Lost in space: the eco-evolutionary impacts of straying on metapopulation robustness

Justin D. Yeakel[1,2,*], Jean Phillipe Gibert[1], Sean Anderson[3], Peter Westley[4], & Jon W. Moore[5]
[1]School of Natural Sciences, University of California, Merced, Merced CA, USA
[2]The Santa Fe Institute, Santa Fe NM, USA
[3]Department of Biology, University of Washington, Seattle WA, USA
[4]Institute for Arctic Biology, University of Alaska, Fairbanks, Fairbanks AK, USA
[5]Earth$_2$Oceans Research Group, Simon Fraser University, Vancouver BC, Canada
*To whom correspondence should be addressed: jdyeakel@gmail.com

I. INTRODUCTION

Coordinated mass migrations are one of the great wonders of the natural world, and the ability of individuals and groups to navigate across great distances have long fascinated naturalists [1]. Anadromous salmonid fishes (genera *Oncorhynchus* and *Salmo*) embody these astonishing migrations by homing with high accuracy and precision to their natal streams for reproduction after years at sea [2–4]. Nothwithstanding their philopatric tendancy, not all individuals home, but rather 'stray' to non-natal sites to spawn [5–7]. Although extensive work has been done to document the extent of straying from donor populations and into recipient populations [4, 8], only recently have the abiotic, biotic, and anthropogenic influences of 'straying' behaviors been investigated systemically [9–11]. Most recently the role of social interactions and collective navigation has been hypothesized [12, 13, ; this volume]. Although the straying of individuals into sites hosting other populations provides connections within the larger metapopulation, potentially promoting ecological and evolutionary rescue, it also serves to introduce maladapted individuals into habitats that are host to different environmental conditions, and this may lower the mean fitness of the local (mixed) population [14].

The dual nature of straying as both promoter of connections among metapopulation demes and potential eroder of locally adapted gene complexes highlights the interplay between ecological dynamics of connected populations as well as the evolutionary dynamics of mixed trait distributions that respond to alternative local conditions. Population-level biodiversity is recognized to increase species persistence (REFS), and the resilience and sustainability of metapopulations (general REF). For example, the long-term sustainability of the Bristol Bay sockeye salmon fishery is due in large part to intact habitat that in conjunction with fine-scale homing and reduced gene flow provides a template for the evolution of countless locally adapted populations [15–18]. In contrast, areas such as California's Central Valley where habitats have been lost, degraded, and homogenized stand in marked contrast. Within species diversity (or lack thereof) can manifest itself by way of asynchronous population dynamics, where the drivers that give rise to changes in population size vary across a metapopulation, decreasing the potential for synchronization, and correspondingly increasing the potential for ecological rescue (REFS). This statistical buffer against extinction has traditionally been quantified as the Portfolio Effect (PE), which is the ratio of the population CV to the CV of the aggregated metapopulation. Weakened portfolio dynamics can also emerge from homogenization resulting from reduced genetic variability among populations, where homogenous stocks are more likely to have similar life-history structures (REFS), be at greater risk disease-induced epidemics (REFS), and recruit sub-optimally in heterogeneous environments (REFS). Of course, these two measures of diversity often occur concurrently: for instance, lower genetic diversity increases the likelihood that two populations respond similarly to the same stressors, and this promotes synchronized dynamics, thus lowering portfolio effects.

That evolutionary forces play out heterogeneously across geographic mosaics is now a foundational concept in ecology and evolutionary biology (REFS). These mosaics are in part driven by environmental differences between habitats that alter the selective forces acting on different phenotypes [19], and a principle underlying assumption is that there is gene flow such that individuals from different habitats mix over space (REFS). Although the evolutionary outcomes of these spatial processes have been explored in depth (REFS), it is less well understood how selective mosaics and their consequent evolutionary forces impact population dynamics over contemporary timescales [20]. How the ecological dynamics of phenotypically diverse metapopulations, wherein constituent populations are subject to different selective regimes, are altered affected by evolutionary forces is less well known.

Migratory populations that return to a breeding ground or natal stream to reproduce are linked to each other by some proportion of the population that permanently disperse, or stray into the 'wrong' site; we might say that there is at least one *Kevin* in every school or flock in every school or flock (figure 1). The rate at which individuals stray, m, has been subject to a growing amount of both theoretical and empirical research [4, 7, 8] and may be linked to errors made at an individual-level that are themselves diminished by migrating in groups and pooling individual choices [12, 13]. Regardless of the mechanism's governing straying, the effect that it has on the dynamics of individual populations and the metapopu-

Figure 1: *Migrating Geese*, a comic from Randall Monroe's xkcd (https://xkcd.com/1729/). A flock of geese travel in the direction of a shared destination, the lone stray named *Kevin*. In this case, the rate of straying is $m = 0.05$, which is not an uncommon rate for migrating populations of salmon [18].

lation as a whole is a topic of considerable interest that has tangible conservation implications [21–23]. Whether, and to what extent, the ecological consequences of straying depend on the evolutionary dynamics that emerge from populations distributed across a selection mosaic is unclear. How the assumed negative evolutionary effects of straying and subsequent gene flow is balanced by the positive effects of demographic rescue is the subject of this contribution.

