

Disturbance-induced emigration: an overlooked mechanism that reduces metapopulation extinction risk

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Abstract. Emigration propensity (i.e., the tendency to leave undisturbed patches) is a key life-history trait of organisms in metapopulations with local extinctions and colonizations. Metapopulation models of dispersal evolution typically assume that patch disturbance kills all individuals within the patch, thus causing local extinction. However, individuals may instead be able to leave a patch when it is disturbed, either by fleeing before being killed or simply because the disturbance destroys the patch without causing mortality. This scenario may pertain to a wide range of organisms from horizontally transmitted symbionts, to aquatic insects inhabiting temporary ponds, to vertebrates living in fragmented forests. We generalized a Levins-type metapopulation model of dispersal evolution by adding a new parameter of disturbance escape probability, which incorporates a second source of dispersal into the model: disturbance-induced emigration. We show that disturbance escape expands the domain of metapopulation viability and selects for lower rates of emigration propensity when disturbance rates are high. The fitness gains from disturbance-induced emigration are generally moderate, suggesting that disturbance escape might act more as a complementary dispersal strategy rather than a replacement to emigration propensity, at least for metapopulations that meet the assumptions of the Levins-type model. Yet disturbance-induced emigration may in some circumstances rescue a metapopulation from long-term extinction when the combination of high disturbance rates and low local population growth rates compromises its viability. Further, a metapopulation could persist exclusively by disturbance escape if local carrying capacities are large enough to counterbalance two sources of mortality: mortality driven by disturbance and mortality during dispersal. This study opens two promising research lines: (1) the investigation of disturbance escape in metapopulations of ephemeral habitats with unsaturated populations and non-equilibrium dynamics and (2) the incorporation of information costs to investigate the joint evolution of disturbance escape and emigration propensity.

Key words: conditional dispersal; dispersal evolution; disturbance escape; disturbance rate; invasion fitness; metapopulation viability.

INTRODUCTION

Dispersal is a fundamental trait of individuals that maintains the regional persistence of metapopulations (Clobert et al. 2004). Dispersal also serves as a bet-hedging strategy against disturbance that reduces kin competition and inbreeding (Ronce 2007). Metapopulation models of dispersal evolution predict how dispersal should evolve as a function of the basic parameters that define a metapopulation, such as patch disturbance rates, local population growth rates, carrying capacities,

and dispersal mortality (e.g., Gandon and Michalakis 1999, Parvinen et al. 2003, Jansen and Vitalis 2007). Multiple mechanisms have been invoked to explain selection for increased dispersal in these models, including spatiotemporal variation in local conditions, overcrowding, competition, non-equilibrium metapopulation dynamics and demographic stochasticity (Ronce 2007, Duputié and Massol 2013).

Early models of dispersal evolution assumed that dispersal is unconditional: individuals emigrate at a constant rate independent of their location or individual condition (Hamilton and May 1977, Comins et al. 1980). Later researchers explored conditional dispersal strategies dependent on an individual's sex (Motro 1991), age (Ronce et al. 2000a), local population

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densities (Travis et al. 1999, Metz and Gyllenberg 2001), or carrying capacities (Poethke and Hovestadt 2002). More recent studies have investigated the evolution of plastic dispersal strategies conditioned on a much wider variety of factors, including body condition (Bonte and de la Peña 2009), local sex ratio (Hovestadt et al. 2014), habitat or patch quality (Enfjäll and Leimar 2009, Weigang 2017), density of suitable habitats (Bartoń et al. 2009), predator abundance (Poethke et al. 2010), or infection rates and virulence of associated parasites (Iritani and Iwasa 2014). Conditional dispersal is predicted to be favored by natural selection, especially in heterogeneous and temporally variable environments with sufficiently low information costs (i.e., costs associated with estimating the factors that control conditional dispersal; Bocedi et al. 2012, Duputié and Massol 2013).

Here, we present a model to study the importance of a type of conditional dispersal that has not been examined in prior literature, i.e., emigration induced by patch disturbance. Metapopulation theory traditionally assumes that patch disturbance kills all the individuals within the patch, leading to local extinction (Hanski 1998). Under this assumption, metapopulation models of dispersal evolution typically focus on the evolution of the tendency to leave undisturbed patches, which we refer to here as “emigration propensity” (e.g., Gandon and Michalakis 1999, Parvinen et al. 2003, Jansen and Vitalis 2007). However, the probability of being killed by disturbance may depend on the properties of the disturbance events (e.g., intensity and speed). In some cases, individuals could escape disturbance simply because disturbance destroys the patch without incurring death. For instance, clear-cut logging or a slow fire in a forest patch would often permit birds to emigrate (Pausas and Parr 2018). Moreover, one might expect selection to favor the ability of organisms to detect cues related to imminent disturbance, vacate a patch where death is certain, and thus possibly survive by dispersing to other patches. For instance, some aquatic insects use rainfall cues as an adaptation to escape floods (Lytle and Poff 2004). Detection-and-escape behaviors against fire have been observed in bats and frogs (Grafe et al. 2002, Scesny and Robbins 2006). Indeed, signal detection theory suggests that traits allowing escape from disturbance can evolve if disturbance events are sufficiently frequent, severe, and/or predictable (Lytle et al. 2008). This is particularly important because a large proportion of individuals may leave disturbed populations (or patches) and so potentially influence the persistence of the metapopulation as a whole. However, no theory has as yet explored the potential consequences of escaping from disturbance on the evolution of dispersal and the persistence of metapopulations.

