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

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# 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 and also decrease the variability of processes that integrate across the metapopulation . For example, different responses to climate variability within populations of a rare plant reduced fluctuations in abundance . 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 . Strengthened portfolio effects are expected to increase the robustness of metapopulations to external disturbances, and by extension promote persistence . In contrast, homogenization of populations that leads 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. Permanent movement of individuals among local populations (i.e., dispersal) can also have a large influence on metapopulation persistence . First, dispersal facilitates evolutionary rescue, whereby immigration of individuals with heritable adapative traits can rescue small populations from local extinction in the context of maladaptive environmental change. On the other hand, high rates of dispersal may synchronize populations and actually increase the risk of extinction of the entire metapopulation . Although the disperasl of individuals into sites hosting other populations provides connections within the larger metapopulation, potentially promoting demographic and evolutionary rescue, it may also introduce maladapted individuals into habitats that are host to different environmental conditions, possibly lowering the mean fitness of the recipient population . More broadly, dispersal can provide a mechanism by which phenotypes are sorted in space rather than time and facilitates the spread of maladaptive genes (Lowe et al. 2015) 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 anthrpogenic factors can control the rate of dispersal among populations . 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, , may be linked to errors made at an individual-level that are themselves diminished by migrating in groups and pooling individual choices . 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 . That evolutionary forces of selection and gene flow play out heterogeneously across geographic mosaics is now a foundational concept in ecology and evolutionary biology . These mosaics are in part driven by environmental differences between habitats that alter the selective forces acting on different phenotypes , and a principle underlying assumption is that there is gene flow such that individuals from different habitats mix over space . 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 as they unfold .

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 reknown for returning to their natal spawning habitats with high accuracy and precision after years at sea , there are generally some individuals that ‘stray’ to non-natal sites to spawn . Salmon may operate as metapopulations, where populations are genetically distinct but linked by some level of straying . Although extensive work has been done to document the extent of straying from donor populations and into recipient populations , only recently have the abiotic, biotic, and anthropogenic influences of ‘straying’ behaviors been investigated systemically . Straying among salmon may be influenced by environmental factors such as water temperature, human activities such as hatchery practices, and population density as predicted by the collective migration hypothesis . These strays can introduce new maladaptive genotypes into the recipient population. Further, straying and genetic homogenization could synchronize population dynamics and erode portfolio effects. Thus, there is opportunity 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 different stray rates, levels of environmental heterogeneity, and the influence of collective movement. This model enables us to explore the multiple and potentially opposing pathways by which straying influences metapopulation robustness such as potentially detrimental erosion of local adaptation, positive effects of demographic rescue, and population synchronization.

[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 metapopulations.]

# Model Description & Analysis

**(a) Metapopulation framework**  
We consider two populations and that inhabit two distinct habitats, each with trait values and determing recruitment rates. We assume that there is an optimum trait value and associated with each habitat, where recruitment is maximized if the trait value of the local population equals the optimum, such that . Moreover, we assume that are normally distributed with means and and have the same standard deviation . As such, the recruitment rate for both populations is determined by the mean trait value of the local population, such that . 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 .

The two populations are assumed to reproduce in spatially separate sites that are close enough such that a proportion of the population 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 , and the recruitment rate for that population will be maximized. If there is straying between populations at rate , then the traits in each respective location will be pulled away from the optimum, and recruitment rates will be lowered. As , the populations are perfectly mixed, acting as a single population.

![ 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. ](data:application/pdf;base64,)

A) The steady state densities of and as a function of a constant stray rate . 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 , as a function of a constant stray rate . FB marks the fold bifurcation.

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

$$\begin{aligned} &N\_i(t+1) = \\ \nonumber &\left((1-m)N\_i(t) + m N\_j(t) \right){\rm e}^{-Z} \\ \nonumber &+ \left(R\_i[\mu\_i(t)] (1-m)N\_i(t) + R\_i[\mu\_j(t)] m N\_j(t)\right) \\ \nonumber &\times {\rm e}^{-\beta ((1-m)N\_i(t) + m N\_j(t))}, \label{eq:N}\end{aligned}$$

where the difference equation for mirrors that for .

