

Managing emergent recovery dynamics in at-risk metapopulations

Supplemental materials: Model details & results

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Metapopulation model

Local & metapopulation dynamics

Our metapopulation was defined by a set of P local populations for a species with a one year generation time with time-dynamics that follows birth (i.e., recruitment R), immigration, death, and emigration processes typical to metapopulation theory and tested the role of multiple spatial, temporal, and density-dependent processes (Anderson et al. 2015; Fullerton et al. 2016; Zelnik et al. 2019; Bowlby & Gibson 2020; Okamoto et al. 2020):

$$N_{i,t} = R_{i,t} + \sum_{\substack{j=1 \\ j \neq i}}^P \omega p_{i,j} R_{j,t} - d_{i,t} R_{i,t} - \omega R_{i,t} \quad (\text{S.1})$$

where $N_{i,t}$ was the number of adults in patch i at time t , $R_{i,t}$ was the number of recruits at time t , $\sum_{\substack{j=1 \\ j \neq i}}^P \omega p_{i,j} R_{j,t}$ was the number of recruits immigrating into patch i from any other patch, ω was the proportion of local recruits to disperse, $p_{i,j}$ was a distance-dependent dispersal function, and $d_{i,t}$ was the proportion of recruits that die due to disturbance regime.

Local patch recruitment at time t depended on adult densities at $t-1$ and followed a reparameterized Beverton-Holt function (Walters & Martell 2004; Forrest et al. 2010):

$$R_{i,t} = \frac{\alpha_i N_{i,t-1}}{1 + \frac{\alpha_i - 1}{\beta_i} N_{i,t-1}} \epsilon_{i,t} \quad (\text{S.2})$$

where α_i was the recruitment compensation ratio, β_i was local patch carrying capacity, and $\epsilon_{i,t}$ was lognormally distributed deviates to introduce stochastic recruitment dynamics.

Resource monitoring often occurs at the scale of the whole metapopulation by aggregating abundances among local populations to (Anderson et al. 2015; Moore et al. 2021), hence we define metapopulation adults as:

$$A_t = \sum_{i=1}^P N_{i,t} \quad (\text{S.3})$$

with metapopulation recruits:

$$K_t = \sum_{i=1}^P R_{i,t} \quad (\text{S.4})$$

Monitoring at the scale of the whole metapopulation can produce productivity relationships that aggregates the population dynamics and productivity among all local populations. For example, take a two patch metapopulation model that varies $\alpha_1 = 2$; $\alpha_2 = 4$ and $\beta_1 = 100$; $\beta_2 = 200$ parameters. Here, recruitment compensation from local patches α_i gets averaged across the metapopulation leading to an average compensation ratio $\bar{\alpha}$ of 3. Likewise, the total carrying capacity of the metapopulation $\bar{\beta}$ becomes the summation of local patch carrying capacities $\sum \beta_i$, which was 300. This scale of monitoring generates the following local patch and metapopulation dynamics:

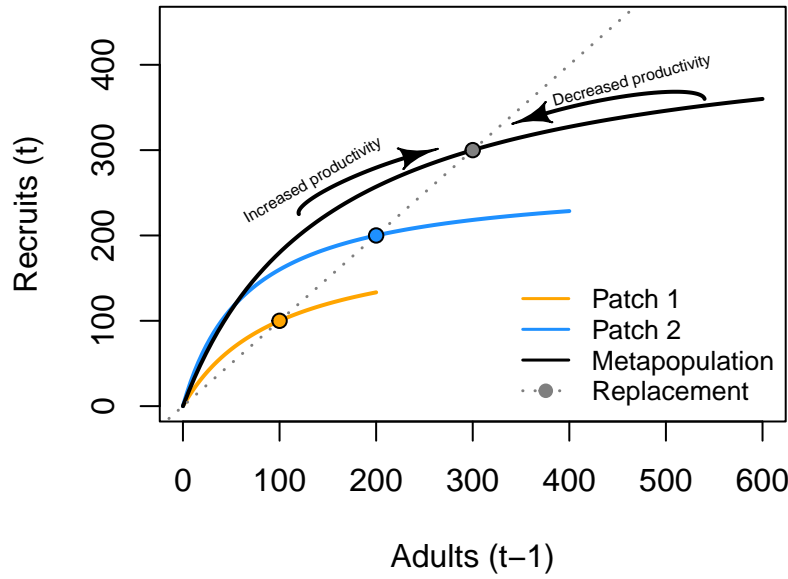


Figure S1: Density dependence in metapopulation and local patch recruitment dynamics. Dashed line indicates the line of replacement, with equilibrium indicated by points. When populations fall below equilibrium points, per-capita productivity improves driving populations back towards equilibrium. When populations exceed their capacity, per-capita productivity decreases driving populations back towards equilibrium. At each point of the x-axis, the distance between the solid and dashed lines indicates the amount of recruitment above replacement, i.e., the surplus recruitment produced via compensatory density dependence.

Creating the spatial networks

The next aspect to our metapopulation model was connecting the set of patches to one another (Yeakel et al. 2014). We need to specify the number of patches, their arrangements (i.e., connections), and how far apart they are from one another. We followed some classic metapopulation and source-sink arrangements to create four networks that generalize across a few real-world topologies: a linear habitat network (e.g., coastline), a dendritic or branching network (e.g., coastal rivers), a star network (e.g., mountain & valley, or lake with inlet tributaries), and a grid network (e.g., grasslands).

To make networks comparable, each spatial network type needs the same leading parameters (e.g., number of patches P and mean distance between neighboring patches \bar{d}). In this case, we set P to 16 and \bar{d} to 1 unit (distance units are arbitrary). We used the `igraph` package (Csardi & Nepusz 2006) and some custom code to arrange our spatial networks as the following:

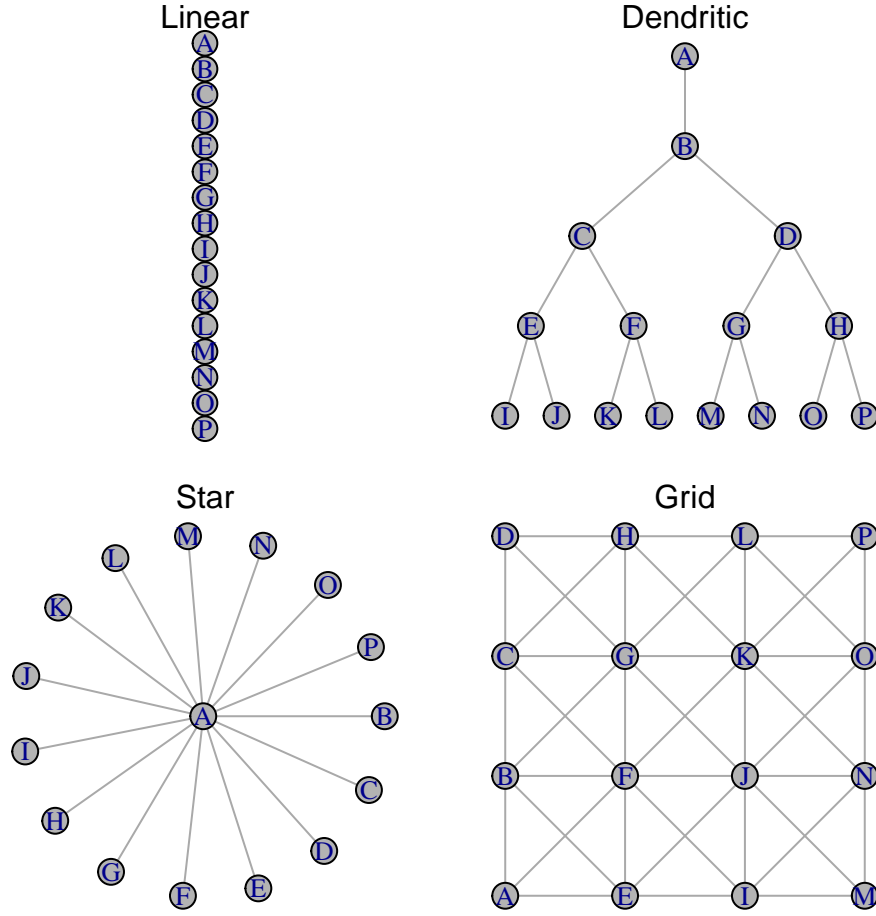


Figure S2: Four spatial network topologies.

57 Note that distances between neighbor patches in the above networks are equal. An example dispersal matrix for
 58 the grid network can be found in Table S1.