An additional empirical motivation that inspires our disturbance escape concept comes from considering species that live in or on other species (their hosts). There are numerous taxa for which, given their life histories,

dispersal is necessary for persistence. These include obligate symbionts on hosts, a very widespread and phylogenetically diverse life-history syndrome (Weinstein and Kuris 2016, Fisher et al. 2017). Each host individual in effect is a patch that can be occupied, or not, by symbionts (Grenfell and Harwood 1997, Borer et al. 2016). Because hosts are born and die, they are ephemeral patches with a finite lifetime, so recurrent colonization of fresh hosts is required for symbiont persistence in a host population. Many symbionts disperse via horizontal transmission from one host to another, and such systems are strongly akin to classical metapopulations, in that host death is in effect a severe patch disturbance for its resident symbionts (Mestre et al. 2020). But host death is not always a dead end for symbionts (Ponton et al. 2006, Klose et al. 2012, Rizvi et al. 2012). Many horizontally transmitted symbionts could abandon a host as it dies and seek other hosts, rather than suffer death along with the original host. Thus, symbiont lifestyles provide another source of empirical examples that motivates our theoretical investigation of the consequences of disturbance escape for metapopulation dynamics and dispersal evolution.

We start by generalizing a Levins-type metapopulation model of dispersal evolution (Jansen and Vitalis 2007) by adding a new parameter that allows for disturbance escape. The new parameter incorporates a second source of emigration: disturbance-induced emigration. We then use a standard analytical approach based on metrics of invasion fitness in a metapopulation context to quantify the biological significance of disturbance escape in a metapopulation subject to disturbances that destroy patches without always killing all occupants. Our study demonstrates the potential of disturbance escape as a mechanism that may enhance persistence of metapopulations threatened by the combination of high disturbance rates and low local population growth rates. We also evaluate the conditions that would allow a metapopulation to persist by disturbance escape as the sole mechanism of dispersal.

METHODS

Disturbance escape model

We extended the model of dispersal evolution developed by Jansen and Vitalis (2007) to allow for disturbance escape. This model is an extension of Levins' metapopulation model that accounts for local population dynamics with logistic growth (model parameters are summarized in Table 1). The metapopulation dynamics are described as follows (Levins 1969):

$$\dot{P} = mP(1 - P) - eP \quad (1)$$

where P is the fraction of occupied patches (a dot indicates change over time), m is the patch colonization rate,

TABLE 1. Variables and parameters of the disturbance escape model.

Symbol	Description	Formula
γ	per capita rate of leaving an undisturbed patch (emigration propensity)	
λ	per capita probability of leaving a patch when the patch is disturbed (disturbance-induced emigration)	
e	patch disturbance rate	
r	per capita local population growth rate	
k	carrying capacity of local populations	
α	probability of finding a patch before dying in the dispersal pool	
u	probability of colonization of an empty patch by an individual disperser that reaches the patch	$u = 1 - \frac{\gamma}{r}$
\bar{x}	average local (patch) population size at equilibrium	$\bar{x} = k(1 - \frac{\gamma}{r})$
\bar{D}	number of new dispersers per unit of time	$\bar{D} = (\gamma + \lambda e)\bar{x}\bar{P}$
m	patch colonization rate	$m = (\gamma + \lambda e)\alpha u k(1 - \frac{\gamma}{r})$
\bar{P}	fraction of patches occupied at equilibrium	$\bar{P} = 1 - \frac{e}{m}$
\bar{P}_1	equilibrium fraction of patches that received one immigrant	$\bar{P}_1 = \frac{m u}{m - e(1 - u)}\bar{P}(1 - \bar{P})$
\bar{P}_2	equilibrium fraction of patches that received two immigrants	$\bar{P}_2 = \frac{m}{m - e(1 - u)}\bar{P}^2$
s	total population of two strains locally co-occurring within a patch	$s = x^o + x^*$
$\bar{s}^\phi(t)$	dynamics of s over time with the initial condition ϕ	$\bar{s}^\phi(t) = \bar{x}^o + f^\phi(t)(\bar{x}^* - \bar{x}^o)$
f	fraction of the mutant strain within a patch where two strains locally co-occur	$f = \frac{x^*}{s}$
$f^\phi(t)$	dynamics of f over time depending on the initial condition ϕ	$f^\phi(t) = \frac{\phi}{\bar{x}^* \phi + (1 - \phi)\exp((\gamma^* - \gamma^o)t)}$; $f^\phi(0) = \phi$
ϕ^*	initial fraction of mutant individuals when a resident individual reinvades a patch already occupied by the mutant strain	$\phi^* = \frac{\bar{x}^*}{\bar{x}^o + 1}$
ϕ^o	initial fraction of mutant individuals when a mutant individual reinvades a patch already occupied by the resident strain	$\phi^o = \frac{1}{\bar{x}^o + 1}$
R	probability of a rare mutant encountering another mutant individual in its patch (relatedness)	$R = \frac{\bar{P}_1 + \bar{P}_2(\phi^{o2} + \phi^{*2})}{P}$
\bar{R}	probability of a rare mutant encountering an unrelated individual in its patch (unrelatedness)	$\bar{R} = 1 - R = \frac{2\phi^o\phi^*\bar{P}_2}{P}$

Notes: Superscripts refer to either a mutant strain (*) or a resident strain (o), both differing marginally in their γ . The model assumes that $r - \gamma \gg e$ and colonization rates are low (see also Jansen and Vitalis 2007).

and e is the patch disturbance rate (which is extinction in the Levins model). Levins metapopulation dynamics have the equilibrium $\bar{P} = 1 - e/m$ (a tilde indicates equilibrium value). Jansen and Vitalis (2007) then added the equation for local population dynamics

$$\dot{x} = rx \left(1 - \frac{x}{k}\right) - \gamma x \quad (2)$$

where x is the average local population size, r is the per capita local population growth rate, k is the local carrying capacity, and γ is the per capita emigration propensity. If $\gamma < r$ and local dynamics are faster than metapopulation dynamics, then local populations reach a stable equilibrium quickly (compared to the patch lifetime) given by $\bar{x} = k(1 - \gamma/r)$ (Goel and Richter-Dyn 1974).

