

# Evolution of dispersal in a spatially heterogeneous population with finite patch sizes

Kalle Parvinen<sup>a,b,1</sup> , Hisashi Ohtsuki<sup>c</sup>, and Joe Yuichiro Wakano<sup>d,e</sup>

<sup>a</sup>Department of Mathematics and Statistics, University of Turku, FI-20014 Turku, Finland; <sup>b</sup>Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria; <sup>c</sup>Department of Evolutionary Studies of Biosystems, School of Advanced Sciences, The Graduate University for Advanced Studies, SOKENDAI, Hayama, Kanagawa 240-0193, Japan; <sup>d</sup>Department of Mathematical Sciences Based on Modeling and Analysis, School of Interdisciplinary Mathematical Sciences, Meiji University, Tokyo 164-8525, Japan; and <sup>e</sup>Mathematical Modeling and Analysis Division, Meiji Institute for Advanced Study of Mathematical Sciences, Tokyo 164-8525, Japan

Edited by Alan Hastings, University of California, Davis, CA, and approved February 18, 2020 (received for review September 12, 2019)

**Dispersal is one of the fundamental life-history strategies of organisms, so understanding the selective forces shaping the dispersal traits is important. In the Wright's island model, dispersal evolves due to kin competition even when dispersal is costly, and it has traditionally been assumed that the living conditions are the same everywhere. To study the effect of spatial heterogeneity, we extend the model so that patches may receive different amounts of immigrants, foster different numbers of individuals, and give different reproduction efficiency to individuals therein. We obtain an analytical expression for the fitness gradient, which shows that directional selection consists of three components: As in the homogeneous case, the direct cost of dispersal selects against dispersal and kin competition promotes dispersal. The additional component, spatial heterogeneity, more precisely the variance of so-called relative reproductive potential, tends to select against dispersal. We also obtain an expression for the second derivative of fitness, which can be used to determine whether there is disruptive selection: Unlike the homogeneous case, we found that divergence of traits through evolutionary branching is possible in the heterogeneous case. Our numerical explorations suggest that evolutionary branching is promoted more by differences in patch size than by reproduction efficiency. Our results show the importance of the existing spatial heterogeneity in the real world as a key determinant in dispersal evolution.**

dispersal | evolutionarily stable strategy | evolutionary branching | metapopulation model

**D**ispersal is a basic characteristic of many living organisms, and its adaptive significance has been widely investigated (1–6). One obvious benefit of dispersal is the potential to find a better habitat, such as colonization of empty sites (3). Counter to our intuition, however, in many models that assume large patch sizes it has been observed that equilibrium population dynamics result in evolution of no dispersal (7–10). Under such circumstances, if the local growth conditions are heterogeneous among patches, equilibrium population sizes are typically larger in patches with larger growth rates. Therefore, a dispersing individual on average arrives in worse conditions than the original ones, leading to evolution of no dispersal.

In contrast to equilibrium population dynamics, cyclic or chaotic local population dynamics may select for positive dispersal and even allow divergence of traits (8, 10–13), a phenomenon called evolutionary branching (14–16). In particular, when local population sizes fluctuate out of phase, so that at some moment in time some local populations are small and others large, and at other times roles are reversed, a dispersing individual may be able to sample mostly good growth conditions, giving the individual selective advantage (8). Also environmental stochasticity, in which for example the carrying capacities of local populations fluctuate (17, 18), may result in temporal heterogeneity promoting dispersal and evolutionary branching. Temporal heterogeneity can be caused

also by local catastrophes, which wipe out a local population but leave the patch habitable, so that dispersers may recolonize the patch (9, 10, 19–22). Especially, local catastrophes result in empty patches, dispersal into which is often beneficial. Therefore, increasing the catastrophe rate moderately may select for dispersal. Evolutionary branching of dispersal has been observed in metapopulation models with local catastrophes, when there are different patch types with different growth conditions or catastrophe rates (22). The contrasting effects of different kinds of heterogeneity suggest that the type of heterogeneity that exists in the population and its interplay with demographic dynamics therein are major determinants of evolutionary consequences.

In addition, small local population size also influences evolution of dispersal. When local patches are small, local population dynamics can be stochastic due to a small number of individuals, and growth conditions fluctuate in time, resulting in yet another form of temporal heterogeneity promoting dispersal (23, 24). Even if there is no stochasticity in local patch size, as is often assumed in population genetics models, another factor promoting dispersal emerges, that is, kin competition (2, 25–30). Each individual may have relatives in the same patch. When the number of patches is large (infinite), a dispersing individual will typically arrive in a patch without relatives, and nondispersing relatives in the original patch will gain advantages for example in a form of better resource availability.

## Significance

**Organisms are known to invest resources to disperse their offspring. Plants produce fruits, although fruit eaters do not promise to disperse seeds to the right places. According to a classical theory, costly dispersal can evolve because dispersing individuals can avoid competition among their own offspring. The textbook formulas of evolutionarily stable dispersal strategies, however, assume the same living conditions everywhere. Here we present formulas predicting the dispersal probability in spatially heterogeneous environments. In the real world, no environment is homogeneous as assumed in the classical theory, so our results bring in important achievements. In heterogeneous environments the evolved dispersal probability can be much lower than in homogeneous ones, and also diversification in dispersal strategies is possible.**

Author contributions: K.P., H.O., and J.Y.W. designed research, performed research, and wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

This open access article is distributed under [Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 \(CC BY-NC-ND\)](https://creativecommons.org/licenses/by-nc-nd/4.0/).

<sup>1</sup>To whom correspondence may be addressed. Email: [kalparvi@utu.fi](mailto:kalparvi@utu.fi).

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1915881117/-DCSupplemental>.