The recruitment of local individuals as a function of their mean trait value at time and the local trait optimum, is

$$\begin{aligned} &R\_i[\mu\_i(t)] = \\ \nonumber &\int\_{-\infty}^\infty r\_{\rm max}\exp\left\{\frac{(x\_i(t)-\theta\_i)^2}{2\tau^2}\right\} {\rm pr}(x\_i(t),\mu\_i,\sigma^2) {\rm d}x\_i(t) +\tilde{P}\\ \nonumber &= \frac{r\_{\rm max} \tau }{\sqrt{\sigma ^2+\tau ^2}}\exp\left\{-\frac{(\theta\_i-\mu\_i(t))^2}{2 \left(\sigma ^2+\tau ^2\right)}\right\} +\tilde{P}, \label{eq:R}\end{aligned}$$

where the mismatch between the local trait mean and the local optimum scales the recruitment rate for the population, and $\tilde{P}\sim {\rm Normal}(0,0.01)$ introduces a small amount of demographic error. The parameter 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 ), which we set as 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 .

![image](data:application/pdf;base64,)

Because we assume that 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, , and for the straying individuals, , where

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. This assumption is supported by patterns in nature Second, we assume that changes in trait variance through time are minimal, such that is assumed to be constant, and this is a common simplification in eco-evolutionary models of population dynamics .

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

where the first two factors determine the mixed normal average of the aggregated local and remote populations. The partial derivative in the Eq. [eq:mu] determines how the mean trait changes through time due to natural selection , which is proportional to the change in mean fitness with respect to .  
**(b) Measuring metapopulation robustness** We evaluated metapopulation robustness by measuring the average-CV portfolio effect (PE) 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

$$\langle{\rm PE}\rangle =\frac{1}{X}\sum\_{i=1}^{X} \frac{\sqrt{{\rm VAR}(N\_i)}}{{\rm E}(N\_i)}\cdot \frac{{\rm E}(N\_T)}{\sqrt{{\rm VAR}(N\_T)}}, \label{eq:pe}$$

where in this case the number of populations is limited to and the expectations $\rm E(\cdot)$ and variances $\rm VAR(\cdot)$ are evaluated at the steady state. As the CV of decreases relative to that of the constituent populations, $\langle{\rm PE}\rangle > 1$, and the metapopulation is presumed to become more stable. Portfolio effects greater than unity corresponds to less synchronization 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 ) 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 , 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 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. We measured the time required for the system 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.  
**(c) The effects of collective movement 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 mounting evidence that at least in some species (including salmon) the straying rate is density dependent with a signature of collective navigation . 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. , given the probability that an individual strays is , the proportion of the local population that strays is

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

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 . We account for this interdependence in our model by assuming that (if the stray rate is constant) or (if the stray rate is density dependent) is a function of the difference between optimal trait values between sites , which can be assumed to be large if the remote site is a great distance away from the local site . If sites and are very close, the stray rate is maximized at $m\_{\rm max} = 0.5$, assuming both sites are equally attractive to the respective populations. Thus, we can integrate these two variables by setting $m,m\_0 = (1/m\_{\rm max} + \epsilon (\theta\_i-\theta\_j))^{-1}$, where sets the sensitivity of a declining to increasing distance (greater values of ).

# Results

![ (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. ](data:application/pdf;base64,)

(a) Median portfolio effect as a function of a constant stray rate (solid line) and density dependent stray rate (point pairs) given heritability is and . 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 for both constant and density dependent stray rates as shown in (a). FB marks the fold bifurcation.

**(a) Nonlinear effects of straying on the portfolio effect and recovery time**  
Taken as a whole straying (both density indepednet and dependent) 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. [fig:traj]). This prediction is in accordance with observations from natural populations . 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 [fig:traj]a, [fig:PE]a). Mean trait values for both populations bifurcate similarly (figure [fig:traj]b), depending on which population attains a low- 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.

