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The Role of Landscape-Dependent Disturbance and Dispersal in Metapopulation Persistence

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ABSTRACT: The fundamental processes that influence metapopulation dynamics (extinction and recolonization) will often depend on landscape structure. Disturbances that increase patch extinction rates will frequently be landscape dependent such that they are spatially aggregated and have an increased likelihood of occurring in some areas. Similarly, landscape structure can influence organism movement, producing asymmetric dispersal between patches. Using a stochastic, spatially explicit model, we examine how landscape-dependent correlations between dispersal and disturbance rates influence metapopulation dynamics. Habitat patches that are situated in areas where the likelihood of disturbance is low will experience lower extinction rates and will function as partial refuges. We discovered that the presence of partial refuges increases metapopulation viability and that the value of partial refuges was contingent on whether dispersal was also landscape dependent. Somewhat counterintuitively, metapopulation viability was reduced when individuals had a preponderance to disperse away from refuges and was highest when there was biased dispersal toward refuges. Our work demonstrates that landscape structure needs to be incorporated into metapopulation models when there is either empirical data or ecological rationale for extinction and/or dispersal rates being landscape dependent.

Keywords: metapopulation dynamics, aggregated disturbance, asymmetric dispersal.

A principal tenet of Levins's (1969, 1970) classic metapopulation model is that extinction and colonization rates are independent of each other and independent of time. However, colonization and extinction may not be uncor-

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related in time and space if the mechanisms driving these processes are influenced by the same landscape features. For example, landscape structure has the potential to dictate the degree to which habitat disturbances are spatially correlated (Channell and Lomolino 2000; Peterson 2002), as well as to influence where and how far animals disperse within their environment (Fahrig and Merriam 1985; Turner 1989; Armsworth and Roughgarden 2005). Although recent articles have examined the effect of spatially aggregated disturbances (Ovaskainen et al. 2002; Johst and Drechsler 2003; Kallimanis et al. 2005) and asymmetric dispersal (King and With 2002; Vuilleumier and Metzger 2006; Vuilleumier and Possingham 2006) on metapopulation dynamics, no one has examined how these spatially explicit processes interact and influence metapopulation persistence.

Spatially correlated disturbances are generally thought to be detrimental to metapopulation persistence (Ovaskainen et al. 2002; Johst and Drechsler 2003; Kallimanis et al. 2005); however, a consensus based on empirical data and theoretical insights has not yet been reached. Spatially correlated disturbances may be detrimental to metapopulation persistence if aggregated disturbances result in the synchronization of the dynamics of local populations (Johst and Drechsler 2003). The resulting synchronization of population growth rates has consistently been found to decrease metapopulation persistence (Ranta et al. 1995, 1999; Heino et al. 1997; Bjornstad et al. 1999; Lande et al. 1999; Ripa 2000). Conversely, aggregated disturbance may produce a landscape in which suitable habitat patches are spatially clustered. If an organism has limited dispersal ability, habitat clustering can result in connectivity being maintained between patches even when some habitat is lost (Doak et al. 1992; With and King 1999; King and With 2002), with the resulting effect of an increase in metapopulation persistence.

If disturbance processes are not only spatially correlated but also have a higher propensity to affect certain sections of the landscape, two types of habitat patches are created: patches that are prone to being destroyed and patches that are less likely to be disturbed that may function as spatial

refuges. A biased distribution of disturbances on a landscape may result from the disturbance being explicitly landscape dependent, for example, flooding occurring only in areas of low elevation. In addition, persistent landscape disturbance patterns may result from positive feedback loops that are created when biotic or abiotic interactions produce a positive correlation between the disturbance history of a patch and the probability that it will be disturbed in the future (Holling 1992; Possingham et al. 1995; Peterson 2002). The presence of refuge patches in a metapopulation is predicted to increase metapopulation viability by providing patches that, over the long term, are more consistently occupied and from which colonizing individuals may be sent (Vuilleumier et al. 2007).

The value to metapopulation viability of a refuge patch will depend on how protected the patch is from disturbance events, its chance of being reoccupied (the likelihood that it will be colonized following a local extinction event), and the ability of the refuge patch to produce and send out propagules to colonize empty patches. The second and third of these attributes will depend on the spatial location of the refuge patch within the metapopulation network, as well as the realized connectivity of the refuge patch (Hanski and Ovaskainen 2000).

Although symmetrical connectivity between patches is often assumed, asymmetric dispersal and colonization probably predominate in many real populations (Vuilleumier and Possingham 2006). Asymmetric colonization may be produced by actively dispersing individuals who are biasing their movement in response to environmental or landscape cues (taxis; Vuilleumier and Perrin 2006) or by the biasing of the movement of passively dispersing individuals by landscape-dependent advection (Armsworth and Bode 1999; Armsworth and Roughgarden 2005). In addition, landscape structures such as barriers or corridors may constrain or guide dispersing individuals, producing asymmetric connectivity (Haddad 1999; Haddad et al. 2003; Pe'er et al. 2006). Therefore, asymmetric movement may be particularly prevalent in organisms that disperse through heterogeneous landscapes.

Asymmetric dispersal has been demonstrated to be detrimental to metapopulation viability in systems where habitat quality is homogeneous (Vuilleumier and Possingham 2006). However, the influence of asymmetric dispersal in metapopulation systems that contain patches of different quality, or refuge patches, is less clear (Doebeli 1995; Kawecki and Holt 2002). In regard to habitat heterogeneity that is driven by landscape-dependent disturbances, two scenarios may occur. First, if landscape structure produces asymmetric movement into refuge patches (negative correlation between disturbance probability and colonization probability), occupancy of refuge patches will be increased but the colonizing pressure from the refuge—and hence

the benefits to the rest of the metapopulation—will be diminished (fig. 1a). Alternatively, if there is asymmetric movement away from refuge patches (positive correlation), occupancy of the refuge will be decreased while colonization from occupied refuges will be enhanced (fig. 1b).