In other words, dispersal can be indirectly beneficial through kin selection because it mitigates kin competition within the same patch.

In a natural population, multiple factors favoring or disfavoring dispersal often exist at the same time, so to fully understand selective forces acting on dispersal traits, it is necessary to reveal relative impacts of each factor and their interactions. In this article we study the evolution of dispersal probabilities in a heterogeneous island model, in which local population sizes are fixed, but may differ between different patch types. Different patch types may also convey different fecundity to native individuals there. Spatial heterogeneity and kin competition, as well as direct cost of dispersal, are thus among mechanisms affecting dispersal evolution in this model.

We analytically derive explicit expressions for the first-order and second-order effects of natural selection acting on dispersal. A direct comparison with a spatially homogeneous model reveals that spatial heterogeneity generally selects against dispersal, and this effect is characterized by an additional term appearing in our formula. We complement the analysis with numerical calculations and unveil the relative impacts of different types of heterogeneity on dispersal evolution and the interaction between spatial heterogeneity and kin competition. Additionally, we observe that spatial heterogeneity favors evolutionary branching of dispersal traits, which is in stark contrast to a homogeneous version of our model where evolutionary branching of dispersal has been shown to be impossible (31).

### Multitype-Island Model

We consider an extended version of Wright's island model (32), which consists of infinitely many habitat patches (demes). We include the possibility for spatial heterogeneity (33), so that patches can be of  $N$  different types. The proportion of patches of type  $k$  is  $\pi_k$ , and naturally their sum is equal to one,  $\sum_{k=1}^N \pi_k = 1$ .

In the beginning of the season each patch of type  $k$  contains  $n_k$  adult individuals. Fecundity in patches of type  $k$  is  $\gamma F_k$  that represents the number of juveniles that each adult produces. Throughout this paper,  $\gamma$  is considered to be very large (actually  $\gamma \rightarrow \infty$ ).

Individuals may differ in their emigration probability  $m$ ,  $0 < m \leq 1$ , which is the proportion of juveniles that will disperse. The proportion  $0 < p \leq 1$  of dispersed juveniles will survive dispersal and land independently in a random patch. The probability to arrive in a patch of type  $k$  is assumed to be  $\phi_k$ , and  $\sum_{k=1}^N \phi_k = 1$ . The relation  $\lambda_k = \phi_k / \pi_k$  describes how strongly patches of type  $k$  attract immigrants. In the standard case  $\lambda_k = 1$ , so that  $\phi_k = \pi_k$  and all patches receive the same amount of immigrants. The present adults are assumed not to survive until the next season. The patch size is assumed to be fixed, so that the  $n_k$  individuals to become adults in a patch of type  $k$  in the next season are randomly chosen among the juveniles in each patch after immigration.

### Evolution of Dispersal

**Metapopulation Reproduction Number and Fitness Gradient.** Next we study how a rare mutant with emigration strategy  $m_{\text{mut}}$  performs in an environment set by a resident with strategy  $m$ . We calculate the metapopulation reproduction number (metapopulation fitness)  $R_m(m_{\text{mut}}, m)$  (21, 23). A mutant may successfully invade the resident, if  $R_m(m_{\text{mut}}, m) > 1$ . We obtain an explicit expression for the fitness gradient  $D_1(m) = \frac{\partial}{\partial m_{\text{mut}}} R_m \Big|_{m_{\text{mut}}=m}$  in *SI Appendix, section 2.A*. The fitness gradient provides the direction of selection pressure: If  $D_1(m) > 0$ , then mutants with  $m_{\text{mut}} \approx m$  may invade the resident only if  $m_{\text{mut}} > m$ . Analogously, for  $D_1(m) < 0$ , invasion is possible only if  $m_{\text{mut}} < m$ .

Patch types, in which the product of patch size  $n_k$  and fecundity  $F_k$  divided by attractiveness  $\lambda_k$  is large compared with other patch types, have large "relative reproductive potential"

$$V_k = \frac{n_k F_k / \lambda_k}{\sum_{l=1}^N \pi_l n_l F_l} = \frac{n_k F_k / \lambda_k}{\sum_{l=1}^N \phi_l n_l F_l / \lambda_l}. \quad [1]$$

This potential is measured from the point of view of an immigrant at a type- $k$  patch. Large  $\lambda_k$  means strong competition because of a large amount of immigrants, so that the relative reproductive potential may be low. We note that this reproductive potential is normalized so that its expectation with respect to the arrival distribution is  $E[V] \equiv \sum_{k=1}^N \phi_k V_k = 1$ .

It is quite natural that  $V_k$  appears in the selection gradient, but it is surprising to observe that spatial heterogeneity is present in the form of variance of the relative reproductive potential

$$\text{Var}[V] = \sum_{k=1}^N \phi_k (V_k - \underbrace{E[V]}_{=1})^2 \geq 0 \quad [2]$$

in the selection gradient

$$\begin{aligned} D_1(m) &= \frac{\partial}{\partial m_{\text{mut}}} R_m \Big|_{m_{\text{mut}}=m} \\ &= -\frac{1-p}{mp} - \frac{1}{mp} \text{Var}[V] + \frac{1}{mp} \sum_{k=1}^N \phi_k V_k^2 R_{2,k} (1-d_k), \end{aligned} \quad [3]$$

where  $d_k$  is the backward migration probability, i.e., the proportion of adults that are immigrant in a monomorphic population in a patch of type  $k$ ,

$$d_k = \frac{mp}{(1-m)V_k + mp}, \quad [4]$$

and  $R_{2,k}$  is the relatedness between two adults (including self) in the same type- $k$  patch

$$R_{2,k} = \frac{1}{n_k - (n_k - 1)(1-d_k)^2}. \quad [5]$$

Eq. 3 can be interpreted also in terms of inclusive fitness; see *SI Appendix, section 2.A.2* for details.

