

# Joint effects of habitat configuration and temporal stochasticity on population dynamics

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**Abstract** Habitat configuration and temporal stochasticity in the environment are recognized as important drivers of population structure, yet few studies have examined the combined influence of these factors. We developed a spatially explicit simulation model to investigate how stochasticity in survival and reproduction influenced population dynamics on landscapes that differed in habitat configuration. Landscapes ranged from completely contiguous to highly fragmented, and simulated populations varied in mean survival probability (0.2, 0.4, 0.8) and dispersal capacity (1, 3, or 5 cells). Overall, habitat configuration had a large effect on populations, accounting for >80% of the variation in population size when mean survival and dispersal capacity were held constant. Stochasticity in survival and reproduction were much less influential, accounting for <1–14% of the variation in population

size, but exacerbated the negative effects of habitat fragmentation by increasing the number of local extinctions in isolated patches. Stochasticity interacted strongly with both mean survival probability and habitat configuration. For example, survival stochasticity reduced population size when survival probability was high and habitat was fragmented, but had little effect on population size under other conditions. Reproductive stochasticity reduced population size irrespective of mean survival and habitat configuration, but had the largest effect when survival probability was intermediate and habitat was well connected. Stochasticity also enhanced the variability of population size in most cases. Contrary to expectations, increasing dispersal capacity did not increase population persistence, because the probability of finding suitable habitat within the dispersal neighborhood declined more for the same level of dispersal capacity when fragmentation was high compared to when it was low. These findings suggest that greater environmental variability, as might arise due to climate change, is likely to compound population losses due to habitat fragmentation and may directly reduce population size if reproductive output is compromised. It may also increase variability in population size.

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## Introduction

Habitat spatial heterogeneity has been increasingly recognized as an important factor in population dynamics. Although theoretical studies have long suggested that space is a critical resource affecting the size, distribution and persistence of species (Andrewartha and Birch 1954; Hanski 1998; Levin 1974), spatially explicit models indicate that the exact arrangement of habitat patches (exclusive of habitat loss) can influence population processes (Fahrig and Paloheimo 1988; Holyoak 2000; Pulliam et al. 1992; Wiegand et al. 2005). Habitat spatial pattern can affect population dynamics by altering the likelihood that organisms will locate and gain access to patches suitable for occupancy (Wiens et al. 1993). In particular, the connectivity of habitat (i.e., the degree to which a landscape facilitates or impedes movement of organisms among resource patches, *sensu* Tischendorf and Fahrig 2000) can determine the rate of local extinctions and thereby affect the survival of regional populations (Fahrig 2002; Fahrig and Merriam 1985; Pearson et al. 1996; Taylor et al. 1993). Because colonization is constrained by the movement ability of organisms, patch isolation due to habitat fragmentation can be especially detrimental to the persistence of dispersal-limited species (Fahrig and Merriam 1994; With and Crist 1995).

Environmental stochasticity can also affect population dynamics by influencing vital rates, such as fecundity and survival, through time. While the ramifications of variability in vital rates are not well understood (Boyce et al. 2006; Doak et al. 2005; Melbourne and Hastings 2008), theory predicts that environmental variation will diminish a population's long-run growth rate and increase the chance of population extinction. This is due to the fact that long-run population growth rate is the geometric mean of growth rates over time, which is always less than or equal to the arithmetic mean (Lande et al. 2003; Lewontin and Cohen 1969). As climate projections and empirical evidence raise the specter of greater variability in precipitation and increases in the frequency of extreme temperatures (Easterling et al. 2000; Karl et al. 1995), such theoretical constructs are becoming increasingly valuable for forecasting the dynamics of biological populations (Drake 2005). Predictions about the effects of

environmental stochasticity may be inaccurate, however, if they fail to consider the spatial pattern of habitat.

Habitat configuration may modulate population response to stochasticity by reducing or enhancing the resilience of populations to temporal fluctuations. In the absence of temporally or spatially correlated stochasticity, habitat patches that are large or well connected may provide local or regional refugia that are higher in population density and therefore recover more quickly from decreased survival (Kallimanis et al. 2005; Petchey et al. 1997). Small patches, on the other hand, may not be of sufficient size to maintain the level of density needed for a local population to recover from a catastrophic event. Likewise, patch isolation may inhibit immigration from source populations and prevent rescue effects from occurring (Brown and Kodric-Brown 1977; Stacey and Taper 1992). In such cases, population fluctuations may amplify and spread across the entire landscape, resulting in spatial synchrony of population dynamics and metapopulation collapse (Liebhold et al. 2004; Münkemüller and Johst 2006; Oborny et al. 2005).

Several studies have examined the effects of habitat configuration and temporal stochasticity on population dynamics focusing on habitat destruction and recovery (DeWoody et al. 2005; Ellner and Fussmann 2003; Johnson 2000; Johst and Drechsler 2003; Keymer et al. 2000; Schrott et al. 2005; Wilcox et al. 2006). These models have generated several key insights, but more work is needed to address how populations might respond to events that affect demographic properties (e.g., survival probability, reproductive output) without influencing habitat availability. Events such as these may occur due to increases in extreme weather, a climate scenario for which there is growing support based on both the current record and model predictions (Easterling et al. 2000; IPCC 2001). Other models that consider the effects of multiple stochastic factors on population persistence often do not account for spatial structure (Lv and Pitchford 2007; Melbourne and Hastings 2008) or do so implicitly, without depicting the spatial distribution of habitat (Harrison and Quinn 1989; Ovaskainen and Hanski 2004). Spatially explicit models can provide additional information about population processes in changing environments and are, thus, an important tool for studying

population dynamics (Bascompte and Sole 1996; Gonzalez-Megias et al. 2005).

We used a spatially explicit model to investigate how temporal stochasticity influences population dynamics on landscapes that differ in habitat configuration. Simulated populations were generalized to represent plant species varying widely in lifespan and dispersal capacity. We explored how different levels of stochasticity in survival and reproductive output affected landscape-scale population size and variability.