![image](data:application/pdf;base64,)

Trait heritability has a large impact on the degree to which straying rate affects both the aggregate population steady state density (; figure [fig:PE]a) as well as the difference between steady state densities (the distance between alternative stable states: ; figure [fig:PE]b). Greater trait heritability results in a faster decline in with increasing straying rates , but leads to only moderate changes to . 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 . The fold bifurcation (the black line in Figs. [fig:PE]a-c) occurs at lower values of the straying rate with decreased trait heritability (Fig [fig:PE]a,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 estimates of life-history traits have an , and we largely focus additional analyses on that range.

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

If we assume that the rate of straying is density dependent, the probability that an individual strays determines the rate of straying within the population, such that becomes lower as increases, likely due to the effects of collective decision-making (Eq. [eq:ddm]). Density dependence alters the straying rate at steady state population densities because , 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 : 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 values by varying the probability that an individual strays , which is positively and linearly related to . 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 ) population is the same as that for a system with a constant (figure [fig:thetaPE]a). As increases, we observe an increase in the PE than for systems with constant .

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 [fig:PE]d), 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 [fig:relax]a) because the surviving population has a mean trait value skewed towards the optimum for that environment (figure [fig:relaxtraj\_hdlh]). Yet, as straying increases, recovery time for the disturbed dominant state population increases, in part because immigrants from the subordinate population pull the trait distribution away from the local optima. 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 population extends the length of time required for it to return to its steady state (figure [fig:relaxtraj\_ldlh]). 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 .

Density-dependent straying alters these recovery times (figure [fig:relax]b). First, in comparison with constant stray 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 ), the recovery times for different disturbance types were very similar to systems with a constant (figure [fig:relax]b; note difference in x-axis scales). As trait heritability increased, the metapopulation always recovered more quickly if the small population was lost (figure [fig:relax\_highh]). The lower recovery time for systems with increased mirrors an elevated PE with higher density dependent straying rates (figure [fig:PEtheta]). 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.

![ 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. ](data:application/pdf;base64,)

Phenotypic diversity () evaluated at the steady state as a function of straying rate and trait heritability . 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.

Increased rates of straying lowers phenotypic diversity (, 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 [fig:traitdiff]). 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 () 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 as . With the onset of straying, we find that increasingly divergent trait optima generally lower and exaggerate (figure [fig:thetadiffN]), 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 [fig:thetaPE]b), reducing recovery time (figure [fig:relaxtheta]). For increased rates of straying, greater habitat heterogeneity erodes the PE (figure [fig:thetaPE]b) and increases the recovery time (figure [fig:relaxtheta]). These results together suggest that habitat heterogeneity, as measured as the differences in trait optima between two habitats , promotes robustness when straying rates are low, and erodes robustness when straying rates are high.  
**(c) Distance dependent straying and habitat heterogeneity**  
We have so far treated and as independent parameters, however we may also assume that if environmental heterogeneity increases with distance between sites, the rate of straying may be expected to decline with habitat heterogeneity, given that individuals will stray less into distant habitats. Alternatively, individuals may be less likely to stray into very different habitats due to the influence of environmental cues on individual decision-making (REFS?). If we incorporate this interdependence of and , low rates of straying correspond to mixing dissimilar (distant) populations, and high rates of straying correspond to mixing similar (nearby) populations.

We find that alternative stable states now appear for very low rates of straying and correspondingly greater habitat heterogeneity (given ). As the straying rate increases, a single stable state emerges as the fold bifurcation is crossed. As straying continues to grow into the single steady state regime, the time required for recovery following extinction of either population declines (to the right of figure [fig:mtheta]) because populations are more similar to each other. However, as straying decreases the system crosses the fold bifurcation, entering the alternative steady state regime (to the left in figure [fig:mtheta]). At low rates of straying, there is a small amount of mixing between dissimilar (distant) populations. Here we find that if the subordinate population is wiped out, the time to recovery is minimized, whereas if the dominant population is wiped out, the time to recovery is maximized; near-collapse of both results in intermediate recovery times.