59 Dispersal

60 Dispersal from patch i into patch j depends on constant dispersal rate ω (defined as the proportion of total local
 61 recruits that will disperse) and an exponential distance-decay function between i and j with distance cost to
 62 dispersal m (Anderson et al. 2015; Fullerton et al. 2016):

$$E_{i,j,t} = \omega R_{i,t} p_{i,j} \quad (\text{S.5})$$

63 where $E_{i,j}$ was the total dispersing animals from patch i into patch j resulting from dispersal rate ω , total number
 64 of local recruits $R_{i,t}$, and probability of dispersal between patches $p_{i,j}$:

$$p_{i,j} = \frac{e^{-md_{i,j}}}{\sum_{\substack{j=1 \\ j \neq i}}^P e^{-md_{i,j}}} \quad (\text{S.6})$$

65 where $d_{i,j}$ was the pairwise distance between patches, m was the distance cost to dispersal. The summation term in

Table S1: Example distance matrix between patches within a grid network to affect dispersal rates.

	A	B	E	F	C	G	D	H	I	J	K	L	M	N	O	P
A	0	1	1	1	2	2	3	3	2	2	2	3	3	3	3	3
B	1	0	1	1	1	1	2	2	2	2	2	2	3	3	3	3
E	1	1	0	1	2	2	3	3	1	1	2	3	2	2	2	3
F	1	1	1	0	1	1	2	2	1	1	1	2	2	2	2	2
C	2	1	2	1	0	1	1	1	2	2	2	2	3	3	3	3
G	2	1	2	1	1	0	1	1	2	1	1	1	2	2	2	2
D	3	2	3	2	1	1	0	1	3	2	2	2	3	3	3	3
H	3	2	3	2	1	1	1	0	3	2	1	1	3	2	2	2
I	2	2	1	1	2	2	3	3	0	1	2	3	1	1	2	3
J	2	2	1	1	2	1	2	2	1	0	1	2	1	1	1	2
K	2	2	2	1	2	1	2	1	2	1	0	1	2	1	1	1
L	3	2	3	2	2	1	2	1	3	2	1	0	3	2	1	1
M	3	3	2	2	3	2	3	3	1	1	2	3	0	1	2	3
N	3	3	2	2	3	2	3	2	1	1	1	2	1	0	1	2
O	3	3	2	2	3	2	3	2	2	1	1	1	2	1	0	1
P	3	3	3	2	3	2	3	2	3	2	1	1	3	2	1	0

the denominator normalizes the probability of moving to any patch to between 0 and 1 with the constraint that dispersers cannot move back into their home patch (i.e., $j \neq i$. With $\bar{d} = 1$, $m = 0.5$, $\omega = 0.1$, $R_{i,t} = 100$ in a linear network):

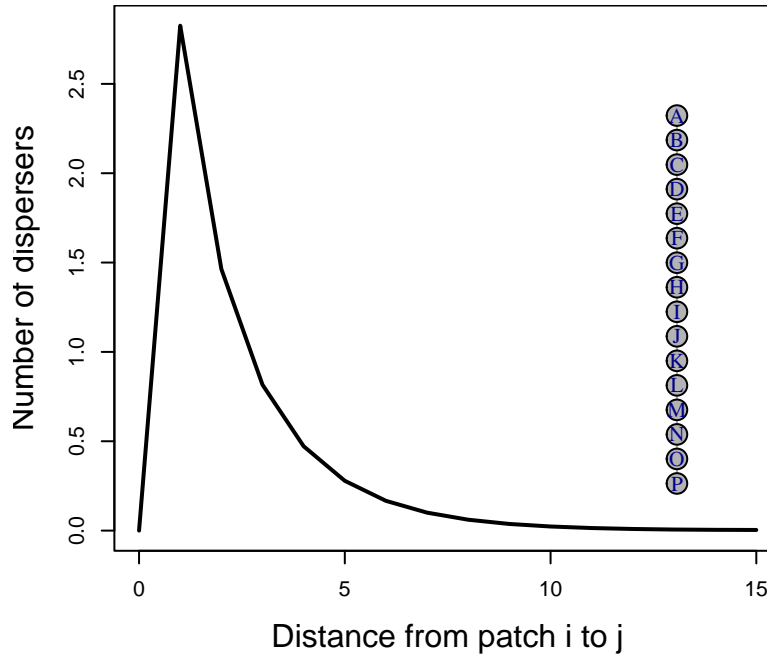


Figure S3: Example dispersal patterns across linear network.

Disturbance regimes

In all scenarios, disturbance was applied after 50 years of equilibrating the metapopulation at pristine conditions. We then applied the disturbance regime at year 50 (the regime varied from *uniform*, *localized*, *even*, and *localized, uneven* - see *Scenarios* below). Disturbance immediately removed a fixed proportion of the metapopulation adults

at that time (i.e., 0.9 of $A_{t=50}$). Once applied, the metapopulation was no longer disturbed and spatio-temporal recovery dynamics emerged from these conditions given the ecological scenarios of network complexity, dispersal rate, spatio-temporal correlations, local patch demographics, and magnitude of stochastic variance.

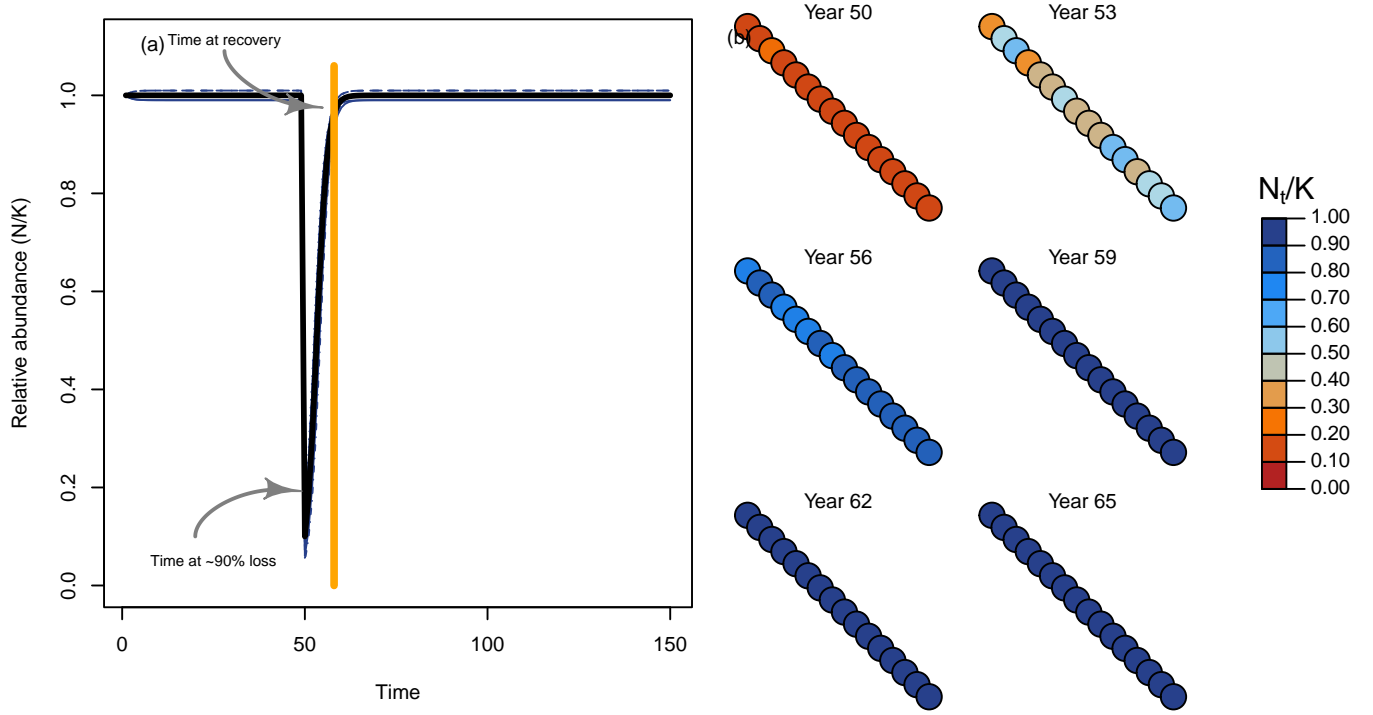


Figure S4: Recovery regime of metapopulation with linear topology through time (a) and space (b).