For the simpler model with just one patch type ( $N = 1$ , so that  $V_1 = 1$ ,  $\pi_1 = \phi_1 = 1$ , and  $\text{Var}[V] = 0$ ), Eq. 3 becomes

$$D_1(m) = \frac{1}{mp} (-(1-p) + R_2(1-d)), \quad [6]$$

which is sign equivalent with a previously derived measure of directional selection for a homogeneous population (29).

Eq. 3 provides an interesting viewpoint for the evolution of dispersal, because all three components have a clear interpretation. The first two terms show the negative effects of the cost of dispersal  $c = 1 - p$  and variance of the relative reproductive potential (spatial heterogeneity)  $\text{Var}[V]$ . In contrast, the third term is always nonnegative. For large patch sizes,  $n_k \rightarrow \infty$ , relatedness goes to zero,  $R_{2,k} \rightarrow 0$ . The third term can thus be understood to incorporate the effect of kin competition on the directional selection of dispersal.

**A Unique Singular Strategy.** If we let  $m$  approach zero, we have

$$\lim_{m \rightarrow 0} m D_1(m) > 0. \quad [7]$$

The strategy boundary  $m = 0$  is thus evolutionarily repelling, and dispersal never evolves to zero in this model. Singular strategies

$m^*$  are such strategies, at which directional selection vanishes; i.e.,  $D_1(m^*) = 0$ . By differentiating  $D_1(m)$  we have  $D_1'(m^*) < 0$ . Therefore, any singular strategy is evolutionarily attracting, and the singular strategy is unique.

We conclude that evolution will take dispersal to the unique singular strategy  $m^*$ . If there is no cost of dispersal ( $p = 1$ ) and there is no variation in reproductive potential ( $\text{Var}[V] = 0$ ), complete dispersal ( $m^* = 1$ ) will evolve; otherwise intermediate dispersal,  $0 < m^* < 1$ , evolves.

In the case that there is just one patch type,  $N = 1$ , the fitness gradient Eq. 3 takes a simpler form Eq. 6, from which the singular strategy can be solved, resulting in (where  $n_1 = n$ )

$$m^* = \frac{1 + 2n(1-p) - \sqrt{1 + 4n(n-1)(1-p)^2}}{2n(1-p)(2-p)}, \quad [8]$$

which with  $c = 1 - p$  is familiar from previous work (ref. 31, equation 14); see also ref. 28. For  $n = 1$  Eq. 8 becomes the classical Hamilton–May (2) result  $m^* = 1/(2 - p)$ .

**Evolutionary Branching.** A singular strategy  $m^*$  is uninvadable, if  $R_m(m_{\text{mut}}, m^*) < 1$  for all  $m_{\text{mut}} \neq m^*$ . Such a strategy is also called an evolutionarily stable strategy (ESS) (34, 35) and it is a fitness maximum with respect to the strategy of the mutant, so that the second derivative  $D_2(m^*) < 0$ , where  $D_2(m) = \frac{\partial^2}{\partial m_{\text{mut}}^2} R_m \Big|_{m_{\text{mut}} = m}$ . However, if  $D_2(m^*) > 0$ , the singular strategy can be invaded by nearby mutants, so that the population will begin to consist of two parts having different strategies, and disruptive selection will cause these strategies to evolve farther away from each other. Such a process is called evolutionary branching (15, 16). For the present model, we have derived an explicit expression also for the second derivative  $D_2(m)$ , and it is given in [SI Appendix, Eq. S2.38](#). The expression includes the second and third moments of  $V$ .

In case there is just one patch type,  $N = 1$ , it has been shown that  $D_2(m^*) < 0$ , so that evolutionary branching is not possible (31). Although it is not so easy to draw general conclusions from [SI Appendix, Eq. S2.38](#), the format suggests that evolutionary branching can happen when there is spatial heterogeneity in the form of variability in relative reproduction potential  $V_k$ . Next we confirm our expectation with numerical investigations.

### Mechanisms Affecting the Evolution of Dispersal

Above, we recognized three mechanisms affecting the selection gradient, Eq. 3, and we next discuss each in turn.

**Direct Cost of Dispersal Selects against Dispersal.** Increasing the direct cost of dispersal  $c = 1 - p$  decreases the first term of the fitness gradient, Eq. 3. One could naively expect that this would cause the singular dispersal strategy  $m^*$  to decrease with  $c$ . However, increasing  $c$  decreases the backward migration probability  $d_k$ , and therefore both  $1 - d_k$  and relatedness  $R_{2,k}$  increase. Therefore, kin competition, depicted in the third term of the fitness gradient, increases with  $c$ . It is not so obvious what the total effect of these two opposing forces on the evolution of dispersal is. Actually, there is a previous work showing that dispersal strategies may even increase with increasing dispersal cost (36). With careful analysis of Eq. 3 presented in [SI Appendix, section 2.B.2](#), we have proved that the fitness gradient  $D_1(m)$  decreases with  $c$ , and therefore the singular strategy  $m^*$  does indeed decrease with  $c = 1 - p$  ([SI Appendix, Fig. S1](#)).

[SI Appendix, Fig. S1](#) also illustrates that evolutionary branching is possible, when the cost of dispersal is small enough. The

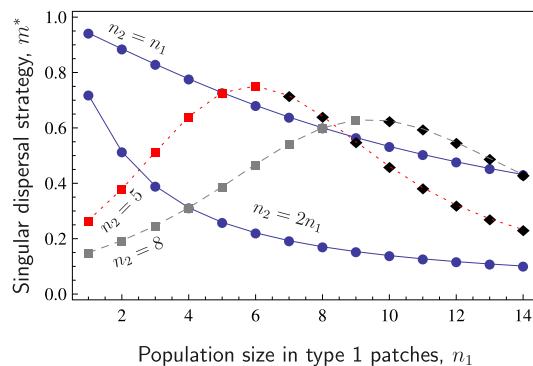
presence of substantial spatial heterogeneity is also necessary, as is discussed below.