When straying rates are low (<ca. 0.10) and the difference in trait optima are correspondingly high (theta values?), we might assume that extinction of the dominant population would result in relatively faster recovery. This would be a logical assumption because the mean trait value of the subordinate population would be skewed towards that of the dominant (larger) population, such that recruitment at the disturbed site should be high and the population should recovery more quickly. Our results show, however, that *this assumption is wrong:* although the mean trait value of the subordinate population *is* skewed towards the optimum of the dominant population, when the latter is wiped out and the rate of straying is low, there is enough time and isolation for the subordinate trait mean to shift towards its own optimum, and away from that of the recovering dominant population (figure [fig:inertia]). This *selective inertia* occurs until the dominant population grows large enough that the evolving subordinate phenotype is overwhelmed by incoming strays, shifting it back to its pre-disturbance (subordinate) state. This effect can lead to much longer recovery times for the dominant population. Importantly, if the rate of straying is below a threshold value, it can also result in a state-switch, wherein increased isolation permits the subordinate population to *escape* the selective pull of the dominant population, leading to a switching in which population is in the dominant/subordinate state. This threshold value of , below which this behavior occurs, is marked by the asterisk in figure [fig:mtheta], and holds for both constant and density dependent straying (figure [fig:mthetamvm]).

![ 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. ](data:application/pdf;base64,)

Distance dependent recovery times for three disturbance types. When straying is distance dependent, increases as decreases. The ‘’ marks the value of below which there is a switch in subordinate/dominant states following extinction of the dominant population. FB marks the fold bifurcation.

# 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 , 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 to return to its steady state following an induced disturbance, which is mechanistically linked to persistence . In our minimal eco-evolutionary model of collective dispersal and natural selection between two populations, we show that these phenomenological and mechanistic descriptors of metapopulation dynamics and robustness are tightly coupled (figure [fig:PE]d). Taken as a whole, we interpret our results to suggest an important role of density-dependent straying in the colonization and recovery dynamics 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.

[This paragraph is interesting to me but could be cut] Although the portfolio effect is negatively correlated with recovery time, there is one exception: the point of transition from a single steady state to alternative steady states, which occurs at the fold bifurcation (REF). At this point, the portfolio effect is maximized, but so is the recovery time (figures [fig:PE], [fig:relax]). This suggests that while the sharply increasing variance of the individual populations is dampened by aggregation, a large disturbance will have a much greater adverse effect due to exponentially longer recovery times. Whether the change in variance, also known as critical slowing down, as the alternative steady state regime is approached could be used as an early warning signal of an oncoming phase transition is a hotly debated topic (REFS). The detectability of such changes in dynamical behavior among salmonids appears to be idiosyncratic across species, though the difficulty in measuring critical slowing down may - ironically - be masked by large portfolio effects .

A salient finding from our results was that straying can push metapopulations into alternative steady states, where one of the populations tends towards a high-density population (the *dominant state; straying source?*), and one to a low-density population (the *subordinate population; straying sink?*). This asymmetry in population densities also leads an asymmetry in the mean trait values, skewed towards the local optimum of the dominant population. The formation of alternative stable states in our system is an example of spatial pattern formation, which only occurs above a threshold straying rate of approximately X% in our model. Pattern formation can occur as a consequence of myriad ecological processes, including habitat selection (REFS), aggregation (REFS), local environmental conditions (REFS), and/or interspecific interactions such as competition or predation(REFS), and is inexorably linked to scale (Reviewed by Levin 1992). Additionally, pattern formation is also well known to occur with the onset of spatially or diffusion-induced instabilities (Turing instabilities, REFS). 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 that results in alternative steady states across sites. While metapopulation approaches have widely recognized the importance of source and sink populations (REFS), here we discover that even similar populations can evolve into diverge states where one population is large while the other populations is smaller and maladapted.