Recruitment stochasticity

Our model allowed for stochastic recruitment that followed a lognormal distribution with average variation in recruitment of σ_R . In cases with stochastic recruitment, the deterministic recruitment in eq. S.4 becomes:

$$R_{i,t} = \frac{\alpha_i N_{i,t-1}}{1 + \frac{\alpha_i - 1}{\beta_i} N_{i,t-1}} e^{(\epsilon_{i,t} - \frac{\sigma_R^2}{2})} \quad (\text{S.7})$$

where lognormal deviates for each patch i at time t were drawn from a multivariate normal distribution (MVN) with bias correction $\frac{\sigma_R^2}{2}$. If σ_R was low, then metapopulation dynamics approach the deterministic case. In some scenarios, we evaluated the role of spatially and/or temporally correlated deviates among local patches to model potential common drivers affecting metapopulation dynamics (e.g., Moran effects). Expected recruitment deviates followed a first-order autoregression model such that:

$$\epsilon_{i,t} = \rho_T \epsilon_{i,t-1} + MVN(\mu = 0, \Sigma = \sigma_R^2 (1 - \rho_T^2) e^{(-\rho_S D_{i,j})}) \quad (\text{S.8})$$

where ρ_T was temporal correlation (bounded 0 – 1) and ρ_S was rate of distance-decay in spatial correlation (bounded 0 – ∞ with higher values leading to independent patches). If ρ_T was 0 and ρ_S was high, then annual recruitment deviates were independent. We modelled the initial conditions for autoregressive recruitment deviates

$\epsilon_{i,1}$ by drawing from a stationary normal distribution with mean $\mu = 0$ and variance σ_R^2 such that:

$$\epsilon_{i,1} \sim N(\mu = 0, \sigma = \sigma_R) \quad (\text{S.9})$$

84 We illustrate the effects of four kinds of recruitment deviates below using the same random number generator seed:

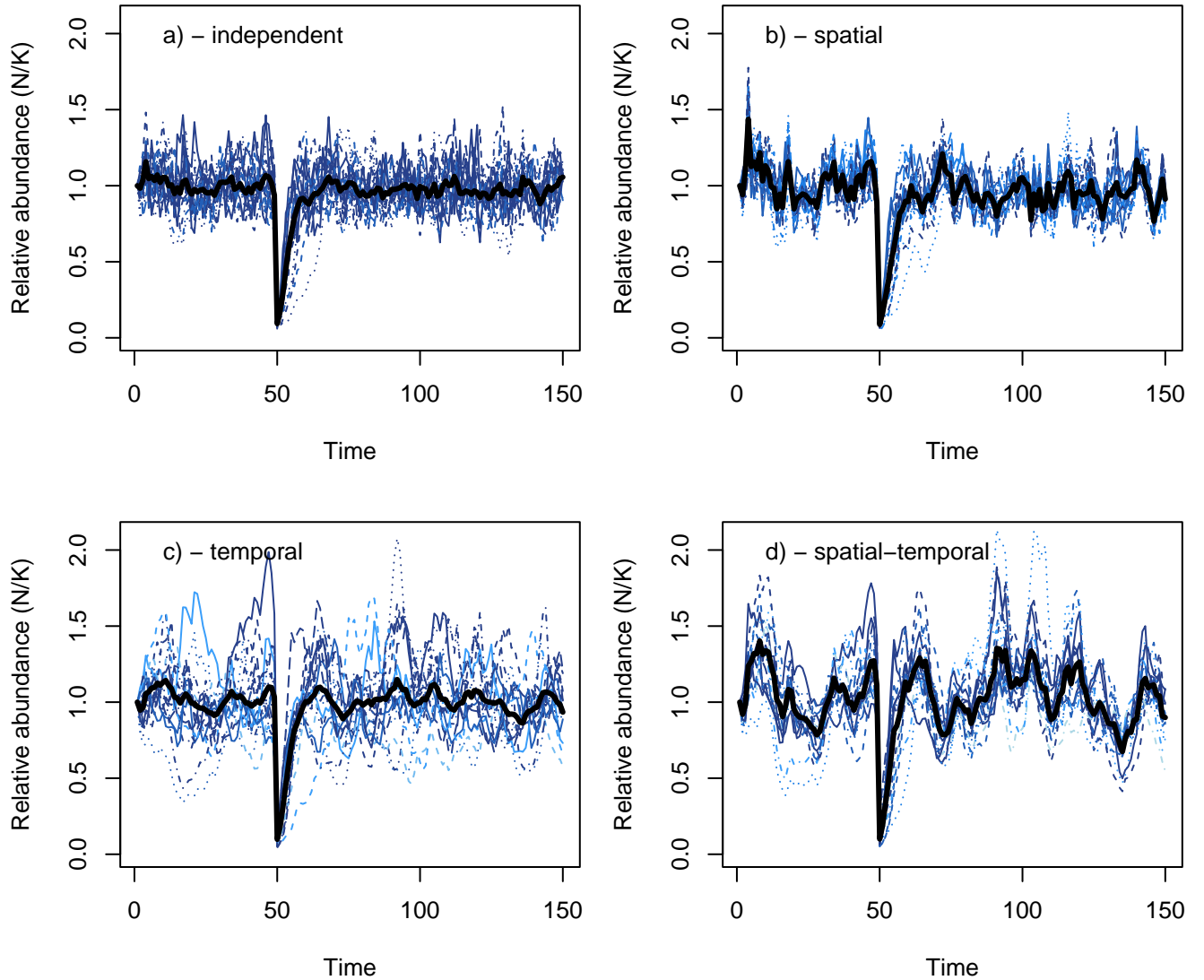


Figure S5: Metapopulation dynamics with independent (a), spatially correlated (b), temporally correlated (c), and spatio-temporally correlated (d) recruitment deviates. Black line indicates metapopulation, and dashed lines indicate local patches with red and blue relating to abundances after 100 years post-disturbance were less than or greater than 1.0 pre-disturbance, respectively.

85 Post-disturbance outcomes

86 Monitoring & management at aggregate-scale

87 While true metapopulation dynamics emerge from local patch dynamics and dispersal in eq. S.1, natural resource
 88 managers often monitor and manage at the scale of the metapopulation. Hence, management at this scale
 89 inherently defines the stock-recruitment dynamics of the aggregate complex of patches (i.e., metapopulation) as:

$$\mathbb{E}(K_t) = \frac{\bar{\alpha}A_{t-1}}{1 + \frac{\bar{\alpha}-1}{\bar{\beta}}A_{t-1}} \quad (\text{S.10})$$

where $\bar{\alpha}$ was the compensation ratio averaged across the metapopulation and $\bar{\beta}$ was the carrying capacity summed across the entire metapopulation.

Recovery metrics

We measured the following post-disturbance outcomes to track the temporal and spatial recovery regime of the metapopulation.

1. Recovery rate after disturbance: Recovery rate represents the proportional post-disturbance recovery towards metapopulation carrying capacity gained per year (1 year = 1 generation in our models). Recovery rate was calculated as $1 - T_{\text{recovery}}/T_{\text{sim}}$ where the recovery time, T_{recovery} , was the number of years/generations it took for the metapopulation to reach five consecutive years pre-disturbance abundance. Recovery rate captures how quickly the aggregate metapopulation recovers from disturbance but doesn't take into account whether any given local patches recover to their pre-disturbance capacity nor did it allow for any uncertainty around recovery criteria.
2. Patch occupancy: The mean number of patches with >0.1 local carrying capacity after disturbance in the short-term (5 years), medium-term (10 years), and long-term (25 years). This value characterizes the expected risk of spatial contractions or local patch collapses, and reflects how interactions between spatial structure, disturbance, and dispersal shape source-sink dynamics and the ability to provide (or not) rescue effects and recover local patches.
3. Relative production: The ratio between the empirical metapopulation adult abundances to the expected adult recruitment if the metapopulation were a single, contiguous population of equivalent size and productivity (i.e., carrying capacities and productivity were equal to the sum β and mean α among patches, respectively). We term Δ_N by calculating the stock-recruitment model to aggregate metapopulation adults (eq. S.10) such that:

$$\Delta_{N_t} = \frac{A_t}{\mathbb{E}(M_t)} \quad (\text{S.11})$$

A value of 1.0 would indicate that the disturbed metapopulation production was equal to a single, contiguous population such that source-sink dynamics were not consuming surplus recruits. In other words, this metric can describe whether the metapopulation acts more than ($\Delta_{N_t} > 1.0$), less than ($\Delta_{N_t} < 1.0$), or equal to the sum of its parts ($\Delta_{N_t} = 1.0$).