**Kin Competition Promotes Dispersal.** A dispersing individual gets an indirect benefit, because dispersal mitigates kin competition within the same patch. The third term of the fitness gradient, Eq. 3, measures this effect. If the relatednesses  $R_{2,k}$  decrease without affecting other relevant quantities, the singular dispersal strategy  $m^*$  obviously decreases. Such a situation takes place, if all patch sizes  $n_1, \dots, n_N$  increase together, while keeping their relative magnitudes  $n_i/n_k$  fixed (while also keeping fecundities  $F_k$  and attractiveness  $\lambda_k$  fixed). Then the relative reproductive potential  $V_k$  does not change although  $R_{2,k}$  decreases, and thus  $m^*$  decreases with patch sizes. Fig. 1 illustrates two such cases ( $n_2 = n_1$  and  $n_2 = 2n_1$ , solid curves).

However, if only one patch size changes, then the relative reproductive potentials also change, and so does their variance  $\text{Var}[V]$ , which appears in the second term of the fitness gradient. When  $n_1 F_1/\lambda_1 \geq n_2 F_2/\lambda_2$ , increasing  $n_1$  will both increase  $\text{Var}[V]$  and decrease relatedness  $R_{2,k}$ , both of which will select against dispersal (Fig. 1, dashed curves with black diamonds). However, when  $n_1 F_1/\lambda_1 < n_2 F_2/\lambda_2$ , increasing  $n_1$  will decrease the variance, and its increasing effect on dispersal may be stronger, so that  $m^*$  increases with  $n_1$  (Fig. 1, dashed curves with squares).

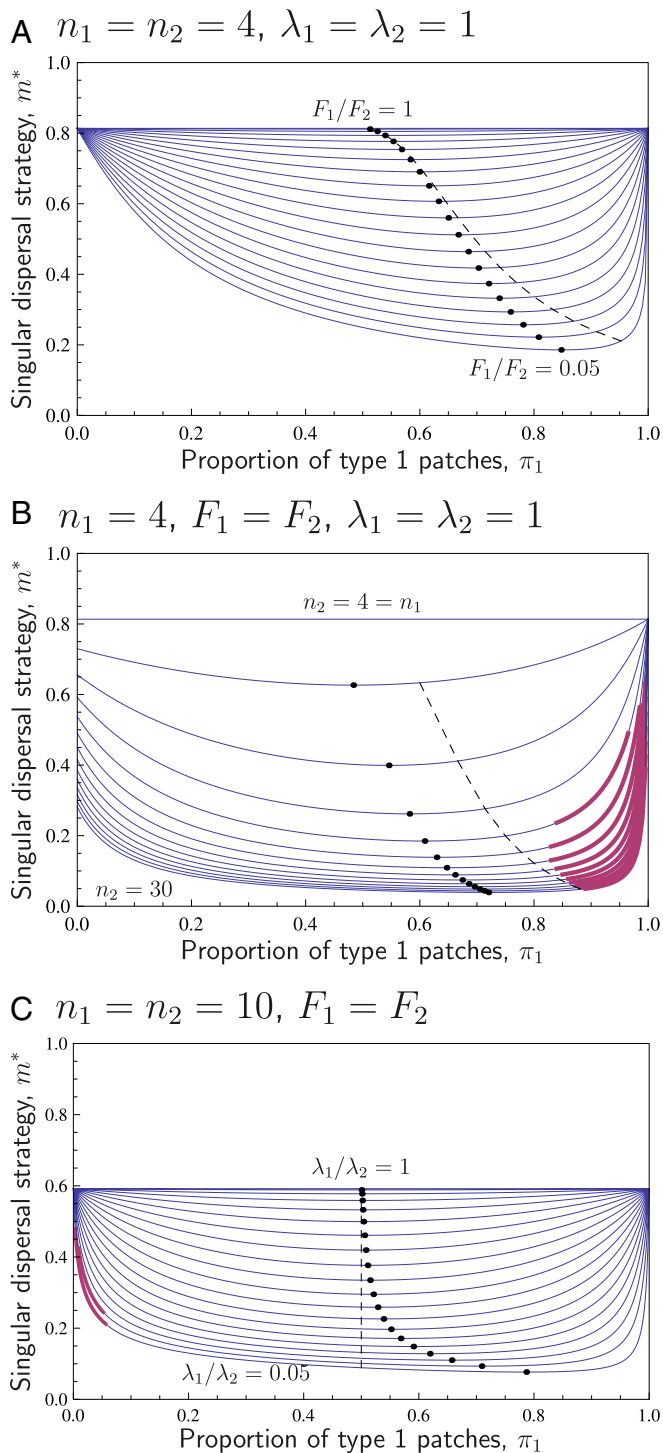
**Spatial Heterogeneity Selects against Dispersal.** The second term of the fitness gradient, Eq. 3, makes it clear that the anticipated effect of spatial heterogeneity against dispersal is depicted through the variance of the relative reproductive potential  $\text{Var}[V]$ , which depends on relative fecundities, patch sizes, and attractiveness.