## Methods

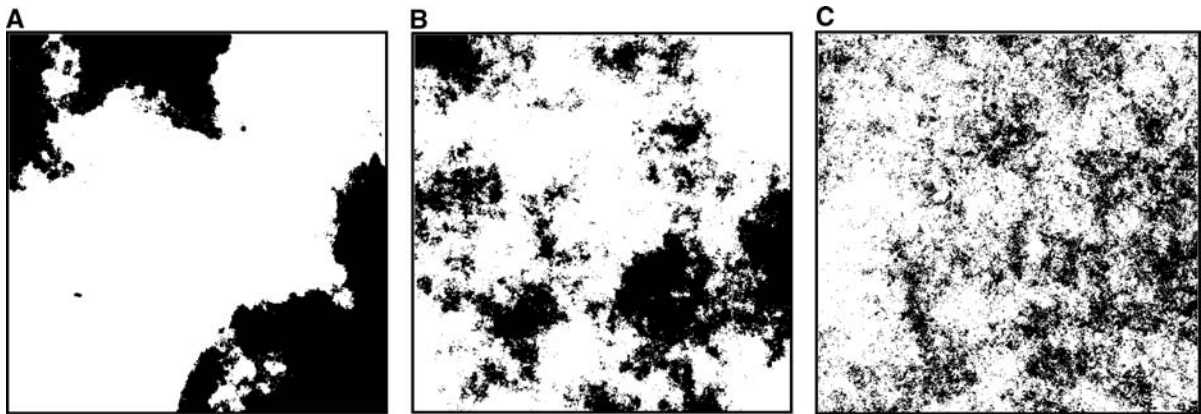
### Model description

The model simulated the survival, reproductive output and dispersal of populations (defined as occupied habitat cells) on simple cell-based maps that differed in the spatial arrangement of habitat but not in the amount of habitat. We introduced temporal environmental stochasticity by changing the probability of survival or reproductive output at each time step, assuming that fluctuations were density-independent. The ecological motivation for this analysis, and hence our initial selection of demographic parameters, was to understand the implications of land-cover and climate change for the spatiotemporal dynamics of herbaceous species found in mesic deciduous forests of the Southern Appalachian Mountains. The populations of many of these herbs decline when their forest habitat is disturbed and fragmented (Pearson et al. 1998). Many of these native herbs are perennials with limited dispersal ability, rendering them unable to cross large gaps of unsuitable habitat to (re)colonize suitable patches (Cain et al. 1998). For example, foam flower (*Tiarella cordifolia*) has small seeds that fall directly below the plant and are dispersed a short distance by gravity or by overland flow of water. Several other herb species (e.g., *Trillium* spp., *Disporum* spp., *T. cordifolia*, *Uvularia* spp. and *Viola canadensis*) are dispersed by ants (Beattie and Culver 1981). In addition, some species, such as *Cimicifuga racemosa*, are long-lived and often reproduce vegetatively; few individuals may flower in a given year. While all these species typically have limited dispersal abilities, they vary considerably in their survivorship and

fecundity. Ultimately, we modeled several combinations of demographic parameters to examine the generality of the results.

The landscape was represented by a square lattice of  $512 \times 512$  cells. Cells could have one of two values: habitat (suitable for occupancy) or nonhabitat. Although the use of binary landscapes is a simplification of the complexity in habitat quality present in real landscapes (Wiegand et al. 1999; Wiegand et al. 2005), such models are useful tools for addressing conceptual questions dealing with spatial processes (With 2004; With and King 1997). Fifteen multifractal landscapes were generated with the program RULE (Gardner 1999) using the midpoint displacement algorithm (Saupe 1988). We chose this method because it has been found to generate landscapes that resemble real landscapes and also allow the amount of habitat and the degree of habitat aggregation to be varied independently (Flather and Bevers 2002). One of three levels of fragmentation was assigned to each map based on  $H$ , the spatial autocorrelation of habitat (Fig. 1): aggregated ( $H = 0.7$ ,  $n = 5$  maps), moderately fragmented ( $H = 0.35$ ,  $n = 5$  maps) and highly fragmented ( $H = 0.0$ ,  $n = 5$  maps). In addition, we generated five maps with completely contiguous habitat (a solid block) to represent unfragmented landscapes. Thirty-three percent of the cells in each map were initialized as habitat. We selected this value for habitat size because the configuration of habitat, and particularly the connectivity of the habitat, can vary substantially among different landscapes at this level of habitat size (Fahrig 2003; Flather and Bevers 2002; Pearson et al. 1996; With et al. 1997). Our simulated landscapes were modeled as closed systems, and populations were not permitted to move outside the lattice. We observed no boundary effects and thus did not make corrections for them.

The basic structure of the model is similar to a spatially explicit implementation of the Levins model (*sensu* Bascompte and Sole 1996). The dynamics of the populations were governed by three demographic parameters: survival (SURV), reproductive output (REPRO) and dispersal (DISP). Survival was the mean probability of a cell remaining occupied from one time step to the next. Reproductive output was the mean probability that an occupied cell produced a propagule that could colonize an unoccupied habitat cell within the neighborhood determined by a



**Fig. 1** Simulated landscapes with different configurations but equal amounts of habitat. Levels of habitat connectivity are: aggregated (a), moderately fragmented (b), and highly

fragmented (c). Maps of unfragmented habitat used in model simulations are not shown

population's dispersal capacity. REPRO was discounted with increasing distance from an occupied cell using a distance decay function. The distance decay function was:

$$\text{DIST} = 1 - [(\text{distance} - 1)/(\text{DISP})]^S \quad (1)$$

where *distance* is the Euclidean distance in cell lengths from the cell being evaluated to an occupied cell, and DISP is the maximum distance (in cells) over which a propagule can move. The function was only evaluated when *distance* < DISP. The shape of the function was controlled by *S* and was set to 0.5, giving a negative exponential shape for all simulations (*sensu* Fahrig 1992). For a suitable but unoccupied cell, the probability of colonization was computed as:

$$\text{Probability of being colonized :} \quad \sum \text{REPRO} \times \text{DIST}_i \times K \quad (2)$$

where  $\text{DIST}_i$  is the coefficient of decay with distance from Eq. 1, and *K* is a constant to normalize  $\text{DIST}_i$  for different values of DISP. The product  $\text{REPRO} \times \text{DIST}_i \times K$  was summed for all *i* cells of habitat within the maximum dispersal distance of a given cell.