4. Risk of non-recovery after disturbance: Non-recovery rate was defined as the % of simulations where metapopulation abundance failed to recover to 1.0 of the average pre-disturbance abundance for 5 consecutive years post-disturbance. This “non-recovery rate” reflects the risk of a long-term state shift in metapopulation dynamics after disturbance in the face of stochasticity.

Scenarios

We tested all combinations of the following eight processes (below) and ran 100 stochastic iterations per scenario to estimate the mean outcome for each of the above recovery metrics:

1. Homogenous and spatially variable recruitment compensation ratio across patches, i.e. intrinsic rate of population growth (α_i).
2. Homogenous and spatially variable local carrying capacity across patches, i.e. asymptote of expected recruits at high adult densities (β_i).
3. Disturbances where a proportion of individuals removed from metapopulation (e.g., 0.90) occurs.

- a. *uniform* - random individuals removed at equal vulnerability across all patches.
 - b. *localized, even* - random individuals removed from randomly selected subset of patches (as long as the target individuals lost in the metapopulation can be achieved in that subset of patches)
 - c. *localized, uneven* - total extirpation of randomly selected subset of patches (as long as the target individuals lost in the metapopulation can be achieved in that subset of patches)
4. Density-independent dispersal rates ω from 0 to 5% of individuals within a patch will disperse.
 5. Topology of the spatial networks with linear, dendritic, star, and grid networks. Each network with $P = 16$ and distance between patches $\bar{d} = 1$.
 6. Stochastic recruitment deviates from low, medium, high coefficient of variation on lognormal error. Generate stochasticity in time-dynamics via random recruitment deviates away from expected.
 7. Temporal correlation in recruitment deviates from low, medium, high correlation (i.e., good year at time t begets good year at time $t+1$).
 8. Spatial correlation in recruitment deviates among patches from low, medium, to high correlation (i.e., neighboring patches go up or down together).

Example results

We demonstrate our metapopulation model with an example outcome for a linear network composed of 16 patches, a dispersal rate of 0.01 and a high enough dispersal cost such that individuals are only willing to move to their closest neighboring patches. This limits the strength of potential rescue effects. For this example, patches varied in their productivity and carrying capacity but will have deterministic population dynamics.

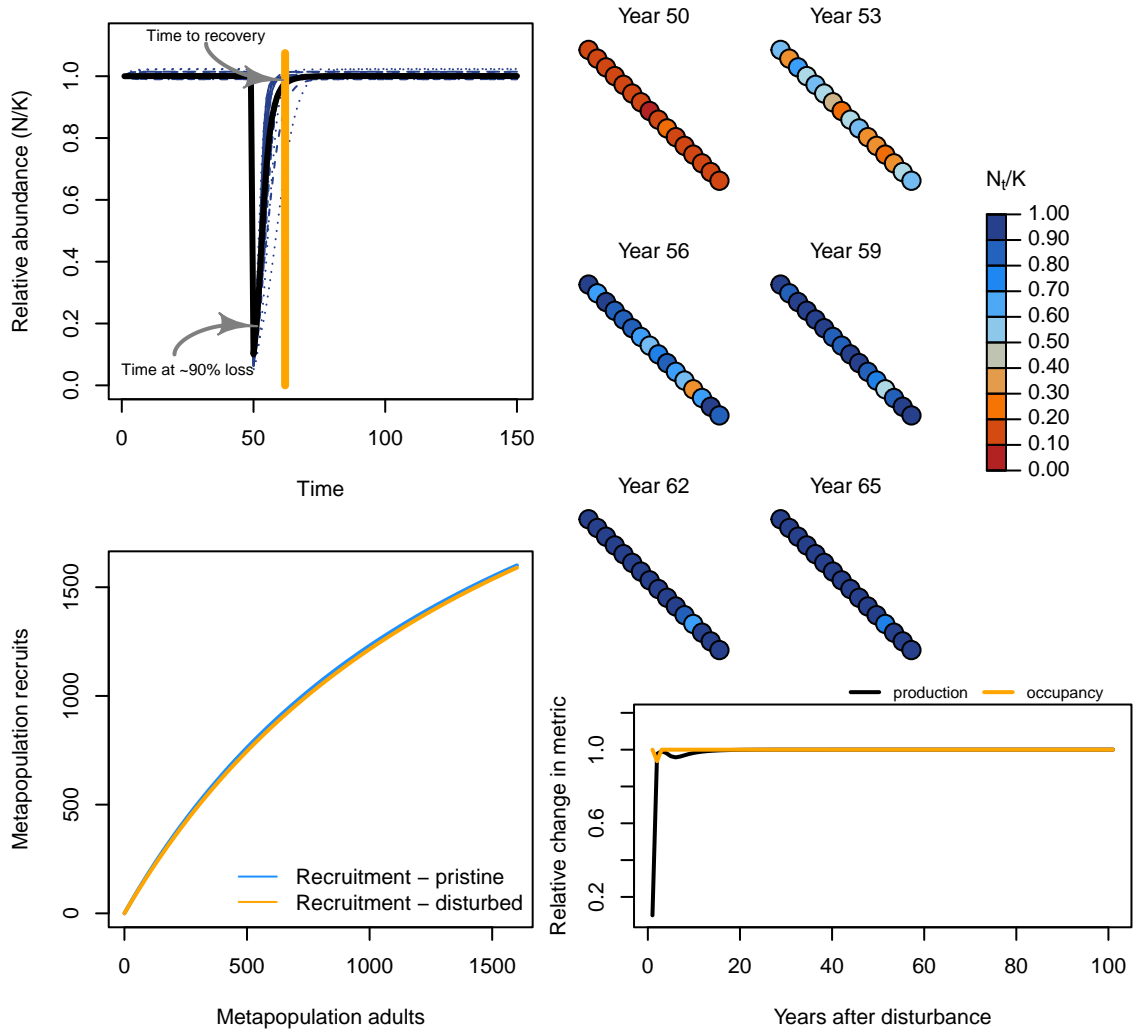


Figure S6: Example iteration of spatial recovery regime of metapopulation with linear topology through time (top left) and space (top right). Recruitment dynamics before and 10 years after disturbance (bottom left). Relative bias in aggregate-scale estimates of carrying capacity, compensation ratio, and recruitment production in recovery phase (bottom right).