Species may be particularly prone to strong correlations between disturbance and dispersal in highly structured landscapes, for example, in river systems, where there are constrained and directional connections between habitat patches (Pringle 2001; Fausch et al. 2002; Allan 2004); in marine systems such as coral reefs, where both organism movement and disturbances are dependent on ocean currents (McClanahan et al. 2005; Dizon and Yap 2006); and in terrestrial systems, where the propagation of major disturbances such as fire is often landscape dependent (Holling 1992). In these systems, an improved understanding of how landscape structure influences the interaction between the key mechanism of dispersal and extinction will provide three benefits: first, it will allow for improved predictions on metapopulation persistence; second, it will improve our evaluation of the importance of individual habitat patches given their spatial location on the landscape and the processes (colonization and disturbance) that link the patches; and finally, it will allow for better predictions about how these systems will respond to future shifts in disturbance patterns and dispersal rates.

In this article, we assess how landscape-dependent correlations between disturbance events and organism dispersal affect metapopulation dynamics, specifically testing whether asymmetric movement into or out of refuge patches increases metapopulation persistence. We then dis-

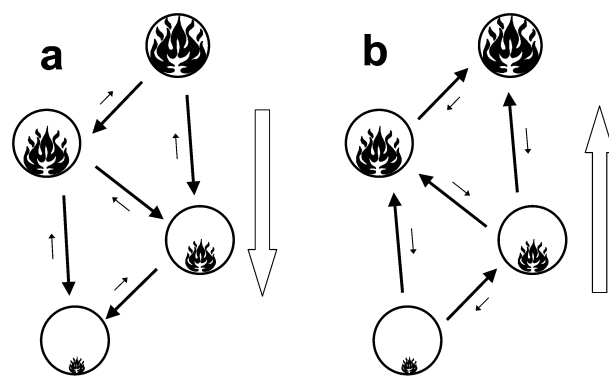


Figure 1: Schematic of landscape-dependent dispersal and disturbances. The probability of a patch being disturbed is represented by the size of the disturbance (shown as fire), and landscape-dependent asymmetric movement is represented by the size of arrows connecting patches. *a*, A negative correlation between colonization probability and disturbance probability as a result of biased movement toward refuges. *b*, A positive correlation with biased movement away from refuges.

cuss the implications of our results for the management of species that occur in systems where disturbance events and movement are landscape dependent.

Methods

We begin by describing the metapopulation framework and the procedures that we used to model landscape-dependent disturbances and landscape-dependent asymmetric dispersal. We then describe the simulation experiments that we conducted. Both of these components require the use of a dispersal kernel that accurately reflects how distance and landscape-dependent movement each influence the dispersal process. The dispersal kernels commonly used in metapopulation models do not incorporate landscape bias (Moilanen and Hanski 2001; Moilanen and Nieminen 2002); thus, we first needed to determine the best method for modeling landscape-dependent dispersal. We did this by testing the accuracy of a range of dispersal kernels using an individual-based simulation model. The model structure, dispersal kernels tested, and results are described in the appendix.

Metapopulation Model

We used a spatially explicit patch occupancy simulation model to explore how the correlation between animal dispersal and the spatial spread of disturbance influences metapopulation persistence. The model was constructed as a continuous-time Markov chain (CTMC) model (Norris 1997; Ross 2006; Cairns et al. 2007) with 100 patches oriented in a 10×10 lattice. All patches were of equal size and quality and differed only in their spatial location and landscape value (elevation; fig. 2). The spatial relationship between all patches was given by a matrix of the distances (d_{ij}) between patches and a matrix that contained the difference in elevations (η_{ij}) between patch i and patch j . Patches could therefore be divided into two broad categories, central and peripheral (fig. 2). The edges of the lattice were modeled as hard boundaries that neither dispersing individuals nor spreading disturbances could cross.

Patches existed in one of two states, occupied ($x_i = 1$) or empty ($x_i = 0$), with the state of the whole metapopulation (x_1, \dots, x_{100}) given by a vector of the states x_i of the individual patches. State transitions occurred as a result of three processes: extinction (κ_i), colonization (c_i), and disturbance (d). The transition matrix (the Q matrix in CTMC terminology) is defined by these rates; we will collectively refer to these rates as q_{ij} , which represents the rate of transition from state i to state j (Norris 1997). The duration that the metapopulation remains in state i before it jumps to state j is exponentially distributed, with the

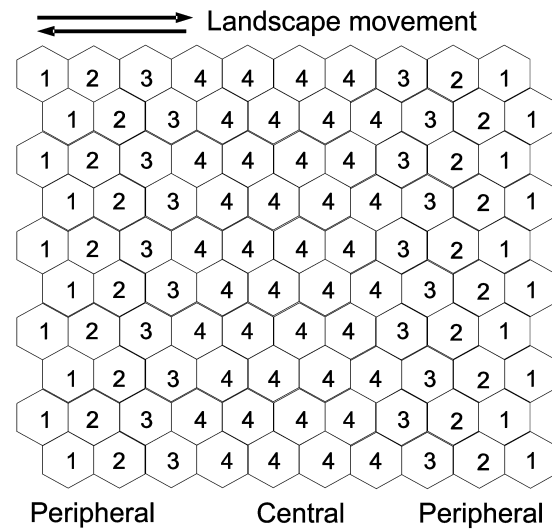


Figure 2: The simulated landscape. Structure was added to the landscape by assigning a landscape value to each cell. The movement of dispersing individuals and the spread of disturbances were made landscape dependent by biasing the probability of moving into a surrounding cell based on the cell's landscape value. Each cell in the landscape contains one habitat patch that is encountered, with a set probability, by a dispersing individual.

rate parameter of the exponential probability density function (PDF) given by

$$\tau_i = \sum_j q_{ij}. \quad (1)$$

The probability that the transition event q_{ij} occurs and that the metapopulation moves from state i to state j is given by

$$p_{ij} = \frac{q_{ij}}{\tau_i}. \quad (2)$$

We simulated transitions by calculating the exponential PDF on the basis of transition rates and then by randomly drawing a transition time from this distribution. The transition that occurred was then randomly selected from the cumulative probability distribution of p_i .

In all simulation runs, κ_i was constant and independent of patch location on the landscape. In simulation runs that included disturbances, d was also constant.