During the life span of an occupied patch (i.e., prior to disturbance), its residents leave the patch at a per capita rate given by γ , as described in Eq. 2. We incorporated a disturbance escape probability (λ) into the model, defined as the per capita probability of leaving a patch before dying when the patch undergoes disturbance. The parameter introduces disturbance-induced emigration in the

metapopulation as a second source of dispersal. The expected number of additional emigrants is proportional to the product of the disturbance escape probability and the rate of patch disturbance (λe). Emigrants from both types of dispersal sources (i.e., γ and λ) enter a dispersal pool from which they will attempt to find and colonize new patches. The equilibrium number of new dispersers per unit of time entering the pool is $\bar{D} = (\gamma + \lambda e)\bar{x}\bar{P}$. A disperser finds a patch with a fixed probability α (otherwise it dies in the dispersal pool). If the patch was empty, the settled individual will attempt to establish a new local population. We expect an initial phase of high extinction risk due to stochastic fluctuations in the local population size until it reaches a certain threshold. If we assume that the per capita birth and death rates are r and rx/k , respectively, and k is large, then the probability of successfully colonizing the patch can be approximated as $u \approx 1 - \gamma/r$. The reasoning for this approximation is based on a fully stochastic version of Jansen and Vitalis' model with local dynamics formulated as a stochastic birth-death model (see Appendix S1 in Jansen and Vitalis 2007). Now, we can provide a definition for the patch colonization rate that links local and metapopulation dynamics (i.e., Eqs. 1 and 2):

$$m = (\gamma + \lambda e) \alpha u k \left(1 - \frac{\gamma}{r}\right) \quad (3)$$

Following Jansen and Vitalis (2007), we assumed that local immigration rates are low enough that multiple reinvasions over the lifetime of a patch are extremely rare and can be disregarded. Therefore, the maximum number of immigrants that arrived in a patch at the end of its lifetime was limited to two. Under this assumption, the fraction of occupied patches (P) can be decomposed into invaded patches that received one immigrant (P_1) and reinvaded patches that received two immigrants (P_2), where $P = P_1 + P_2$. The dynamics of invaded and reinvaded patches are given by

$$\dot{P}_1 = mP(1 - P) - eP_1 - \frac{m}{u}PP_1 \quad (4a)$$

$$\dot{P}_2 = \frac{m}{u}PP_1 - eP_2 \quad (4b)$$

where $mP(1 - P)$ is the flux of patches turning from empty to invaded, and $(m/u)PP_1$ is the flux of patches turning from invaded by a single individual to reinvaded. The terms eP_1 and eP_2 are the rates of loss of invaded and reinvaded patches, respectively, due to disturbance. The presence of u in the denominator of the reinvasion rate compensates the u integrated within the definition of m (see Eq. 3). This compensation addresses the fact that extinction risks associated with demographic stochasticity are not expected during the reinvasion of an occupied patch. The equilibrium values for the fractions of invaded and reinvaded patches are $\tilde{P}_1 = \frac{mu}{m-e(1-u)}\tilde{P}(1-\tilde{P})$ and $\tilde{P}_2 = \frac{m}{m-e(1-u)}\tilde{P}^2$.

The model has two major assumptions: (1) local dynamics are fast relative to metapopulation dynamics so that local equilibrium is reached instantaneously ($r - \gamma \gg e$) and (2) a patch receives no more than two immigrants over its lifetime. The second assumption implies that colonization rates are low, so that the metapopulation has empty patches [$r - \gamma > 10(e + \alpha\tilde{D})$].

Adaptive dynamics method

We applied the adaptive dynamics method of trait evolution based on the fitness of a rare mutant with a marginally different strategy than the resident (Geritz et al. 1998). For that, we used a model variant that describes the dynamics of competition between two strains cohabiting in a metapopulation (Jansen and Vitalis 2007). The strains only differ in their emigration propensity (γ , i.e., the trait under selection). The competition between both strains occurs at two levels: within local populations, and across the entire metapopulation. One competing strain is a monotypic resident with $\gamma = \gamma^0$, which is assumed to be established in the metapopulation at its equilibrium. The other strain is a rare mutant with $\gamma = \gamma^*$ that might be able to invade the

metapopulation. Strains compete locally within shared patches. We define $s = x^0 + x^*$ as the total number of individuals of both strains cohabiting in a shared patch, and $f = x^*/s$ is the fraction of the mutant strain within the patch. The equations for local dynamics of shared patches are

$$\dot{s} = s \left(r \left(1 - \frac{s}{k}\right) - \gamma^0(1-f) - \gamma^*f \right) \quad (5a)$$

$$\dot{f} = (\gamma^0 - \gamma^*)f(1-f) \quad (5b)$$

Assuming local population dynamics to be faster than metapopulation dynamics for both strains, s reaches a quasi-steady state and approximately follows $\tilde{s}^\phi(t) = \tilde{x}^0 + f^\phi(t)(\tilde{x}^* - \tilde{x}^0)$, where t is the time of local reinvasion. The superscript ϕ represents the value of f at the beginning of the patch reinvasion that initiated the shared local dynamics (i.e., $f^\phi(0) = \phi$). This superscript is used because the dynamic variables $\tilde{s}(t)$ and $f(t)$ depend on the initial fraction of mutants at the time of reinvasion. The state of ϕ (either ϕ^* or ϕ^0) is determined by the order of arrival of both strains in the patch. If a resident individual reinvades a patch colonized by the mutant strain, then $\phi^* = f^{\phi^*}(0) = \tilde{x}^*/(\tilde{x}^* + 1)$, while if a mutant individual reinvades a patch colonized by the resident strain then $\phi^0 = f^{\phi^0}(0) = 1/(\tilde{x}^0 + 1)$. If we assume that strains differ only marginally in their emigration propensity, the more philopatric strain will tend to replace the more dispersing strain, locally. But the replacement will be a slow process, so that the local dynamics of the mutant fraction can be approximated by the following logistic equation (Jansen and Vitalis 2007):

$$f^\phi(t) = \frac{\phi}{\phi + (1 - \phi)\exp[(\gamma^* - \gamma^0)t]} \quad (6)$$

The strains also compete at the metapopulation level through colonization processes, including invasions of empty patches generated by local disturbance and immigration into occupied patches. We can derive from this two-strain model the fitness of a rare mutant with an emigration propensity (γ^*) that is marginally different from the one established in the metapopulation (γ^0). Analyzing this fitness function, we can predict the evolutionary change in emigration propensity, the endpoint of the evolutionary process, and how it will be affected by disturbance escape.