Here we ask the overarching question: how does collective behavior mediated dispersal and gene flow interact to influence the robustness of locally adapted populations? 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. An important and relatively novel component of this model is the inclusion of a parameter that defines the difference in local conditions that favor different trait optima, increasing values of which correlates to populations that mix across increasingly heterogeneous environments [12, though see]. Although our proposed model is was constructed with the dynamics of salmon populations in mind, the framework is general and the conclusions are likely relevant to a diverse range of migratory organisms where locally adapted populations are linked by dispersal. We first show that specific rates of straying and trait heritability can have large effects on the qualitative dynamics of populations over time, in many cases giving rise to alternative steady states where one site is pushed towards very low biomass. The emergence of alternative steady states results in a nonlinear response of the portfolio effect as well as the time required for the metapopulation to recover after an induced disturbance, suggesting that metapopulation robustness can be quite sensitive to the combined influences of dispersal across a selective landscape.

A second important finding of our minimal model reveals that systems with greater habitat heterogeneity (measured by an increased difference in the trait values that are optimal between sites) host an intermediate range of straying rates where the portfolio effect increases to a local maximum, signaling that under certain conditions moderate amounts of straying between populations can increase the likelihood of persistence despite the deleterious evolutionary effects overall. However, if we suppose that the rate of straying between two sites is correlated with distance (as indicated by empirical evidence), and that the difference in trait optima increases with distance as would be the case if the optima were associated with alternative temperature regimes (especially if sites are distributed latitudinally rather than longitudinally), even a very small amount of straying can drastically reduce the portfolio effect. Importantly, the qualitative nature of our results do not depend on whether the stray rate is density dependent or constant, suggesting a limited role of collective dispersal on the dynamics considered herein.

II. MODEL DESCRIPTION & ANALYSIS

(a) Metapopulation framework

We consider two populations N_1 and N_2 that are separated in space in 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 $x = \theta$. 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 population mean and the local trait optimum at a given point in time [24, 25].

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 $x_1 \to \theta_1$, 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 will be pulled away from the optimum, and recruitment rates will be lowered. As $m \to 0.5$, the populations are perfectly mixed, acting as a single population.

We use the discrete Ricker population dynamic framework described by Shelton and Mangel [26] as the basis

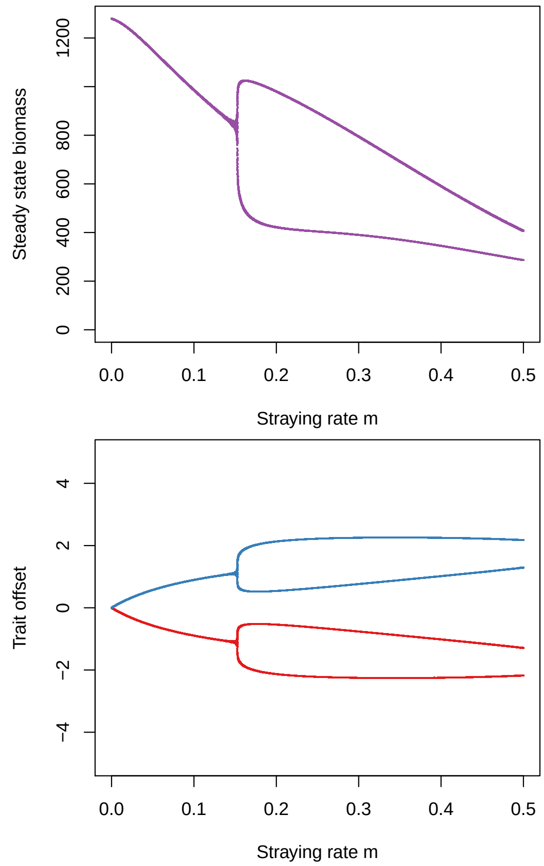

Figure 2: A) The steady state densities of N_1 and N_2 as a function of a constant stray rate m. Which population attains the low- or high-density state is random due to small applied fluctuations in the initial conditions. B) The steady state trait values measured as $\theta_i - x_i$, as a function of a constant stray rate m.

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 $((1-m)N_i(t) + mN_j(t))\,\mathrm{e}^{-Z}$. 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

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

where the difference equation for N_j mirrors that for N_i.

The combined recruitment of local individuals $(1-m)N_i(t)$ and incoming strays $mN_j(t)$, as a function of their mean trait value at time t. Given the local trait optimum is θ_i, recruitment is

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

where the mismatch between the local trait mean $\mu_i(t)$ and the local optimum θ_i determines scales the recruitment rate for the population, and $\tilde{P} \sim \mathrm{Normal}(0, 0.01)$ 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, which we set as $\tau = 1$ here and throughout.