Colonization and Asymmetric Dispersal

The rate at which an occupied patch x_i colonizes an unoccupied patch x_j was modeled as a function of d_{ij} and η_{ij} . On the basis of our dispersal simulation (see the appen-

dix), we assumed a sigmoidal dispersal kernel. The rate c_i is the summation of the colonization rates from all occupied patches,

$$c_i = \sum_{i \neq j} c_0 \times x_j \times \{1 - e^{[-\lambda e^{(-\alpha d_{ij} + \beta \eta_{ij})}]}\}, \quad (3)$$

where c_0 is a basal colonization rate, $x_j = 1$ if the sending patch is occupied, and $x_j = 0$ if the patch is unoccupied. Dispersal distance is determined by α and is equivalent to the reciprocal of the mean dispersal distance (Moilanen and Nieminen 2002). When α is set to 0, the rate at which an occupied patch colonizes an unoccupied patch is independent of distance. The influence of landscape structure on dispersal was determined by β (table 1); a positive β resulted in individuals dispersing up an elevation gradient, whereas negative values of β resulted in movement down an elevation gradient. We tested connectivity across a range of α and β values (table 1).

As a result of this landscape-biased movement, patch connectivity is asymmetric. Previous studies that have examined asymmetric dispersal have produced asymmetric connections between patches but have not situated the asymmetric movement within a landscape perspective (Vuilleumier and Possingham 2006). In contrast, because we assume that dispersal is driven by landscape structure, connectivity will be directly correlated with the landscape and indirectly correlated with landscape-dependent disturbances.

Landscape-Dependent Disturbance

Individual disturbance events affected multiple patches simultaneously and occurred at rate d . When a disturbance occurred, the number of patches that were affected (μ) was drawn from the binomial distribution,

$$\text{Bin}(\mu; N, \theta) = \binom{N}{\mu} \theta^\mu (1 - \theta)^{N-\mu}, \quad (4)$$

where θ is the probability of a patch being disturbed, reflecting the disturbance intensity, and N is the total number of patches in the environment. Suitable patches and patches that had been removed during previous disturbance events had the same probability of being disturbed, such that N was constant.

The patch in which the disturbance originated was selected from the cumulative probability distribution,

$$p(\text{origin}_i) = \frac{\eta_i^{(\delta)}}{\sum_{k=1}^{100} \eta_k^{(\delta)}}, \quad (5)$$

where η_i is the elevation of the patch and δ determines the degree to which disturbances have a higher probability of occurring at either high-elevation (positive δ) or low-elevation (negative δ) sites. Once a site of origin was selected, the disturbances spread across the landscape from patch to patch in a successive manner until μ patches were disturbed. The probability of a disturbance spreading from patch i into patch j was a function of the relative distance between the patches and was calculated as

$$p(\text{spread}_j) = \left(\frac{e^{(-\varphi \times d_{ji} + \delta \times \eta_{ji})}}{\sum_{j=1}^{100} e^{(-\varphi \times d_{ji} + \delta \times \eta_{ji})}} \right) \cdot \omega_j, \quad (6)$$

where φ determines the degree to which the disturbance is spatially aggregated, δ determines the propensity for the disturbance to spread into lower-elevation (central) or higher-elevation (peripheral) patches, and ω specifies whether the patch is already disturbed ($\omega = 0$) or not disturbed ($\omega = 1$) such that a disturbance will not move into a patch that has already been disturbed during the current disturbance event.

If an occupied patch was disturbed, the population was eliminated and the patch state was set to “unoccupied.” Disturbed patches were immediately suitable for colonization following a disturbance. This representation of disturbances as events that cause population extinctions but

Table 1: Parameter values used in each metapopulation simulation experiment

Parameter	Experiment 1: aggregated disturbance	Experiment 2: asymmetric dispersal	Experiment 3: correlated dispersal and disturbance
Extinction rate (κ_i)	.2	.2	.2
Base colonization rate (c_0)	1	1	1
Dispersal distance (α)	1	0 to 1.6	1
Landscape-dependent dispersal (β)	0	-1 to 1	-1 to 1
Disturbance rate (d)	1	0	1
Disturbance intensity (θ)	.2, .25, .3, .35	0	.2, .25, .3, .35
Spatial aggregation of disturbance (φ)	0 to 1.6	0	1
Landscape-dependent disturbance (δ)	-1 to 1	0	-1 to 1

that do not influence habitat suitability approximates the effect of extrinsic disturbances such as disease or environmental disturbances (e.g., flood or severe weather events), where populations are adversely affected but where the quality of the habitat remains relatively unchanged. Whereas the rate at which disturbed patches recover has been shown to be important for metapopulation dynamics (Amarasekare and Possingham 2001; Wilcox et al. 2006), here our focus is on the spatial arrangement of disturbances and not on the rate at which patches recover.

Metapopulation Simulations

At the beginning of each simulation, all patch states were set to "suitable and occupied." Metapopulation dynamics were simulated across 5,000 transition events. We used two metrics to assess the state of the metapopulation, metapopulation viability and quasi-stationary distribution. The quasi-stationary distribution is the probability distribution of metapopulation occupancy states given that the metapopulation is still viable (Day and Possingham 1995; Pollett 2001). If one or more patches were occupied after 5,000 transition events, the metapopulation was recorded as viable. The first 1,000 transition events were used as a burn-in period during which the metapopulation moved toward its quasi-stationary distribution. Preliminary analysis demonstrated that simulations quickly approached the quasi-stationary distribution, usually within the first 200 transitions. If the metapopulation was viable, we recorded the number of occupied patches after each transition and calculated the mean number of occupied patches (our measure of the quasi-stationary state). We used these two metrics of metapopulation state to get a clear idea of how correlated disturbances and dispersal influence metapopulations but also because these two metrics reflect the difference between what population managers and ecologists care about (the long-term viability of a metapopulation) and the metric that is commonly recorded to assess the state of a metapopulation (the number of patches that are occupied).

