
Global Dispersal

We start by considering the original model developed by Hamilton and May (1977) where dispersal is global (dispersing individuals have an equal probability of landing at any site). In this model, a parthenogenetic species inhabits an environment with a fixed number of sites, $S$, that can each support only one adult. Each adult produces $n$ offspring and then dies immediately after reproduction. A fraction $v$ of these offspring disperses, while the rest $(1 - v)$ remains at the natal site. Only a fraction $p$ of dispersing offspring survives and are distributed equally among all other sites (fig. A1). All offspring compete equally for a site, regardless of whether they were born there or arrived via dispersal. The evolutionarily stable strategy (ESS) value of $v$ (the fraction of offspring that should be dispersed) is the strategy that when adopted by all individuals within a population cannot be invaded by a mutant individual playing any other strategy. Let $\tilde{v}$ be the resident strategy adopted by all individuals in the population, and let $v'$ be the mutant strategy played by a single mutant individual. The fitness of this mutant will be the probability that it retains its home site plus the expected number of new sites it gains in the next generation.

![Model schematic for global dispersal](image)

**Figure A1:** Model schematic for global dispersal. A fraction $1 - v$ of offspring remains at the natal site, while the remaining offspring $v$ disperse, a fraction $p$ of which survives and is distributed evenly across the other $S - 1$ sites. Here $S = 7$.

The mutant produces $n$ offspring, of which $1 - v'$ stay at its home site, for a total of $(1 - v')n$ individuals. There are $S - 1$ resident-type individuals in the population, each of which produce $n$ offspring, of which $\tilde{v}$ then disperse and $p$ survive dispersal, for a total of $(S - 1)vnp$ resident-type individuals that disperse and survive. These individuals are then distributed equally among the remaining $S - 1$ sites. So there will be a total of $(S - 1)vnp/(S - 1)$ resident-type offspring arriving at the mutant’s home site. The probability that the mutant retains its home site is

$$w_1 = \frac{(1 - v')n}{(1 - v')n + (S - 1)vnp/(S - 1)}.$$

$$w_1 = \frac{1 - v'}{1 - v' + \tilde{v}p}.$$  \(A1\)

The mutant also produces $v'np$ offspring that disperse and survive and are distributed randomly among the other $S - 1$ sites. At each site, they will compete with the $(1 - \tilde{v})n$ nondispersing offspring that are born and stay at that site, plus the offspring that disperse in from other sites. There are $S - 2$ other sites (i.e., excluding this focal site plus the
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mutant’s home site), each of which has an adult that produces \( vnp \) offspring that survive dispersal, a fraction \( 1/(S - 1) \) of which lands at this focal site. The probability that the mutant wins a new site is

\[
q = \frac{v'np/(S - 1)}{v'np/(S - 1) + (1 - v)n + (S - 2)\bar{v}np/(S - 1)}.
\] (A2)

The expected number of new sites the mutant gains is the number of possible sites to gain times the probability of gaining each of them, or

\[
w_2 = (S - 1)q, \quad \text{or} \quad w_2 = \frac{v'p}{v'p/(S - 1) + (1 - \bar{v}) + (S - 2)\bar{v}p/(S - 1)}. \] (A3)

The total fitness of the mutant type \( v' \) in a population of resident types \( \bar{v} \) is given by adding the probability of the mutant type retaining its home site (A1) and the expected number of sites the mutant gains (A3) together to get

\[
w(v', \bar{v}) = \frac{1 - v'}{1 - v' + \bar{v}p} + \frac{\bar{v}p}{\bar{v}p/(S - 1) + (1 - \bar{v}) + (S - 2)\bar{v}p/(S - 1)}. \] (A4)

If we make the assumption of a very large number of sites \( (S \to \infty) \), this simplifies to

\[
w(v', \bar{v}) = 1 - v' + \bar{v}p + \bar{v}p. \] (A5)

The ESS value of \( v \), if it exists, is defined as the strategy \( v' \), where

\[
w(v', v') = 1, \quad w(v', v') \leq 1 \quad \forall v'. \] (A6a) (A6b)