To add temporal variability to survival and reproductive output, we stochastically varied SURV and/or REPRO at each time step by drawing a random number from a beta distribution. The beta distribution, which is bounded by 0 and 1, was parameterized by solving for  $\alpha$  and  $\beta$  for the desired

mean and variance (see Mood et al. 1974 for equations). For example, if SURV = 0.2 and survival variability was 50%, we set the mean to 0.2 and variance to 0.01 (SD = 0.1) and solved for  $\alpha$  and  $\beta$ . At each time step, a new value of SURV or REPRO was applied to all occupied cells in the landscape for the current time step. Thus, temporal variability in these parameters was synchronous across space.

### Model operation

At the beginning of each run of the model, the demographic parameters were specified and 75% of the habitat cells were randomly occupied. We chose this level of occupancy so that landscape occupancy could initially change in either direction. Simulations run with other values of initial occupancy indicated that initial conditions had no effect on model behavior (data not shown).

During a given time step, changes in the occupancy of habitat cells were determined by first evaluating the probability of survival for occupied cells and then evaluating the probability of colonization for unoccupied habitat cells at each time step using Eqs. 1 and 2. The model was run for 200 time steps on each map (dynamics typically stabilized after 100 time steps) and for each parameter set the model was run 10 times. We recorded the proportion of habitat occupied at the end of each time step. In the rest of the paper, we use the terms 'global population'

to refer to the landscape-wide collection of occupied cells and ‘local population’ to refer to a cluster of occupied cells or cells within a habitat patch and in nearby patches.

### Simulation experiments

We performed three simulation experiments to investigate the model’s behavior under different demographic conditions (Table 1). In the first experiment we used a factorial design to examine how changing the mean probability of survival influenced the effects of habitat configuration and temporal stochasticity in survival on population dynamics, while holding REPRO and DISP constant. Using this design as a backdrop, we then investigated the effects of temporal stochasticity in REPRO (experiment 2) and dispersal capacity (experiment 3) on model behavior. We did not vary the overall mean of REPRO in these experiments because previous work indicated that doing so would alter the effective population growth rate (S. Pearson, unpublished data), and we accomplished the same result by varying overall mean survival. In experiment 3, we varied maximum dispersal distance (DISP). In order to control recruitment rate when modifying dispersal distance, we normalized the distance decay function by multiplying DIST by a normalization constant ( $K$ ) which varied with DISP (Table 1). This constant was derived by normalizing the integrals of Eq. 1 over the interval of one to DISP. The values of this constant were 3.154, 1.000, and 0.468 for DISP values of 1, 3, and 5 cells, respectively. In biological terms,  $K$  controls the number of seeds reaching an empty cell to equalize recruitment rates under different levels of dispersal.

### Data analysis

We focused our analysis on the response of the global population to habitat configuration and temporal stochasticity. Landscape occupancy at time step 200 was averaged over replicates and used as a measure of global population size. Variability in global population size was determined by calculating the standard deviation of landscape occupancy (logit transformed) at each time step over replicates and then averaging over time steps.

Response variables were logit transformed (appropriate for proportional data [Sokal and Rohlf 1995]) where appropriate to meet normality assumptions, and a general linear model was used to test for main effects and interactions among all terms. All factors were treated as categorical variables in accordance with the experimental design. Plots of residual versus predicted values were inspected and indicated that error variances were homogenous among groups in all experiments.

## Results

### Experiment 1: habitat configuration and temporal stochasticity in survival

As expected, global population size declined significantly as habitat fragmentation increased (Table 2, Fig. 2a). Populations with low or moderate mean survival were the most sensitive to habitat configuration, and quickly approached extinction as fragmentation increased (Fig. 2a). In these cases, habitat configuration accounted for >99% of the variation in population size. In contrast, a high level of mean survival (0.8) buffered the negative effects of habitat fragmentation, resulting in appreciable but relatively small losses in population size as fragmentation increased (Fig. 2a).

By itself, survival stochasticity had a minor effect on population size and accounted for a limited amount of variation in population size (Table 2). As fragmentation increased, however, the impact of survival stochasticity became more pronounced (Fig. 2b). This effect varied with mean survival (Table 2). When mean survival was high, stochasticity in survival exacerbated the negative effects of fragmentation (Fig. 2b). In contrast, survival stochasticity had little effect on global population size when mean survival was low or intermediate, as a result of the dominant effect of habitat configuration.

Mean survival, survival stochasticity, and habitat configuration interacted in complex ways to affect variability in population size. For example, habitat fragmentation caused an increase in population variability when mean survival was low, but had little influence when mean survival was intermediate or high (SURV  $\times$  habitat:  $F_{6,240} = 914.4$ ,  $P < 0.001$ ). In contrast, the effect of survival stochasticity on variability was appreciably greater when mean survival

**Table 1** Model parameters for the three simulation experiments performed in this study

Simulation experiment	Mean survival (SURV)	Stochasticity in survival	Mean reproductive output (REPRO)	Stochasticity in reproductive output	Maximum dispersal distance (DISP)
1	0.2	0, 10%, 30%, 50%	0.11	0	3
	0.4	0, 10%, 30%, 50%	0.11	0	3
	0.8	0, 10%, 30%, 50%	0.11	0	3
2	0.2	0, 10%, 30%, 50%	0.11	0, 10%, 30%, 50%	3
	0.4	0, 10%, 30%, 50%	0.11	0, 10%, 30%, 50%	3
	0.8	0, 10%, 30%, 50%	0.11	0, 10%, 30%, 50%	3
3	0.2	0, 10%, 30%, 50%	0.11	0	1, 3, 5
	0.4	0, 10%, 30%, 50%	0.11	0	1, 3, 5
	0.8	0, 10%, 30%, 50%	0.11	0	1, 3, 5

Simulations were run on maps representing four different levels of habitat fragmentation

**Table 2** Results of an analysis of variance on the global size of populations subjected to habitat fragmentation and stochasticity in survival probability

Source	df	Percentage total SS <sup>a</sup>	F ratio	P
Survival	2	68.86	11,592.40	<0.0001
Habitat	3	25.11	2,818.12	<0.0001
Survival × habitat	6	5.83	327.43	<0.0001
Surv-stoch	3	0.05	5.28	0.0016
Survival × surv-stoch	6	0.05	2.80	0.0123
Surv-stoch × habitat	9	0.04	1.51	0.1465
Survival × surv-stoch × habitat	18	0.06	1.15	0.3054

Global size is based on the proportion of occupied habitat at time step 200. Values are nested means from ten replicate simulations of the model on each of five maps per type of habitat configuration. For all simulations, maximum dispersal distance was three cells and mean reproductive output was 0.11

SS sums of squares, *surv-stoch* survival stochasticity

was high compared to when it was intermediate or low (SURV × survival stochasticity:  $F_{6,240} = 610.1$ ,  $P < 0.001$ ).

