTION & ANALYSIS

(a) Metapopulation framework

We consider two populations N_1 and N_2 that inhabit two distinct habitats, each with trait values x_1 and x_2 determining recruitment rates. We assume that there is an optimum trait value θ_1 and θ_2 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 assume that $x_{1,2}$ are normally distributed with means μ_1 and μ_2 and have the same standard deviation σ . As such, the recruitment rate for both populations is determined by the mean trait value of the local population, such that $r_1 = R_1[\mu_1(t), \theta_1]$. Trait means for each population are subject to selection, the strength of which depends on the difference between the trait mean and the local trait optimum at a given point in time [33, 34].

The two populations are assumed to reproduce in spatially separate sites that are close enough such that a proportion of the population m can stray into the other site, and where mortality occurs before individuals return to reproduce. If there is no straying between these populations (such that they are independent), then the mean trait evolves towards the optimal value such that $x_1 \rightarrow \theta_1$, and the recruitment rate for that population will be maximized. If there is straying between populations at rate m , then the traits in each respective location

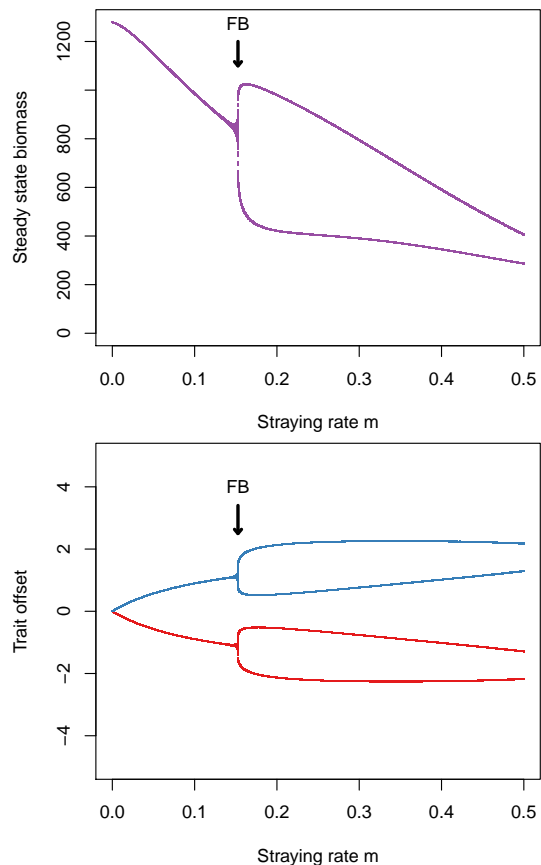


Figure 1: A) The steady state densities of N_1 and N_2 as a function of a constant stray rate m . Which population attains the low- or high-density state is random due to small applied fluctuations in the initial conditions. B) The steady state trait values measured as $\theta_i - x_i$, as a function of a constant stray rate m . FB marks the fold bifurcation.

will be pulled away from the optimum, and recruitment rates will be lowered. As $m \rightarrow 0.5$, the populations are perfectly mixed, acting as a single population.

We use the discrete Ricker population dynamic framework described by Shelton and Mangel [35] as the basis for our two-site model, with the added effect of the local population N_i mixing with a set proportion m of a remote population N_j that is straying into it. In this sense, both populations serve as donor and recipient populations. We first assume that the proportion e^{-Z} of both populations survive such that the surviving aggregated population, composed of both local individuals (at site i) and incoming strays (from site j), is $((1 - m)N_i(t) + mN_j(t))e^{-Z}$. Because local individuals will recruit differently than incoming strays, the recruitment of the aggregate must incorporate two recruitment functions, given by $(R_i[\mu_i(t)](1 - m)N_i(t) + R_i[\mu_j(t)]mN_j(t))$. This mix of individuals is subject to the same compensatory effects, which is determined by the parameter β . Taken together, the difference equation that determine changes in population size is

$$\begin{aligned}
N_i(t+1) = & \\
& ((1-m)N_i(t) + mN_j(t)) e^{-Z} \\
& + (R_i[\mu_i(t)](1-m)N_i(t) + R_i[\mu_j(t)]mN_j(t)) \\
& \times e^{-\beta((1-m)N_i(t) + mN_j(t))},
\end{aligned} \tag{1}$$

where the difference equation for N_j mirrors that for N_i .

The recruitment of local individuals $(1-m)N_i(t)$ as a function of their mean trait value at time t and the local trait optimum, is

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

where the mismatch between the local trait mean $\mu_i(t)$ and the local optimum θ_i scales the recruitment rate for the population, and $\tilde{P} \sim \text{Normal}(0, 0.01)$ introduces a small amount of demographic error. The parameter τ 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 τ), 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 have indeed found that straying individuals have lower life-time fitness than individuals that do not stray, although it unknown at what life-stage this selection occurs [29].

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 mixed normal with weights corresponding to the proportion of the mixed population that are local individuals, w_i , and for the straying individuals, $1 - w_i$, where

$$w_i = \frac{(1-m)N_i(t)}{(1-m)N_i(t) + mN_j(t)}. \tag{3}$$

We make two simplifying assumptions. First, we assume that the distribution resulting from the mix of remote and local individuals, following reproduction, is also normal with a mean value equal to that of the mean for the mixed-normal distribution. Thus, we assume that strays can successfully reproduce and introduce their genotypes into the recipient population, which is supported by observations in wild populations [36]. Second, we assume that changes in trait variance through time are minimal, such that σ^2 is assumed to be constant, and this is a common simplification in eco-evolutionary models of population dynamics [34, 37–39].

An increasing flow of incoming strays is generally expected to pull the mean trait value of the local population away from its optimum over time, which will decrease its rate of recruitment. Following Lande [34], the mean trait value thus changes through time according to the difference equation

$$\begin{aligned}
\mu_i(t+1) = & w_i\mu_i(t) + (1-w_i)\mu_j(t) \\
& + h^2\sigma^2 \frac{\partial}{\partial \mu_i} \ln(w_i R_i[\mu_i(t)] + (1-w_i)R_i[\mu_j(t)]),
\end{aligned} \tag{4}$$

where the first two factors determine the mixed normal average of the aggregated local and remote populations. The partial derivative in the Eq. 4 determines how the mean trait changes through time due to natural selection [34], which is proportional to the change in mean fitness with respect to μ_i .

(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) the straying rate is density-dependent with a signature of collective navigation [13, 16]. 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. [16, 40], 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. We note that at the limit $C \rightarrow \infty$, the density-dependent straying rate becomes constant such that $m(t) \rightarrow m_0$, and this corresponds to the original formulation where $m = m_0$. A similar observation shows that when the population density is very high, $m(t) \rightarrow 0$, and when it is small, individuals operate without regard to collective behavior, meaning $m(t) \rightarrow m_0$. Thus, for realistic population densities, $m(t) < m_0$.