In other words, an individual playing the strategy \( v' \) in a population of individuals playing \( v' \) will exactly replace itself in the next generation. In contrast, an individual playing any other mutant strategy \( v' \) will not be able to increase in number in the next generation. To find \( v' \), we look for critical points by differentiating (A5) with respect to \( v' \):

\[
\frac{\partial w(v', \bar{v})}{\partial v'} = -\frac{p\bar{v}}{(1 - v' + p\bar{v})^2} + \frac{p}{1 - \bar{v} + p\bar{v}}. \] (A7)

We evaluate (A7) at \( v' = \bar{v} = v' \), set it to zero, and solve for \( v' \). Doing this, we get

\[
v' = \frac{1}{2 - p}. \] (A8)

Note that this is equivalent to the model in the main manuscript with \( z = S \to \infty \). To determine whether this point is in fact an ESS, we check the sign of the second derivative evaluated at this point:

\[
\frac{\partial^2 w(v', \bar{v})}{\partial v'^2} \bigg|_{v' = \bar{v} = v'} = -\frac{2p\bar{v}}{(1 - v' + p\bar{v})^3}, \quad \text{if} \quad 0 \leq p \leq 1
\] (A9)

Since \( 1 - p \) and \( 2 - p \) are both nonnegative (\( 0 \leq p \leq 1 \)), the second derivative is negative. This confirms that this critical point is a maximum (instead of a minimum) and is therefore an ESS.

Local Dispersal, Two Distance Classes

Next, consider a spatially structured version of this model with local dispersal. Here the $S$ viable sites are arranged in a two-dimensional lattice with wrapping (periodic) boundaries. A fraction $v$ of the newborn offspring disperses a distance of 1 to one of the four sites that directly border the natal site, while the rest of the offspring $(1 - v)$ remain at the natal site (fig. B1). As before, only a fraction $p$ of dispersing offspring survives and is distributed equally among each of these four sites. As above, we let $v$ and $v'$ be the resident and mutant dispersal strategies, respectively, and look for $v^*$, the ESS dispersal strategy.

![Model schematic for local dispersal with two distance classes. A fraction $1 - v$ of offspring remains at the natal site, while the remaining offspring $v$ disperse, a fraction $p$ of which survives and is distributed evenly in four sites.](image)

The mutant produces $(1 - v')n$ offspring that stay at its home site. The resident-type individuals in the four neighboring sites each produce $vnp$ offspring that disperse and survive, a quarter of which arrive at the mutant’s home site. So there will be a total of $4vnp/4$ resident-type offspring arriving at the mutant’s home site. The probability that the mutant retains its home site is...
We evaluate (B4) at times the probability of gaining each of them, or at the focal site. The expected number of new sites the mutant gains is the number of possible sites to gain (four) offspring that survive dispersal, a quarter of which land at this focal site, for a total of \( \frac{3vnp}{4} \) resident offspring arriving at the focal site. The expected number of new sites the mutant gains is the number of possible sites to gain (four) times the probability of gaining each of them, or

\[
 w_1 = \frac{(1 - v')n}{(1 - v')n + 4vnp/4}, \\
= \frac{1 - v'}{1 - v' + v'p}.
\]

(B1)

The mutant also produces \( v'np \) offspring that disperse and survive and are distributed randomly among the four neighboring sites. At each site, they will compete with the \((1 - \bar{v})n\) nondispersing offspring that are born and stay at that site, plus the offspring that disperse from other sites. Each adult at the other three neighboring sites produces \( v'ns \) offspring that survive dispersal, a quarter of which land at this focal site, for a total of \( \frac{3vnp}{4} \) resident offspring arriving at the focal site. To get the fitness of the mutant type \( v' \) in a population of resident types \( \bar{v} \) is given by adding the probability of the mutant type retaining its home site (B1) and the expected number of sites at distance 1 that the mutant gains (B2) together to get

\[
 w(v', \bar{v}) = \frac{1 - v'}{1 - v' + \bar{v}p} + \frac{4v'p}{v'p + 4(1 - \bar{v}) + 3v'p}.
\]

(B3)

Note that unlike the first model above, this expression does not depend on the number of sites \( S \) in the world.