(b) Recruitment over a selective landscape Because individuals from the local population are mixed with individuals from the remote population via staying, 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

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

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 being that of the mixed-normal. Second, we assume that changes in trait variance through time are minimal, such that σ^2 is assumed to be constant.

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. The mean trait value thus changes through time according to the difference equation

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

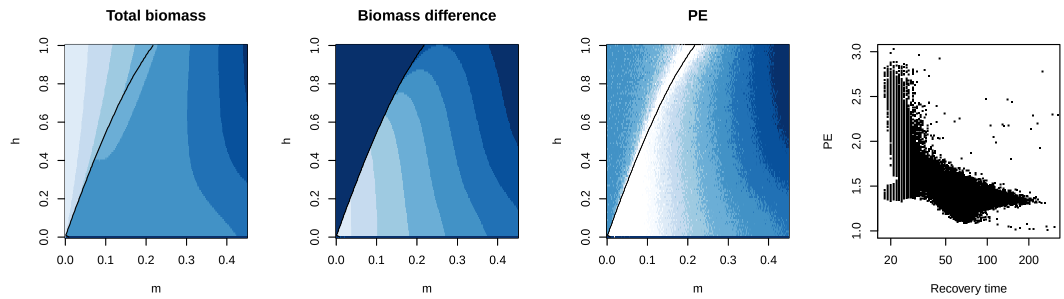

Figure 3: (a) Total means N_t, (b) difference in means ΔN, and (c) the portfolio effect PE as a function of heritability h^2 and a constant stray rate m. Light colors = high values. The black line shows the fold bifurcation separating a single steady state (left) from alternative steady states (right). (d) The relationship between the time to recovery following a disturbance and the portfolio effect.

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 [25], which is proportional to the change in mean fitness with respect to μ_i.

(c) Measuring metapopulation robustness We evaluated metapopulation robustness by measuring the average-CV portfolio effect (PE) [28**?**] 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 [**?**]. The average-CV portfolio effect is, as the name implies, the average CV across each population divided by the CV of the aggregate [**?**], such that

$$\langle \mathrm{PE} \rangle = \frac{1}{X}\sum_{i=1}^{X}\frac{\sqrt{\mathrm{VAR}(N_i)}}{\mathrm{E}(N_i)}\cdot\frac{\mathrm{E}(N_T)}{\sqrt{\mathrm{VAR}(N_T)}}, \qquad (5)$$

where in this case the number of populations is limited to $X = 2$ and the expectations $\mathrm{E}(\cdot)$ and variances $\mathrm{VAR}(\cdot)$ are evaluated at the steady state. As the CV of N_T decreases relative to that of the constituent populations, $\langle \mathrm{PE} \rangle > 1$, and the metapopulation is presumed to become more stable. A similar measure of metapopulation robustness can be evaluated by measuring the synchronization ϕ between populations, where

$$\phi = \frac{\mathrm{VAR}(N_T)}{\left(\sum_{i=1}^{N}\sqrt{\mathrm{VAR}(N_i)}\right)^2}. \qquad (6)$$

By rearranging and substituting eq. (6) into eq. (5), we can observe that $\langle \mathrm{PE} \rangle \propto \sqrt{\phi}^{-1}$. Thus, the dynamical diversity of the metapopulation offers a mirror to the portfolio effect, where perfect synchrony ($\phi = 1$) also means $\langle \mathrm{PE} \rangle = 1$. Portfolio effects greater than unity corresponds to less synchronization ($\phi < 1$) [27–29] 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). Measuring the time that it takes for a perturbed system to relax also permits a more detailed perspective of the potential fragility of the metapopulation. For example, if populations settle to alternative steady states (alternative steady 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. 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.

(d) The effects of density and distance on the rate of straying We have so far assumed that the proportion of strays leaving and entering a population is constant, however there is good evidence that at least in some species the straying rate is density dependent [8, 13]. 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. [13], given the probability that an individual strays is m_0, the proportion of the local population $N_i(t)$ that strays is

$$m(t) = m_0\left(1 - \frac{N_i(t)}{C + N_i(t)}\right), \qquad (7)$$

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

The straying rate is intrinsically linked to the distance between the donor and recipient population. The greater the distance between two populations, the lower the expected rate of straying (REF). We can 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 $m_{\max} = 0.5$, 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 $\theta_i - \theta_j$).

III. RESULTS

(a) Nonlinear effects of straying on the portfolio effect and recovery time

Straying generally 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, and this accords with observations from natural populations [8] 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 steady states: one at high biomass, and one at low biomass density (figure 2a, 3a). Mean trait values for both populations bifurcate similarly (figure 2b), depending on which population attains a low- vs. high-density, which in our system is random due to a small amount of introduced variation in the initial conditions. The fold bifurcation (the black line in Figs. 3a-c) occurs at lower values of the straying rate m with decreased trait heritability h^2 (Fig 3a,b), indicating that weaker coupling between ecological and evolutionary dynamics in addition to higher rates of straying promotes the appearance of alternative stable states.