(c) Habitat heterogeneity

The straying rate is largely influenced by the spatial distance between the donor and recipient population. The greater the distance between two populations, the lower the expected rate of straying [11, 27]. We account for this interdependence in our model by assuming that m (if the stray rate is constant) or m_0 (if the stray rate is density-dependent) is a function of the difference between optimal trait values between sites $\theta_i - \theta_j$, which can be assumed to be large if the remote site j is a great distance away from the local site i . If sites i and j are very close, the stray rate is maximized at $m_{\max} = 0.5$,

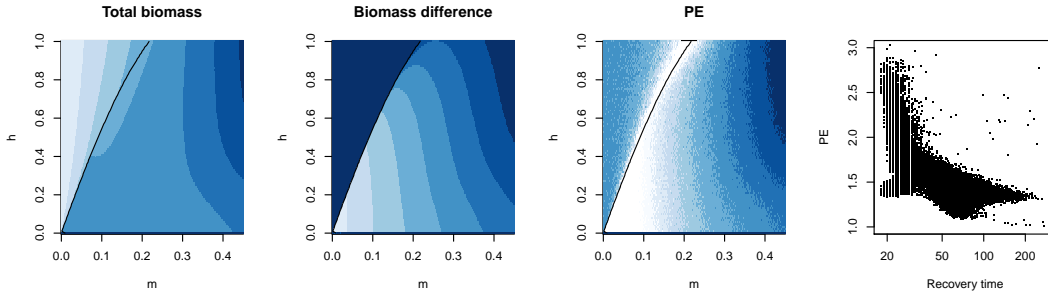


Figure 2: (a) Total means N_t , (b) difference in means ΔN , and (c) the portfolio effect PE as a function of heritability h^2 and a constant stray rate m . Light colors = high values. The black line shows the fold bifurcation separating a single steady state (left) from alternative stable states (right). (d) The relationship between the time to recovery following a disturbance and the portfolio effect. The black line denotes the fold bifurcation.

assuming both sites are equally attractive to the respective populations. Thus, we can integrate these two variables by setting $m, m_0 = (1/m_{\max} + \epsilon(\theta_i - \theta_j))^{-1}$, where ϵ sets the sensitivity of a declining m to increasing distance (greater values of $\theta_i - \theta_j$).

(d) Measuring metapopulation robustness We evaluated metapopulation robustness by measuring the average-CV portfolio effect (PE) [25, 41] as well as the time required for the system to return to a steady state following an induced disturbance to one or both of the populations [42]. The average-CV portfolio effect is, as the name implies, the average CV across each population divided by the CV of the aggregate [43], 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. 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 become more stable. Portfolio effects greater than unity corresponds to less synchronization [25, 44, 45] 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 it takes the system (measured as the aggregate biomass N_T) to recover its steady state abundance 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 [46], because we aimed to 1) assess the effects of a large perturbation, and 2) estimate the time required for all transient effects to decay (including dampened oscillations), we used a simulation-based numerical procedure.

Numerically estimating the time that it takes for a perturbed system to relax also permits a more detailed perspective of metapopulation fragility. For example, if populations settle to alternative stable states (alternative stable states in our model requiring one population to be high-density and one low-density), comparing recovery times after a disturbance applied to the high, low, and/or both populations allows for an assessment of which component of the metapopulation has a longer-lasting influence on the system's recovery. We measured the time required for the system N_T to recover to its steady state 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 the system is in the single steady state regime); (iii) near-collapse of both populations where just 1.0% of each survives. Throughout, we will refer to an increase in the portfolio effects and/or reduction in recovery times as promoting metapopulation robustness, which is expected to have a positive effect on persistence.

III. 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 fold bifurcation whereby the single steady state for the metapopulation bifurcates into two alternative stable states: one at high biomass, and one at low biomass density (figure 1a, 2a). Mean trait values for both populations bifurcate similarly (figure 1b), depending on which population attains a low-

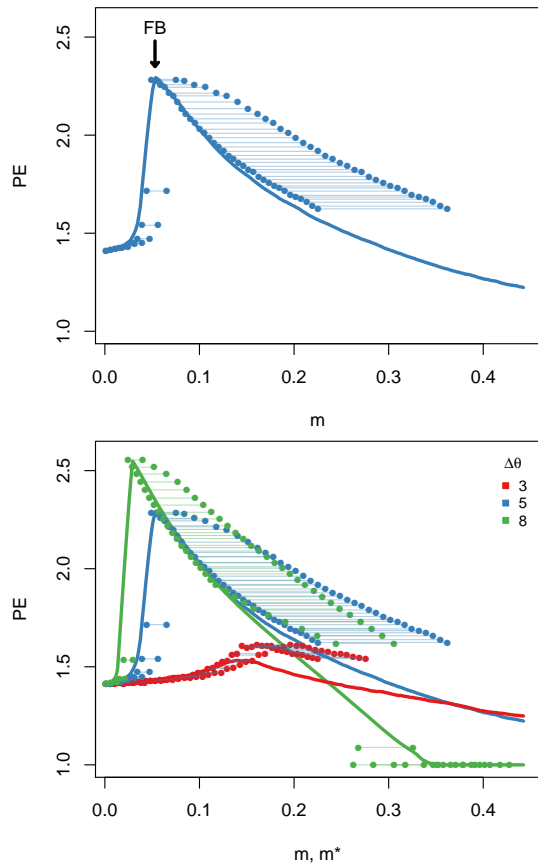


Figure 3: (a) Median portfolio effect as a function of a constant stray rate m (solid line) and density-dependent stray rate (point pairs) given heritability is $h^2 < 0.5$ and $\Delta\theta = 5$. Point pairs connected by a horizontal line represent the PE as a function of density-dependent straying rates, evaluated for both low- and high-density populations at equilibrium. The lower straying rate of a pair is for the larger population; the higher straying rate is for the smaller population. (b) Median portfolio effects for habitats with increasing heterogeneity as measured by the difference in regional trait optima $\Delta\theta$ for both constant and density-dependent stray rates as shown in (a). FB marks the fold bifurcation.

vs. high-density. Above the threshold straying rate defined by the fold bifurcation, there are two alternative eco-evolutionary states: the *dominant state* population will have a higher a higher density and higher degree of local adaptation (lower trait offset from the local optimum), while the *subordinate state* population will have lower density with maladapted trait values (higher trait offset from the local optimum). Whether a specific population goes to one state or the other in our model is random, which is due to a small amount of introduced variance in the initial conditions.

Trait heritability has a large impact on the degree to which straying rate affects both the aggregate population steady state density ($N_T^* = N_1^* + N_2^*$; figure 2a) as well as the difference between steady state densities (the dis-

tance between alternative stable states: $\Delta N = |N_1^* - N_2^*|$; figure 2b). Greater trait heritability results in a faster decline in N_T^* with increasing straying rates m , but leads to only moderate changes to ΔN . Conversely, in the context of lower trait heritability, an increase in the straying rate has little impact on the total biomass density but contrastingly large effects on ΔN . The fold bifurcation (the black line in Figs. 2a-c) occurs at lower values of the straying rate m with decreased trait heritability h^2 (Fig 2a,b), indicating that weaker coupling between ecological and evolutionary dynamics in addition to higher rates of straying promotes the appearance of alternative stable states. Although trait heritability among salmonids is variable, most life history traits have an $h^2 < 0.5$ [47], and we largely focus additional analyses on that range.

As the fold bifurcation is approached with increasing m , the portfolio effect increases sharply due to an amplification in variance within both donor and recipient populations $\text{VAR}(N_{i,j})$. This variance increase is the product of a dynamical process known as *critical slowing down* that occurs near fold bifurcations [48], a phenomenon that some have suggested may serve as an early warning indicator for approaching phase transitions [48–51]. For larger values of m (to the right of the fold bifurcation in Fig 2a-c), where alternative stable states occur, the portfolio effect declines steadily as the CV of N_T increases. The decline over m is more gradual if trait heritability is low, and steeper if trait heritability is high (figure 2c).

As the portfolio effect is highly sensitive to the rate of straying between populations, so is the time required for the system to recover to a steady state following a large disturbance. In general, we find that the average-CV portfolio effect is negatively correlated with recovery time (figure 2d), indicating that, for our system, both measures are valuable indicators of metapopulation robustness. Because we can assess the time to recovery in response to the various disturbance types described above, this allows us to gain an in-depth perspective into the fragility of the metapopulation as a function of straying rate.