To find the ESS \( v' \), we look for critical points by differentiating (B3) with respect to \( v' \):

\[
 \frac{\partial w(v', \bar{v})}{\partial v'} = \frac{-p\bar{v}}{(1 - v' + \bar{v}p)^2} + \frac{16p(1 - \bar{v}) + 12p\bar{v}}{(pv' + 4(1 - \bar{v}) + 3p\bar{v})^2}.
\]

(B4)

We evaluate (B4) at \( v' = \bar{v} = v' \), set it to zero, and solve for \( v' \). Doing this, we get

\[
 v' = \frac{4}{8 - 3p}.
\]

(B5)

Note this is equivalent to the model in the main manuscript with \( z = 4 \). To determine whether this point is in fact an ESS, we check the sign of the second derivative evaluated at the following point:

\[
 \frac{\partial^2 w(v', \bar{v})}{\partial v'^2} \bigg|_{v' = \bar{v} = v'} = \frac{-2p\bar{v}}{(1 - \bar{v}) + \bar{v}p} + \frac{-2p[16p(1 - \bar{v}) + 12p\bar{v}]}{4(1 - \bar{v}) + 4p\bar{v}},
\]

\[
= \frac{-2p\bar{v}}{(1 - v') + pv'} + \frac{-2p[16p(1 - v') + 12pv']}{4(1 - v') + 4pv'}.
\]

By grouping terms and noting that \( 1 - v' \) is positive, we can conclude that the second derivative is negative (even without plugging in the specific value for \( v' \)). This confirms that this critical point is a maximum (instead of a minimum) and is therefore an ESS.

Local Dispersal, Three Distance Classes

Next, consider a modified version of the previous model where a fraction $v_1$ of the newborn offspring disperses a distance of 1 to one of the four sites that directly border the natal site, another fraction $v_2$ of the newborn offspring disperses a distance of 2 to one of eight sites, while the rest of the offspring $(1 - v_1 - v_2)$ remain at the natal site (fig. C1). As before, only a fraction $p$ of dispersing offspring survives. Offspring dispersing a distance of 1 and surviving are distributed equally among each of the four sites, and offspring dispersing a distance of 2 and surviving are distributed equally among each of the eight sites. Here we let $\{v_1, v_2\}$ and $\{v'_1, v'_2\}$ be the resident and mutant dispersal strategies, respectively, and look for $\{v_1^*, v_2^*\}$, the ESS dispersal strategy.

The mutant produces $(1 - v_1' - v_2')n$ offspring that stay at its home site. The resident-type individuals in the four sites at distance 1 from the mutant’s home site each produce $pv_1n$ offspring that disperse and survive, a quarter of which arrive at the mutant’s home site, for a total of $4pv_1n/4$. The resident-type individuals in the eight sites at distance 2 from the mutant’s home site each produce $pv_2n$ offspring that disperse and survive, an eighth of which arrive at the mutant’s home site...
site, for a total of $8v_np/8$. So there will be a grand total of $4v_np/4 + 8v_np/8$ resident-type offspring arriving at the mutant’s home site. The probability that the mutant retains its home site is

$$w_1 = \frac{(1 - v'_i - v'_j)n}{(1 - v'_i - v'_j)n + 4v_np/4 + 8v_np/8},$$

$$= \frac{1 - v'_i - v'_j}{(1 - v'_i - v'_j) + p(v'_i + v'_j)}.$$  \hspace{1cm} (C1)

The mutant also produces $v_np$ offspring that disperse a distance 1 and survive, a quarter of which land at this focal site, for a total of three sites at distance 1 from this focal site produce offspring that are born and stay at that site, plus the offspring that disperse in from other sites. Each adult at the other three sites at distance 1 from this focal site produce $v_np$ offspring that disperse a distance 1 and survive, a quarter of which land at this focal site, for a total of $3v_np/4$. Each adult at the eight sites at distance 2 from this focal site produce $v_np$ offspring that disperse a distance 2 and survive, an eighth of which land at this focal site, for a total of $8v_np/8$. The expected number of new sites at distance 1 that the mutant gains is the number of possible sites to gain (four) times the probability of gaining each of them, or

$$w_1 = 4 \left(\frac{v'_np/4}{4v'_p} \right),$$

$$= \frac{v'_np/4}{4v'_p} + 4(1 - v'_i - v'_j) + 3v'_p + 4v'_p.$$  \hspace{1cm} (C2)