147 We can then contrast this with a different network shape, like a dendritic network.

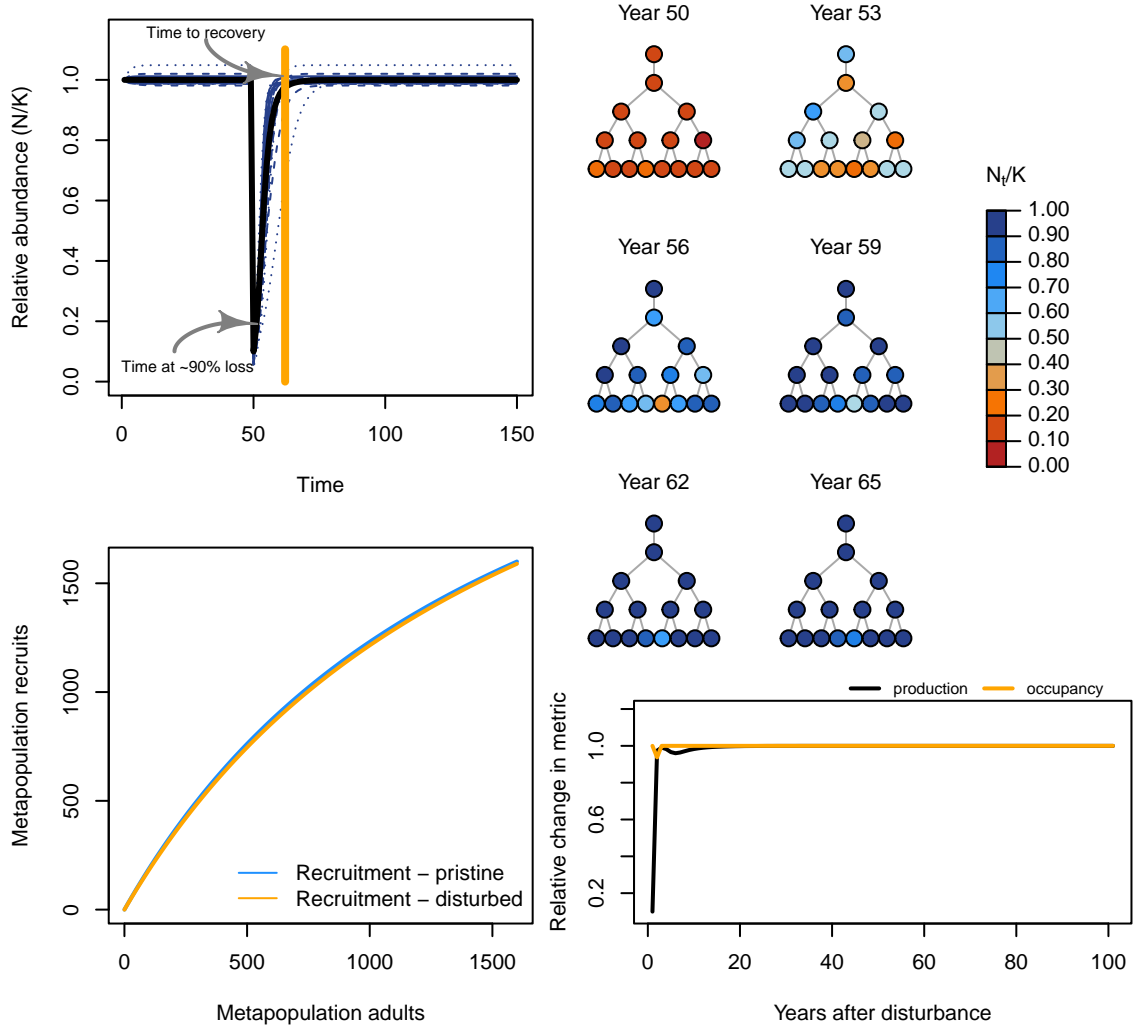


Figure S7: Example iteration of spatial recovery regime of metapopulation with dendritic topology.

148 Now, let's add some stochasticity to recruitment and see how this affects the recovery regime.

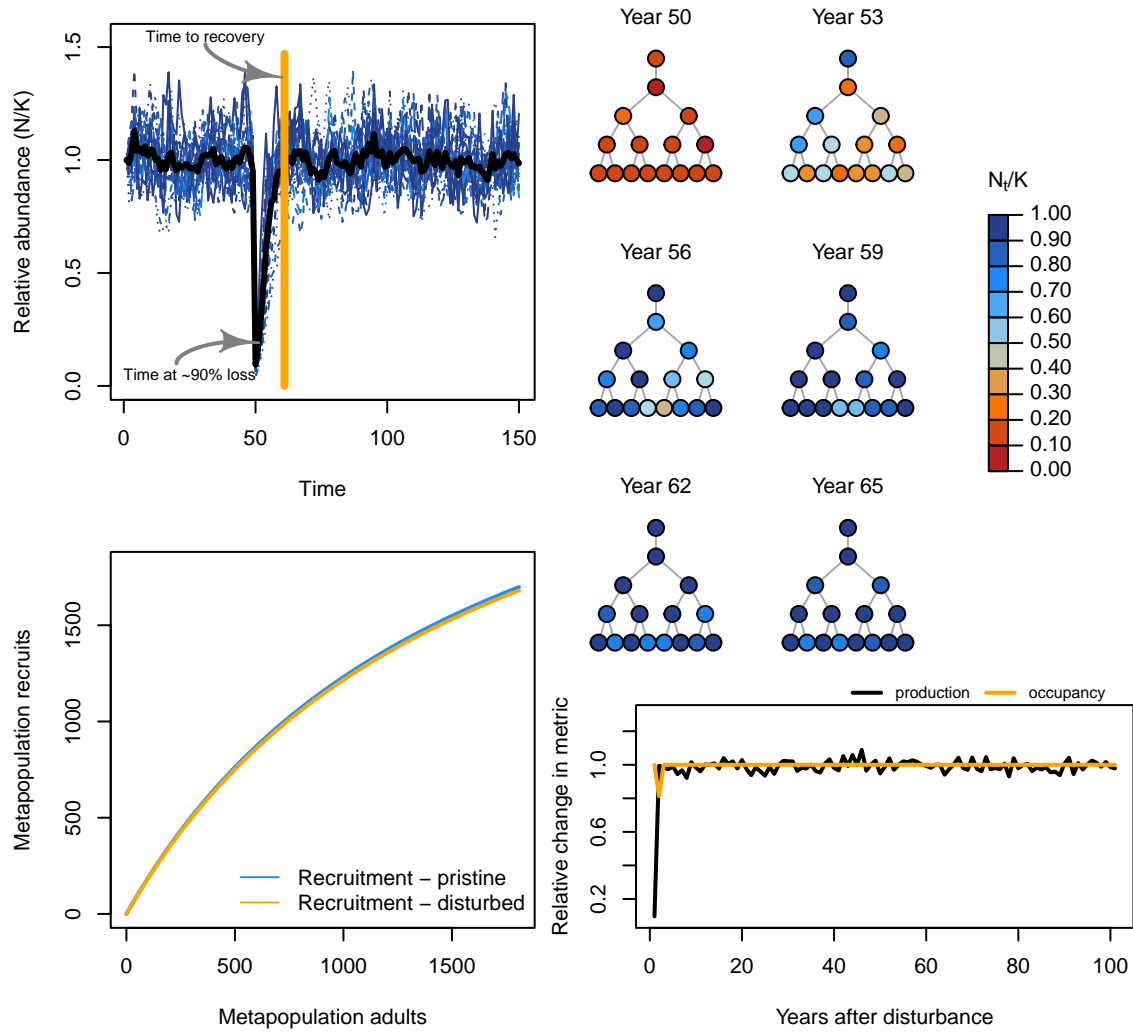


Figure S8: Example iteration of spatial recovery regime of stochastic metapopulation.

Next, we can contrast with a disturbance regime where the disturbance is concentrated on local patches that can be completely extirpated (rather than the disturbance being applied proportionally across all patches e.g., a mixed-stock fishery).

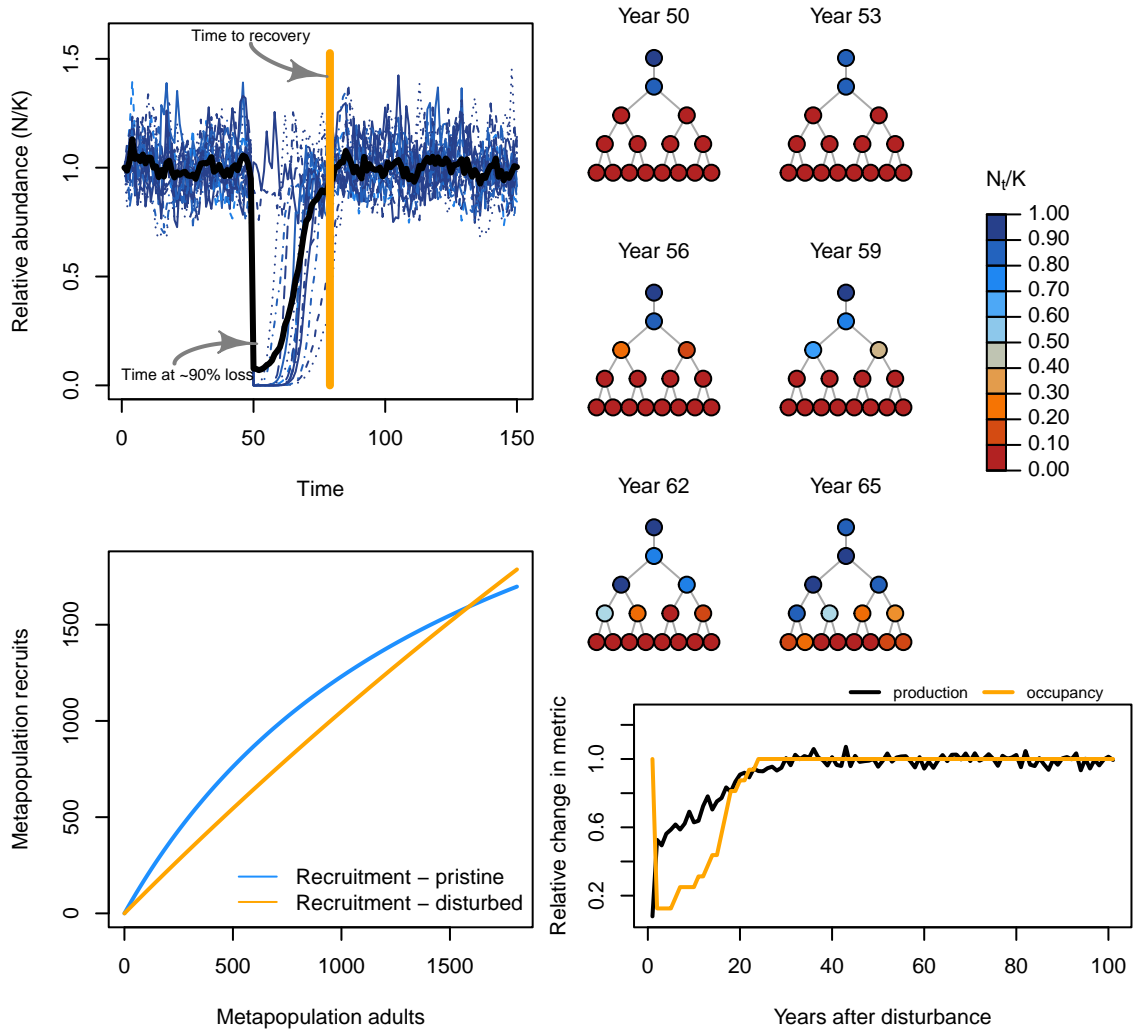


Figure S9: Example iteration of spatial recovery regime of stochastic metapopulation.