Straying had non-linear impacts on the recovery time of populations. When the dominant state (well adapted and high density) is wiped out, high levels of straying allow it to recover quickly (figure 4a) because the surviving population has a mean trait value skewed towards the optimum of the recovering population (figure S2). Yet, as straying decreases, recovery time for the disturbed dominant state population increases, in part because there is enough time for the trait distribution to move back towards the trait optimum of the subordinate state population. In contrast, when the subordinate state population (maladapted and low density) is wiped out, recovery rates are fastest at low to intermediate levels of straying. Because the mean trait values of both populations are skewed towards those of the dominant population, when the subordinate population collapses under high rates of straying, selection against the flood of maladapted individuals that stray into the recovering

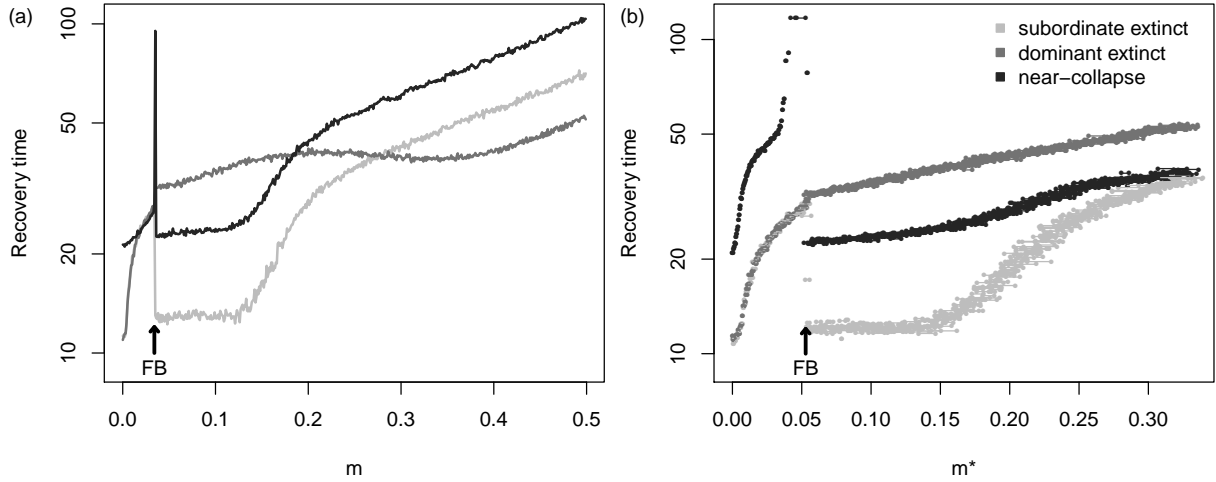


Figure 4: Recovery time of N_T following the extinction of either the low-density (light gray) or high-density (gray) population, or the near-collapse of both (dark gray) assuming (a) constant straying rates m and (b) density-dependent straying rates (evaluated at the steady state m^*) with trait heritability $h^2 = 0.2$. 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. FB marks the fold bifurcation.

population extends the length of time required for it to return to its steady state (figure S1). When both populations are both dramatically reduced, recovery time is generally fastest at lower levels of straying, while near the onset of the fold bifurcation, recovery time increases explosively and this is – as the name implies – characteristic of *slowing* dynamics that occur near critical transitions [48, 52].

(b) The effects of collective migration and density dependent straying

If we assume that the rate of straying is density-dependent, the probability that an individual strays m_0 determines the rate of straying within the population, such that $m(t)$ becomes lower as $N(t)$ increases, likely due to the effects of collective decision-making [16] (Eq. 5). Density dependence alters the straying rate at steady state population densities because $0 < m^* < m_0$, and this serves to rescale both the strength of the PE as well as the recovery time, but does not change the qualitative nature of our findings. In the alternative stable state regime, because each population exists at different steady state densities, there are likewise two alternative straying rates (m_i^*, m_j^*): the higher straying rate is associated with the low-density population, and the lower straying rate is associated with the high-density population. We assessed metapopulation robustness across a range of (m_i^*, m_j^*) values by varying the probability that an individual strays m_0 , which is positively and linearly related to (m_i^*, m_j^*). We find that the portfolio effects generated in systems with density-dependent straying are qualitatively similar to systems with constant straying, however there are some important quantitative differences. First, the PE associated with the high-density (low m^*) population is the same as that for a system with a constant

m (figure 3a). As m^* increases, we observe an increase in the PE than for systems with constant m .

Density-dependent straying alters these recovery times (figure 4b). First, in comparison with constant straying rates, density-dependent straying made recovery more rapid at elevated stray rates when both populations collapsed and when the subordinate population was extirpated. At low straying rates, near-collapse of both populations resulted in longer than expected recovery times, whereas in the alternative stable state regime (higher m^*), the recovery times for different disturbance types were very similar to systems with a constant m (figure 4b; note difference in x-axis scales). As trait heritability increased, the metapopulation always recovered more quickly if the small population was lost (figure S3). The lower recovery time for systems with increased m^* mirrors an elevated PE with higher density-dependent straying rates (figure 3). In tandem, analysis of both PE and recovery time suggests that although density-dependent straying does not appear to change the ‘dynamic landscape’ in our minimal model, it does appear to promote robustness, particularly when the aggregate biomass is low and straying is correspondingly high.

Increased rates of straying lowers phenotypic diversity ($\Delta\mu^* = |\mu_i(t) - \mu_j(t)|$, evaluated at the steady state) because both local and remote populations are increasingly homogenized. The loss of phenotypic diversity with increased straying is greater if trait heritability is low because traits take longer to go back to their local optima than they do when heritability is large. Hence straying counters the effect of diversifying local adaptation. Less intuitively, we observe a discrete jump towards low phenotypic diversity as the fold bifurcation is crossed (figure 5). Although the development of alternative stable states elevates the portfolio effect

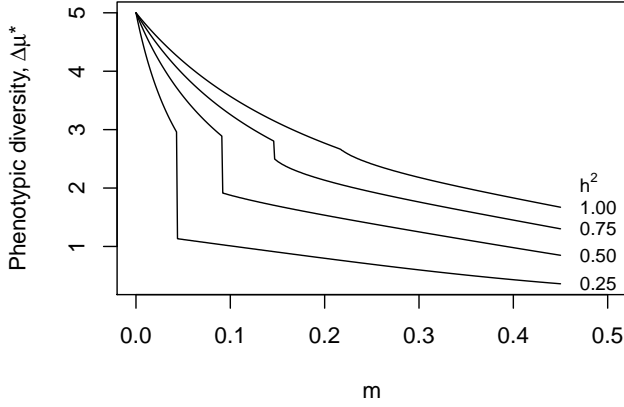


Figure 5: Phenotypic diversity ($\Delta\mu^*$) evaluated at the steady state as a function of straying rate m and trait heritability h^2 . The discrete jump occurs as the system crosses the fold bifurcation; lower phenotypic diversity emerges with higher straying rates and in the alternative stable state regime.

due to the variance-dampening effects of the aggregate, entering this dynamic regime also results in a substantial decline in phenotypic diversity, which may have less predictable adverse effects on the population.