We divided our analysis of the metapopulation simulation into three experiments. The range of parameter values used in each experiment is given in table 1. The first experiment examined how spatially aggregated disturbances that were or were not landscape dependent influence metapopulation persistence. In this experiment, all patches were equally and symmetrically connected. We varied the degree to which disturbances were spatially aggregated (φ) and the degree to which the probability of a disturbance occurring was landscape dependent (δ) and examined a range of disturbance intensities. In the second experiment, we focused on asymmetric dispersal and tested how landscape-dependent asymmetric movement influ-

ences metapopulation persistence. We varied dispersal distance (α) and the degree to which dispersal was asymmetric (β). Disturbance events were not included. The third experiment combined these two factors to address the question of how correlation between landscape-dependent disturbances and landscape-dependent dispersal influences metapopulation persistence. The parameter values that we used for the extinction rate ($\kappa_i = 0.2$), base colonization rate ($c_0 = 1, 0.3$), and disturbance rate ($d = 1$) were selected on the basis of preliminary analysis. We ran 1,000 metapopulation simulation replicates for each parameter set.

Our interest was not only to determine how correlated disturbances and dispersal influence metapopulations but also to assess the relative importance of each factor. To accomplish this, we calculated the effect size for each of the parameters that we varied in the stochastic metapopulation simulations. Effect size (Tabachnick and Fidell 2007) represents the proportion of the total variance that is attributable to an effect and is calculated as the sum of squares of the effect divided by the total sum of squares that results from an ANOVA. We used an ANOVA that included all second-order interactions of the independent variables that were manipulated in each experiment (table 1).

To facilitate the comparison of our stochastic simulation results with the results obtained from classic metapopulation models that are based on mean field approximations (e.g., Levins 1969), we compared the quasi-stationary distribution predictions from our model with the number of occupied patches predicted using the model formulation of Johnson (2000; see Vuilleumier et al. 2007 for a full description of the model validation procedure that we used). Similar to the results obtained by Vuilleumier et al. (2007), we found that our simulation results closely corresponded to the results of the mean field models when the simulations were devoid of explicit spatial structure (no spatial aggregation of disturbance, no asymmetrical dispersal, all patches capable of sending colonists to all other patches). However, as soon as explicit spatial structure was included, the results diverged. Therefore, classic metapopulation predictions are approximated by our results when disturbances are not aggregated ($\varphi = 0$) or landscape dependent ($\delta = 0$) and when dispersal is not constrained ($\alpha \sim 0$) or asymmetrical ($\beta = 0$).

Results

Question 1: What Is the Impact of Aggregated Disturbance on Metapopulation Dynamics (Experiment 1)?

In our model, spatially aggregated disturbances with symmetric migration decreased both metapopulation viability

and the mean number of patches occupied from the quasi-stationary distribution; because spatially aggregated disturbance had the same qualitative effect on both metapopulation viability and quasi-stationary distribution, we present only the metapopulation viability (fig. 3a). The influence of disturbance aggregation depended on the intensity of the disturbance (fig. 3a; table 2). When the disturbance intensity (which determines the number of patches disturbed) was either low or high, there was only a marginal decrease in viability and the number of occupied patches as disturbances became more aggregated. At high disturbance intensities, metapopulation viability is already low and increased aggregation results in viability becoming 0. At intermediate disturbance intensities, the degree that a disturbance is aggregated has a large influence on viability (fig. 3a).

Although the spatial aggregation of disturbances decreases metapopulation viability, increasing the probability that disturbances occur in one portion of the landscape (either central or peripheral patches) increased metapopulation viability (fig. 3b). Metapopulation viability is increased to a greater extent when disturbances are localized in central patches compared with peripheral patches. To test the generality of this finding, we reran our model using higher disturbance rates ($d = 1-2$) and lower colonization rates ($c_0 = 0.5-1$). Using disturbance and colonization rates beyond these values produced nonviable metapopulations. Even when high disturbance rates were used, metapopulation viability was higher when disturbances were biased toward central patches. Only very low colonization rates ($c_0 = 0.5$) created conditions where metapopulation viability was lower when disturbances were biased toward central patches.

This seemingly counterintuitive result, that disturbances in central patches are less detrimental than disturbances concentrated in peripheral patches, reflects the relative rate at which disturbed central and peripheral patches are recolonized. When dispersal is symmetrical, a disturbed peripheral patch will be recolonized more slowly than a central patch. Therefore, although disturbances localized to central patches will initially decrease the probability that unoccupied patches will be colonized, the longer-term impact on metapopulation dynamics is smaller because these patches themselves will be recolonized more quickly.

Question 2: What Is the Impact of Asymmetric Dispersal on Metapopulation Dynamics (Experiment 2)?

Asymmetric dispersal reduces both metapopulation viability and occupancy state (fig. 4; table 2). This was true regardless of whether the asymmetry favored central or peripheral patches. When the dispersal distance was short, asymmetric movement toward peripheral patches was