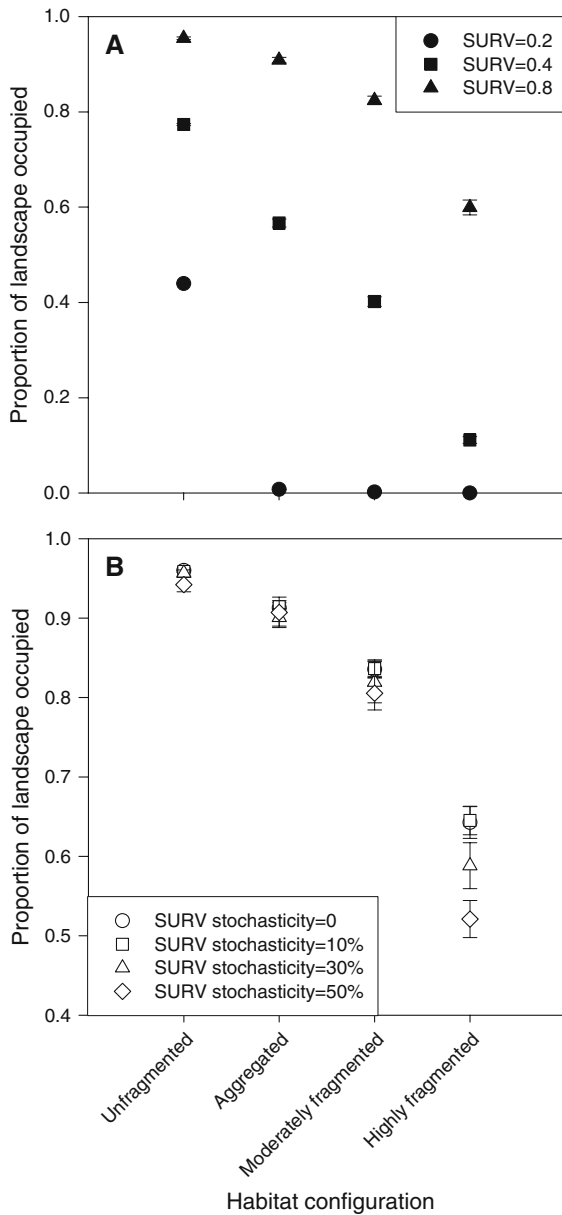
Habitat configuration also influenced the extent to which survival stochasticity altered variability in population size. In well connected landscapes, survival stochasticity enhanced population variability, but this effect diminished as habitat became increasingly fragmented (habitat × survival stochasticity:  $F_{6,240} = 21.1$ ,  $P < 0.001$ , Fig. 3).

#### Experiment 2: temporal stochasticity in reproductive output

Stochasticity in reproductive output significantly reduced global population size, but explained relatively little variation compared with habitat

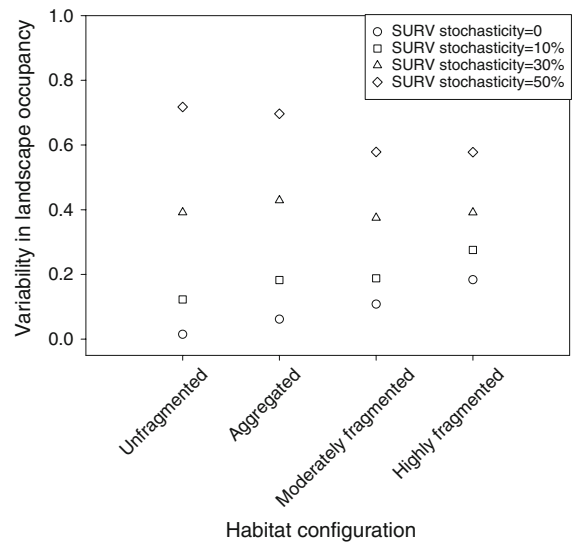
configuration (Table 3). At low mean survival, the effect of habitat configuration effectively masked the influence of reproductive stochasticity on population size. As a result, a decrease in population size due to reproductive stochasticity was only evident on contiguous landscapes (Fig. 4a). Stochasticity in reproductive output had a more pronounced effect at intermediate and high mean survival (Fig. 4b, c), where it accounted for 12 and 3% of the variation in population size, respectively. Interestingly, the magnitude of the effect was dampened by fragmentation at intermediate mean survival but enhanced by fragmentation at high mean survival. Survival stochasticity did not interact with reproductive stochasticity.

Stochasticity in reproductive output significantly increased variability in global population size



**Fig. 2** Mean landscape occupancy ( $\pm 1$  SE) at different levels of habitat fragmentation when mean survival (a) and survival stochasticity (b) vary. In panel b, mean survival is 0.8. Values are nested means from ten replicate simulations of the model on each of five maps per type of habitat configuration. For all simulations, maximum dispersal distance was three cells and mean reproductive output was 0.11

( $F_{3,960} = 11,189.3, P < 0.001$ ). The strength of this effect was sufficient to enhance population variability across all levels of mean survival (Fig. 5a), habitat configuration (Fig. 5b), and survival stochasticity



**Fig. 3** Variability in landscape occupancy for different levels of survival stochasticity and habitat fragmentation. Variability was computed by first taking the standard deviation of logit-transformed occupancy data at each time step over map replicates and then averaging over time steps. Data shown are means from five maps per type of habitat configuration, averaged over mean survival

(Fig. 5c), but each of these factors modulated the influence of reproductive stochasticity to some extent (SURV  $\times$  REPRO stochasticity:  $F_{6,960} = 249.0, P < 0.001$ ; Habitat  $\times$  REPRO stochasticity:  $F_{9,960} = 94.8, P < 0.001$ ; SURV stochasticity  $\times$  REPRO stochasticity:  $F_{9,960} = 964.1, P < 0.001$ ). Although absolute variability in landscape occupancy was highest when both reproductive and survival stochasticity were high, relative increases in variability were greater in populations subjected to reproductive stochasticity when survival stochasticity was low (Fig. 5c).