The mutant also produces $v_np$ offspring that disperse a distance 2 and survive and are distributed randomly among the four neighboring sites at distance 1. At each of these sites, they will compete with the $(1 - v'_i - v'_j)n$ nondispersing offspring that are born and stay at that site, plus the offspring that disperse in from other sites. Each adult at the other three sites at distance 1 from this focal site produce $v_np$ offspring that disperse a distance 1 and survive, a quarter of which land at this focal site, for a total of $3v_np/4$. Each adult at the eight sites at distance 2 from this focal site produce $v_np$ offspring that disperse a distance 2 and survive, an eighth of which land at this focal site, for a total of $8v_np/8$. The expected number of new sites at distance 2 that the mutant gains is the number of possible sites to gain (eight) times the probability of gaining each of them, or

$$w_1 = 8 \left(\frac{v'_np/8}{8v'_p} \right),$$

$$= \frac{v'_np/8}{8v'_p} + 8(1 - v'_i - v'_j) + 8v'_p.$$  \hspace{1cm} (C3)

The total fitness of the mutant type $v'$ in a population of resident types $v$ is given by adding the probability of the mutant type retaining its home site (C1), the expected number of sites at distance 1 that the mutant gains (C2), and the expected number of sites at distance 2 that the mutant gains (C3) together to get

$$w = \frac{1 - v'_i - v'_j}{(1 - v'_i - v'_j) + p(v'_i + v'_j)} + \frac{4v'_p}{8v'_p} + \frac{v'_i - v'_j}{8v'_p} + 8v'_i + 8v'_j.$$  \hspace{1cm} (C4)

To find the ESS $v'$, we look for critical points by differentiating (C4) with respect to each $v'_i$ and $v'_j$:

$$\frac{\partial w}{\partial v'_i} = \frac{-p(v'_i + v'_j)}{[1 - v'_i - v'_j + p(v'_i + v'_j)]^2} + \frac{4p[4(1 - v'_i - v'_j) + 3v'_i + 4v'_j]}{[4(1 - v'_i - v'_j) + pv'_j + 3v'_i + 4v'_j]^2},$$

$$\frac{\partial w}{\partial v'_j} = \frac{-p(v'_i + v'_j)}{[1 - v'_i - v'_j + p(v'_i + v'_j)]^2} + \frac{8p[8(1 - v'_i - v'_j) + 8v'_i + 7v'_j]}{[8(1 - v'_i - v'_j) + pv'_j + 8v'_i + 7v'_j]^2}.$$  \hspace{1cm} (C5a, C5b)

We evaluate (C5) at \( v'_1 = v'_2 = v'_3 = v'_4 = v'_5 \), set both equations to zero, and solve for \( \{v'_1, v'_2\} \). Doing this, we get

\[
v'_1 = \frac{4}{24 - 11p}, \tag{C6a}\]

\[
v'_2 = 2v'_1 = \frac{8}{24 - 11p}. \tag{C6b}\]

Note this is equivalent to the model in the main manuscript with \( z = 12 \), split into two distance classes. In order for this point to be an ESS, it must be a maximum with respect to both \( v_1 \) and \( v_2 \). To check this, we calculate the quantity

\[
D = \left[ \frac{\partial^2 W}{\partial v^2} \right]_{\{v'_1, v'_2\} = \{\bar{v}, \bar{v}\} = \{v_1, v_2\}} \left[ \frac{\partial^2 W}{\partial v^2} \right]_{\{v'_1, v'_2\} = \{\bar{v}, \bar{v}\} = \{v_1, v_2\}} - \left[ \frac{\partial^2 W}{\partial v'_1 \partial v'_2} \right]_{\{v'_1, v'_2\} = \{\bar{v}, \bar{v}\} = \{v_1, v_2\}}^2 \tag{C7}\]

and check that two conditions hold:

\[
D > 0, \tag{C8a}\]

\[
\frac{\partial^2 W}{\partial v^2} \bigg|_{\{v'_1, v'_2\} = \{\bar{v}, \bar{v}\} = \{v_1, v_2\}} < 0. \tag{C8b}\]