Trait heritability has a large impact on the sensitivity of the straying rate to both the aggregate population steady state density ($N_T^* = N_1^* + N_2^*$; figure 3a) as well as the difference between steady state densities (the distance between alternative stable states: $\Delta N = |N_1^* - N_2^*|$; figure 3b). 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, if the trait is less heritable, an increase in the straying rate has little impact on the total biomass density but contrastingly large effects on ΔN.

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 $\mathrm{VAR}(N_{i,j})$. This variance increase is the product of a dynamical process known as critical slowing down that occurs near fold bifurcations [30], a phenomenon that some have suggested may serve as an early warning indicator for approaching phase transitions [30**?** –32]. For larger values of m (to the right of the fold bifurcation in Fig 3a-c), where alternative steady 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 3c).

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. We measured the time required for the system N_T to relax 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. In general, we find that the average-CV portfolio effect is negatively correlated with recovery time (figure 3d), 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.

At low rates of straying both populations are subject to the same steady state, such that extinction of either population results in the same recovery time, and when trait heritability is low, the time required to recover following the extinction of either population is generally less than or equal to the recovery time after near-collapse of both (figure 4a). In the alternative stable state regime where straying rates are higher, extinction of the smaller population results in the shortest recovery time, whereas as m increases, extinction of the larger population results in the shortest recovery time. Because the mean trait values of both populations are skewed towards those of the high-density site, when the low-density population collapses under high rates of straying, selection against the flood of maladapted individuals that stray into the recovering extends the length of time required for it to return to its steady state (figure S1). Alternatively, when the high-density population collapses under high straying rates, the low-density population suffers loss as well due to the absence of incoming strays such that both populations must recover (figure S2).

Increased trait heritability flips this relationship by increasing the response of trait evolution to changes in demography (figure 4b). When straying rates are low,