### Experiment 3: dispersal capacity

Decreasing the REPRO parameter reduced global population size despite increasing dispersal capacity (Fig. 6). When we increased dispersal capacity without adjusting REPRO, population size increased substantially in response to increased recruitment rates (data not shown).

Nonetheless, dispersal capacity and habitat configuration interacted as expected (Table 4). Habitat fragmentation caused greater losses in populations with low dispersal capacity than in populations with

**Table 3** Results of an analysis of variance on the global size of populations subjected to habitat fragmentation, and stochasticity in survival probability and reproductive output

Source	<i>df</i>	Percentage total SS	<i>F</i> ratio	<i>P</i>
Survival	2	68.58	33,932.25	<0.0001
Habitat	3	23.80	7,850.19	<0.0001
Survival × habitat	6	4.80	791.73	<0.0001
Repro-stoch	3	1.19	391.39	<0.0001
Survival × repro-stoch	6	0.93	153.14	<0.0001
Surv-stoch	3	0.12	40.59	<0.0001
Survival × surv-stoch	6	0.09	14.68	<0.0001
Survival × repro-stoch × habitat	18	0.22	12.16	<0.0001
Repro-stoch × habitat	9	0.10	11.15	<0.0001
Surv-stoch × repro-S	9	0.02	2.72	0.0039
Survival × surv-stoch × habitat	18	0.05	2.60	0.0003
Surv-stoch × habitat	9	0.02	2.24	0.0181
Survival × surv-stoch × repro-stoch	18	0.03	1.45	0.1023
Survival × surv-stoch × repro-stoch × habitat	54	0.04	0.70	0.953
Surv-stoch × repro-stoch × habitat	27	0.02	0.67	0.8942

Global size is based on the proportion of occupied habitat at time step 200. Values are nested means from ten replicate simulations of the model on each of five maps per type of habitat configuration. For all simulations, maximum dispersal distance was three cells and mean reproductive output was 0.11

SS sums of squares, *repro-stoch* stochasticity in reproductive output, *surv-stoch* survival stochasticity

high dispersal capacity (dispersal × habitat:  $F_{6,720} = 180.3$ ,  $P < 0.001$ , Fig. 6). Survival stochasticity had no influence on this effect (SURV stochasticity × dispersal × habitat:  $F_{18,720} = 0.29$ ,  $P = 0.99$ ).

Increasing dispersal capacity generally enhanced variability in population size ( $F_{2,720} = 312.3$ ,  $P < 0.001$ ). Population variability was 0.06 when dispersal was limited to 1 cell, and 0.33 and 0.35 when dispersal was limited to 3 and 5 cells, respectively. There were, however, significant interactions with mean survival and habitat configuration, such that greater variability was observed when habitat was aggregated ( $F_{6,720} = 122.1$ ,  $P < 0.001$ , Fig. 7a) and mean survival was high ( $F_{6,720} = 40.5$ ,  $P < 0.001$ , Fig. 7b).

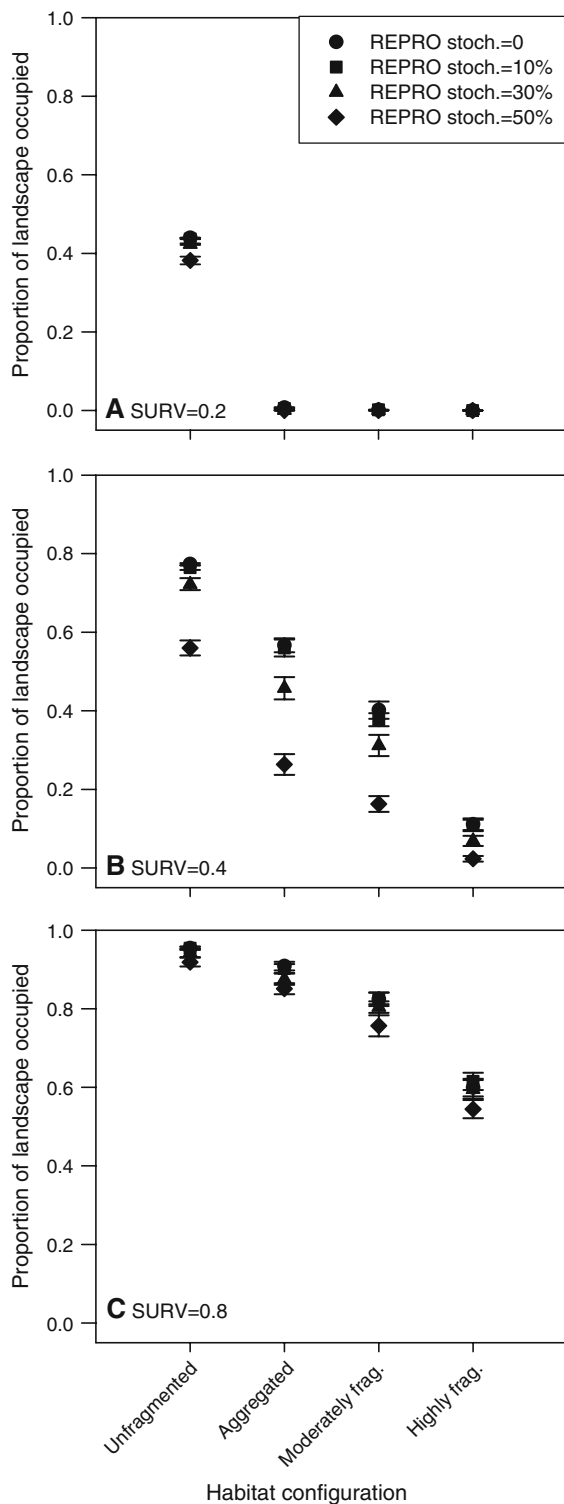
## Discussion

Survival probability was the primary factor governing global population size and also played a key role in determining the effects of habitat fragmentation and temporal stochasticity on population dynamics at the landscape scale. In general, habitat fragmentation

reduced the size of global populations and increased their variability, but populations with a high mean survival were less sensitive to differences in broad-scale habitat configuration (Fig. 8). At the same time, populations with higher survival probabilities exhibited the largest absolute response to stochasticity, although stochasticity had a greater relative impact on populations with lower survival probabilities. In particular, reproductive stochasticity had the most influence on populations with low mean survival, while survival stochasticity had the most influence on populations with high mean survival (Fig. 8).