Disturbance escape and invasion fitness

We applied the concept of invasion fitness extended to metapopulations (Gyllenberg and Metz 2001, Metz and Gyllenberg 2001). Much of our derivation of equations in this section follows the methods of Jansen and Vitalis (2007), but with the addition of disturbance-induced

emigration. We characterized the fitness of a rare mutant that attempts to invade a metapopulation dominated by a resident strain that has converged to a point equilibrium. The rare mutant is almost identical to the resident strain, only differing marginally in its emigration propensity. The invasion fitness is the expected number of new emigrants produced by an emigrating mutant individual, considering the different fates it may meet: (1) death in the dispersal pool, (2) colonization of an empty patch that is never reinvaded, (3) reinvasion of a patch already occupied by the resident, and (4) colonization of an empty patch that is later reinvaded by the resident. The case of successive invasion of two mutants into the same patch was disregarded because we are calculating the fitness while the mutant is rare. Thus, we are assuming a very small initial density of mutant individuals in the metapopulation.

The invasion fitness of the disturbance escape model incorporates the contribution of two sources of dispersal: emigration propensity (individuals that leave a patch continually while it remains a viable habitat) and disturbance-induced emigration (departure in a pulse near the time of disturbance). Considering all the fates that the focal individual may undergo and their corresponding probabilities, we accounted for the expected number of emigrants produced by both dispersal sources. Putting these together, we obtained the following invasion fitness equation (for derivation and details see Appendix S1: Section S1):

$$W(\gamma^*, \gamma^0) = \gamma^* \alpha \tilde{P}_1 \left[\frac{\tilde{x}^* u^*}{\alpha u^0 \tilde{D}} + \frac{\lambda e \tilde{x}^* u^*}{\gamma^* \alpha u^0 \tilde{D}} \right] + \int_0^\infty \left[f^{\Phi^0}(t) \tilde{s}^{\Phi^0}(t) + \frac{u^*}{u^0} f^{\Phi^*}(t) \tilde{s}^{\Phi^*}(t) \right] \exp(-et) dt + \int_0^\infty \left[\frac{\lambda}{\gamma^*} f^{\Phi^0}(t) \tilde{s}^{\Phi^0}(t) + \frac{\lambda u^*}{\gamma^* u^0} f^{\Phi^*}(t) \tilde{s}^{\Phi^*}(t) \right] e \exp(-et) dt \quad (7)$$

The invasion fitness (W) can be divided into two parts, one dependent on γ and the other on λ . At the limit when the resident and the mutant are the same ($\gamma^* = \gamma^0 = \gamma$), both parts can be expressed as follows (Appendix S1: Section S2):

$$W_\lambda = \frac{\lambda e}{\gamma + \lambda e}; W_\gamma = \frac{\gamma}{\gamma + \lambda e}; \frac{W_\lambda}{W_\gamma} = \frac{\lambda e}{\gamma} \quad (8)$$

where W_λ is the fitness component associated with disturbance escape, and W_γ is the fitness component associated with emigration propensity ($W = W_\lambda + W_\gamma$). We used the W_λ/W_γ ratio to quantify the relative contribution of the disturbance-induced emigration to the invasion fitness.

From Eq. 7, we derived the marginal fitness (i.e., selection gradient) that describes the change in fitness due to a marginal change in the emigration propensity (Appendix S1: Section S3):

$$\frac{\partial W(\gamma^*, \gamma^0)}{\partial \gamma^*} \Big|_{\gamma^* = \gamma^0 = \gamma} = \frac{1}{\gamma} \left(1 - \frac{\lambda e}{\gamma + \lambda e} \right) + \frac{d\tilde{x}}{\tilde{x} d\gamma} \frac{\tilde{P}_1 + \tilde{P}_2(\Phi^{02} + \Phi^{*2})}{\tilde{P}} - \frac{2\Phi^0 \Phi^* \tilde{P}_2}{e \tilde{P}} + \frac{du}{u d\gamma} + \frac{\tilde{P}_2 d\Phi^*}{\tilde{P} d\gamma^*} \Big|_{\gamma^* = \gamma} \quad (9)$$

As shown by Jansen and Vitalis (2007), the marginal fitness can be represented in a clearer form that facilitates its biological interpretation by using measures of relatedness (R) and unrelatedness (\bar{R} ; Appendix S1: Section S4):

$$\frac{\partial W(\gamma^*, \gamma^0)}{\partial \gamma^*} \Big|_{\gamma^* = \gamma^0 = \gamma} \approx \frac{1}{\gamma} W_\gamma - \frac{1}{r - \gamma} R - \frac{1}{e} \bar{R} - \frac{1}{r - \gamma} \quad (10)$$

Relatedness, $R = \frac{\tilde{P}_1 + \tilde{P}_2(\Phi^{02} + \Phi^{*2})}{\tilde{P}}$, is the probability that a rare mutant encounters an identical mutant individual in its patch; whereas unrelatedness, $\bar{R} = 1 - R = \frac{2\Phi^0 \Phi^* \tilde{P}_2}{\tilde{P}}$, is the probability of a rare mutant encountering an unrelated individual produced by local growth in its patch. Eq. 10 gives information about the effects of having a marginally higher emigration propensity. The first term on the right represents the fitness gain due to an increase in the number of dispersers driven by emigration propensity. This fitness gain only affects the fitness component associated with emigration propensity (i.e., W_γ). The second term represents the fitness reduction due to a decrease in the local population size at equilibrium. The third term represents the fitness reduction due to a decrease in the competitive ability within a patch shared by the resident strain. The fourth term represents the fitness reduction due to a decrease in the probability of colonizing an empty patch, which is related to the ability to avoid extinction driven by demographic stochasticity (see Appendix S1: Section S4 for more details).