There appears to be a sweet spot for straying that can maximize metapopulation robustness. The presence of *just enough* straying to cause formation of alternative stable states both increases the portfolio effect (figure [fig:PE]c) and increases recovery rate. Density-dependent straying appears to increase metapopulation robustness across a range of stray rates(figures [PEtheta]a, [fig:relax]b).

In terms of relative biomass lost, the largest perturbation that we investigate is the near-collapse of both populations, where only 1% of the pre-perturbation densities survive, however whether this disturbance results in the longest recovery time depends largely on the rate of straying and trait heritability. For example, when straying and trait heritability are low (figure [fig:relax]) the extinction of the larger population maximizes return times, whereas if straying is high, near-collapse maximizes return time. The latter is always true in the alternative stable state regime if trait heritability is high (figure [fig:relax\_highh]).

This themed issue formalizes a 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, density-dependent straying reduces the time to recovery following an induced disturbance, and this is particularly true in the case of near-collapse of both populations (figure [fig:relax]b). This dynamic emerges although both populations are near-collapse, and the mean trait values of both are scewed towards those of the dominant population, the straying rates are also higher because of the low-densities after collapse, and this permits faster recovery (figure [fig:relaxtraj\_bothlh]). Second, density dependent straying increases the portfolio effect when the steady-state straying rate is at an intermediate level (for both low- and high-density populations). This finding is at odds with previous theoretical work on density dependent straying in herring populations, showing that the PE is lowered with increased connectivity, but did not include natural selection of local phenotypes . Third, while habitat heterogeneity is interpreted here in elevating the difference in trait optima between sites, it both increases the portfolio effect and lowers recovery time at low rates of straying, but has the opposite effect at higher rates of straying. Surprisingly, we find that density dependent straying both exaggerates the negative effects when is low (marginally lower portfolio effects, but substantially longer return times; figures [fig:thetaPE]b, [fig:relaxtheta]a,b) and exaggerates the positive effects when is high (higher portfolio effects, and shorter return times).

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 . Our surrogate measure for habitat heterogeneity is the difference in trait optima between sites . 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 [fig:thetaPE]b, solid lines). This may be particularly consequential for populations that are spatially adjacent but separated by sharp environmental boundary, 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-produce 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 . 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

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(REF). Correspondingly, it is reasonable to expect a larger number of straying individuals between sites that are geographically proximate and indeed evidence corroborates this prediction . Alternatively, salmon that cue to specific environmental conditions may be more likely to stray into sites that have structurally and physiognamically similar habitats (REFS) even if other potential sites are closer. These considerations justify imposing a direct relationship between the rate of straying 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 subordinant 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 [fig:mtheta]). This may have particular conservation implications for considerations of aiding dispersal following disturbances or reconnections of lost habitats.... Moreover, local temperature regimes are known to play a central role in dictating local adapation of salmon populations (REFS). If temperature is the primary determinant of in terms of our model, this would suggest that populations spanning North-South gradients are more predisposed to distance dependent dynamics. In constrast, 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. (Bristal Bay vs. California???)

Our model is a simple framework for an initial consideration of the eco-evolutionary dynamics of metapopulation and accordingly made assumptions that are important to clarify. First, our model did not consider the role of straying and dispersal in introducing new genetic material that can combat genetic challenges of small populations such as inbreeding. Second, our model did not incorporate the potential genetic underpinnings of response diversity and asynchrony. We anticipate that including a link between genetic divergence and population stochasticity would exacerbate the rate at which higher straying would synchronize populations. Third, our model assumed that strays were incorporated into the trait distribution of the recipient populations—in natural systems it is possible that strays may die prior to reproduction when the two habitats are highly divergent. Fourth, natural systems are quite temporally? variable, which could push systems out of steady-state dynamics, which is what our model focused on. Fifth, we focused on an extremely simple system of two linked populations. While more linked populations would introduce additional complexity, we predict that our qualitative results would apply to more complicated systems. It is clear that understanding the eco-evolutionary dynamics of metapopulations is a rich area for further research.