These results reflect the limitations imposed on populations by their demographic characteristics. A population with a low probability of survival has a short life span; thus, its persistence relies heavily on the ability of individuals to colonize new areas. Because habitat fragmentation can severely restrict the spread of organisms, particularly those with a poor capacity for dispersal (Fahrig and Merriam 1994; Wiegand et al. 2005; With and Crist 1995), it has the greatest relative effect on population dynamics. In contrast, stochasticity in survival does little to modulate a short life span and consequently has less





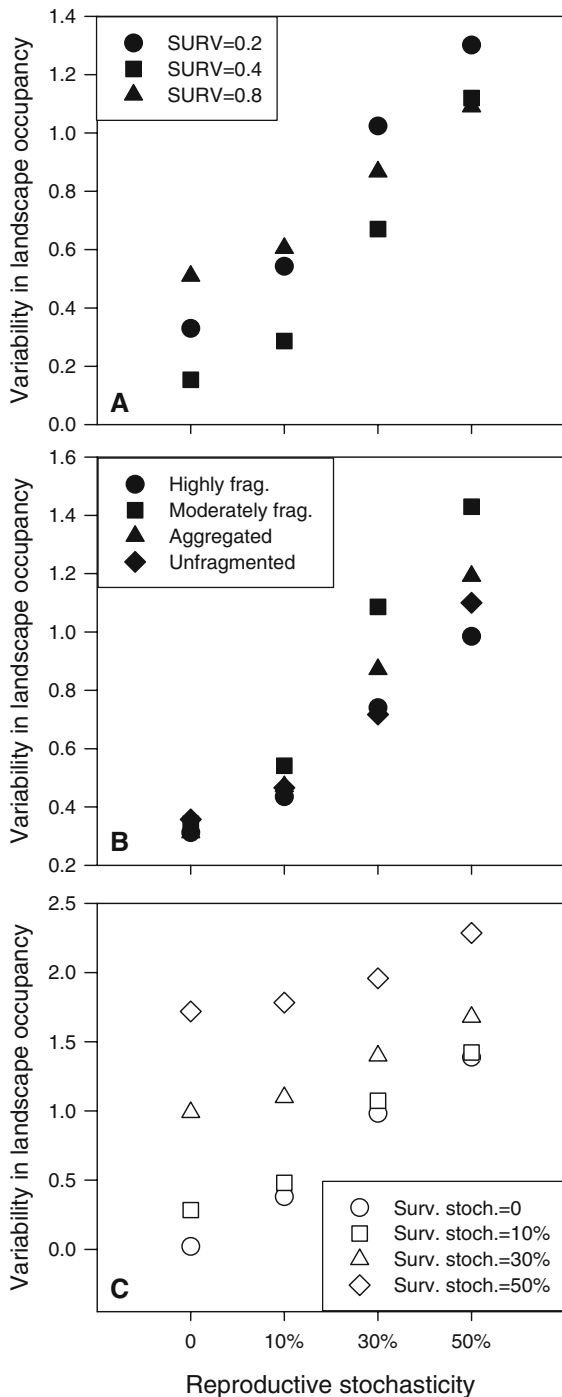
impact on dynamics in these populations. Stochasticity in reproductive output could affect spread by altering propagule availability, but the influence of

**Fig. 4** Mean landscape occupancy ( $\pm 1$  SE) at different levels of reproductive stochasticity and habitat fragmentation when mean survival is low (a), intermediate (b), and high (c). Values are nested means from ten replicate simulations of the model on each of five maps per type of habitat configuration. Maximum dispersal distance was three cells and mean reproductive output was 0.11

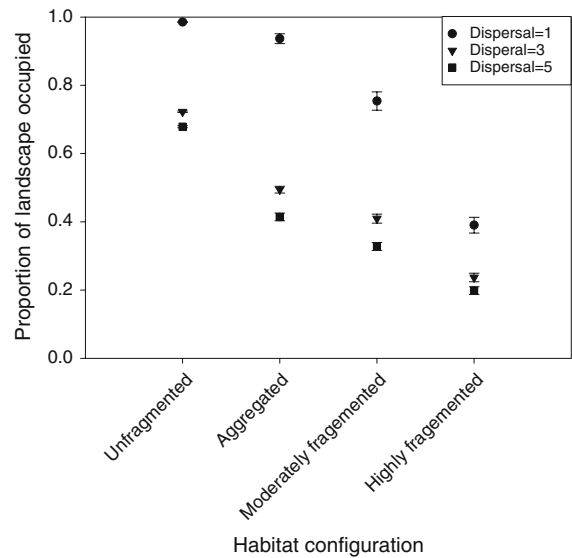
this factor would only be relevant when there are ample opportunities for colonization. Consistent with this hypothesis, our results showed that the effect of reproductive stochasticity on population size declined as habitat fragmentation increased (Fig. 8).

In populations with higher survival probabilities, persistence still depends on colonizing new habitat; however, because life spans are longer, temporal stochasticity can also be important (Fig. 8). The precise effects of each type of stochasticity we examined (reproductive and survival) were a function of both survival probability and habitat configuration. Graphical output indicated that populations with high mean survival could withstand both survival and reproductive stochasticity in connected habitats because there was sufficient colonization to sustain local populations. However, populations in fragmented habitats were unable to rebound entirely from stochastic events leading to local extinctions because some patches were too isolated to be recolonized. Introducing reproductive stochasticity amplified the joint effects of habitat fragmentation and survival stochasticity by further diminishing the availability of new colonists. By comparison, populations with an intermediate survival probability were affected by reproductive stochasticity regardless of the level of habitat fragmentation. These results indicate that population persistence relied substantially on the availability of new colonists. Survival stochasticity exacerbated the effect of reproductive stochasticity, but had little influence on population size on its own.