We obtained the evolutionary singular values of emigration propensity (ES_γ) by calculating the value of γ for which the marginal fitness (Eq. 9) is 0 with the R package `rootSolve` (Soetaert and Herman 2009). We used numerical approximation of second partial derivatives of the invasion fitness to evaluate the stability of the ES_γ (see Appendix S1: Section S5). We assessed two stability properties of the ES_γ : evolutionary stability and convergence stability (Geritz et al. 1997, 1998). An ES_γ is evolutionarily stable if it is resistant to invasion by a neighboring strategy. An ES_γ is convergence stable if the system dynamics return the population's strategy back to ES_γ following a perturbation (Apaloo et al. 2009). First, we used the model to explore the effects of disturbance escape on metapopulation viability. A metapopulation is viable when patch occupancy at equilibrium is greater than 0, or when patch colonization rates are greater than patch disturbance rates. Second, we analyzed the effects of disturbance escape on ES_γ and their interactions with the other model parameters. We show how disturbance escape modifies the maximum value theoretically

attainable for ES_γ . This maximum value would be selected if all the individuals were genetically identical, so that the common good was the only driving force (i.e., $\bar{R} = 0$; Appendix S1: Section S4). Finally, we assessed the influence of model parameters on the W_λ/W_γ ratio (Eq. 8) to determine under which conditions disturbance-induced emigration should be more relevant as a contributor to the invasion fitness.

RESULTS

The condition for metapopulation persistence in our model can be expressed as

$$1 - \frac{e}{(\gamma + \lambda e)\alpha k \left(1 - \frac{\gamma}{r}\right)^2} > 0 \quad (11)$$

Our results show that disturbance escape expands the domain of metapopulation viability at high disturbance rates (Fig. 1). Disturbance escape increases patch occupancy, especially when disturbance rates are relatively high (Fig. 1a). At very high disturbance rates, disturbance-driven emigration can positively shift the colonization-extinction balance, thereby becoming critical for long-term metapopulation persistence (Fig. 1b). Note that in our numerical results, we use the maximum value of $\lambda = 1$, meaning individuals always leave a disturbed patch, to show the maximum effect of disturbance escape.

Disturbance escape decreases the evolutionary singular emigration propensity (ES_γ) at high disturbance rates (Figs. 1b and 2a). In general, the relative importance of disturbance-induced emigration to invasion fitness

(W_λ/W_γ) increases with disturbance rate (Fig. 2b; but see below). The effects of disturbance escape on the ES_γ remain similar for different values of local population growth rate (Fig. 2a). However, the W_λ/W_γ ratio is higher at lower population growth rates (Fig. 2b). This is because a decrease in the local population growth rate selects for lower emigration propensity without affecting the rates of disturbance-induced emigration. By contrast, a decrease in either local carrying capacities or the probability of finding a patch decreases the W_λ/W_γ ratio (Appendix S1: Figs. S3 and S4). The reason is that in both cases a decrease in the parameter selects for higher emigration propensity. Moreover, lowering local carrying capacities also affects W_λ directly by decreasing the number of disturbance-induced dispersers per disturbance event. This can even lead to a negative relationship between disturbance rate and the W_λ/W_γ ratio (Appendix S1: Fig. S3b). Finally, disturbance escape lowers the upper limit of ES_γ and makes it decrease with increasing disturbance rate (Fig. 2a; Appendix S1: Figs. S3a and S4a; see also Appendix S1: Section S4). The vast majority of ES_γ presented in this paper satisfied the conditions for being both evolutionarily and convergence stable (see Appendix S1: Section S5, Figs. S1, S2).

DISCUSSION

Prior metapopulation theory assumes that disturbances always cause local extinctions. Here, we explored the biological significance of relaxing this assumption by using a Levins-type metapopulation model. In