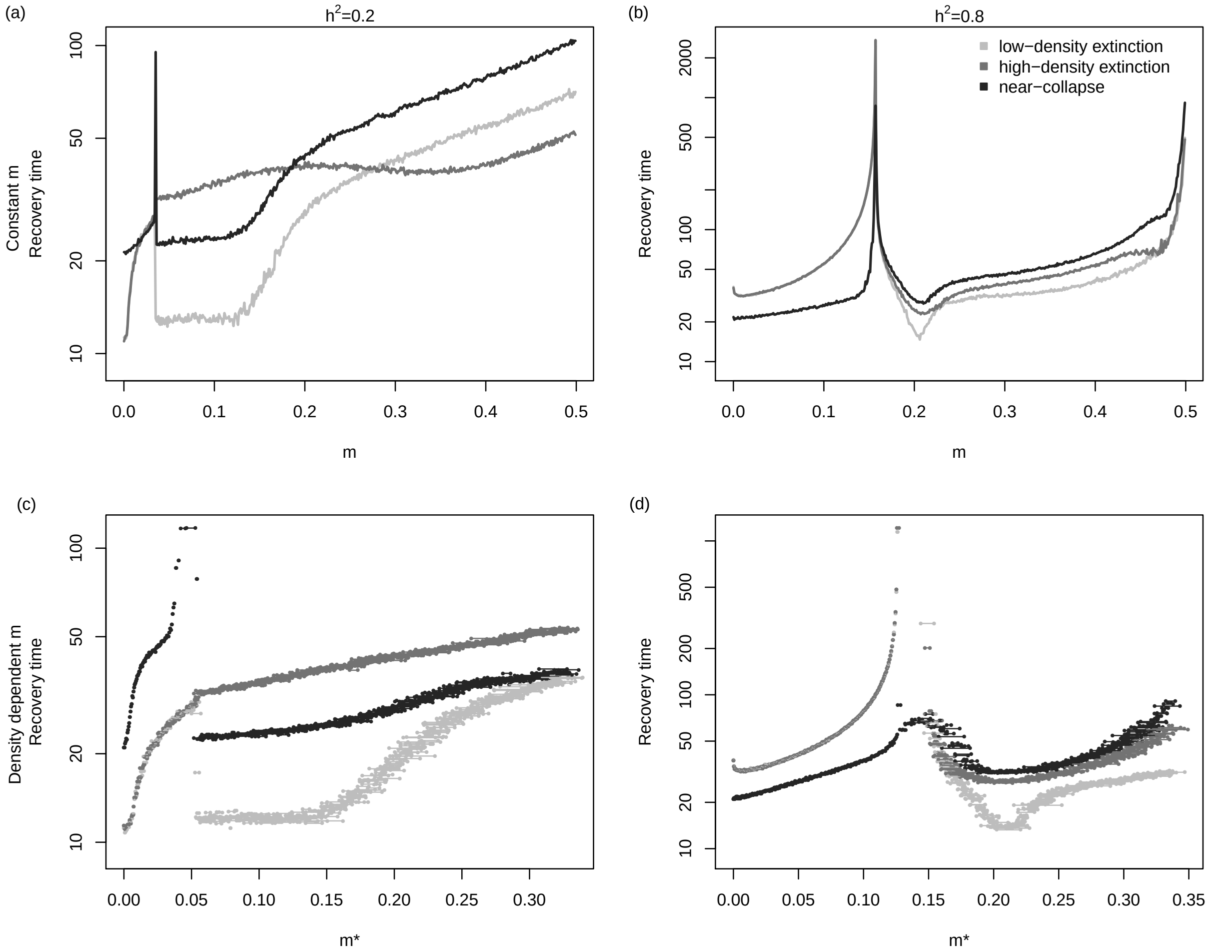

Figure 4: (a, b) Recovery time of N_T following the extinction of either the low-density (light gray) or high-density (gray) population, or the near-collapse of both (dark gray) assuming constant straying rates m and (c, d) density dependent straying rates (evaluated at the steady state m^*). If m is density dependent, in the alternative steady 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.

metapopulations that suffer near-collapse of both populations recover more quickly than systems suffering extinctions of either population. When straying rates are higher such that the system is in the alternative stable state regime, the metapopulation always recovers more quickly if the small population is lost (figure S3), whereas the time to recovery is maximized if both populations suffer near-collapse. When the high-density population goes extinct, the stronger response of selection permits the surviving low-density population to grow quickly and fill the high-density state (figure S4). Near the onset of the fold bifurcation, recovery times increase explosively regardless of straying rate, heritability, or disturbance type.

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 the selective forces acting against trait means far from the local optima are lessened. 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 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.

(b) The influence of habitat heterogeneity on metapopulation robustness

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. Although trait heritability among salmonids is variable, most life history traits show $h^2 < 0.5$ [34], and we largely focus additional analyses on that range. If both populations are isolated, natural

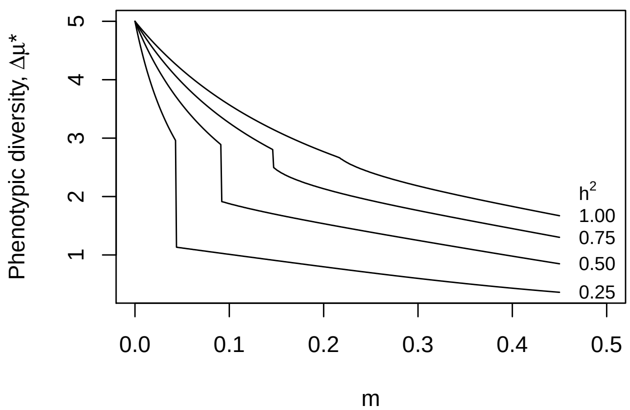

Figure 5: Phenotypic diversity ($\Delta\mu^*$) evaluated at the steady state as a function of straying rate m and trait heritability h^2. The descrete jump occurs as the system crosses the fold bifurcation; lower phenoytic diversity emerges with higher straying rates and in the alternative steady state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

selection will direct the mean trait values of both populations towards their respective optima, such that $\mu_i(t) \to \theta_i$ as $t \to \infty$. With the onset of straying, we find that increasingly divergent trait optima generally lower N_T and exaggerate ΔN (figure S5), 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 for 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 increases (figure 6a), reducing recovery time (figure S6). For increased rates of straying, greater habitat heterogeneity erodes the PE and increases the recovery time (figure 6a, figure S6) Taken together, habitat heterogeneity, as measured as the differences in trait optima between two habitats, promotes robustness when straying rates are low, but erodes robustness when straying rates are high.

(c) The effects of 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 due to the effects of collective decision-making [13] (Eq. 7). 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 importantly does not change