General patterns

Effects of disturbance regime

The strongest lever influencing recovery in our simulated metapopulations was, by far, the characteristics of the disturbance regime. Specifically, the degree to how locally concentrated the disturbance was on the set of patches was more influential than variable density dependence, dispersal rates, or network topology. This was surprising and not expected in our initial hypotheses. Localized disturbances increased the risk of spatial contraction, reduced recovery rates and aggregate compensation, and increased the risk of non-recoveries. By altering aggregate compensation, localized disturbance reduced the relative production of the metapopulation. In other words, through changes in source-sink dynamics, metapopulations under localized disturbance acted less than the sum of their parts – the more localized the impacts, the worse these effects. Uniform disturbances generally left the metapopulation dynamics unaffected with few ecological surprises. These above spatial and temporal recovery processes also appeared tied to one another such that changes to any of them had feedbacks with other recovery metrics.

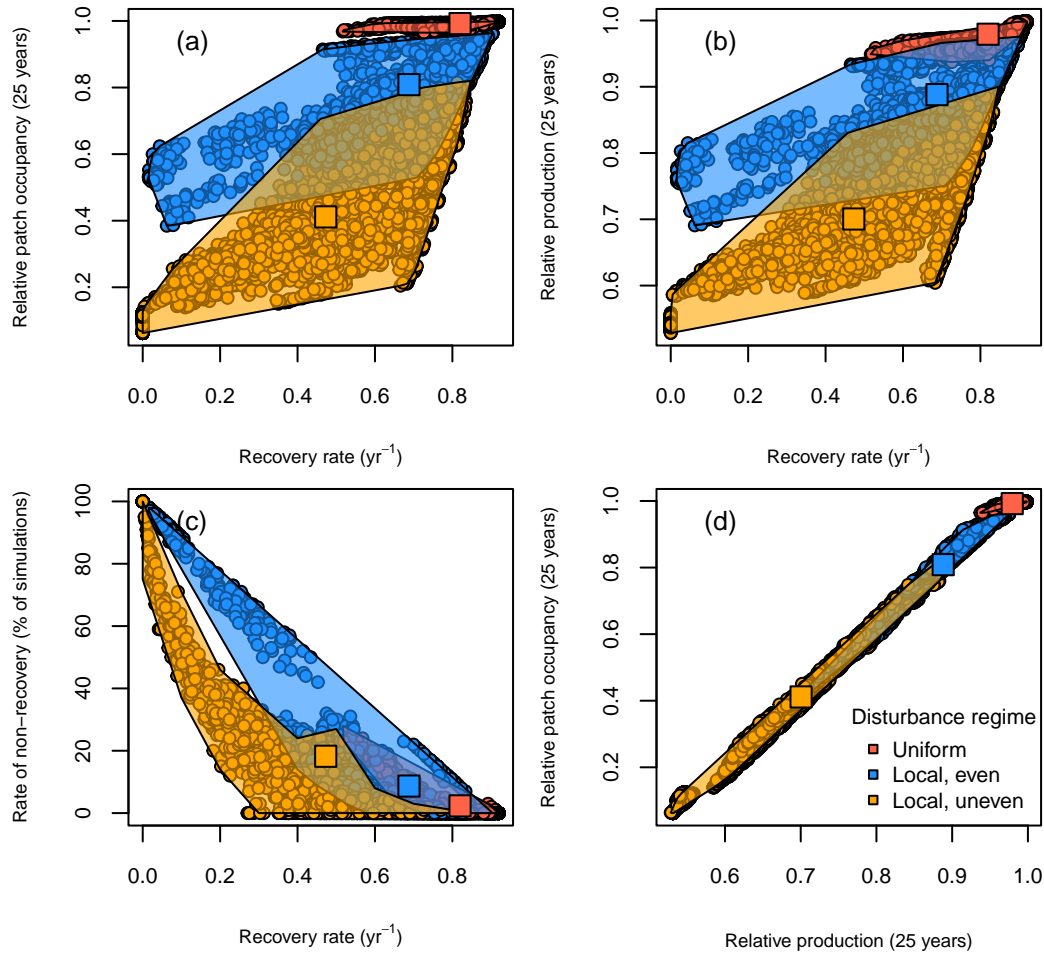


Figure S10: Spatial and temporal recovery patterns along disturbance regimes across all scenarios.

Role of network structure & dispersal

We now show some general patterns in how variable patch demographic rates, network structure, dispersal, disturbance, recruitment stochasticity, and spatio-temporal correlations variation affects metapopulation *recovery rates*, *maximum sustainable yield* (analogous to the maximum rate of loss the system can sustain), and *collapse rate* (i.e., the number of simulations where the metapopulation fails to recover), and *patch occupancy* (i.e., number of patches with local abundance <10% of pre-disturbance).

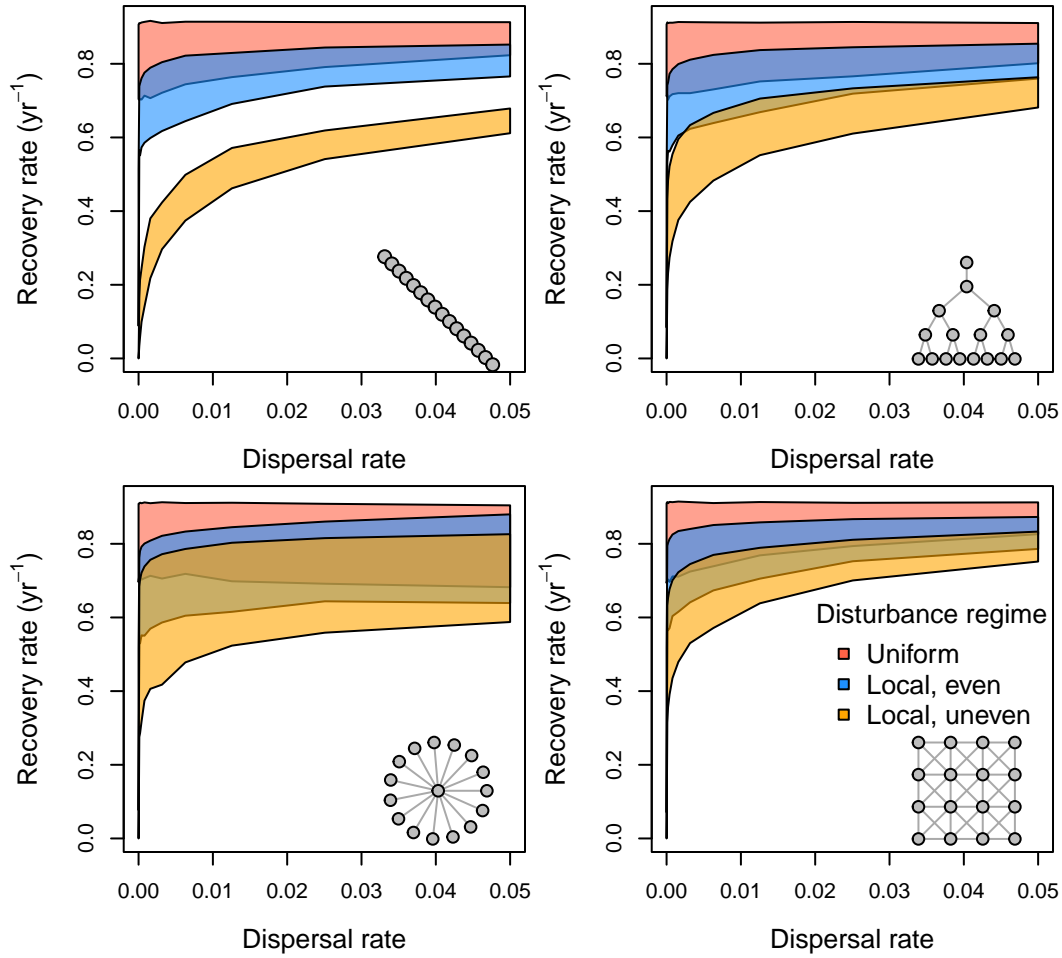


Figure S11: Metapopulation recovery rates along gradients of network configuration, dispersal rates, and spatial distribution of disturbance. The shaded region describes the interquartile range across all scenarios.