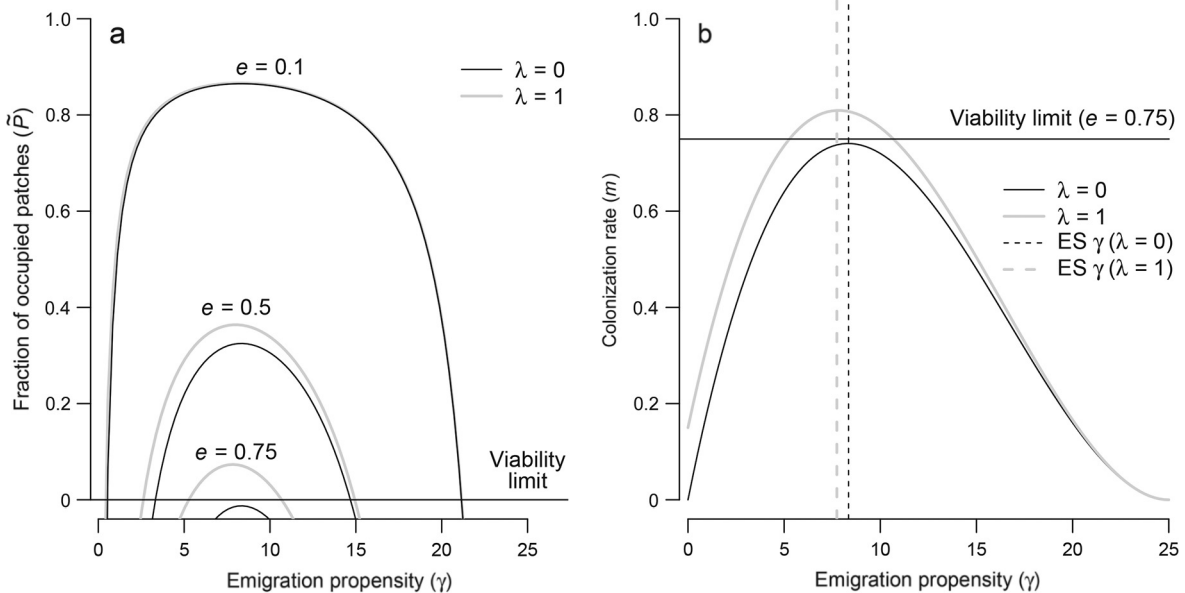


FIG. 1. Expansion of the domain of metapopulation viability when disturbance escape is present (i.e., $\lambda = 1$): (a) effects of disturbance escape on the equilibrium fraction of occupied patches under three scenarios of disturbance rate (e) and (b) effects of disturbance escape on patch colonization rates in a case wherein disturbance escape rescues the metapopulation (i.e., $e = 0.75$). Parameters are $r = 25$, $k = 200$, and $\alpha = 0.001$. The vertical lines in panel b are the evolutionary singular rates of emigration propensity (ES_γ) when disturbance escape is absent and present, respectively.

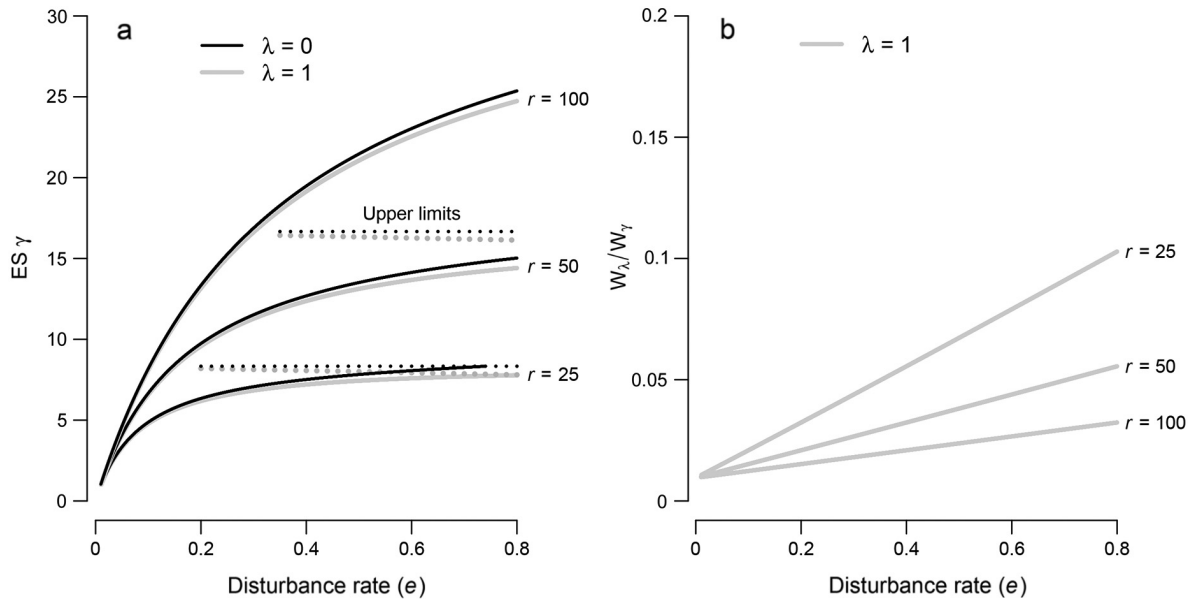


Fig. 2. Evolutionary singular rate of emigration propensity (ES_γ) and invasion fitness (W) when disturbance escape is possible (i.e., $\lambda = 1$): (a) effects of disturbance escape on ES_γ under three scenarios of local population growth rate (r), and (b) effects of disturbance rate on the W_λ/W_γ ratio under the same three scenarios of r , where $W_\lambda/W_\gamma = \lambda e/ES_\gamma$. The dotted lines in panel a are the upper limits of ES_γ (see Appendix S1: Section S4). W_λ is the fitness component associated with disturbance-induced emigration, whereas W_γ is the fitness associated with emigration propensity (see Appendix S1: Section S2). Parameters are $k = 200$ and $\alpha = 0.001$. All the curves meet the condition $r - \gamma > 10(e + \alpha\bar{D})$. More than 99.9% of the ES_γ shown in this figure satisfied the conditions for being both evolutionarily stable and convergence stable (see Appendix S1: Section S5, Figs. S1, S2).

particular, we investigated the role of disturbance-induced emigration as a potential driver of metapopulation dynamics and the evolution of unconditional emigration. We show that escaping from disturbance expands the persistence domain (Fig. 1) and selects for a lower emigration propensity (Fig. 2). Moreover, we identified the circumstances that would make disturbance escape useful as a rescue mechanism in a threatened metapopulation: (1) high disturbance rates, (2) low local population growth rates, and (3) local carrying capacities not too low. First, high patch disturbance rates directly foster disturbance-induced emigration. Second, lowering local population growth rates increases the relative fitness associated with disturbance escape indirectly, by reducing the ES_γ . Third, if local carrying capacities are very low, kin competition strongly selects for high rates of emigration propensity, and the smaller local population sizes at equilibrium also directly decrease the number of disturbance-induced emigrants.

Pros and cons of disturbance escape as a dispersal strategy in a metapopulation

There are both potential advantages and disadvantages of disturbance-induced emigration as a source of dispersal, complementary or alternative to emigration propensity in a metapopulation. These pros and cons reflect differences between both dispersal strategies in

three main aspects: (1) their impacts on local dynamics, (2) the maximum number of emigrants that they can produce per colonized patch, and (3) their relationships with disturbance (the ways disturbance affects them).