Fig. 2 shows the evolutionarily singular dispersal strategies in a metapopulation with two patch types as a function of  $\pi_1$ , the proportion of patches of type 1. For  $\pi_1 = 0$  and  $\pi_1 = 1$  the metapopulation is spatially homogeneous, and the singular dispersal strategies are those given by Eq. 8, which is independent of fecundity. For spatially heterogeneous metapopulations (intermediate proportion  $\pi_1$ ), singular dispersal strategies can be considerably smaller than in the homogeneous ones, independent of the cause (different fecundities, patch sizes, or attractiveness) of variance of the relative reproductive potential  $\text{Var}[V]$ . One should, however, note that the relative reproductive potential affects also the third term of the fitness gradient, and therefore



**Fig. 1.** Kin competition promotes dispersal. Shown are singular strategies for different patch sizes  $n_1$  and  $n_2$  in a model with two patch types ( $N = 2$ ). Solid lines connect cases in which both patch sizes are changed while keeping their proportion  $n_1/n_2$  fixed (circles). Dashed lines connect cases in which only  $n_1$  is changed and  $n_2$  remains fixed (squares and diamonds). For squares  $n_1 F_1/\lambda_1 \geq n_2 F_2/\lambda_2$  and for diamonds  $n_1 F_1/\lambda_1 < n_2 F_2/\lambda_2$ . Parameters:  $\pi_1 = 0.5$ ,  $F_1/F_2 = 0.8$ ,  $p = 0.95$ ,  $\lambda_1 = \lambda_2 = 1$ .





**Fig. 2.** (A–C) Heterogeneity in (A) fecundities only, (B) patch sizes only, and (C) attractiveness only. Shown are singular dispersal strategies as a function of  $\pi_1$  for different values of (A)  $F_1/F_2$ , (B)  $n_2$ , and (C)  $\lambda_1/\lambda_2$ , when other parameters are as given in the panel headings. Branching points are shown as thick solid lines. The minimal dispersal strategies with respect to  $\pi_1$  are marked with dots. The dashed curve marks where  $\text{Var}[\mathbf{V}]$  reaches its maximum. Parameters:  $\rho = 0.95$ .

the smallest dispersal strategy (marked with a dot) is not reached at the point at which  $\text{Var}[\mathbf{V}]$  reaches its maximum (marked with a dashed curve).

In Fig. 2B, increasing  $n_2$  not only increases  $\text{Var}[\mathbf{V}]$ , but also decreases relatedness  $R_{2,2}$ . For this reason evolutionarily singular

dispersal strategies are considerably lower in Fig. 2B than in Fig. 2A for the same  $\text{Var}[\mathbf{V}]$ . As Fig. 2 does not directly show  $\text{Var}[\mathbf{V}]$ , it is easier to make such a conclusion based on Fig. 3, which shows singular dispersal strategies with respect to  $\text{Var}[\mathbf{V}]$ .

### Evolutionary Branching Is Promoted by Differences in Patch Size.

In contrast to the qualitative behavior of magnitude of singular strategies, the potential for evolutionary branching is very much affected by the cause of variance of the relative reproductive potential  $\text{Var}[\mathbf{V}]$ . Fig. 2A illustrates the case when patch sizes are the same, but fecundities are different. Evolutionary branching is possible in such situations, but the parameter range where it can happen is extremely narrow (illustrated in *SI Appendix, section 3*). The area increases when the patch sizes are increased, but remains narrow (*SI Appendix, Fig. S3*). In contrast, when patch sizes are different, but fecundities are the same, evolutionary branching happens in a wide parameter range (Fig. 2B and *SI Appendix, Fig. S4*). Evolutionary branching is thus promoted by differences in patch size.

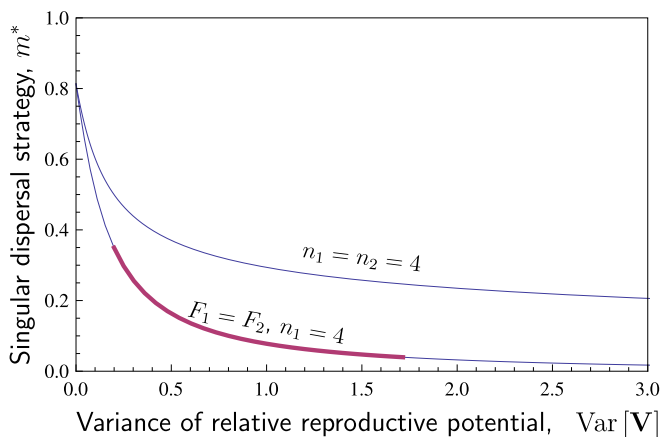
Fig. 2C illustrates that evolutionary branching is possible also when patches differ only in attractiveness. However, patch attractiveness proportional to its size,  $\lambda_k \propto n_k$  (*SI Appendix, Eq. S3.1*), can mitigate the effect of variability in patch size on the variance of the relative reproductive potential, so that  $\text{Var}[\mathbf{V}] = 0$ , preventing evolutionary branching (*SI Appendix, Fig. S5*).

Fig. 4 illustrates the consequences of evolutionary branching. Fig. 4A is based on analyzing the metapopulation fitness, whereas Fig. 4B illustrates an individual-based simulation. The complementary approaches show that evolutionary branching in this case results in the evolutionarily stable coexistence of two rather different dispersal strategies. See also *SI Appendix, section 4*.

### Discussion

Understanding the effect of heterogeneity in the population on evolution of dispersal requires considering many relevant factors; some favor more dispersal, others favor less, and some other conditions cause even disruptive selection. Here we assumed a heterogeneous Wright's island model and analytically derived general expressions of first- and second-order effects of natural selection on dispersal trait,  $m$ . Our model contains heterogeneity in three aspects. First, patches of different types may have different size, or adult carrying capacity,  $n_k$ . Second, individuals in patches of different types may have different types of interactions with environments, which yield different fecundities,  $F_k$ . Third, different patches attract immigrants with different attractiveness  $\lambda_k$ . In the presence of those heterogeneous factors, we asked how they affect the evolution of dispersal traits and which heterogeneity is important.