Our findings offer a perspective on the joint effects of habitat configuration and environmental stochasticity that differs from that of models in which habitat is ephemeral. In those studies, metapopulation persistence in dynamic landscapes is determined by mean patch lifetime and size relative to colonization and/or extinction rates (Brachet et al. 1999; DeWoody et al. 2005; Ellner and Fussmann 2003; Johnson 2000; Keymer et al. 2000). Additionally, Wilcox et al. (2006) demonstrated that persistence



**Fig. 5** Variability in landscape occupancy for different levels of reproductive stochasticity, mean survival (a), habitat fragmentation (b), and survival stochasticity (c). Variability was computed by first taking the standard deviation of logit-transformed occupancy data at each time step over map replicates and then averaging over time steps



**Fig. 6** Mean landscape occupancy ( $\pm 1$  SE) at different levels of dispersal capacity and habitat fragmentation. Values are nested means from ten replicate simulations of the model on each of five maps per type of habitat configuration and were averaged over mean survival. Mean reproductive output was adjusted to hold recruitment constant (see Table 1 for details)

can depend on the variance in patch lifetime and the synchrony in patch dynamics that results from disturbance. In our model, habitat is static, and stochasticity affects vital rates directly. Under these conditions, we found that habitat fragmentation is of overwhelming importance for determining population dynamics. Reproductive stochasticity can have independent effects, but only within a particular range of mean survival. Survival stochasticity has no independent effects, but can exacerbate the effects of fragmentation.

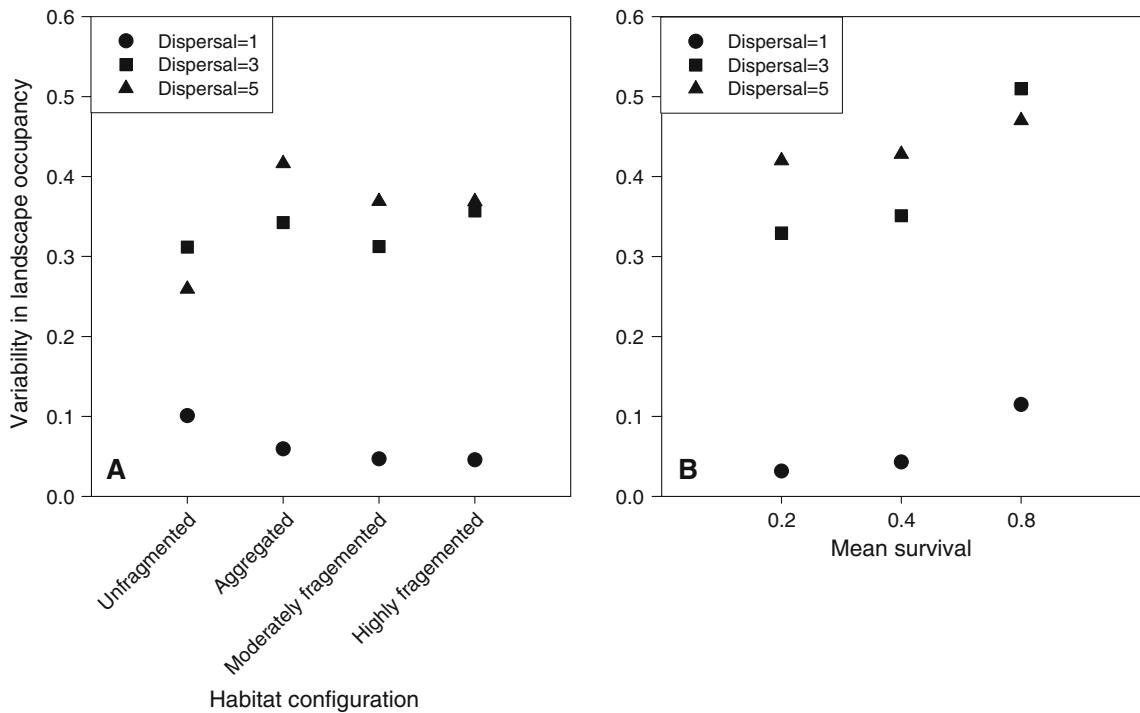
Many of our findings are comparable to those from spatially explicit models that simulate population dynamics, despite the fact that modeling approaches differ. For example, Bossuyt and Honnay (2006) showed that survival probability (or species lifespan) can influence how global populations respond to environmental stochasticity. They reported that metapopulations of species with short lifespans have higher extinction rates and are more sensitive to environmental stochasticity than those with longer lifespans (Bossuyt and Honnay 2006). We found a similar pattern when populations were subjected to stochasticity in reproductive output, i.e., higher

**Table 4** Results of an analysis of variance on the global size of populations varying in dispersal capacity and subjected to habitat fragmentation and stochasticity in survival probability

Source	<i>df</i>	Percentage total SS	<i>F</i> ratio	<i>P</i>
Survival	2	35.63	12,733.35	0.0000
Dispersal	2	20.10	7,182.950	0.0000
Habitat	3	28.63	6,820.992	0.0000
Survival × dispersal	4	8.84	1,580.367	<.0001
Survival × habitat	6	2.49	296.7734	<.0001
Dispersal × habitat	6	2.42	288.7519	<.0001
Survival × dispersal × habitat	12	1.73	102.9135	<.0001
Surv-stoch	3	0.04	8.3601	<.0001
Survival × surv-stoch	6	0.03	3.1475	0.0048
Surv-Stoch × dispersal	6	0.01	1.4567	0.1909
Survival × surv-stoch × habitat	18	0.03	1.2139	0.2436
Surv-stoch × habitat	9	0.01	0.9387	0.4907
Survival × surv-stoch × dispersal	12	0.01	0.5038	0.9127
Surv-stoch × dispersal × habitat	18	0.01	0.3851	0.9902
Survival × surv-stoch × dispersal × habitat	36	0.02	0.3023	1.0000

Global size is based on the proportion of occupied habitat at time step 200. Values are nested means from ten replicate simulations of the model on each of five maps per type of habitat configuration

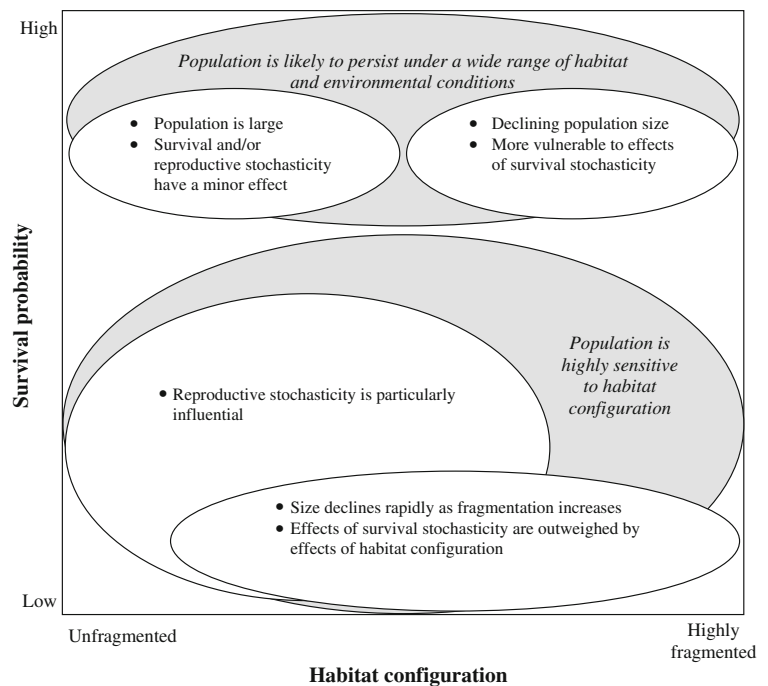
SS sums of squares, *surv-stoch* survival stochasticity