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

Increasing differences in optimal trait values between sites ($\Delta\theta = |\theta_i - \theta_j|$) corresponds to greater regional differences in the conditions that favor alternative trait complexes, which we interpret here as greater habitat heterogeneity (REFS). If both populations are isolated, natural selection will direct the mean trait values of both populations towards their respective optima, such that $\mu_i(t) \rightarrow \theta_i$ as $t \rightarrow \infty$. With the onset of straying, we find that increasingly divergent trait optima generally lower N_T and exaggerate ΔN (figure S4), such that the biomass distribution becomes increasingly uneven. The impact of habitat heterogeneity on the portfolio effect and recovery time is more complex, serving to emphasize the nonlinear relationship between rates of straying and metapopulation robustness. As habitat heterogeneity increases, alternative stable states appear at lower straying rates – with the crossing of the fold bifurcation, accompanied by a peak in the PE – whereas the magnitude of increase in the PE also increases (figure 3b), reducing recovery time (figure S5). For increased rates of straying, greater habitat heterogeneity erodes the PE (figure 3b) and increases the recovery time (figure S5). These results together suggest that habitat heterogeneity, as measured as the differences in trait optima between two habitats $\Delta\theta$, promotes robustness when straying rates are low,

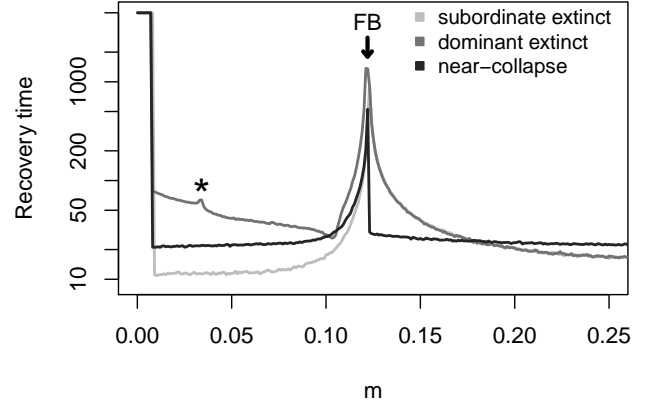


Figure 6: Distance dependent recovery times for three disturbance types. When straying is distance dependent, m increases as $\Delta\theta$ decreases. The '*' marks the value of $(m, \Delta\theta)$ below which there is a switch in subordinate/dominant states following extinction of the dominant population. FB marks the fold bifurcation.

and erodes robustness when straying rates are high.

If we assume that environmental heterogeneity increases with distance between sites, or that individuals may have behaviors that minimize their chances of straying into very different habitats, the rate of straying will decline with habitat heterogeneity. Accordingly, $\Delta\theta$ will decrease as m increases, such that there are low rates of straying between dissimilar populations and high rates of straying between similar populations. We find that under these conditions alternative stable states now appear for very low rates of straying $0 < m \leq 0.43$. As the straying rate increases and $\Delta\theta$ decreases, a single stable state emerges as the fold bifurcation is crossed, which is opposite the pattern observed when these parameters are independent. There are two notable dynamics that emerge following extinction of the dominant population at low rates of straying between dissimilar (high $\Delta\theta$) sites: (i) above a threshold m value, the dominant population recovers quickly enough that the evolving subordinate phenotype is overwhelmed by incoming strays, and it shifts back to its pre-disturbance (subordinate) state; (ii) below a threshold m value, there is enough time and isolation for the subordinate trait mean to shift towards its local optimum, and away from that of the recovering dominant population, such that the dominant population becomes subordinate, and the subordinate population becomes dominant (figure S7). This threshold value of m , below which this behavior occurs, is marked by the asterisk in figure 6, and holds for both constant and density-dependent straying (figure S8).

IV. 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 directly impacting the robustness of metapopulations against external disturbances. Specifically, we observed robustness in terms of: 1) the average-CV portfolio effect [3, 43], 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 [42]. In our minimal 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 among different metrics of stability [53]. Taken as a whole, we interpret our results to suggest an important role of density-dependent straying in the colonization and recovery dynamics for populations in shifting river mosaics, while also underscoring the risk of straying by individuals with maladaptive traits to reduce the productivity of locally adapted stock complexes.

A salient finding from our results was that straying can push metapopulations into alternative stable states, pushing one of the populations to a high density population (the *dominant state*), and one to a low density population (the *subordinate population*). This asymmetry in population densities also leads to an asymmetry in the mean trait values, both of which are skewed towards the local optimum of the dominant population. The formation of alternative stable states in our system is a relatively common example of spatial pattern formation, which only occurs above a threshold straying rate, the value of which depends on trait heritability and the difference in trait optima between sites. Pattern formation can occur as a consequence of myriad ecological processes, including habitat selection, aggregation, local environmental conditions, and/or interspecific interactions such as competition or predation, and is inexorably linked to scale [54]. Additionally, pattern formation is also well known to occur with the onset of spatially or diffusion-induced instabilities, or Turing instabilities [55]. Here, we describe an additional mechanism through which pattern formation in local densities can occur, when the onset of collective movement-mediated maladaptation leads to local differences in reproductive rates resulting in alternative stable states across sites. While metapopulation approaches have widely recognized the importance of source and sink populations [56] and have observed formation of alternative states [57], here we show that even similar populations can evolve into divergent states where one population is large and the other is smaller and maladapted.

There is a ‘sweet spot’ for straying that maximizes

metapopulation robustness. Results from our model reveal that the presence of just enough straying to cause formation of alternative stable states increases the portfolio effect (figure 2a). Previous theoretical work has shown that increased connectivity may erode portfolio effects in herring metapopulations, where straying is also thought to be density-dependent [58]. Although high levels of dispersal in our system shows a similar trend, the interplay between dispersal and PE is more subtle when selection for local adaptations is considered, such that low to intermediate levels of density-dependent straying result in an elevated PE, increasing the buffering capacity of the metapopulation. Although PE is measured at the steady state, low to intermediate rates of straying also appear to have a beneficial effect on transient dynamics. When there is just enough straying to cause alternative stable states, recovery times following induced disturbances decline, though – as with the PE – the time to recovery then grows if straying becomes too large (figure 4a).

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. We observed three salient results that contribute to our understanding of collective movement that combine to suggest that density-dependent straying may play an important role in the persistence of metapopulations over evolutionary time. First, the inclusion of density-dependent straying does not qualitatively alter either (i) steady state or (ii) transient dynamics of our minimal eco-evolutionary model, but effectively rescales measures of robustness to the straying rates the emerge from the coupled dynamics. Second, compared to systems with constant dispersal, density-dependent straying appears to increase the portfolio effect across a range of straying rates (figure 3a). Third, density-dependent straying reduces the time to recovery following disturbance, and this is particularly true in the case of near-collapse of the metapopulation (figure 4b). In the case of near-collapse, although both populations inherit low population densities, the mean trait values of both are skewed towards the optimum of the dominant population. Due to density-dependent straying, low population densities evince greater dispersal, and while this increased connectivity primarily facilitates the growth of the dominant population (because the trait means are closer to the dominant optimum), because the dominant population is the bulk of the aggregate biomass, the overall recovery time is significantly lessened (figures 4b, S9).

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 [27]. Our surrogate measure for habitat heterogeneity is the difference in trait optima between sites $\Delta\theta$. In general, our findings indicate that increased habitat heterogeneity promotes robustness (higher PE, shorter time to recovery) when straying rates are low, but may erode robustness when straying rates are high (figure 3b, solid lines). This may be particularly consequential for popu-

lations 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 adjacent 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].

All else being equal, habitats that are closer in space generally have greater similarity in environmental conditions than habitats that are geographically distant, and correspondingly phenotypes of more proximately located populations should be more similar to those that are distant [62]. Correspondingly, it is reasonable to expect a larger number of straying individuals between sites that are geographically proximate and indeed evidence corroborates this prediction [63, 64]. Alternatively, salmon that cue to specific environmental conditions may be more likely to stray into sites that have structurally and physiognomically similar habitats [29] even if other potential sites are closer. These considerations justify imposing a direct relationship between the rate of straying m and habitat heterogeneity: as site dissimilarity increases, so too should the straying rate decrease. As site dissimilarity increases, so to should the optima in trait values for the resident populations.