Directional selection, which was calculated as  $D_1(m)$  in Eq. 3, is used to determine the singular level of dispersal. We have proved that this singular dispersal strategy is unique and evolutionarily attracting (convergence stable). The directional selection consists of three terms, each corresponding to a negative effect of dispersal cost, a negative effect of heterogeneity, and a positive effect of kin competition. The first and the third terms can be considered as the generalized versions of direct cost and indirect benefit (due to kin competition) in classical studies on a homogeneous population (ref. 29 and *SI Appendix, section 2.A.2*). The second term is specific to heterogeneous populations. Very interestingly, we find that the second negative effect is proportional to the variance of (relative) "reproductive potential" of patches. This reproductive potential,  $V_k$ , is a normalized product of  $n_k$ ,  $F_k$ , and  $1/\lambda_k$ . From this result we have concluded that heterogeneity in reproductive potential plays a major role in hindering evolution of dispersal. It has been known that the mixture of good and poor patches in the population may lead to a lower dispersal strategy (22, 30), but we have found that such defined reproductive potential is the appropriate measure



**Fig. 3.** Singular dispersal strategies plotted with respect to the variance of relative reproductive potential  $\text{Var}[V]$  in two cases. In one case, the variance is caused by heterogeneity in fecundities only, so that patch sizes are equal,  $n_1 = n_2 = 4$ , and relative fecundity  $F_1/F_2$  varies from 1 to 0.07. In the other, there is heterogeneity in patch sizes only, so that fecundities are equal,  $F_1/F_2 = 1$ , the patch size  $n_1 = 4$  is fixed, and the patch size  $n_2$  varies from 4 to 58. Parameters:  $\pi_1 = 0.90$ ,  $p = 0.95$ ,  $\lambda_1 = \lambda_2 = 1$ .

of patch goodness. An intuition behind our reproductive potential is that, from a viewpoint of an immigrant, a large patch size means more empty spots, small attractiveness means less competitors there, and large fecundity means more productivity once the immigrant settles there.

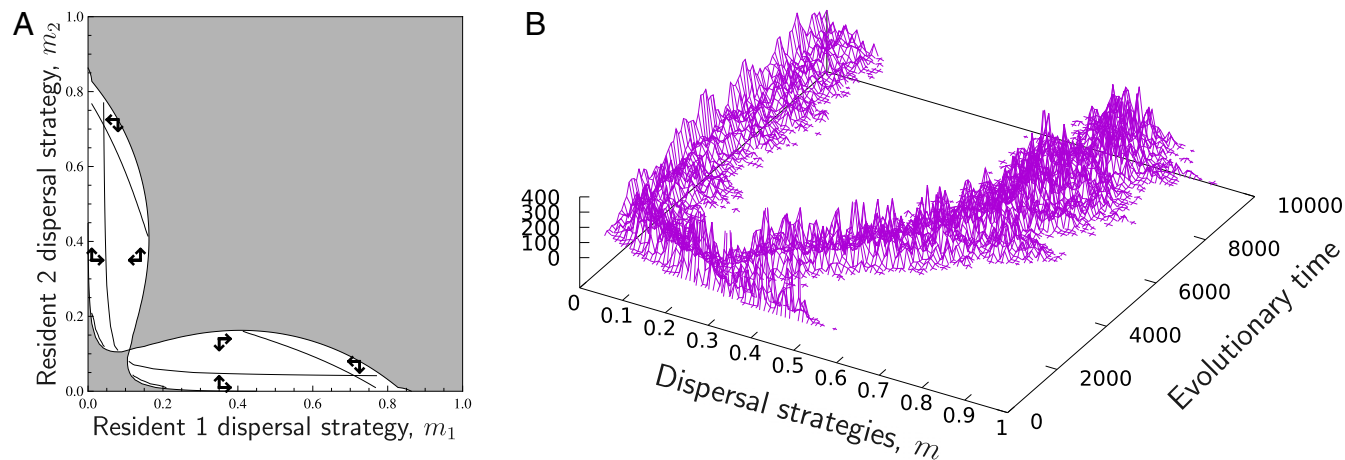
However, we have observed that the kin-competition term in  $D_1(m)$  also includes  $n_k$ ,  $F_k$ , and  $\lambda_k$  in a complex manner, so we have performed numerical calculations, which confirmed that the mixture of two patch types typically leads to smaller dispersal probability (Fig. 2).

Regarding disruptive selection, we have derived its general expression (SI Appendix, section 2.C). We once again found that some moments of reproductive potential matter, and we found that its heterogeneity has a promoting effect on evolutionary branching. Through numerical analysis, we confirmed this. Typically, branching occurs when there are many small patches and few large patches. Heterogeneity in fecundity has only a weak effect on evolutionary branching. Heterogeneity in attractive-

ness only can promote disruptive selection (Fig. 2C), but when attractiveness is proportional to patch size, disruptive selection is greatly hindered (SI Appendix, Fig. S5D) as it cancels the effect of patch size in Eq. 1 and homogenizes the difference in reproductive potentials between patches.

In the real world, no environment is completely homogeneous. Consider, e.g., seed dispersal by wind. All patches might be similar with slight differences. Alternatively, only few small patches might be good, while most patches might be poor (low survivorship or fecundity). If no seeds can survive or reproduce in the poor patches, the situation corresponds to a homogeneous model with only good patches and increased cost of dispersal. Actually, when there are two patch types and the fecundity in a poor type tends to zero, our formula reproduces a classical homogeneous result with increased cost of dispersal (SI Appendix, section 2.B.3). However, if seeds can survive and reproduce even in the poor patches, we cannot neglect such patches. When does heterogeneity have a major impact on the evolution of dispersal? SI Appendix, Fig. S2 suggests that when the proportion of poor patches  $\pi_1$  is small, the homogeneous approximation is relatively good. However, when  $\pi_1$  is large, the poor patches cannot be neglected. In all cases, the homogeneous approximation underestimates the evolutionarily singular dispersal probability.