**Fig. 7** Variability in landscape occupancy for different levels of dispersal capacity when habitat fragmentation (a) and mean survival (b) vary. Variability was computed by first taking the

standard deviation of logit-transformed occupancy data at each time step over replicates and then averaging over time steps

**Fig. 8** State space diagram summarizing global population response to different factors as a function of mean survival probability and habitat configuration



survival probability buffered populations from the effect of reproductive stochasticity. The dominant influence of reproductive versus survival stochasticity is also broadly consistent with the findings of previous studies by Fahrig (2001) and With and King (1999b), who found that reproductive output had a larger effect on extinction thresholds than fragmentation.

In contrast, the effects of dispersal in our study did not fully agree with the conclusions of others. Many studies report that increasing dispersal distance promotes the persistence of populations occupying fragmented landscapes through the rescue effect (Brown and Kodric-Brown 1977; Johst et al. 2002; Opdam 1990; Stacey and Taper 1992; Thomas 2000). Increasing dispersal distance reduces inter-patch distance, effectively enhancing landscape connectivity, when there is directed dispersal (With and King 1999a). If dispersal is not directed, however, an increasing number of dispersal attempts will actually be unsuccessful as dispersal capacity and fragmentation increase (Wiegand et al. 1999; Wiegand et al. 2005). This is because the probability of finding suitable habitat within the dispersal neighborhood declines more for the same level of dispersal capacity when fragmentation is high compared to when it is low. For instance, in our model,

the mean proportion of habitat cells within the dispersal neighborhood when dispersal capacity was 1 cell was 0.73 on highly fragmented maps and 0.98 on aggregated maps. In contrast, the mean proportion of habitat cells within the dispersal neighborhood when dispersal capacity was 5 cells was 0.57 on highly fragmented maps and 0.95 on aggregated maps. Other conditions may exist when long-range dispersal is disadvantageous for long-term persistence on fragmented landscapes, such as when the number of potential dispersers is low (Johst et al. 2002), or the level of dispersal mortality is high (Doak et al. 1992; Fahrig 2002; León-Cortés et al. 2003; Thomas 2000). A decline in the number of potential dispersers can occur if fragmentation reduces the size of populations to the extent that edge effects and/or genetic erosion compromise reproductive output (Honnay et al. 2005; Jacquemyn et al. 2002; Jules 1998; Ouborg et al. 1991). Dispersal mortality, on the other hand, may increase if fragmentation causes organisms to spend more time in nonbreeding habitat (or "matrix" areas) where reproduction is not possible and the rate of mortality is higher (Fahrig 2002; León-Cortés et al. 2003). In these cases, more dispersal leads to a greater drain of individuals from existing populations, resulting in increased extinction.

Habitat configuration may not always have a substantial effect on population dynamics. In her review of fragmentation effects, Fahrig (2002) concluded that the effects of habitat amount on population persistence typically outweigh those of habitat pattern, except when habitat amount is low (Pearson et al. 1996; With et al. 1997). Simulation modeling studies have further demonstrated that habitat arrangement has an appreciable influence on population persistence only when habitat covers 30–50% of a landscape (Flather and Bevers 2002). In our study, 33% of the cells were initialized as habitat. At this level, habitat connectivity varied substantially among the landscapes. We computed the average area of habitat patches in each map for individuals that could cross gaps of a maximum of three cells. The average area of habitat patches was 439, 453, and 620 cells, in the highly fragmented, moderately fragmented, and aggregated maps, respectively. This suggests that populations in the highly fragmented maps experienced landscapes with smaller patches that were less connected overall. There remains a need to understand the conditions under which habitat configuration influences population dynamics when populations are simultaneously faced with fluctuating environmental conditions. Additional work will be necessary to determine the levels at which habitat amount trumps the effects of habitat configuration when stochastic processes are also operating.

Overall, our results point to the importance of preserving landscape connectivity in the face of increasing climatic variability. Landscapes with intact habitat have the best chance of sustaining populations when their survival and reproductive rates fluctuate. From a different perspective, it seems that neither fragmentation nor environmental stochasticity will limit the persistence of organisms with high probabilities of survival. Because many weedy species fall into this category, we might conclude that once such a population becomes established in an area, it will endure even under the most extreme conditions, and may even thrive as populations of less robust species decline.

Because we opted for generality at the expense of realism in our modeling approach, there are several issues that we could not address but which merit attention. We did not examine the influence of land-use change in our model despite recent research suggesting that the creation and destruction of habitat

can have a dramatic influence on the size and persistence of populations, particularly those that are dispersal-limited (DeWoody et al. 2005; Johst and Drechsler 2003; Matlack and Monde 2004; Wilcox et al. 2006). Given the observed effects of habitat fragmentation, however, we would expect that temporal changes in habitat availability would depress population size and diminish persistence, even if overall habitat amount were held constant. We also did not consider how seed banks or seed dormancy may affect the results. Although these factors could potentially buffer plant response to temporal stochasticity (Pake and Venable 1999), they would do little to temper the negative impacts of habitat fragmentation. Finally, we did not address how local (versus global) stochastic events that are temporally autocorrelated may alter population dynamics. Others have demonstrated that positively autocorrelated local events that desynchronize population processes can increase both the size of populations and their probability of persistence (Roy et al. 2005), while negatively autocorrelated local events can have the opposite effect (Pike et al. 2004). This topic warrants closer investigation, and spatially explicit models may be useful in resolving the conditions under which populations experience growth and decline.

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