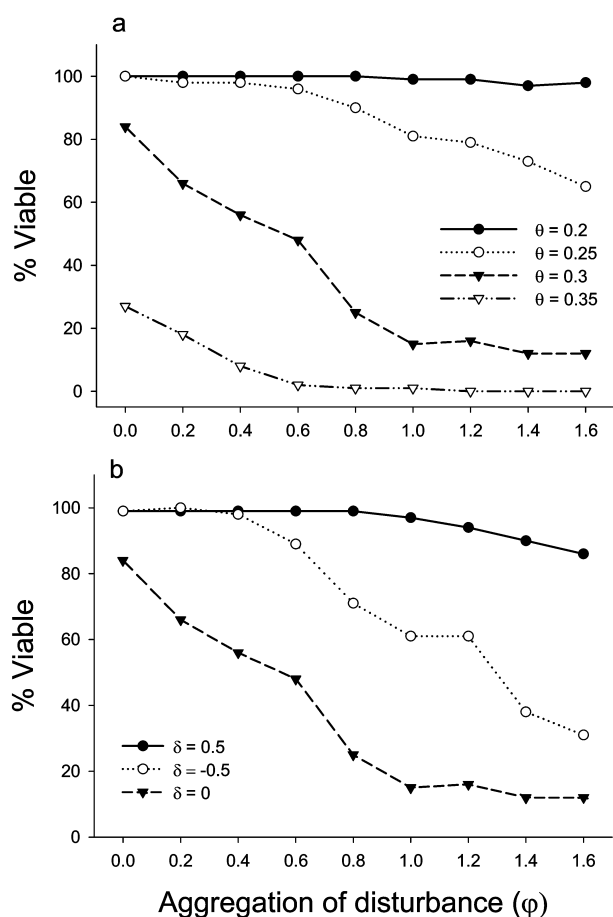


Figure 3: Percent of metapopulations that were viable following 5,000 transition events in simulations that incorporated different levels of spatial aggregation of disturbances ($\phi = 0$, no spatial aggregation; $\phi = 1.6$, highly aggregated disturbances). *a*, Influence of disturbance intensity (θ = percent of habitat patches destroyed) on metapopulation viability, in simulations with no landscape-dependent bias to disturbance occurrence ($\delta = 0$). *b*, Influence of landscape-dependent disturbance on metapopulation viability ($\delta = -0.5$, disturbance biased toward peripheral patches; $\delta = 0.5$, disturbance biased toward central patches), in simulations with a disturbance intensity of $\theta = 0.3$.

more detrimental than asymmetric movement toward central patches. Conversely, when dispersal distance was longer, asymmetric movement toward peripheral patches was initially less detrimental to population viability (down to a β value of -0.5). However, when there was a strong movement bias toward peripheral patches ($\beta < -0.5$) and dispersal distance was longer, metapopulation viability quickly decreased. Whereas asymmetric dispersal had the same qualitative affect on both metapopulation viability and occupancy state, the magnitude of the influence on metapopulation viability was much greater (fig. 4).

Table 2: Effect size for each parameter that was varied in the metapopulation simulation experiment

Parameter	Experiment 1: aggregated disturbance	Experiment 2: asymmetric dispersal	Experiment 3: correlated dispersal and disturbance
α		19.7 (20.4)	
β		23.6 (43.7)	6.9 (19.6)
$\alpha \times \beta$		3.2 (1.5)	
θ	27.2 (57)		27.4 (16.4)
φ	5.2 (7.5)		
$\theta \times \varphi$	4 (.5)		
δ	13.1 (12.2)		11 (2.2)
$\theta \times \delta$	11.7 (.9)		5.6 (.4)
$\varphi \times \delta$	2.1 (1.8)		
$\beta \times \theta$			22.4 (.8)
$\beta \times \delta$			14.8 (2)

Note: Effect size expresses the percent of variation attributable to each parameter. The first value is the percent of variation in metapopulation viability, and the value in parentheses is the variation in the mean metapopulation occupancy state (mean of the quasi-stationary distribution). α = dispersal distance; β = landscape-dependent dispersal; θ = disturbance intensity; φ = spatial aggregation of disturbance; δ = landscape-dependent disturbance.

Question 3: What Is the Impact of Correlated Disturbance and Dispersal on Metapopulation Dynamics (Experiment 3)?

The response of metapopulation viability and occupancy state to landscape-dependent dispersal and disturbance was qualitatively the same for each disturbance intensity that we simulated. Although the interaction between disturbance intensity and landscape-dependent dispersal influenced metapopulation viability and occupancy state (table 2), changes in disturbance intensity did not qualitatively alter how the interaction between landscape-dependent dispersal and landscape-dependent disturbances influenced either metapopulation viability or occupancy state. For presentation purposes, we focus on the results from simulations that included a disturbance intensity of 0.3.

Metapopulation viability was highest when there was a negative correlation between landscape-dependent dispersal and landscape-dependent disturbances (fig. 5, *top*). In these situations, partial refuges are created on the landscape and landscape-dependent asymmetric dispersal results in biased movement of organisms toward the partial refuges and reduced movement away from the refuges. A negative correlation between dispersal and disturbance can reflect two states: (1) peripheral patches that are functioning as partial refuges and biased movement toward the periphery or (2) central refuge patches with biased movement toward the center. Both refuge states result in high metapopulation viability, with peripheral patches being slightly superior (fig. 5, *top*).

The strength of partial refuge patches (i.e., peripheral patches if there is a higher likelihood of disturbance in central patches) depended on the strength of the landscape-dependent disturbance bias. If disturbances were strongly landscape dependent ($\delta > 0.5$ or $\delta < 0.5$), then functionally the refuge was strong because the likelihood of a disturbance occurring in the refuge was low. As a result, the worst metapopulation viability results occurred when individuals had a propensity to move away from partial refuges (positive correlation between dispersal and disturbance movement) and when landscape-dependent disturbance spread was at intermediate levels ($\delta \sim 0.25$ or $\delta \sim -0.25$; fig. 5, *top*). Under these conditions, the patches that were more likely to be colonized were more likely to be disturbed, but the spatial segregation of disturbances was not sufficiently pronounced to produce strong refuges in the landscape.

Surprisingly, the number of patches occupied at equilibrium (the mean of the quasi-stationary distribution) exhibited the same qualitative response to changes in landscape-dependent disturbance rates as metapopulation viability, but the response to landscape-dependent dispersal was markedly different (fig. 5, *bottom*). Asymmetric dispersal (toward either peripheral or central patches) resulted in the number of occupied patches being lower, irrespective of whether there was a positive or negative correlation with landscape-dependent disturbance. As a result, the number of patches occupied was highest when there was no asymmetric dispersal and disturbances were strongly biased to either peripheral or central patches.

The relative effect size of landscape-dependent dispersal and disturbance on metapopulation dynamics depended on whether metapopulation viability or the number of occupied patches was examined. Landscape-dependent asymmetric dispersal had a large impact on metapopulation occupancy state but a relatively minor effect on viability (table 2). Conversely, landscape-dependent disturbance strongly influenced metapopulation viability but had a small effect on occupancy state. In addition, the effect size for the interaction between landscape-dependent dispersal and disturbance was large with respect to metapopulation viability but small in its effect on occupancy state.

In summary, our results demonstrate that disturbances that are both spatially aggregated and landscape dependent produce habitat patches that have lower extinction risk, that is, partial refuges that increase metapopulation viability. The value of these partial refuges depended on whether dispersal was also landscape dependent. Metapopulation viability was increased when individuals had a propensity to disperse toward partial refuges, and viability was decreased if individuals were more likely to disperse away from refuges.