The second derivatives are

\[
\frac{\partial^2 W}{\partial v^2} \bigg|_{\{v'_1, v'_2\} = \{\bar{v}, \bar{v}\} = \{v_1, v_2\}} = \frac{-2p(v_1 + v_2)}{[1 - v_1 - v_2 + p(v_1 + v_2)]^3} + \frac{-8p^2[4(1 - v_1 - v_2) + 3pv_1 + 4pv_2]}{[4(1 - v_1 - v_2) + 4p(v_1 + v_2)]^3}, \tag{C9a}\]

\[
\frac{\partial^2 W}{\partial v^2} \bigg|_{\{v'_1, v'_2\} = \{\bar{v}, \bar{v}\} = \{v_1, v_2\}} = \frac{-2p(v_1 + v_2)}{[1 - v_1 - v_2 + p(v_1 + v_2)]^3} + \frac{-16p^2[8(1 - v_1 - v_2) + 8pv_1 + 7pv_2]}{[8(1 - v_1 - v_2) + 8p(v_1 + v_2)]^3}, \tag{C9b}\]

\[
\frac{\partial^2 W}{\partial v^2} \bigg|_{\{v'_1, v'_2\} = \{\bar{v}, \bar{v}\} = \{v_1, v_2\}} = \frac{-2p(v_1 + v_2)}{[1 - v_1 - v_2 + p(v_1 + v_2)]^3}. \tag{C9c}\]
By grouping terms and noting that $1 - v_1$ and $1 - v_1 - v_2$ are both nonnegative, we can see that the right-hand side of equation (C9a) is negative, and so condition (C8b) holds. We can write out the quantity $D$ as

\[
D = \left[\frac{-2p(v_1 + v_3)}{[1 - v_1 - v_2 + p(v_1 + v_2)]}\right]^2 + \left[\frac{-2p(v_1 + v_3)}{[1 - v_1 - v_2 + p(v_1 + v_2)]}\right]^2 + \left[\frac{-2p(v_1 + v_3)}{[1 - v_1 - v_2 + p(v_1 + v_2)]}\right]^2 + \left[\frac{-2p(v_1 + v_3)}{[1 - v_1 - v_2 + p(v_1 + v_2)]}\right]^2.
\]

Again, by grouping terms, we see that $D > 0$, so condition (C8a) holds. This confirms that this critical point is a maximum with respect to both $v_1$ and $v_2$ and is therefore an ESS.

Local Dispersal, \( D \) Distance Classes

Finally, we can extend this last model up to \( D \) dispersal distances. As before, only a fraction \( p \) of dispersing offspring survives. Offspring dispersing a distance of 1 and surviving are distributed equally among each of the four sites, offspring dispersing a distance of 2 and surviving are distributed equally among each of the eight sites, and generally, offspring dispersing a distance \( i \) and surviving are distributed equally among each of the \( 4i \) sites (up to distance \( i = D \)). Here we let \( \{v_1, v_2, ..., v_D\} \) and \( \{v'_1, v'_2, ..., v'_D\} \) be the resident and mutant dispersal strategies, respectively, and look for \( \{v^*_1, v^*_2, ..., v^*_D\} \), the ESS dispersal strategy.

The mutant produces

\[
\left(1 - \sum_{i=1}^{D} v'_i\right)n
\]

offspring that stay at its home site. The resident-type individuals in the four sites at distance 1 from the mutant’s home site each produce \( v_1 np \) offspring that disperse and survive, a quarter of which arrive at the mutant’s home site, for a total of \( 4v_1 np/4 \). The resident-type individuals in the eight sites at distance 2 from the mutant’s home site each produce \( v_2 np \) offspring that disperse and survive, an eighth of which arrive at the mutant’s home site, for a total of \( 8v_2 np/8 \). Generally, the resident-type individuals in the \( 4i \) sites at distance \( i \) from the mutant’s home site each produce \( v_i np \) offspring that disperse and survive, \( 1/(4i) \) of which arrive at the mutant’s home site, for a total of \( 4iv_i np/(4i) \). So there will be a grand total of

\[
\sum_{i=1}^{D} \frac{4iv_i np}{4i}
\]

resident-type offspring arriving at the mutant’s home site. The probability that the mutant retains its home site is

\[
w_1 = \frac{\left(1 - \sum_{i=1}^{D} v'_i\right)n}{\left(1 - \sum_{i=1}^{D} v'_i\right)n + \sum_{i=1}^{D} (4iv_i np/(4i))}
\]

\[
= \frac{1 - \sum_{i=1}^{D} v'_i}{1 - \sum_{i=1}^{D} v'_i + p \sum_{i=1}^{D} v_i}.
\]