When habitat heterogeneity and the rate of straying are linked, we show that small amounts of either constant or density-dependent straying result in longer recovery times for the dominant population because there is enough isolation to allow the surviving subordinate population to slowly adapt towards its own optimum and

therefore strays from that population will be maladaptive in the dominant site. As selection pushes the subordinate population away from the dominant trait optimum, the recovery of the extinct population is slowed (figure 6). This may have particular conservation implications for considerations of aiding dispersal following disturbances or reconnections of lost habitats [65, 66]. Moreover, local temperature regimes are known to play a central role in dictating local adaptation of salmon populations (REFS). If temperature is the primary determinant of $\Delta\theta$ in terms of our model, this would suggest that populations spanning North-South gradients are more predisposed to distance dependent dynamics. In contrast, the relationship between the rate of straying and habitat heterogeneity may be less clear-cut for populations spanning an East-West gradient, where distant habitats may equally fitting for straying populations.

The importance of selection and its influence on the dynamics of populations is increasingly recognized as vital for assessing species' fragility. Of particular interest is how selection might influence spatially coupled metapopulations distributed across environmental gradients. We have shown that two measures of metapopulation robustness – the portfolio effect and the time to recovery following a disturbance – are strongly influenced by the rate at which individuals from a donor population stray into habitats occupied by a recipient population. Importantly, density-dependent straying, which may occur when individuals collectively navigate, can both increase the portfolio and lower the time to recovery following a disturbance, which is anticipated to promote persistence. We suggest that understanding the spatial complexity of metapopulations dispersing across heterogeneous environments, combined with the mosaic of selective forces acting on those environments, may be key to discovering those factors that promote persistence.

-
- [1] J. H. Brown and A. Kodric-Brown, "Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction," *Ecology*, vol. 58, pp. 445–449, Mar. 1977.
 - [2] D. J. D. Earn, S. A. Levin, and P. Rohani, "Coherence and conservation," *Science*, vol. 290, pp. 1360–1364, Jan. 2000.
 - [3] D. E. Schindler, J. B. Armstrong, and T. E. Reed, "The portfolio concept in ecology and evolution," *Front. Ecol. Environ.*, vol. 13, pp. 257–263, June 2015.
 - [4] R. E. Abbott, D. F. Doak, and M. L. Peterson, "Portfolio effects, climate change, and the persistence of small populations: analyses on the rare plant *Saussurea weberi*," *Ecology*, vol. 98, pp. 1071–1081, Apr. 2017.
 - [5] L. M. Thibaut and S. R. Connolly, "Understanding diversity-stability relationships: towards a unified model of portfolio effects," *Ecol. Lett.*, vol. 16, pp. 140–150, Feb. 2013.
 - [6] E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair, *Animal Migration*. A Synthesis, Oxford University Press, Jan. 2011.
 - [7] G. Bell and A. Gonzalez, "Adaptation and Evolutionary Rescue in Metapopulations Experiencing Environmental Deterioration," *Science*, vol. 332, pp. 1327–1330, June 2011.
 - [8] S. M. Carlson, C. J. Cunningham, and P. A. H. Westley, "Evolutionary rescue in a changing world," *Trends Ecol. Evol.*, vol. 29, pp. 521–530, Sept. 2014.
 - [9] C. C. Muhlfeld, R. P. Kovach, L. A. Jones, R. Al-Chokhachy, M. C. Boyer, R. F. Leary, W. H. Lowe, G. Luikart, and F. W. Allendorf, "Invasive hybridization in a threatened species is accelerated by climate change," *Nature Climate Change*, vol. 4, pp. 620–624, July 2014.
 - [10] W. H. Lowe, C. C. Muhlfeld, and F. W. Allendorf, "Spatial sorting promotes the spread of maladaptive hybridization," *Trends Ecol. Evol.*, vol. 30, pp. 456–462, Aug. 2015.
 - [11] P. A. H. Westley and T. P. Quinn, "Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus*

- spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and . . . ,” *Canadian Journal of . . .*, vol. 70, no. 5, pp. 735–746, 2013.
- [12] M. L. Keefer and C. C. Caudill, “Homing and straying by anadromous salmonids: a review of mechanisms and rates,” *Reviews in Fish Biology and Fisheries*, vol. 24, no. 1, pp. 333–368, 2014.
 - [13] N. N. Bett, S. G. Hinch, N. J. Burnett, M. R. Donaldson, and S. M. Naman, “Causes and Consequences of Straying into Small Populations of Pacific Salmon,” *Fisheries*, vol. 42, pp. 220–230, Mar. 2017.
 - [14] A. M. Simons, “Many wrongs: the advantage of group navigation,” *Trends Ecol. Evol.*, vol. 19, pp. 453–455, Sept. 2004.
 - [15] A. Berdahl, C. J. Torney, E. Schertzer, and S. A. Levin, “On the evolutionary interplay between dispersal and local adaptation in heterogeneous environments,” *Evolution*, vol. 69, pp. 1390–1405, June 2015.
 - [16] A. Berdahl, “Collective behavior as a driver of critical transitions in migratory populations,” *Movement Ecology*, vol. 4, pp. 1–12, June 2016.
 - [17] R. E. Brenner, S. D. Moffitt, and W. S. Grant, “Straying of hatchery salmon in Prince William Sound, Alaska,” *Environmental Biology of Fishes*, vol. 94, pp. 179–195, Feb. 2012.
 - [18] R. C. Johnson, P. K. Weber, J. D. Wikert, M. L. Workman, R. B. MacFarlane, M. J. Grove, and A. K. Schmitt, “Managed Metapopulations: Do Salmon Hatchery ‘Sources’ Lead to In-River ‘Sinks’ in Conservation?,” *PLoS ONE*, vol. 7, pp. e28880–11, Feb. 2012.
 - [19] A. H. Fullerton, S. T. Lindley, G. R. Pess, B. E. Feist, E. A. Steel, and P. McElhany, “Human Influence on the Spatial Structure of Threatened Pacific Salmon Metapopulations,” *Conservation Biology*, vol. 25, pp. 932–944, July 2011.
 - [20] T. P. Quinn, *The Behavior and Ecology of Pacific Salmon and Trout*. UBC Press, Nov. 2011.
 - [21] B. Jonsson and N. Jonsson, *Ecology of Atlantic Salmon and Brown Trout*. Habitat as a template for life histories, Dordrecht: Springer Science & Business Media, May 2011.
 - [22] T. P. Quinn, “A review of homing and straying of wild and hatchery-produced salmon,” *Fisheries Research*, vol. 18, pp. 29–44, Oct. 1993.
 - [23] A. P. Hendry, T. Bohlin, B. Jonsson, and O. K. Berg, “The evolution of philopatry and dispersal: homing versus straying in salmonids,” in *Evolution Illuminated* (A. P. Hendry and S. C. Stearns, eds.), Oxford University Press on Demand, 2004.
 - [24] N. Schtickzelle and T. P. Quinn, “A metapopulation perspective for salmon and other anadromous fish,” *Fish Fish.*, vol. 8, no. 4, pp. 297–314, 2007.
 - [25] S. C. Anderson, J. W. Moore, M. M. McClure, N. K. Dulvy, and A. B. Cooper, “Portfolio conservation of metapopulations under climate change,” *Ecol. Appl.*, vol. 25, no. 2, pp. 559–572, 2015.
 - [26] M. L. Keefer, C. C. Caudill, C. A. Peery, and S. R. Lee, “Transporting juvenile salmonids around dams impairs adult migration,” *Ecol. Appl.*, vol. 18, pp. 1888–1900, Dec. 2008.
 - [27] P. A. H. Westley, A. H. Dittman, E. J. Ward, and T. P. Quinn, “Signals of climate, conspecific density, and watershed features in patterns of homing and dispersal by Pacific salmon,” *Ecology*, vol. 96, pp. 2823–2833, Oct. 2015.
 - [28] M. H. Bond, P. A. H. Westley, A. H. Dittman, D. Holecek, T. Marsh, and T. P. Quinn, “Combined effects of barge transportation, river environment, and rearing location on straying and migration of adult snake river fall-run chinook salmon,” *Transactions of the American Fisheries Society*, vol. 146, pp. 60–73, Dec. 2016.
 - [29] D. A. Peterson, R. Hilborn, and L. Hauser, “Local adaptation limits lifetime reproductive success of dispersers in a wild salmon metapopulation,” *Nature Communications*, vol. 5, p. 3696, Apr. 2014.
 - [30] J. W. Moore, M. McClure, L. A. Rogers, and D. E. Schindler, “Synchronization and portfolio performance of threatened salmon,” *Conserv. Lett.*, vol. 3, pp. 340–348, Apr. 2010.
 - [31] S. M. Carlson, W. H. Satterthwaite, and I. A. Fleming, “Weakened portfolio effect in a collapsed salmon population complex,” *Can. J. Fish. Aquat. Sci.*, vol. 68, pp. 1579–1589, Sept. 2011.
 - [32] D. C. Braun, J. W. Moore, J. Candy, and R. E. Bailey, “Population diversity in salmon: linkages among response, genetic and life history diversity,” *Ecography*, vol. 39, pp. 317–328, Mar. 2016.
 - [33] G. G. Simpson, *The major features of evolution*. Simon and Schuster, 1953.
 - [34] R. Lande, “Natural Selection and Random Genetic Drift in Phenotypic Evolution,” *Evolution*, vol. 30, p. 314, June 1976.
 - [35] A. O. Shelton and M. Mangel, “Fluctuations of fish populations and the magnifying effects of fishing,” *Proc. Natl. Acad. Sci. USA*, vol. 108, pp. 7075–7080, Apr. 2011.
 - [36] J. R. Jasper, C. Habicht, S. Moffitt, R. Brenner, J. Marsh, B. Lewis, E. C. Fox, Z. Grauvogel, S. D. R. Olive, and W. S. Grant, “Source-Sink Estimates of Genetic Introgression Show Influence of Hatchery Strays on Wild Chum Salmon Populations in Prince William Sound, Alaska,” *PLoS ONE*, vol. 8, p. e81916, Dec. 2013.
 - [37] S. J. Schreiber, R. Bürger, and D. I. Bolnick, “The community effects of phenotypic and genetic variation within a predator population,” *Ecology*, vol. 92, pp. 1582–1593, Aug. 2011.
 - [38] J. P. Gibert and C. E. Brassil, “Individual phenotypic variation reduces interaction strengths in a consumer–resource system,” *Ecol. Evol.*, vol. 4, no. 18, pp. 3703–3713, 2014.
 - [39] J. P. Gibert and J. P. DeLong, “Individual variation decreases interference competition but increases species persistence,” *Advances in Ecological Research*, vol. 52, pp. 45–64, 2015.
 - [40] A. Berdahl, P. A. H. Westley, S. A. Levin, I. D. Couzin, and T. P. Quinn, “A collective navigation hypothesis for homeward migration in anadromous salmonids,” *Fish Fish.*, vol. 17, pp. 525–542, June 2014.
 - [41] D. E. Schindler, J. B. Armstrong, and T. E. Reed, “The portfolio concept in ecology and evolution,” *Front. Ecol. Environ.*, vol. 13, pp. 257–263, June 2015.
 - [42] O. Ovaskainen and I. Hanski, “Transient Dynamics in Metapopulation Response to Perturbation,” *Theor. Popul. Biol.*, vol. 61, pp. 285–295, May 2002.
 - [43] S. C. Anderson, A. B. Cooper, and N. K. Dulvy, “Ecological prophets: quantifying metapopulation portfolio effects,” *Methods Ecol. Evol.*, vol. 4, no. 10, pp. 971–981, 2013.
 - [44] M. Loreau and C. de Mazancourt, “Species Synchrony

- and Its Drivers: Neutral and Nonneutral Community Dynamics in Fluctuating Environments,” *Am. Nat.*, vol. 172, pp. E48–E66, Aug. 2008.
- [45] J. D. Yeakel, J. W. Moore, P. R. Guimarães Jr, and M. A. M. de Aguiar, “Synchronisation and stability in river metapopulation networks,” *Ecol. Lett.*, vol. 17, no. 3, pp. 273–283, 2014.
- [46] J. Guckenheimer and P. Holmes, *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields*. New York: Springer, 1983.
- [47] S. M. Carlson and T. R. Seamons, “SYNTHESIS: A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change,” *Evolutionary Applications*, vol. 1, pp. 222–238, Apr. 2008.
- [48] M. Scheffer, J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Nes, M. Rietkerk, and G. Sugihara, “Early-warning signals for critical transitions,” *Nature*, vol. 461, pp. 53–59, Sept. 2009.
- [49] S. J. Lade and T. Gross, “Early warning signals for critical transitions: A generalized modeling approach,” *PLoS Comp. Biol.*, vol. 8, no. 2, p. e1002360, 2012.
- [50] C. Boettiger, N. Ross, and A. Hastings, “Early warning signals: the charted and uncharted territories,” *Theor. Ecol.*, vol. 6, pp. 255–264, Aug. 2013.
- [51] V. Dakos and J. Bascompte, “Critical slowing down as early warning for the onset of collapse in mutualistic communities,” *Proc. Natl. Acad. Sci. USA*, vol. 111, pp. 201406326–17551, Nov. 2014.
- [52] C. Kuehn, “A mathematical framework for critical transitions: Bifurcations, fast-slow systems and stochastic dynamics,” *Physica D*, vol. 240, no. 12, pp. 1020–1035, 2011.
- [53] I. Donohue, O. L. Petchey, J. M. Montoya, A. L. Jackson, L. McNally, M. Viana, K. Healy, M. Lurgi, N. E. O’Connor, and M. C. Emmerson, “On the dimensionality of ecological stability,” *Ecol. Lett.*, vol. 16, pp. 421–429, Apr. 2013.
- [54] S. A. Levin, “The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture,” *Ecology*, vol. 73, pp. 1943–1967, Dec. 1992.
- [55] H. Meinhardt, “Turing’s theory of morphogenesis of 1952 and the subsequent discovery of the crucial role of local self-enhancement and long-range inhibition,” *Interface Focus*, vol. 2, no. 4, pp. 407–416, 2012.
- [56] I. Hanski, *Metapopulation Ecology*. Oxford University Press, Mar. 1999.
- [57] D. A. Boughton, “EMPIRICAL EVIDENCE FOR COMPLEX SOURCE–SINK DYNAMICS WITH ALTERNATIVE STATES IN A BUTTERFLY METAPOPULATION,” *Ecology*, vol. 80, pp. 2727–2739, Dec. 1999.
- [58] D. H. Secor, L. A. Kerr, and S. X. Cadrin, “Connectivity effects on productivity, stability, and persistence in a herring metapopulation model,” *ICES Journal of Marine Science*, vol. 66, pp. 1726–1732, Sept. 2009.
- [59] M. R. Christie, M. L. Marine, R. A. French, and M. S. Blouin, “Genetic adaptation to captivity can occur in a single generation,” *PNAS*, vol. 109, pp. 238–242, Jan. 2012.
- [60] M. W. Chilcote, “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.*, vol. 60, pp. 1057–1067, Sept. 2003.
- [61] H. Araki, B. Cooper, and M. S. Blouin, “Genetic Effects of Captive Breeding Cause a Rapid, Cumulative Fitness Decline in the Wild,” *Science*, vol. 318, pp. 100–103, Oct. 2007.
- [62] P. A. H. Westley, Corinne M. Conway, and I. A. Fleming, “Phenotypic divergence of exotic fish populations is shaped by spatial proximity and habitat differences across an invaded landscape,” *Evol. Ecol. Res.*, vol. 14, no. 2, pp. 147–167, 2012.
- [63] J. R. Candy and T. D. Beacham, “Patterns of homing and straying in southern British Columbia coded-wire tagged chinook salmon (*Oncorhynchus tshawytscha*) populations,” *Fisheries Research*, vol. 47, pp. 41–56, June 2000.
- [64] R. S. Schick and S. T. Lindley, “Directed connectivity among fish populations in a riverine network,” *J. Appl. Ecol.*, vol. 44, no. 6, pp. 1116–1126, 2007.
- [65] J. H. Anderson, P. L. Faulds, W. I. Atlas, and T. P. Quinn, “Reproductive success of captive bred and naturally spawned Chinook salmon colonizing newly accessible habitat,” *Evolutionary Applications*, vol. 6, pp. 165–179, Feb. 2013.
- [66] G. R. Pess, T. P. Quinn, S. R. Gephard, and R. Saunders, “Re-colonization of Atlantic and Pacific rivers by anadromous fishes: linkages between life history and the benefits of barrier removal,” *Reviews in Fish Biology and Fisheries*, vol. 24, pp. 881–900, Jan. 2014.