Dispersal, landscape structure, and local density-dependence also affected metapopulation recovery patterns in three key ways, though to a lesser extent. First, recovery rates increased with increased dispersal. However, this effect was nonlinear with diminishing benefits of dispersal occurring at ~1-3%, depending on spatial structure and disturbance. Second, more linearized networks had slower recovery times than more connected networks suggesting that rescue effects take some time to cascade through the entire network of patches; but this interacted with the disturbance regime as only local, extirpation exhibited this change in any substantial manner. Last, diversity in local patch compensation and carrying capacities tended to slow metapopulation recoveries - this effect interacted with other factors like stochasticity.

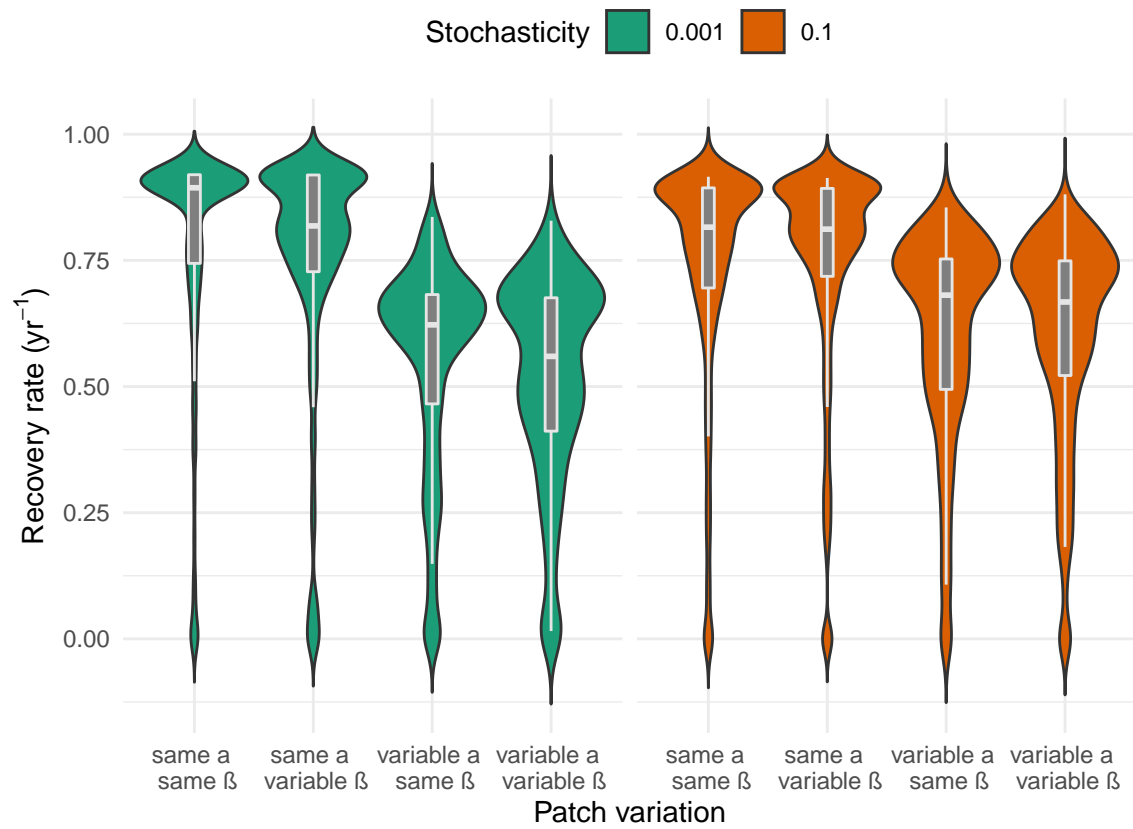


Figure S12: Effects of variable local patch productivities on metapopulation recovery across all scenarios.

Clustering analyses

We used hierarchical clustering analyses (implementing Ward's criterion) of a dissimilarity matrix from our four recovery metrics to evaluate whether there was evidence for common recovery regimes among our simulation results across all ecological and disturbance scenarios (Murtagh & Legendre 2014). Based on advice laid out in Hennig (2014), we determined that the best number of unique clusters in metapopulation recoveries should satisfy the following statistical criteria:

1. recovery outcomes from within a cluster are closer to one another than to other clusters (i.e., the two Dunn indices are relatively high)
2. the number of clusters explains much of the point variation within the dataset (i.e., diminishing returns in minimizing the sums-of-squared residuals)
3. the point observations within clusters are relatively tight (i.e., both the average silhouette width and the widest within-cluster gap are relatively low)
4. clusters are relatively unique and there is good separation between the clusters (i.e., the separation index is still high, while considering that low numbers of clusters should always have the highest separation)

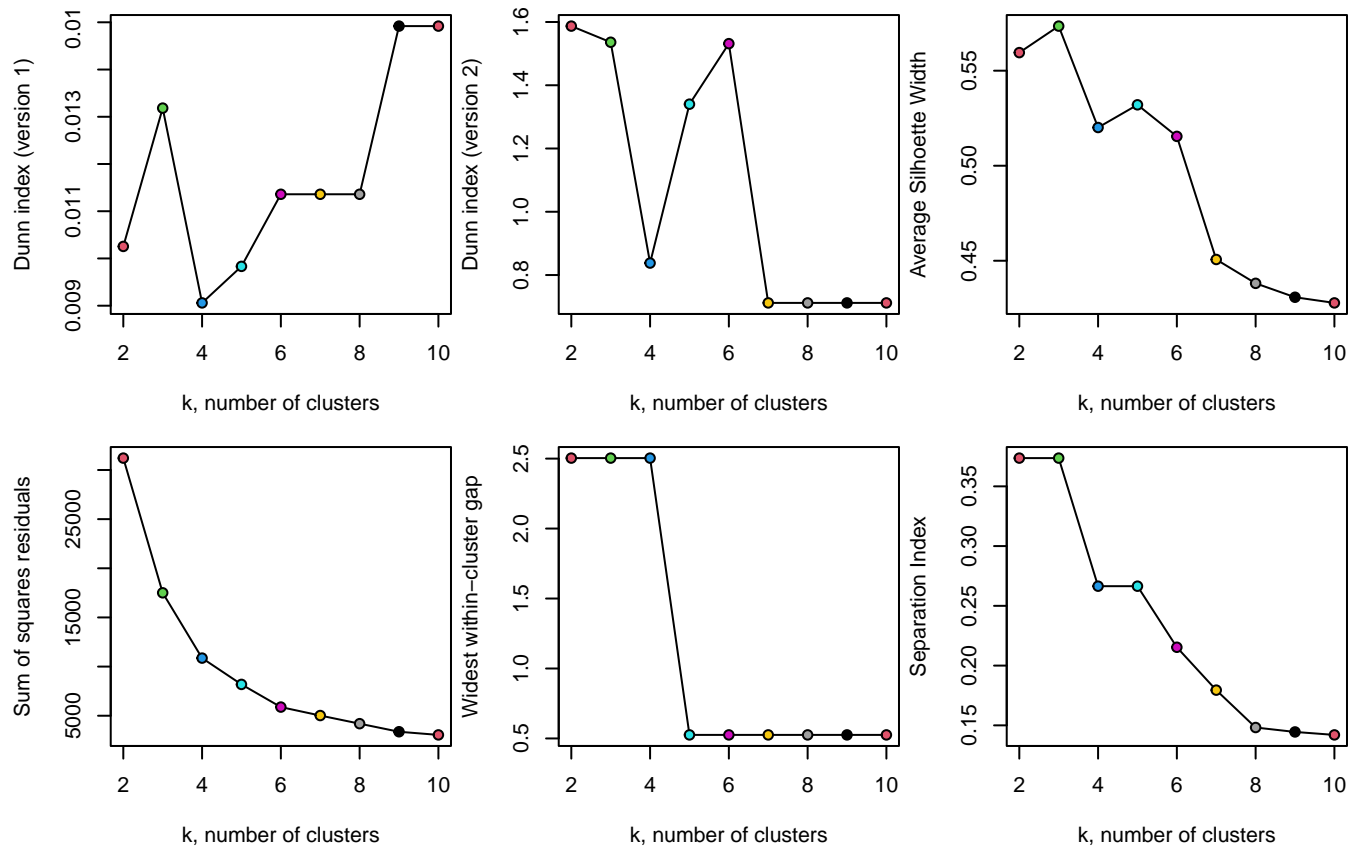


Figure S13: The relationships between number of potential clusters and multiple statistical criteria used to test support for the best number of clusters within the simulated recovery outcomes

Based on the above criteria, we chose 5 unique clusters as satisfying most of the above criteria in the figure above, although there was good support for between 3 and 6 unique clusters. The principal components analysis indicates that five clusters has substantial explanatory power of metapopulation recovery metrics (explained ~89% of the point variation).