The mutant produces \( v'_1 np \) offspring that disperse a distance 1 and survive and are distributed randomly among the four neighboring sites at distance 1. At each of these sites, they will compete with the

\[
\left(1 - \sum_{i=1}^{D} v_i\right)n
\]

nondispersing offspring that are born and stay at that site, plus the offspring that disperse in from other sites. Each adult at the other three sites at distance 1 from this focal site produce \( v_i np \) offspring that disperse a distance 1 and survive,

a quarter of which land at this focal site, for a total of $3v_1np/4$. Each adult at the eight sites at distance 2 from this focal site, produce $\bar{v}_1np$ offspring that disperse a distance 2 and survive, an eighth of which land at this focal site, for a total of $8\bar{v}_1np/8$. Generally, each adult at the $4i$ sites at distance $i$ from this focal site produce $\bar{v}_1np$ offspring that disperse a distance $i$ and survive, $1/(4i)$ of which land at this focal site, for a total of $4i\bar{v}_1np/(4i)$. The expected number of new sites at distance 1 that the mutant gains is the number of possible sites to gain (four) times the probability of gaining each of them, or

$$w_i = 4\left(\frac{v_1np/4}{v_1np/4 + (1 - \sum_{j=1}^{p}v_1)\pi + 3\bar{v}_1np/4 + \sum_{j=2}^{p}(4i\bar{v}_1np/4i)}\right),$$

$$= \frac{v_1p}{v_1p/4 + 1 - \sum_{j=1}^{p}v_1 + 3\bar{v}_1p/4 + p\sum_{j=1}^{p}v_1}, \quad (D5)$$

$$= \frac{v_1p}{(p/4)(v_1 - \bar{v}_1) + 1 - (1 - p)\sum_{j=1}^{p}v_1}.$$  

Generally, the mutant produces $v_1np$ offspring that disperse a distance $i$ and survive and are distributed randomly among the $4i$ sites at distance $i$. At each site, they will compete with the nondispersing offspring that are born and stay at that site, plus the offspring that disperse in from other sites. Each adult at the $4j$ sites at distance $j$ from this focal site produce $\bar{v}_1np$ offspring that disperse a distance $j$ and survive, $1/(4j)$ of which land at this focal site, for a total of $4j\bar{v}_1np/(4j)$ (except for $j = i$ where there are only $(4j - 1)\bar{v}_1np/(4j)$ resident offspring dispersing in, since one site at distance $i$ is occupied by the mutant). The expected number of new sites at distance $i$ that the mutant gains is the number of possible sites to gain $(4i)$ times the probability of gaining each of them, or

$$w_i = (4i)\left(\frac{v_1np/(4i)}{v_1np/(4i) + (1 - \sum_{j=1}^{p}v_1)\pi - \bar{v}_1np/(4i) + \sum_{j=1}^{p}(4j\bar{v}_1np/4j)}\right),$$

$$= \frac{pv_1'}{(1/4i)p(v_1' - \bar{v}_1) + 1 - (1 - p)\sum_{j=1}^{p}v_1'}. \quad (D7)$$

The total fitness of the mutant type $v'$ in a population of resident types $\bar{v}$ is given by adding the probability of the mutant type retaining its home site (D3) to the expected number of sites at distance $i$ that the mutant gains (D7), summed across $i = 1, ..., D$:

$$w = \frac{1 - \sum_{j=1}^{p}v_1'}{1 - v_1'\sum_{j=1}^{p}v_1' + p\sum_{j=1}^{p}v_1'} + \sum_{i=1}^{p}\left\{\frac{pv_1'}{(1/4i)p(iv_1' - \bar{v}_1i) + 1 - (1 - p)\sum_{j=1}^{p}v_1'}\right\}. \quad (D8)$$