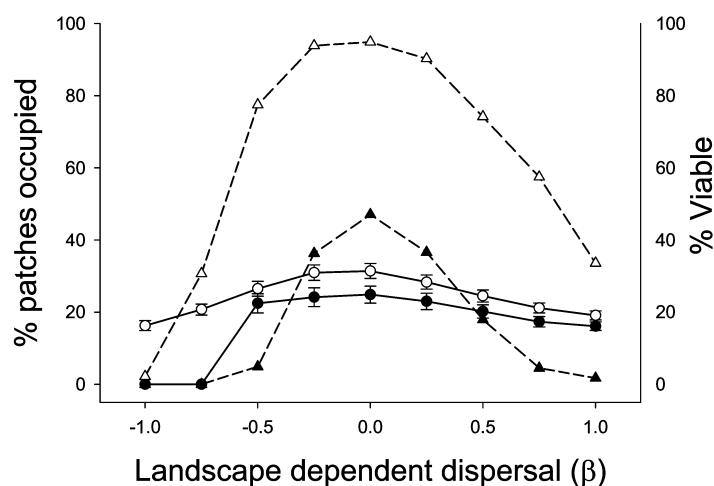


Figure 4: Percent of metapopulations that were viable (*triangles*) and mean metapopulation occupancy state (mean and variance of quasi-stationary distribution; *circles*) from metapopulation simulation that incorporated different degrees of landscape-dependent dispersal. Negative values of β indicate biased dispersal toward peripheral patches, while positive values indicate biased dispersal toward central patches. *Open symbols*, results from simulations with using longer dispersal distance ($\alpha = 0.6$); *closed symbols*, results from simulations using shorter dispersal distance ($\alpha = 1.6$).

Discussion

Landscape-dependent correlations between habitat-disturbance events and organism dispersal can have large impacts on metapopulation dynamics. Positive correlations between these processes, whereby individuals exhibit biased movement toward habitat patches that are more likely to be disturbed, substantially decrease metapopulation viability, whereas negative correlations result in metapopulations that are much less likely to become extinct. The beneficial effect that negative correlations had on metapopulation viability indicates that maintaining the occupancy state of habitat patches that are less likely to be disturbed and become extinct (partial refuge patches) is very important for metapopulation persistence. Our results are in accord with those of Ross (2006) who, using a mainland-island metapopulation model (Alonso and McKane 2002), demonstrated that the presence of patches that have very low extinction rates, “mainland-like patches,” significantly increases metapopulation persistence. Landscape-dependent disturbances produce a situation that is also analogous to source/sink population models (Pulliam 1988); over a long duration, refuge patches within a metapopulation function as “pseudo-source” populations in that they contribute colonizing propagules to empty habitat patches more frequently than do nonrefuge patches. Similar to source populations, the presence of refuge patches will make metapopulations more resistant to stochastic extinction.

Surprisingly, our results also indicate that the beneficial influence of having partial refuge patches in a landscape

is maintained even when the propensity for individuals to disperse away from refuges toward more “risky” habitat patches is very low. We found that metapopulation viability is highest even when there was very strong asymmetric dispersal toward partial refuge patches (fig. 5). The beneficial influence of maintaining the occupancy state of refuges is also demonstrated by the fact that, although the viability of metapopulations continued to increase as the strength of asymmetric dispersal increased, the mean occupancy state of the metapopulation decreased. However, we predict that strong asymmetric dispersal toward refuge patches will be detrimental to metapopulation persistence under some conditions. If some refuge patches are relatively isolated from other refuge patches, strong asymmetric dispersal will decrease the number of dispersers that are exchanged between refuges (fig. 3*b*; fig. 5, *bottom, lower left*). Because refuge patches are not expected to be immune to extinction, they will eventually become extinct. If the probability of their being recolonized is low, the persistence of the metapopulation will also be low.

Similar to previous studies (Ovaskainen et al. 2002; Johst and Drechsler 2003; Kallimanis et al. 2005), we found that spatial aggregation of disturbances decreases metapopulation persistence. The detrimental effects of aggregated disturbance will, however, be partially ameliorated if disturbances are landscape dependent and partial refuge patches are present. Our results indicate that spatial refuge patches do not need to be immune to disturbance to significantly decrease a metapopulation’s extinction risk; the rate at which a disturbance occurs in a patch just needs