The classical source of dispersal assumed in previous metapopulation models occurs continually over the life span of a patch until the patch becomes disturbed, typically at a constant rate defined by the emigration propensity (γ). Consequently, γ directly affects local dynamics (see Eqs. 2 and 5) with negative repercussions on the invasion fitness at three levels (see Eq. 10 and Appendix S1: Section S4). First, γ slows down the initial local population growth necessary to overcome stochastic extinction risk at the initial phase of a patch invasion. Note that the probability of colonizing an empty patch is $u = 1 - \gamma/r$ (based on the assumption that the per capita birth and death rates are r and rx/k , respectively). Second, γ keeps limiting the local population growth after successful colonization, thus decreasing the local population size at equilibrium: $\bar{x} = k(1 - \gamma/r)$. Third, γ compromises the ability of a strain to compete with other strains with lower γ within shared patches (Eq. 6). Besides its negative repercussions on local dynamics, γ has the advantage of providing a continuous flux of emigration that covers the entire lifetime of a patch since colonization. The expected number of γ emigrants over the life span of a colonized patch (n_γ) can be higher than the local population size at equilibrium: $n_\gamma = \gamma\bar{x}/e$ (note

that γ is a rate, and thus can be higher than 1). However, n_γ is negatively affected by disturbance rate ($1/e$ is the time elapsed before the patch becomes disturbed). In addition, because emigration propensity occurs before disturbance, γ is not affected by the intensity of disturbance (i.e., its capacity to cause damage).

By contrast, disturbance escape is a discrete event that occurs at the end of a patch life span along with disturbance, when the patch becomes no longer viable. The disturbance escape parameter (λ) incorporated as the novel feature in our model required the modification of the definitions for the total dispersal rate at equilibrium, $\bar{D} = (\gamma + \lambda e)\bar{x}\bar{P}$, and the colonization rate of empty patches (m ; Eq. 3). The fractions of occupied patches at equilibrium (\bar{P} , \bar{P}_1 , and \bar{P}_2) also depend on λ through m . Because here we did not consider costs associated with disturbance escape, the equations describing the local dynamics (Eqs. 2, 5 and 6) are not affected by λ in our model. As such, λ affects the system at the metapopulation level through m (Eqs. 1 and 4). Assuming no costs, disturbance escape does not affect local dynamics because it is a post-disturbance source of dispersal. Thus, a first potential advantage of disturbance escape compared to emigration propensity is the lack of direct fitness costs associated with negative effects on local population growth. Moreover, the expected number of λ emigrants over the life span of a colonized patch (n_λ), assuming the population is at its equilibrium at the time of disturbance, is given by $n_\lambda = \lambda\bar{x}$. Provided that a local population has reached its equilibrium size, the time elapsed before disturbance occurs does not affect n_λ (i.e., n_λ is independent of e). Thus, disturbance rate increases the frequency of disturbance-induced emigration without affecting the number of emigrants per event (i.e., n_λ). This can be a second advantage of disturbance escape compared to emigration propensity when disturbance rates are high. However, in a more realistic situation, very high disturbance rates could lower n_λ because populations may not have time to reach their equilibrium size. Moreover, n_λ cannot exceed the local population size at equilibrium: $\lambda\bar{x} \leq \bar{x}$ (note that λ is a probability and cannot be higher than 1). This is an important limitation of λ when local carrying capacities are low. Without emigration propensity, disturbance escape alone does not allow dispersal when a viable patch is overcrowded. Another potential disadvantage of disturbance escape is its sensitivity to the disturbance intensity. That is, the value of λ may depend on the nature of the disturbance or its intensity. Unpredictable and strongly harmful disturbance events, such as a major hurricane, a big fire, or predation on hosts for their symbionts, could cause λ to be very low (after all, it is often assumed to be 0). Finally, disturbance escape could have associated fitness costs due to resource allocation trade-offs. For instance, investment in the acquisition of sensory mechanisms to detect disturbance, or specific morphological or behavioral adaptations to flee from disturbance, could require

a reduced investment in reproduction, anti-predatory mechanisms, etc. In this case, disturbance escape would impact local dynamics indirectly.

The fitness ratio, $W_\lambda/W_\gamma = \lambda e/\gamma$, clearly indicates that disturbance rate is the key parameter determining the relative contributions of emigration propensity and disturbance escape to the invasion fitness, by favoring λ against γ . Also, the role of disturbance rate in the persistence of a metapopulation governed by a single dispersal source differs between sources. This remark can be inferred from a simple evaluation of the Eq. 11 as follows. The condition for metapopulation persistence shows the importance of having a favorable balance of disturbance and colonization rates (see numerator and denominator of Eq. 11). This condition can be rewritten as $(\gamma/e + \lambda)\alpha k(1 - \gamma/r)^2 > 1$. Considering a metapopulation without disturbance-induced emigration (i.e., $\lambda = 0$), the previous expression simplifies to $(\gamma/e)\alpha k(1 - \gamma/r)^2 > 1$. The term $(1 - \gamma/r)^2$ reflects the impacts of γ on local dynamics, as described above. The e in the denominator of the first term on the left indicates that disturbance rate has a negative effect on persistence of a metapopulation governed by γ . The effect is explained by the positive dependence of n_γ on the patch life span (i.e., $1/e$), as explained above in this section. Conversely, if we apply the same evaluation to a metapopulation exclusively governed by disturbance escape (i.e., $\gamma = 0$), we obtain the following condition for metapopulation persistence: $\lambda\alpha k > 1$. We can get three insights from this expression. First, persistence is independent of disturbance rate in a metapopulation fully governed by disturbance-induced emigration. This is because colonization rates driven by disturbance-induced emigration are strictly proportional to e , thus counterbalancing variation in local extinction rates. Second, a metapopulation of this type can be released from constraints on persistence derived from the impacts of γ on local dynamics (assuming that λ is free of costs). Third, our model suggests that a metapopulation can persist exclusively by disturbance escape if local carrying capacities (k) are large enough to counterbalance two sources of mortality: mortality driven by disturbance $(1 - \lambda)$ and mortality during dispersal $(1 - \alpha)$.