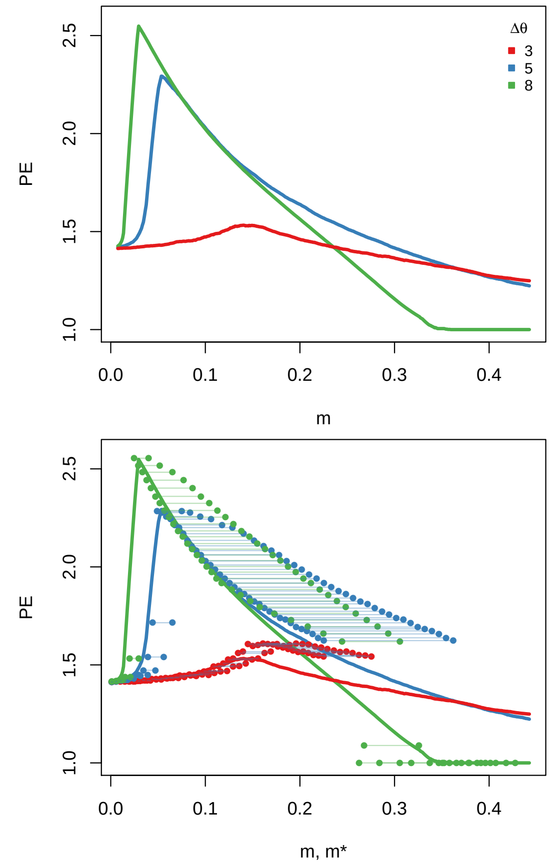

Figure 6: (a) Median portfolio effect as a function of stray rate m given heritability is $h^2 < 0.5$ for habitats with increasing heterogeneity as measured by the difference in regional trait optima $\Delta\theta$. (b) Median portfolio effects as shown in (a) are denoted by the solid lines. Point pairs 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. The different steady state regimes that give rise to the range of straying rates were obtained by varying the individual straying probability m_0 (where m_0 and m^* are linearly related).

the qualitative nature of our findings for constant straying rates. In the alternative stable state regime, because the 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 m_0, which is positively and linearly related to (m_i^*, m_j^*).

The recovery times for systems with constant and density dependent straying both show similar trends for a given m and m^* (figure 4c,d), however there are some distinct quantitative differences. When the straying rate and trait heritability are low, near-collapse of both populations result in longer than expected recovery times, whereas in the alternative stable state regime (higher m^*), the recovery times for different disturbance types are very similar to systems with a constant m (figure 4c; note difference in x-axis scales). There is greater similarity in the recovery times for constant and density dependent m systems when trait heritability is high.

As with recovery time, 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 6b). As such, the difference in m^* among low- and high-density populations appears to matter less than the straying generated by the high-density population. However, as m^* increases, we observe a higher PE than that generated by systems with constant m. This higher PE at increased m^* is mirrors recovery times that are also lower than those observed for systems with constant m (figure 4). Together this suggests that although density-dependent straying does not appear to change the 'dynamic landscape' in our minimal model, we do find evidence that it can promote robustness, particularly when populations are low and straying is correspondingly high.

(d) Distance dependent straying and habitat heterogeneity

We have so far treated $\Delta\theta$ and m as independent parameters, however we may also assume that if environmental heterogeneity increases with distance, the rate of straying may be expected to decline given that individuals will stray less into distant habitats. If we incorporate this interdependence of m and $\Delta\theta$, low rates of straying correspond to mixing dissimilar (distant) populations, and high rates of straying would correspond to mixing similar (nearby) populations.

Here we find that alternative stable states now appear for low straying rates ($m < 0.15$). As the straying rate increases, a single stable state emerges with a correspondingly high N_T. As before, there is a spike in the PE at the fold bifurcation separating the alternative stable state regime from the single stable state regime, and a sharp decline in the PE as the straying rate becomes very low. This is in accordance with intuition as increasing straying rates mean that two very similar populations are mixing, such that the rate of recruitment is less influenced by gene flow.

That alternative stable states appear and that PE becomes severely depressed for very low rates of straying is surprising: this means that even a small amount of mixing of populations from distant or dissimilar populations can qualitatively alter the dynamics of the metapopulation, regardless of trait heritability.

IV. DISCUSSION

We have shown that the natural selection of mixed populations adapted to different environments can result in large effects on population dynamics and the degree to which the metapopulation is buffered against extinction, quantified here as the portfolio effect. The immigration of dispersing strays with trait values far from the local optimum generally lowers the combined steady state biomass N_T and increases the likelihood that the system gives way to alternative steady states, pushing one of the populations close to extinction. Although the emergence of alternative steady states can result in very large portfolio effects near the bifurcation, alternative steady state regimes tend to result in very low portfolio effects, indicating that the metapopulation is less likely to persist in the long run.

The detectability of such changes in dynamical behavior among salmonids appears to be idiosyncratic across species, and the difficulty in measuring critical slowing down may - ironically - be masked by large portfolio effects [33] [this might be more appropriate for the discussion].

The degree to which the PE is lowered depends to a large extent on *i*) trait heritability h^2 and *ii*) habitat heterogeneity $\Delta\theta$. Increased heritability results in greater response to natural selection on the metapopulation, increasing the coupling between evolutionary and ecological dynamics. Our minimal model of straying between two populations shows that greater h^2 buffers the metapopulation against the emergence of alternative stable states, but magnifies the negative effects of alternative stable states (captured by increased ΔN and decreased PE; figure 3B,C) once this regime is encountered at higher straying rates. We note that although the rate of straying has been shown to be density dependent (REFS), the qualitative results of our model are relatively insensitive to this dynamic (figure **??**) and we limit discussion to the simplified case of a constant stray rate m with the understanding that our findings also apply to the case density dependent stray rates $m(t)$.