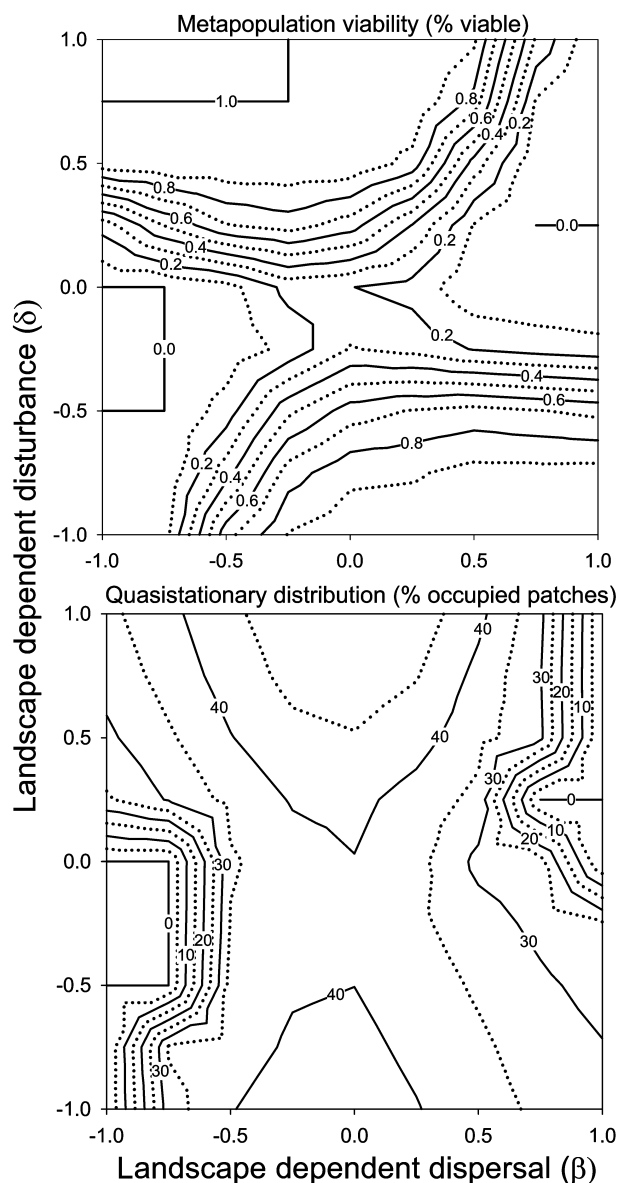


Figure 5: Influence of landscape-dependent disturbance (δ) and dispersal (β) on metapopulation viability (*top*) and mean metapopulation occupancy state (mean of quasi-stationary distribution; *bottom*). Results are shown for simulations that incorporated a disturbance intensity $\theta = 0.3$.

to be lower. Kallimanis et al. (2005) identified a similar effect when they noted that spatially autocorrelated disturbances are most detrimental to metapopulation viability when the disturbance occurs at the same scale at which habitat patches are clustered. When aggregated disturbances operate on either a larger or a smaller scale compared with the scale of habitat clustering, there is a higher probability that some patches will not be destroyed. These

undisturbed patches are equivalent to the spatial refuge patches in our study in that they will increase the probability that disturbed patches will be recolonized. Holling (1992) and Peterson (2002) have proposed that, for many disturbances that exhibit spatial autocorrelation, such as fire, disease outbreaks, or floods, the occurrence and spread of the disturbance is also landscape dependent. If this is the case, then refuge habitat patches that are less likely to be disturbed are probably also prevalent in these landscapes. From this perspective, when researchers and ecosystem managers are assessing the impact of a disturbance on a metapopulation persistence, it may be as important to determine whether refuge habitat patches exist as it is to assess how spatially aggregated disturbances are likely to be.

In this article, we have premised our model on landscape-dependent disturbance and dispersal that are driven by abiotic landscape features, such as elevation or temperature gradients. However, correlations between disturbance and dispersal may also be produced by biotic interactions. Gilliam and Fraser (2001) describe how a combination of direct and indirect interactions between predators and prey in a stream system can render some habitat patches inhospitable for prey while at the same time influence the movement rates of prey between patches. This therefore creates a condition where a spatially aggregated disturbance (e.g., a predation threat that is constrained to occur only in some habitat patches) is correlated with the movement of individuals between patches. This highlights the fact that habitat patches may function as spatial refuges because they have experienced lower levels of abiotic disturbance or as a result of biological processes such as predation or competition that are less intense or not present at the site. Under these conditions, the dynamics and persistence of the metapopulation will be accurately represented only by models that both are spatially explicit and account for the within-patch biological conditions that produce refuge and nonrefuge sites.

Vuilleumier and Possingham (2006) examined the influence of asymmetric dispersal on metapopulation persistence, and they noted two main conclusions. First, asymmetric dispersal decreases metapopulation viability, a conclusion that our results support. Second, with asymmetric dispersal, the viability of a metapopulation is determined primarily by the number of connected patches and not by the colonization probability. They note that this conclusion implies that the standard conservation tactic of modifying movement corridors to increase colonization probability between patches may be inefficient in systems with highly asymmetric dispersal. Although our results generally support this conclusion, they also suggest that conservation efforts that maintain or increase the con-

nectivity to refuge habitat patches will increase metapopulation persistence.

A key finding of our work is that metapopulation viability exhibits a different response to correlated disturbance and dispersal compared with the effect on the metapopulation's quasi-stationary distribution state. Metapopulation viability increases as the strengths of positively correlated landscape-dependent processes increase (fig. 5). Conversely, the mean number of patches occupied (the metapopulation's quasi-stationary distribution) is highest when there is no correlation between dispersal and disturbance and when disturbances are biased toward occurring in one area of the landscape (either peripheral or central patches). Therefore, landscape-dependent disturbance and dispersal parameters that maximize the number of occupied patches will not maximize metapopulation viability.

This difference is important because, while the objective of most management or conservation actions is to increase the probability that a species will remain extant in an area (i.e., increase metapopulation viability), the data that managers use to model and assess the status of a metapopulation are often based on a "snapshot" or a short time series of patch occupancy. Two problems may arise. First, management actions that are designed to increase the number of occupied patches (e.g., by modifying dispersal routes to make connectivity between patches more symmetrical) may actually decrease metapopulation viability if dispersal and disturbances are negatively correlated. Second, and potentially more important, when there is a negative correlation between disturbance and dispersal and when individuals move toward partial refuge patches, an assessment of metapopulation viability based on the number of occupied patches will systematically underestimate the viability of the metapopulation network. To avoid these problems, managers need to evaluate whether dispersal and disturbances are landscape dependent and, if they are, to assess metapopulation viability using models that explicitly account for these landscape-dependent processes.

To effectively manage metapopulation systems, it is important to be able to value the contribution that individual patches make to metapopulation persistence (Ovaskainen and Hanski 2003; Frank 2005; Nicholson et al. 2006). This valuation will typically account for the spatial location of the patches and whether the patch is a source population or a sink population. Our work suggests that it may be equally important to value a patch on the basis of its probability of being a spatial refuge and to a lesser degree by whether there is biased movement into or out of the patch. Estimating whether a patch is a partial refuge would ideally be done by directly estimating patch-specific extinction rates. Likewise, determining whether some patches have higher colonization rates due to asymmetric

movement would ideally be done by directly observing a large number of colonization events or by measuring the number of potential colonizers arriving at sites. However, deriving whether a patch is a partial refuge and whether there is asymmetric colonization only on the basis of patch occupancy data will be very difficult if not impossible in most systems because time series data that would allow for patch-specific extinction and colonization events to be estimated are not available. An alternative approach is to begin with a hypothesis of biologically realistic mechanisms that will produce landscape-dependent disturbances and dispersal rates and explicitly incorporate them into spatially explicit metapopulation models. This approach will require a greater understanding of disturbance and dispersal processes and how they relate to landscape features and therefore will require a larger amount of data compared with conventional metapopulation models. However, if one is using a model structure that is similar to what we used in our simulation experiment, whereby colonization and extinction rates can be linked to landscape features, we think that relatively simple landscape-explicit metapopulation models can be produced. These models represent a trade-off between increased ecological realism and increased data requirements and parameter uncertainty. On the basis of our theoretical findings, that landscape-dependent dispersal and disturbances can significantly influence metapopulation persistence, we would advocate that in many systems this trade-off is justified.