Also ref. 30 studied the first- and second-order effects of selection on the evolution of dispersal when local patch sizes are finite. While they considered heterogeneity only in patch sizes and revealed the impact of second- and third-order moments of patch size distribution, we considered three different sources of heterogeneity and revealed the importance of the moments of reproductive potentials. Qualitatively, our result is in line with their finding that disruptive selection occurs when the environment consists of many small and few large patches. A technical yet important difference to position our results in the literature is that we have adopted the Wright–Fisher updating, which has been assumed in many previous studies of dispersal evolution, whereas ref. 30 adopted death–birth Moran updating, which enabled them to derive much simpler analytic expressions than ours. Due to this difference, our result does not quantitatively contain results of ref. 30 as special cases. One advantage of our results is that we can directly compare our formula with classical ones (2, 28, 29).



**Fig. 4.** Evolutionary branching. (A) Area of protected coexistence (white area), in which  $R_m(m_2, m_1) > 1$  and  $R_m(m_1, m_2) > 1$ , together with the isoclines and direction of the dimorphic selection gradient. The dimorphic evolutionarily stable strategy coalition ( $m_1 \approx 0.042$ ,  $m_2 \approx 0.71$ , or vice versa) is located at the intersection of the isoclines. (B) Individual-based evolutionary simulation, in which evolutionary branching results in the coexistence of two strategy groups, centered around the dimorphic strategy coalition. Parameters:  $n_1 = 4$ ,  $n_2 = 20$ ,  $\lambda_1 = \lambda_2 = 1$ ,  $F_1/F_2 = 1$ ,  $\pi_1 = 0.9$ ,  $p = 0.95$ . Details of B are described in SI Appendix, section 4.

Kin competition due to patch finiteness is the only mechanism that favors dispersal in our model. Therefore, when each patch size goes to infinity, dispersal never evolves in our model, analogous to models with equilibrium population dynamics (7–10). In many previous heterogeneous population models, in which positive dispersal can evolve, different mechanisms promoting dispersal, such as temporal heterogeneity, are present (18, 22, 37), and explicit expressions for directional selection have not been presented. Thus, a direct comparison with those models is difficult, but we can compare our results with them qualitatively. Our results are qualitatively consistent with previous results of spatial heterogeneity disfavoring dispersal (22) and, also in that aspect, that when at least one mechanism promoting dispersal is present, heterogeneity (temporal or spatial) can promote evolutionary branching of dispersal (8, 10–13, 18, 22, 37). In addition, we revealed how to measure relative impacts of different types of heterogeneity on dispersal evolution.

We have considered spatial heterogeneity in patch size, fecundity consequences therein, and patch attractiveness. We can conceive, however, other types of heterogeneity. For example, survivorship of adults has been assumed to be zero in all patches in this paper, but it can generally be different between different patches. Moreover, seed survival probability may depend on dispersal distance, because we can naturally assume that longer dispersal may be riskier. Also, the impact of the combination of spatial and temporal heterogeneity on dispersal evolution will be an interesting future topic.

To conclude, we have found through analytical formulas with reproductive potential that spatial heterogeneity generally selects against evolution of dispersal but promotes evolutionary branching. The impact of heterogeneity in patch size on

evolutionary branching is greater than that in fecundity. These insights tell us that the existence of many low-quality patches in nature, which has not drawn much attention so far in the literature, indeed generates strong evolutionary force on dispersal traits.

## Materials and Methods

The metapopulation reproduction number (metapopulation fitness) is the expected number of dispersing mutant juveniles that are produced by the potential mutant colony of one dispersing mutant juvenile (21, 23). For the present model, its calculation involves first determining the probability that a disperser survives dispersal and manages to settle as an adult in a patch. That adult and all its descendant adults in the focal patch form a mutant colony. The adults of the focal patch in the next generation are randomly chosen among juveniles present in the patch after dispersal. Therefore, the number of adult mutants in the mutant colony forms a stochastic process, a discrete-time Markov chain. The mutant colony will eventually go extinct. Using matrix algebra, including solving a system of linear equations, we calculate the expected number of dispersing juveniles that the mutant colony will produce during its lifetime. That amount is the metapopulation reproduction number  $R_m(m_{\text{mut}}, m)$ . Although we do not obtain an explicit expression for  $R_m(m_{\text{mut}}, m)$ , with the help of the implicit function theorem, we are able to obtain an explicit expression for the fitness gradient  $D_1(m) = \left. \frac{\partial}{\partial m_{\text{mut}}} R_m(m_{\text{mut}}, m) \right|_{m_{\text{mut}}=m}$  and the second derivative  $D_2(m) = \left. \frac{\partial^2}{\partial m_{\text{mut}}^2} R_m(m_{\text{mut}}, m) \right|_{m_{\text{mut}}=m}$ . These expressions provide valuable

information about evolution of dispersal in this model, as explained in detail in *SI Appendix*. All data are contained in the main text and *SI Appendix*.

**ACKNOWLEDGMENTS.** This work was supported by the SOKENDAI Advanced Sciences Synergy Program. J.Y.W. acknowledges support by Japan Society for the Promotion of Science, Grants-in-Aid for Scientific Research 16K05283 and 16H06412.