Disturbance escape as a rescue mechanism

What is the expected role of disturbance-induced emigration as a rescue mechanism when a metapopulation approaches extinction? A main insight from our model is that it depends on the type of mechanism that is driving the metapopulation towards extinction. In particular, it depends, in part, on how the extinction driver selects for emigration propensity. Metapopulation models of dispersal evolution have considered four common drivers of metapopulation extinction (Comins et al. 1980, Gandon and Michalakis 1999, Heino and Hanski 2001, Parvinen et al. 2003, Jansen and Vitis 2007): (1)

increased disturbance rate, (2) increased mortality rate during dispersal (akin to $1 - \alpha$ in our model), (3) decreased local population growth rates, and (4) decreased local carrying capacities. The fitness equations of the disturbance escape model clearly indicate that disturbance escape would be relevant to both the evolution of emigration propensity and the invasion fitness when disturbance rates are high and ES_y is low (see Eqs. 8 and 10). Thus, the metapopulation extinction drivers that select for lower emigration propensity should tend to indirectly increase the relative importance of disturbance escape. In the model of Jansen and Vitalis (2007), which we have extended here, the only extinction driver that selects for lower emigration propensity is a decrease in local population growth rates. Lowering local population growth rates negatively affects ES_y in two different ways, as indicated by the marginal fitness equation (Eq. 10). First, it strengthens the expected fitness reduction associated with the local population sizes at equilibrium. Second, it worsens the ability to avoid extinction driven by demographic stochasticity during the colonization of an empty patch.

We found that an increased mortality rate during dispersal (i.e., decreased α) lowers the relative importance of disturbance escape because it selects for higher emigration propensity. Dispersal mortality (akin to $1 - \alpha$) is generally considered a selective pressure against dispersal (Bonte et al. 2012). However, emigration propensity can sometimes evolve toward higher values when dispersal mortality increases. This occurs when the dispersal mortality is high enough that it produces such a pronounced drop in patch occupancy that metapopulation persistence becomes threatened (Comins et al. 1980, Ronce and Olivieri 2004, Delgado et al. 2011). The assumption of low colonization rates and the existence of empty patches explains this relationship in the disturbance escape model (Jansen and Vitalis 2007). Our model also assumes that local populations reach equilibrium quickly. Other models that relax this assumption provide two main different predictions. First, demographic stochasticity selects for higher emigration propensity when disturbance rates are low (Parvinen et al. 2003). Second, increased disturbance rate selects for lower emigration propensity when disturbance rates are very high (Ronce et al. 2000b). Therefore, we expect that the observed positive effects of disturbance rate on the fitness component associated with disturbance escape will be even stronger in situations with unsaturated populations and non-equilibrium dynamics.

Future perspectives

Our results suggest that disturbance escape seems to act more as a complementary dispersal strategy rather than representing a feasible alternative to replace unconditional emigration. But we illustrated a theoretical situation wherein this complementary role becomes critical

for persistence of a threatened metapopulation (see Fig. 1b). Furthermore, the condition for persistence (Eq. 11) indicates that a metapopulation could persist entirely due to disturbance escape provided $\lambda\alpha k > 1$. Metapopulation models of the Levins' type, such as the one used here, assume that local dynamics equilibrate within a time much shorter than the average lifetime of a patch. However, the metapopulation concept has been extended to describe dynamics of organisms that inhabit ephemeral habitats, in which habitat life span is similar to or shorter than population life span (Reigada et al. 2015). For instance, dynamics of horizontally transmitted symbionts may fit this metapopulation archetype if hosts are conceptualized as ephemeral patches (Mestre et al. 2020). Host death can be viewed as a patch disturbance for its resident symbionts. Interestingly, some horizontally transmitted symbionts are known to abandon a host as it dies, an example of disturbance escape in action (e.g., Klose et al. 2012). The ephemeral lifetime of patches may leave insufficient time to reach local equilibrium and start investing in emigration prior to disturbance. Thus, investment in reproduction and local population growth would become a priority. Disturbance escape could play a major role in governing dispersal in metapopulations of this type. Therefore, we envision the investigation of disturbance escape in metapopulations of ephemeral habitats to be a promising research line.

We did not consider costs associated with disturbance escape. However, it would be sensible in future studies to incorporate costs when considering disturbance escape as an adaptation. One such cost is the ability to detect disturbance in the first place. Many organisms have evolved sensory mechanisms that can anticipate disturbance based on environmental cues. For instance, the giant waterbug *Abedus herberti* uses rainfall cues to abandon streams with a heightened risk of flash floods (Lytle et al. 2008). Juveniles of the reed frog *Hyperolius nitidulus* detect the sound of approaching fires and use it as a cue to flee (Grafe et al. 2002). Smoke detection allows eastern red bats (*Lasiurus borealis*) to rouse from torpor and escape from fire (Scesny and Robbins 2006). Entire aphid colonies flee their host plant as a response to the warmth and humidity of mammalian breath, permitting them to avoid being consumed by herbivores (Gish et al. 2010). Costs associated with information acquisition can play an important role in the evolution of context-dependent dispersal (Bocedi et al. 2012). Thus, the incorporation of information costs to investigate the joint evolution of disturbance escape and emigration propensity will be a natural step further in this novel research line. Finally, we have assumed a binary strategy of dispersal: a basic emigration propensity, together with a pulse of dispersal associated directly with a disturbance. Given that cues associated with patch disturbance are uncertain, one could also imagine graded responses. Symbionts might for instance inhabit hosts with an expected life span, and dispersal rates might

increase gradually as the host ages and gets closer to death. Analyzing such continuous, plastic dispersal strategies would be another valuable direction to pursue beyond the results we have presented.

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