Above, we found that for a maximum dispersal distance of 2 ($D = 2$), we get $v_1' = 2v_1'$, since an individual can reach twice as many sites at distance 2 as at distance 1. Following this pattern, we make the general assumption that $v_1' = iv_1'$, since an individual can reach $i$ times as many sites at distance $i$ as at distance 1. Using this, we can rewrite (D8) as

$$w = \frac{1 - v_1'\sum_{j=1}^{p}iv_1'}{1 - v_1'\sum_{j=1}^{p}iv_1' + p\sum_{j=1}^{p}iv_1'} + \sum_{i=1}^{p}\left\{\frac{ipv_1'}{(1/4i)p(iv_1' - \bar{v}_1i) + 1 - (1 - p)\sum_{j=1}^{p}iv_1'}\right\}. \quad (D9)$$
Noting that $\sum_{i=1}^{D} i = (1/2)D(D + 1)$, we can further simplify this to

$$w = \frac{1 - (1/2)D(D + 1)v_i}{1 - (1/2)D(D + 1)(v_i - p\pi_i)} + \sum_{i=1}^{D} \left\{ \frac{ipv_i}{(1/4)p(v_i - \pi_i) + 1 - (1 - p)(1/2)D(D + 1)\pi_i} \right\},$$

(D10)

To find the ESS $v^*$, we look for critical points by differentiating (D10) with respect to $v_i'$ and dropping the 1 subscript:

$$\frac{\partial w}{\partial v'} = \frac{[2 - D(D + 1)(v - \bar{v})][D(D + 1)] - [2 - D(D + 1)v'][D(D + 1)]}{[2 - D(D + 1)(v' - \bar{v})]^2} + \frac{[4 + p(v' - \bar{v}) - 2D(D + 1)(1 - p)v'] [2D(D + 1)] - [2D(D + 1)p v'][p]}{[4 + p(v' - \bar{v}) - 2D(D + 1)(1 - p)\bar{v}]^2}.$$  

(D11)

We evaluate (D11) at $v' = \bar{v} = v^*$, set it to zero, and solve for $v^*$. Doing this, we get

$$v^* = \frac{4}{p + 2D(D + 1)(2 - p)},$$

(D12)

the probability of dispersing a distance of 1, with the probability of dispersing a distance $i = 2, \ldots, D$ given by $v_i^* = iv^*$. Note this is equivalent to the model in the main manuscript with $z = 2D(D + 1)$, split into $D$ distance classes.

As above, we check whether this point is an ESS by checking the sign of the second derivative, evaluated at the following point:

$$\frac{\partial^2 w}{\partial v'^2} \bigg|_{v' = v^*} = -\frac{2pv[D(D + 1)]^2}{[2 - D(D + 1)(1 - p)v]^3} + \frac{-4D(D + 1)p\bar{v}[4 - pv - 2D(D + 1)(1 - p)v]}{[4 - 2D(D + 1)(1 - p)v]^3}. $$

(D13)

Individual-Based Model Details

Initialization

At the start of a simulation, one individual is placed in each viable site in the environment. Every individual starts with an initial dispersal strategy of \( K = \{1, 0, 0, \ldots, 0\} \). In other words, all individuals start by always staying at the natal site (dispersing a distance of 0). The final evolved probabilities were not qualitatively different if different initial conditions (e.g., a uniform distribution among all dispersal probabilities) were used (fig. E1A vs. E1B). However, running simulations with uniform initial conditions in the seascape simulations (31 dispersal classes) led to population extinction in approximately six generations.

![Figure E1: Examples of the average probability \( (k_d) \) in the population of dispersing a distance \( d \) over the course of a single simulation in an unbounded world with potential dispersal distances \( d = \{0, 1, 2, 3\} \) and probability of surviving dispersal \( p = 0.2 \). These simulations were run with two different initial conditions: all individuals started by always dispersing a distance of 0 (a) and all individuals started by having an equal probability of dispersing a distance of 0, 1, 2, or 3 (b), yet both generate approximately the same final result.](image)