1. L. Van Valen, Group selection and the evolution of dispersal. *Evolution* **25**, 591–598 (1971).
2. W. D. Hamilton, R. M. May, Dispersal in stable habitats. *Nature* **269**, 578–581 (1977).
3. H. N. Comins, W. D. Hamilton, R. M. May, Evolutionarily stable dispersal strategies. *J. Theor. Biol.* **82**, 205–230 (1980).
4. U. Dieckmann, B. O'Hara, W. Weisser, The evolutionary ecology of dispersal. *Trends Ecol. Evol.* **14**, 88–90 (1999).
5. J. Clobert, E. Danchin, A. A. Dhondt, J. D. Nichols, Eds., *Dispersal* (Oxford University Press, 2001).
6. O. Ronce, How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.* **38**, 231–257 (2007).
7. A. Hastings, Can spatial variation alone lead to selection for dispersal. *Theor. Popul. Biol.* **24**, 244–251 (1983).
8. K. Parvinen, Evolution of migration in a metapopulation. *Bull. Math. Biol.* **61**, 531–550 (1999).
9. M. Gyllenberg, K. Parvinen, U. Dieckmann, Evolutionary suicide and evolution of dispersal in structured metapopulations. *J. Math. Biol.* **45**, 79–105 (2002).
10. K. Parvinen, Evolution of dispersal in a structured metapopulation model in discrete time. *Bull. Math. Biol.* **68**, 655–678 (2006).
11. R. D. Holt, M. A. McPeck, Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.* **148**, 709–718 (1996).
12. M. Doebeli, G. D. Ruxton, Evolution of dispersal rates in metapopulation models: Branching and cyclic dynamics in phenotype space. *Evolution* **51**, 1730–1741 (1997).
13. K. Johst, M. Doebeli, R. Brandl, Evolution of complex dynamics in spatially structured populations. *Proc. R. Soc. Lond. B* **266**, 1147–1154 (1999).
14. J. A. J. Metz, S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs, J. S. van Heerwaarden, "Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction" in *Stochastic and Spatial Structures of Dynamical Systems*, S. J. van Strien, S. M. Verdun Lunel, Eds. (North-Holland, Amsterdam, The Netherlands, 1996), pp. 183–231.
15. S. A. H. Geritz, J. A. J. Metz, É. Kisdi, G. Meszéna, Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.* **78**, 2024–2027 (1997).
16. S. A. H. Geritz, É. Kisdi, G. Meszéna, J. A. J. Metz, Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**, 35–57 (1998).
17. M. A. McPeck, R. D. Holt, The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* **140**, 1010–1027 (1992).
18. A. Mathias, É. Kisdi, I. Olivieri, Divergent evolution of dispersal in a heterogeneous landscape. *Evolution* **55**, 246–259 (2001).
19. S. Gandon, Y. Michalakis, Evolutionarily stable dispersal rate in a metapopulation with extinctions and kin competition. *J. Theor. Biol.* **199**, 275–290 (1999).
20. O. Ronce, F. Perret, I. Olivieri, Evolutionarily stable dispersal rates do not always increase with local extinction rates. *Am. Nat.* **155**, 485–496 (2000).
21. M. Gyllenberg, J. A. J. Metz, On fitness in structured metapopulations. *J. Math. Biol.* **43**, 545–560 (2001).
22. K. Parvinen, Evolutionary branching of dispersal strategies in structured metapopulations. *J. Math. Biol.* **45**, 106–124 (2002).
23. J. A. J. Metz, M. Gyllenberg, How should we define fitness in structured metapopulation models? Including an application to the calculation of ES dispersal strategies. *Proc. R. Soc. Lond. B* **268**, 499–508 (2001).
24. K. Parvinen, U. Dieckmann, M. Gyllenberg, J. A. J. Metz, Evolution of dispersal in metapopulations with local density dependence and demographic stochasticity. *J. Evol. Biol.* **16**, 143–153 (2003).
25. U. Motro, Optimal rates of dispersal. I. Haploid populations. *Theor. Popul. Biol.* **21**, 394–411 (1982).
26. U. Motro, Optimal rates of dispersal. II. Diploid populations. *Theor. Popul. Biol.* **21**, 412–429 (1982).
27. U. Motro, Optimal rates of dispersal. III. Parent offspring conflict. *Theor. Popul. Biol.* **23**, 159–168 (1983).
28. S. A. Frank, Dispersal polymorphisms in subdivided populations. *J. Theor. Biol.* **122**, 303–309 (1986).
29. P. D. Taylor, An inclusive fitness model for dispersal of offspring. *J. Theor. Biol.* **130**, 363–378 (1988).
30. F. Massol, A. Duputié, P. David, P. Jarne, Asymmetric patch size distribution leads to disruptive selection on dispersal. *Evolution* **65**, 490–500 (2011).
31. É. Ajar, Analysis of disruptive selection in subdivided populations. *BMC Evol. Biol.* **3**, 1–12 (2003).
32. S. Wright, Evolution in Mendelian populations. *Genetics* **16**, 97–159 (1931).
33. K. Parvinen, H. Ohtsuki, J. Y. Wakano, Spatial heterogeneity and evolution of fecundity-affecting traits. *J. Theor. Biol.* **454**, 190–204 (2018).
34. J. Maynard Smith, G. R. Price, The logic of animal conflict. *Nature* **246**, 15–18 (1973).
35. J. Maynard Smith, Evolution and the theory of games. *Am. Sci.* **64**, 41–45 (1976).
36. S. Gandon, Kin competition, the cost of inbreeding and the evolution of dispersal. *J. Theor. Biol.* **200**, 245–364 (1999).
37. K. Parvinen, J. A. J. Metz, A novel fitness proxy in structured locally finite metapopulations with diploid genetics, with an application to dispersal evolution. *Theor. Popul. Biol.* **73**, 517–528 (2008).