Table S2: The mean recovery metrics and metapopulation abundance (N/K) for each of five common metapopulation recovery regimes supported by hierarchical clustering analyses.

Regime	Recovery rate	% non-recovery	Occupancy	Relative production	Relative abundance
Resilient	0.81	3	0.98	0.97	0.99
Slow recovery	0.71	3	0.76	0.87	0.99
Hidden collapses	0.48	12	0.40	0.70	0.98
Lost capacity	0.16	78	0.58	0.78	0.65
Critical risk	0.00	100	0.10	0.54	0.08

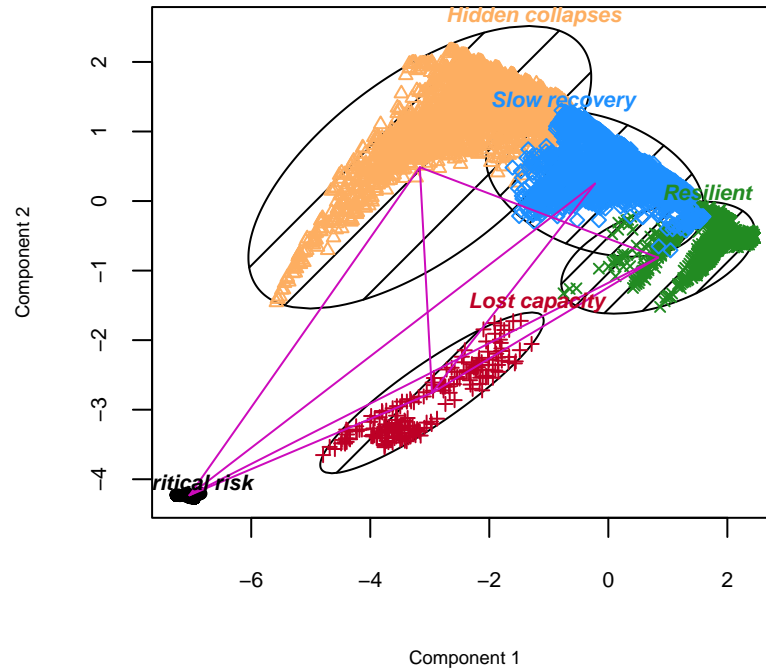


Figure S14: Bivariate cluster plot of the principal components explaining point variation in metapopulation recovery metrics across all simulated scenarios grouped into five distinct clusters.

Emergent recovery outcomes

Overall, we used hierarchical clustering analyses to describe five common metapopulation recovery outcomes. These outcomes were: (1) resilient recovery – metapopulations recovered to pre-disturbance abundances quickly with all patches occupied, (2) slow recovery – metapopulation recovery was slow but there were no other changes in metrics, (3) hidden collapses – metapopulations tended to recover, metapopulation abundance was high, but many local patches remained unoccupied, (4) lost capacity – recovery rates was very slow, risk of non-recovery was high, long-term production was low, and many local patches remained unoccupied and (5) critical risk – metapopulation abundances remained in a collapsed state and risk of non-recovery was high.

These five spatial recovery regimes emerged from the interplay of density-dependent productivity (shown in Figure 6 of the main text), network structure (shown here), dispersal, stochasticity, and spatial disturbance regimes. Resilient recovery regimes were most common when disturbance was evenly applied across the network and local patches were identical. Any localized disturbances could create ecological surprises, and the frequency of these surprises were often exacerbated when patches were diverse. Localized, even disturbances tended to reduce recovery by 50% compared to even disturbances (from 16 years to 24 years on average). The riskiest recovery outcomes emerged when disturbance was localized and allowed for extirpation. In these scenarios, recovery was slowed by >100% (from 16 years to >32 years on average), relative production was often reduced by >50%, long-term patch occupancy was reduced by >35%. Last, note that linear networks tended to have higher risks for long-term spatial contractions.

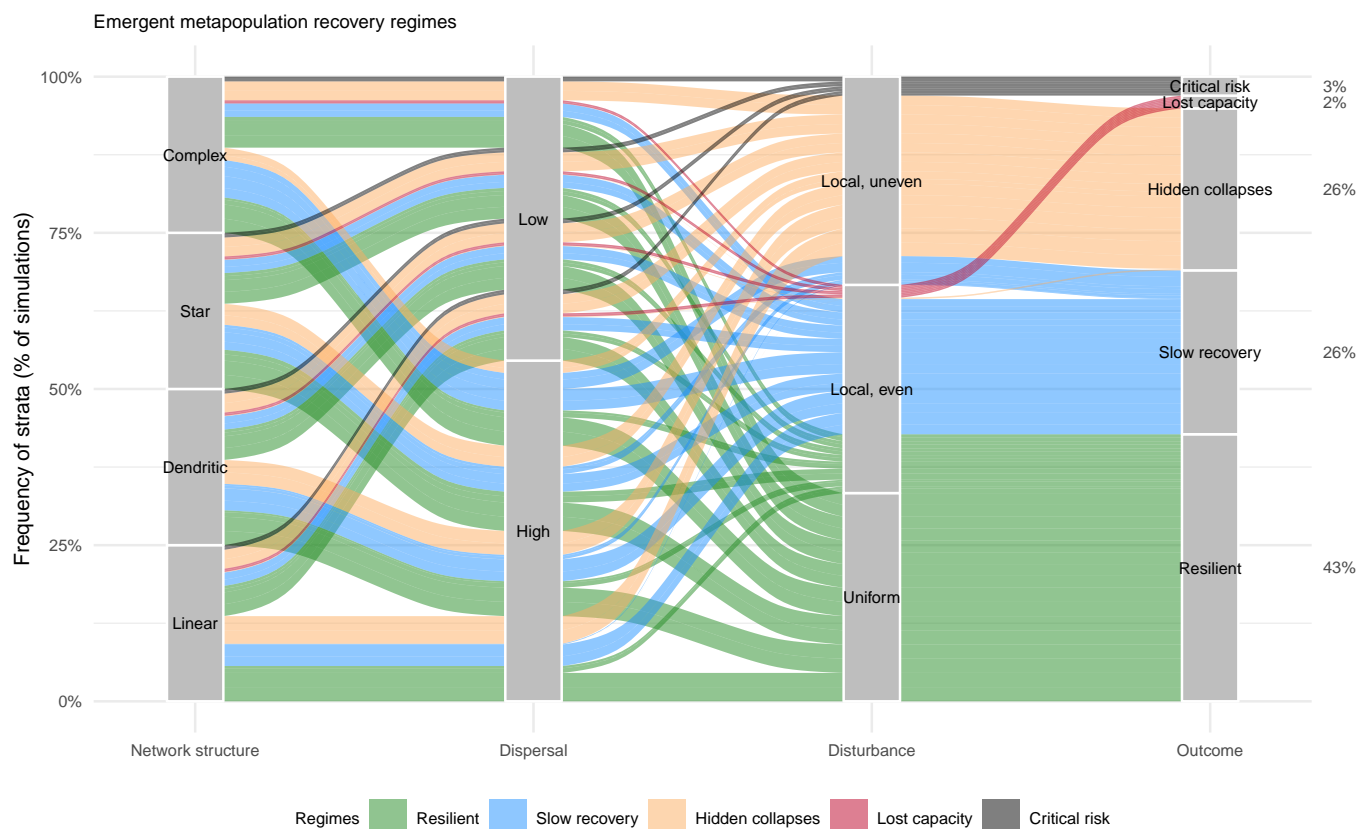


Figure S15: Interplay between network structure, disturbance, and dispersal can lead to surprising recovery outcomes.

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