Trait heritability determines the coupling between ecological and evolutionary dynamics, effectively setting the strength of natural selection. Among salmon species, recruitment among local populations is highly sensitive to local climatic conditions, with temperature thought to play a central role (REFS). Populations distributed across a temperature gradient are assumed to be locally adapted to different temperature regimes, such that migration between them should take into account differential environmental effects on the recruitment of mixed populations. **(author?)** showed heritability 0.1-0.3. Our results show that trait heritability has large effects on both metapopulation persistance as well as phenotypic diversity, particularly in the regime of low-to-moderate straying rates.

Recovery times: largest perturbations lead to the longest recovery times [**?**]. This is not true in our

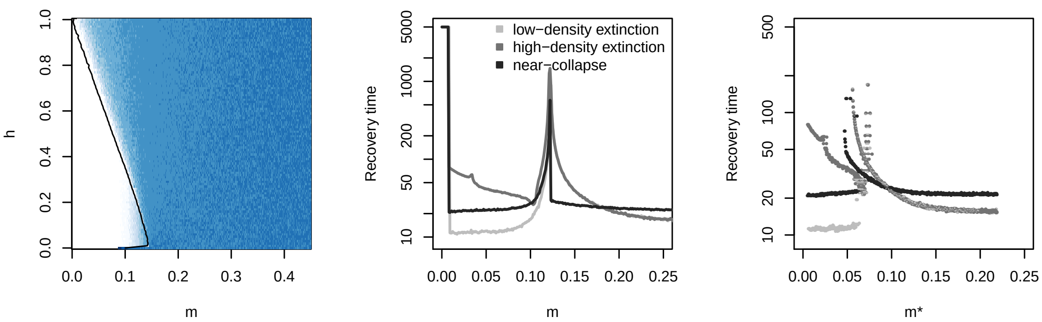

Figure 7: Assuming that the rate of straying is linked directly to habitat heterogeneity. A low stray rate corresponds to very different (or distant) habitats (high $\Delta\theta$), whereas a higher rate of straying corresponds to very similar (or nearby) habitats (low $\Delta\theta$). Light colors = high values.

systems when (*i*) heritability and (*ii*) straying are low. Why?

That recovery times and PE are similar for constant m vs. density dependent m suggests that both transient dynamics as well as asymptotic dynamics are not largely impacted.

[JP - could use some help here] The onset of alternative stable states in a spatial context describes the emergence of spatial pattern formation (REFS), which is more generally defined as a Turing instability (REFS). The mathematical conditions that lead to Turing instabilities are well-known in both continuous (REFS) and discrete spatial contexts (REFS)

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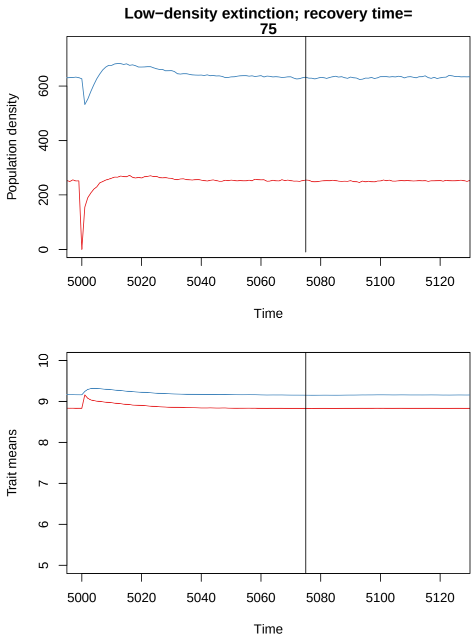

Figure S1: Extinction of low-density population with a high constant straying rate $m = 0.4$ and low trait heritability $h^2 = 0.2$ (see figure 4a). Black line marks the calculated point of recovery post-perturbation. Trait optima are $\theta_1 = 10$ (blue population trajectory) and $\theta_2 = 5$ (red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

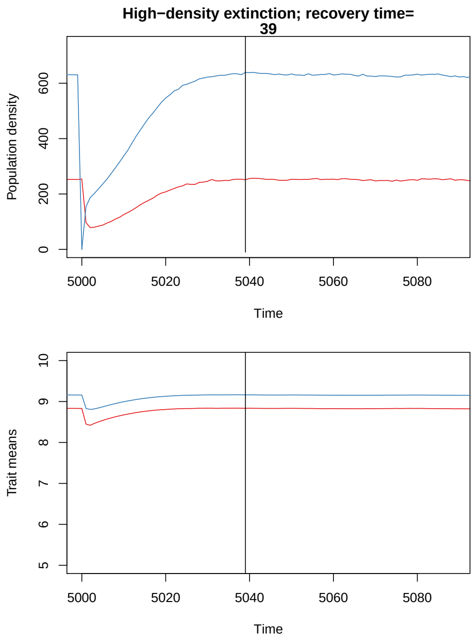

Figure S2: Extinction of high-density population with a high straying rate $m = 0.4$ and low trait heritability $h^2 = 0.2$ (see figure 4a). Black line marks the calculated point of recovery post-perturbation. Trait optima are $\theta_1 = 10$ (blue population trajectory) and $\theta_2 = 5$ (red population).