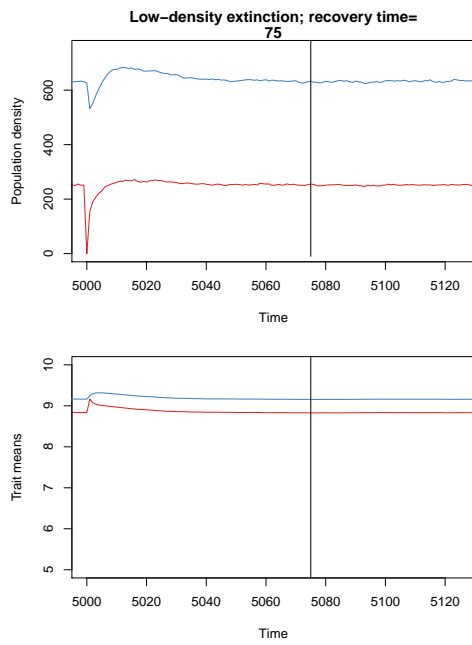


Figure S1: Extinction of low-density population with a high constant straying rate $m = 0.4$ and low trait heritability $h^2 = 0.2$ (see figure 4a). Black line marks the calculated point of recovery post-perturbation. Trait optima are $\theta_1 = 10$ (blue population trajectory) and $\theta_2 = 5$ (red population).

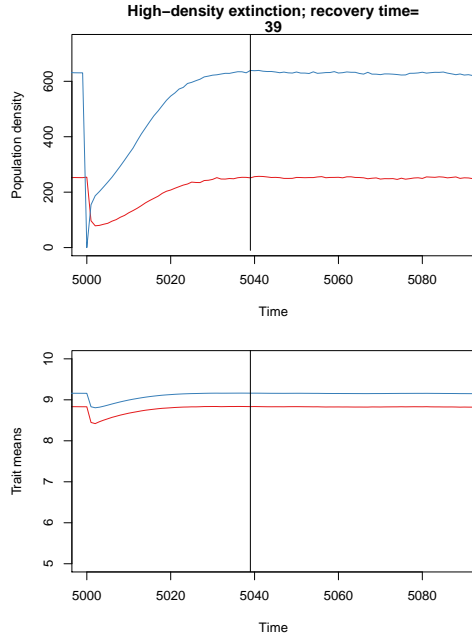


Figure S2: Extinction of high-density population with a high straying rate $m = 0.4$ and low trait heritability $h^2 = 0.2$ (see figure 4a). Black line marks the calculated point of recovery post-perturbation. Trait optima are $\theta_1 = 10$ (blue population trajectory) and $\theta_2 = 5$ (red population).

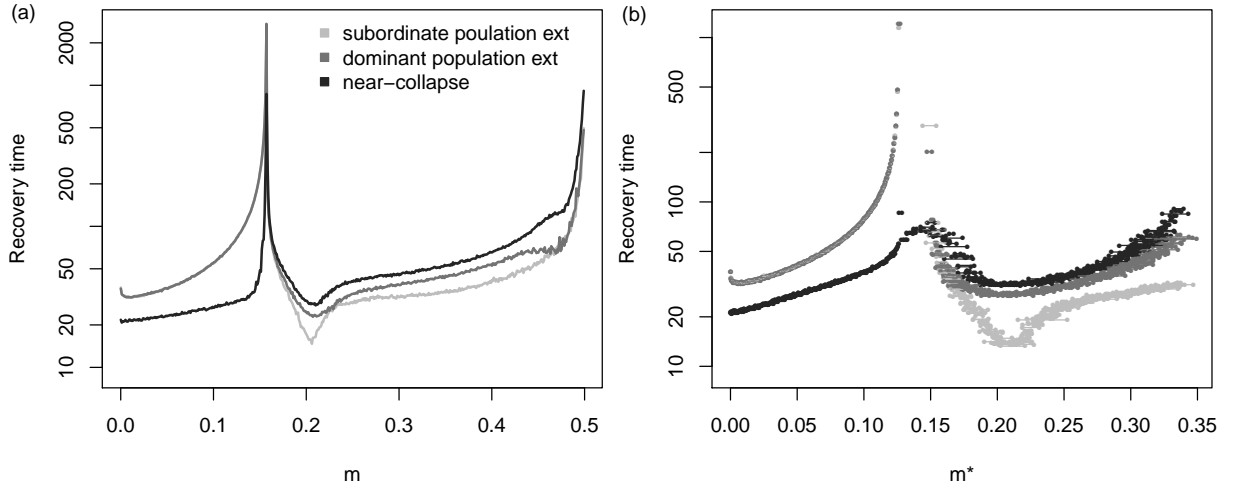


Figure S3: Recovery time of N_T following the extinction of either the low-density (light gray) or high-density (gray) population, or the near-collapse of both (dark gray) assuming (a) constant straying rates m and (b) density-dependent straying rates (evaluated at the steady state m^*) with trait heritability $h^2 = 0.8$. 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.

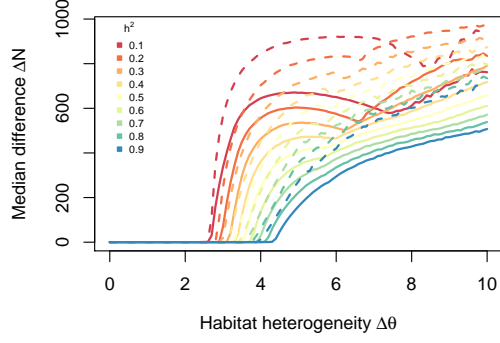


Figure S4: Median difference in population densities taken over the straying rate as a function of habitat heterogeneity $\Delta\theta$. Solid lines are for constant m ; dashed lines are for density-dependent m .