Input Data

The model takes as input data the environmental structure, which is generated before the simulations start and does not change during the course of a simulation or between simulations that are run in the same environment. The environmental structure consists of two components. First, a two-dimensional array that denotes which sites are viable and which are nonviable. Four different types of two-dimensional environmental structures were used (fig. 1): (1) a set of viable sites with periodic boundary conditions (wrapping boundaries); (2) a set of homogeneous viable sites, surrounded by nonviable sites; (3) a patchy (heterogeneous) set of viable sites, surrounded by nonviable sites; and (4) a seascape of viable sites, surrounded by nonviable sites (for confrontation with real data). Second, a three-dimensional array that
denotes which sites in the environment can be reached by traveling any dispersal distance (0, 1, ..., \(d_{\text{max}}\)) starting from any of the viable sites as a starting point.

The first environment was constructed as a set of \(S(S = 1,024)\) viable sites arranged in a square. The second environment was similarly a set of \(S(S = 1,024)\) viable sites but surrounded on each side by \(d_{\text{max}} + 1\) nonviable sites, to ensure that an individual dispersing from a viable site could not possibly disperse off the edge of the total environment. Three different arrangements of the \(S\) viable sites were considered: \(32 \times 32, 8 \times 128,\) and \(2 \times 512\) arrays. This kept the total habitat area constant, while increasing the edge. The third environment was again a set of \(2 \times 512\) viable sites, surrounded by \(d_{\text{max}} + 1\) nonviable sites, but with each viable site assigned a breeding resource value \(b_i\), drawn from a uniform random distribution. We considered three levels of breeding resource heterogeneity (all with the same average value of \(b\)): low \((b_i\) between 7 and 13), medium \((b_i\) between 3 and 17), and high \((b_i\) between 0 and 20).

The final, seascape environment was generated from a map of the Belize Barrier Reef in ArcMap 10.1 (ESRI). We focused only on the forereef zone, where Elacatinus lori is most abundant (D’Aloia et al. 2011). We trimmed the reef so that the forereef was never \(>1\) km wide because \(E. lori\) are found on the outer reef slope, which never exceeds this width (C. C. D’Aloia and P. M. Buston, personal observation). To produce a map of potential habitat sites within the seascape, we created a grid of \(1\) km\(^2\) polygons. We overlaid the forereef onto the grid and coded individual polygons as 1 (suitable) or 0 (unsuitable) based on whether the grid contained forereef. In the seascape environment, there were \(S = 507\) viable sites.

To generate the dispersal array, for each of the \(S\) possible starting sites and for each dispersal distance \((i = 0, 1, ..., d_{\text{max}})\), we recorded the \(4i\) sites located a distance \(i\) away from the starting site (the Von Neumann neighborhood at distance \(i\)).

Simulations

We ran four sets of simulations, for a total of 94 simulation runs. Simulations were run in the homogeneous world without edges for 10 values of \(p\) \((0.1, 0.2, ..., 1)\), and three values of maximum dispersal distance \(d_{\text{max}}\) \((1, 2, \text{and } 3)\). Simulations were run in the homogeneous world with edges for three site configurations \((32 \times 32, 8 \times 128, \text{and } 2 \times 512)\), 10 values of \(p\) \((0.1, 0.2, ..., 1)\), and with \(d_{\text{max}} = 3\). Third, simulations were run in the patchy bounded world for three levels of heterogeneity in the breeding resource per site, \(b\) (low, medium, high), for 10 values of \(p\) \((0.1, 0.2, ..., 1)\), with \(d_{\text{max}} = 3\). Finally, simulations were run in the seascape for four levels of heterogeneity in the breeding resource per site (none, low, medium, high), with \(p = 1\) and \(d_{\text{max}} = 30\).

**Figure E2:** Examples of the average probability \((k_i)\) in the population of dispersing a distance \(d\) over the course of a single simulation in the seascape with potential dispersal distances, \(d = \{0, 1, ..., 30\}\). The reproductive payoff of each viable patch was drawn from a distribution between three and 17. Here distances above three are indistinguishable from each other.
Figure E3: Comparison of simulated and empirical dispersal in the Belizean seascape. Relative frequency plots across all dispersal distance bins for empirical data versus simulated data in a seascape with no patchiness (a), low patchiness (b), medium patchiness (c), and high patchiness (d).