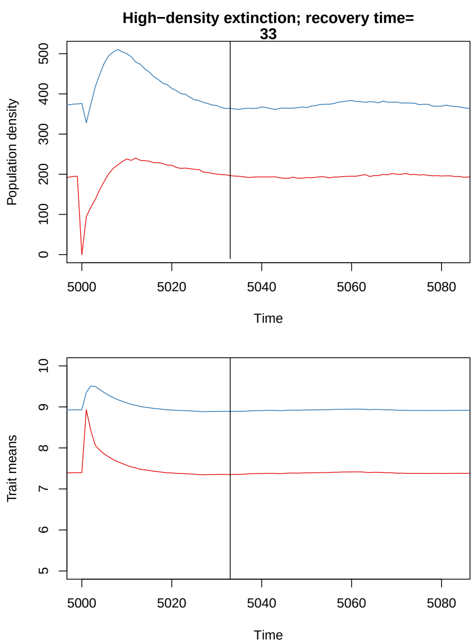

Figure S3: Extinction of low-density population with a high constant straying rate $m = 0.4$ and high trait heritability $h^2 = 0.8$ (see figure 4a). Black line marks the calculated point of recovery post-perturbation. Trait optima are $\theta_1 = 10$ (blue population trajectory) and $\theta_2 = 5$ (red population).

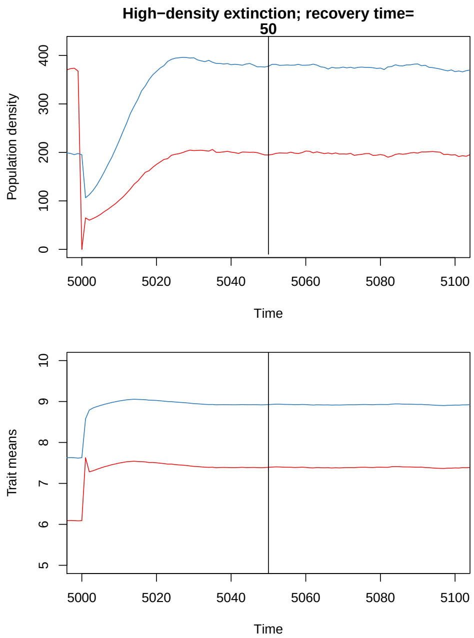

Figure S4: Extinction of high-density population with a high straying rate $m = 0.4$ and high trait heritability $h^2 = 0.8$ (see figure 4a). Black line marks the calculated point of recovery post-perturbation. Trait optima are $\theta_1 = 10$ (blue population trajectory) and $\theta_2 = 5$ (red population).

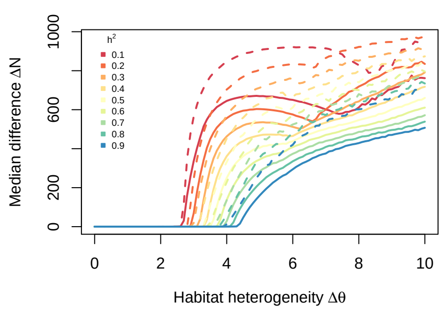

Figure S5: Median difference in population densities taken over the straying rate as a function of habitat heterogeneity $\Delta\theta$. Solid lines are for constant m; dashed lines are for density dependent m

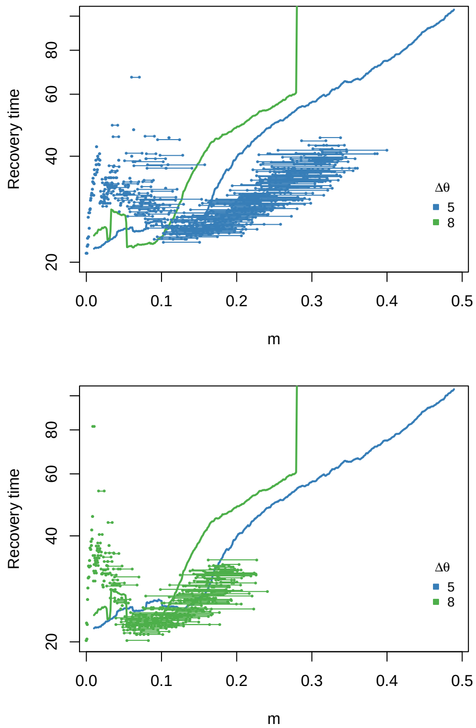

Figure S6: Recovery time as a function of straying rate m and habitat heterogeneity $\Delta\theta$.