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APPENDIX

Simulation of Landscape-Dependent Asymmetric Dispersal

Using an individual-based dispersal simulation, we tested how well phenomenological dispersal kernels fit dispersal distributions derived from individual-based movement rules. Dispersal was simulated on a 10×10 square lattice landscape. This landscape structure was the same as that used in our metapopulation simulation models. Individual cells in the lattice were assigned a landscape value (elevation) that produced a unidirectional landscape bias (fig. 1). Movement and settlement of dispersing individuals depended on landscape value and basic movement rules but were independent of the movement and settlement of other dispersers. During each time step, an individual

could move into an adjacent cell or settle. We ran simulations using a series of self-recruitment probabilities ($p(\text{settle}) = 0.4, 0.5, 0.6, 0.7, 0.8,$ and 0.9) to produce a range of dispersal distances. If an individual did not self-recruit, the probability that it moved into an adjacent cell is

$$m_i = \frac{V_i^\gamma}{\sum_{k=1}^4 V_k^\gamma}, \tag{A1}$$

where V_i specifies the landscape value of the adjacent cell and γ is a movement parameter that biases movement according to the landscape value. A γ value of 0 results in individuals' movements being independent of landscape value, whereas large γ values produce a propensity for individuals to move toward higher (positive γ) or lower (negative γ) landscape values. Movement patterns between cells therefore approximate a random walk, with the degree of correlation in the walk determined by γ . We simulated different degrees of landscape-dependent correlation by testing a range of γ values ($\gamma = -5, -3, -1, 1, 3,$ and 5). The simulation was run until all individuals settled. To derive dispersal distributions, we simulated the dispersal of 10,000 individuals for each settlement probability and γ value combination.

We fit six phenomenological dispersal kernel models to this simulated data to determine which model best encapsulated dispersal distance and the influence of biased movement along landscape structure. Although phenomenological dispersal kernels of this type are not mechanism based, past studies have found that they can closely approximate the dispersal of many organisms (Moilanen and Nieminen 2002). The first three models were based on a negative exponential dispersal kernel. The first model that we tested was simply a negative exponential dispersal kernel, where d_{ij} is the distance moved from the starting cell (i) to the cell that the individual settled in (j) and α determines the rate of decrease:

$$r_{1i} = e^{(-\alpha d_{ij})}. \tag{A2}$$

The second model incorporated the difference in landscape value between sites, z_{ij} , as a linear term controlled by the coefficient β :

$$r_{2i} = e^{(-\alpha d_{ij}) + \beta z_{ij}}. \tag{A3}$$

The third dispersal kernel model we tested incorporated the influences of both distance and landscape values as exponential terms:

$$r_{3i} = e^{(-\alpha d_{ij} + \beta z_{ij})}. \tag{A4}$$

The other three models were based on a sigmoidal dispersal kernel that has been proposed to be a superior description of realistic dispersal pathways compared with the exponential function (Heinz et al. 2005, 2006). We started with a sigmoidal model that does not incorporate a landscape value but does include distance and an additional fitting parameter λ :

$$r_{3i} = 1 - e^{[-\lambda e^{(-\alpha d_{ij})}]}. \tag{A5}$$

We then included a landscape value as a linear term in the second exponential component of the model, corresponding to how landscape was incorporated in dispersal kernel 2:

$$r_{3i} = 1 - e^{\{-\lambda [e^{(-\alpha d_{ij})} + \beta z_{ij}]\}}. \tag{A6}$$

The sixth model that we tested incorporated the landscape value as an exponential term, corresponding with dispersal kernel 3:

$$r_{3i} = 1 - e^{[-\lambda e^{(-\alpha d_{ij} + \beta z_{ij})}]}. \tag{A7}$$

We fit the dispersal models to the simulated data using maximum likelihood. Model fit was compared using Akaike Information Criterion (AIC; Burnham and Anderson 2002).

In all cases, dispersal kernel model 6 had the highest likelihood values. Based on AIC values, model 6 was the best model whenever landscape value had an intermediate or strong influence on dispersal ($\gamma \neq 1, \gamma \neq -1$) and dispersal distance was reasonably long ($p(\text{settle}) < 0.6$). Under these conditions, where the landscape value had a strong influence on dispersal, model 6 provided a more superior fit, with the mean ΔAIC value being 13.2 (max $\Delta\text{AIC} = 33.3,$ min $\Delta\text{AIC} = 4$). When the landscape value had a weak influence on dispersal ($\gamma = 1, \gamma = -1$) and individuals settled after dispersing a short distance ($p(\text{settle}) > 0.6$), model 4 had the lowest AIC values. However, under these conditions there was little difference between model 4 and model 6 (mean $\Delta\text{AIC} = 1.96,$ max $\Delta\text{AIC} = 2,$ min $\Delta\text{AIC} = 1.9$). On the basis of these findings, we concluded that landscape-dependent movement is best encapsulated by model 6, a sigmoidal dispersal

Table A1: Fitted parameter values for the best dispersal model describing landscape-dependent dispersal (model 6)

Landscape movement (γ)	Dispersal distance			
	$p(\text{stop})$	λ	α	β
5	.4	.14	1.30	+ .93
5	.9	.20	1.11	+ .52
1	.4	.15	.86	+ .11
1	.9	.19	.88	+ .08

kernel with landscape value incorporated as an exponential term. The fitted values for λ , α , and β using model 6 are shown in table A1 for low and high stopping values and for strong and weak landscape-dependent movement.

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