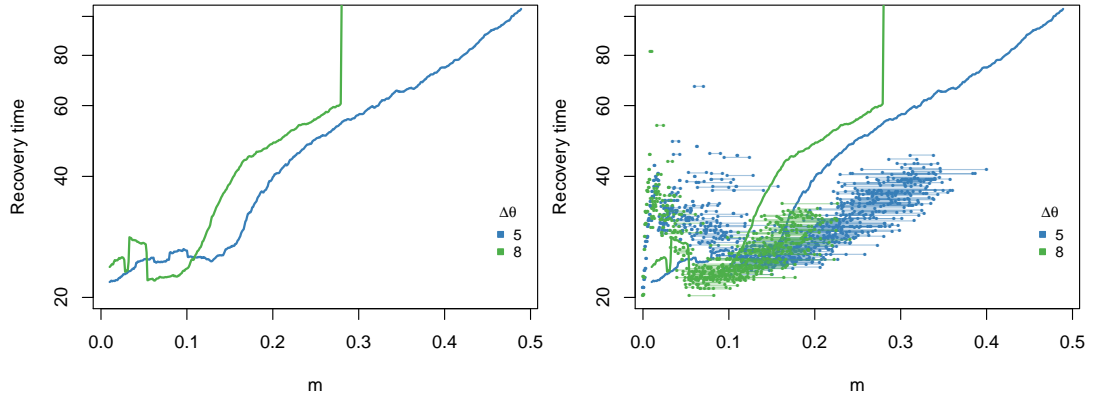


Figure S5: (a) Recovery time after near collapse of both populations as a function of straying rate m and habitat heterogeneity $\Delta\theta$. (b) The same as (a) but including recovery times when straying is density-dependent, shown by linked pairs of points. Recovery times for systems with density-dependent straying are longer at low straying rates and shorter at higher straying rates, mirroring the change in portfolio effects shown in figure 3.

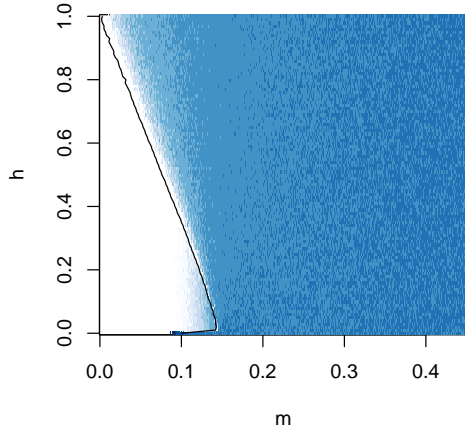


Figure S6: Distance dependent portfolio effects as a function of straying rate m and trait heritability h^2 . When straying is distance dependent, m increases as $\Delta\theta$ decreases.

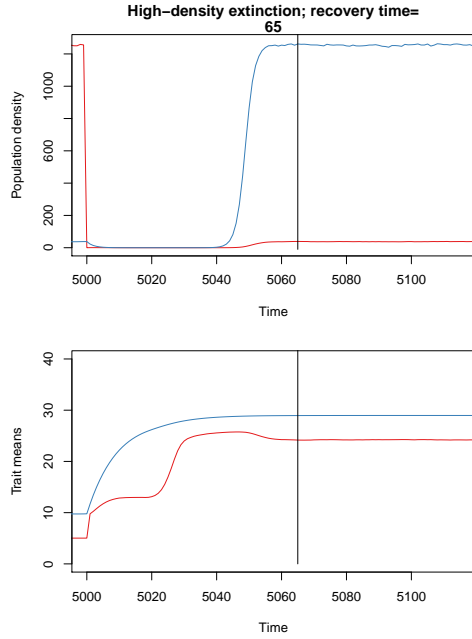


Figure S7: Distance dependent straying, where increased differences in trait optima between sites $\Delta\theta$ corresponds to lower rates of straying m . At low rates of straying $m = 0.02$ ($\Delta\theta = 24$), extinction of the dominant population leads to slower-than-expected recovery times because the subordinate population is isolated enough to evolve towards its own trait optimum. In this case, m is less than $m = 0.034$ (denoted by the asterisk in figure 6), such that isolation allows the subdominant population to ‘run away’ from the influence of the dominant population, leading to a switch in states. If m is low but greater than 0.034, isolation permits the subdominant population to ‘run away’ from the influence of the dominant population, until it is overwhelmed by the recovering dominant population, and reverts back to its previous trait mean prior to the disturbance.

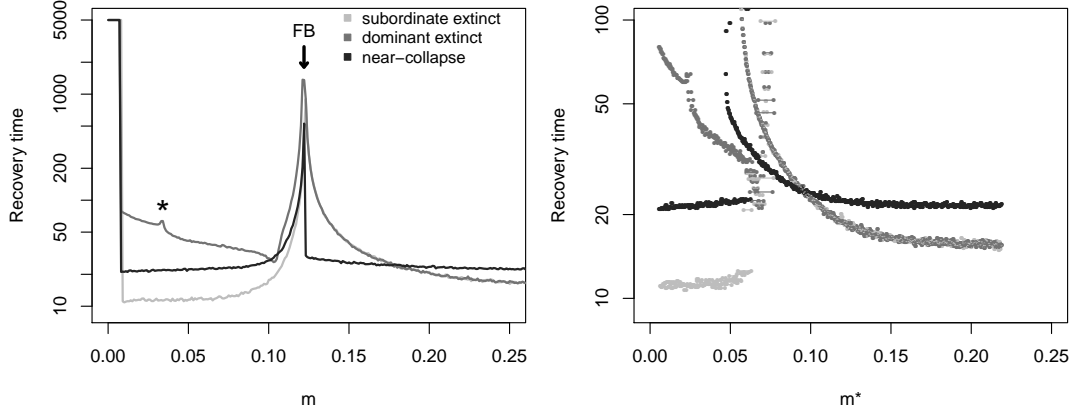


Figure S8: Distance dependent recovery times for three disturbance types. When straying is distance dependent, m increases as $\Delta\theta$ decreases for constant (a) and density-dependent (b) staying rates. The fold bifurcation is not as clear in (b) because $\Delta\theta$ is a function of the individual straying rate m_0 , whereas the x-axis in (b) is the straying rate at the steady state m^* . Despite this difference, the general trends shown in (a) are also present in (b).

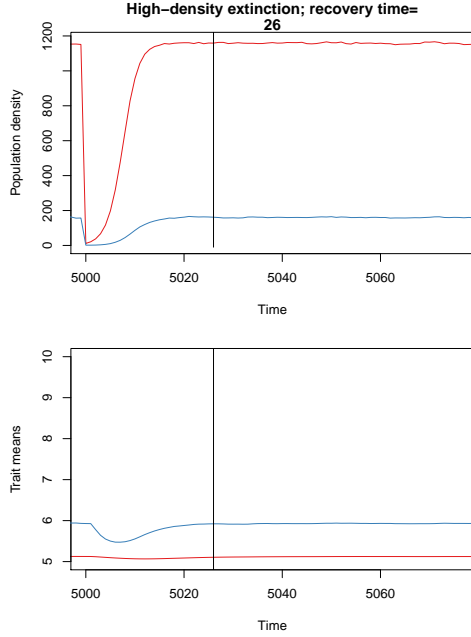


Figure S9: Near collapse of both populations with a low straying rate $m = 0.1$ and low trait heritability $h^2 = 0.2$ (see figure 4a). Black line marks the calculated point of recovery post-perturbation. Trait optima are $\theta_1 = 10$ (blue population trajectory) and $\theta_2 = 5$ (red population).