Although our study was inspired by salmon metapopulation systems yet we suggest that our results have important implications for the conservation and management of salmon and potentially for other migratory metapopulations as well. First, we find that high stray rates generally decrease the robustness of metapopulations through both ecological and evolutionary processes. Thus, human activities that alter straying rates could have unintended consequences. For example, salmon produced by hatcheries often stray into proximate wild populations . Wild populations with more strays generally have lower fitness likely due in part to the introduction of maladapted genes (). Further, hatchery production could erode asynchrony and portfolio effects in wild salmon meta-populations (Carlson et al. , Moore et al. ). Alternatively, salmon stocking to try to speed up recovery times following dam removal could actually decrease recovery over longer time scales. Ongoing examinations of experimental restocking in the recently re-opened Elwha River (Washington State) will provide empirical insight into the potential short- and long-term consequences of facilitated recovery (REF). More generally, the current attributes and resilience of salmon metapopulations are likely a function of their history of evolving in dynamic river systems that periodically went through massive disturbances such as landslides, glaciers, and floods over different climatic regimes (Waples et al. 2009; Waples et al. 2008). Given a massive disturbance that would reduce the numbers and extent of salmon, density-dependent straying would enable the small remaining population to rapidly recolonize across space via high straying rates. As population numbers increase and stray rates decrease, the metapopulation could achieve higher production due to fine-scale local adaptation unhindered by high rates of maladaptive strays. Indeed, we found that density-dependent migration appears to increase the robustness of metapopulations faced with large-scale disturbance. While collective migration is thought to be an emergent property based on individual decision-making, it may actually enable robust metapopulations in dynamic and disturbed environments. Indeed our results indicate that 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.

![ Extinction of low-density population with a high constant straying rate m=0.4 and low trait heritability h^2=0.2 (see figure [fig:relax]a). 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). ](data:application/pdf;base64,)

Extinction of low-density population with a high constant straying rate and low trait heritability (see figure [fig:relax]a). Black line marks the calculated point of recovery post-perturbation. Trait optima are (blue population trajectory) and (red population).

![ Extinction of high-density population with a high straying rate m=0.4 and low trait heritability h^2=0.2 (see figure [fig:relax]a). 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). ](data:application/pdf;base64,)

Extinction of high-density population with a high straying rate and low trait heritability (see figure [fig:relax]a). Black line marks the calculated point of recovery post-perturbation. Trait optima are (blue population trajectory) and (red population).

![image](data:application/pdf;base64,)

![ 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](data:application/pdf;base64,)

Median difference in population densities taken over the straying rate as a function of habitat heterogeneity . Solid lines are for constant ; dashed lines are for density dependent

![image](data:application/pdf;base64,)

![ 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. ](data:application/pdf;base64,)

Distance dependent portfolio effects as a function of straying rate and trait heritability . When straying is distance dependent, increases as decreases.

![ 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 [fig:mtheta]), 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. ](data:application/pdf;base64,)

Distance dependent straying, where increased differences in trait optima between sites corresponds to lower rates of straying . At low rates of straying (), 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, is less than (denoted by the asterisk in figure [fig:mtheta]), such that isolation allows the subdominant population to ‘run away’ from the influence of the dominant population, leading to a switch in states. If is low but greater than , 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.

![image](data:application/pdf;base64,)

![ Near collapse of both populations with a low straying rate m=0.1 and low trait heritability h^2=0.2 (see figure [fig:relax]a). 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). ](data:application/pdf;base64,)

Near collapse of both populations with a low straying rate and low trait heritability (see figure [fig:relax]a). Black line marks the calculated point of recovery post-perturbation. Trait optima are (blue population trajectory) and (red population).