Habitat Destruction Versus Degradation in Metapopulations

Abstract: Habitat destruction is considered one of the greatest threats to species conservation. In metapopulations, or spatially patchy populations with limited inter-patch dispersal, research has shown that destroying even a small number of patches can drive a species extinct. Despite the known consequences of habitat destruction in metapopulations, there has been little research on the importance of this destruction relative to global changes that degrade the quality of habitat, as may occur with species invasions, eutrophication or climate change. We use metapopulation models with simulated landscapes to determine how habitat destruction and degradation affect a metapopulation. In particular, we simulate three types of habitat loss, which we call the patch destruction, habitat degradation and island degradation models. The patch destruction model eliminates patches from the habitat at random, while the habitat degradation model reduces the carrying capacity of each patch by an amount equivalent to that lost by the patch destruction model. Finally, the island model also causes a similar reduction in the carrying capacity of each patch, but does so by reducing the size of the patch. Our results indicate that patch destruction is the lesser of evils when there is a large number of patches – in this scenario, habitat degradation and island degradation consistently lead to higher extinction probabilities. However, as more habitat is lost, this trend reverses so that patch destruction becomes more threatening than habitat or island degradation. The switch between degradation and destruction as the most important determinant of extinction varies with three ecological variables: the variation in patch size, the variation in patch spatial arrangement and the dispersal ability of the focal species. We use these relationships to identify how to best preserve diversity in patchy populations that are threatened with different levels of degradation or destruction.

Introduction

Human activities are often responsible for destroying portions of habitat or reducing the overall habitat quality (Bender, Contreras, and Fahrig, 1998). This loss of habitat often plays a large role in extinctions, so it is of great interest to conservation biologists to be able to predict its effect on the probability of species' persistence (Casagrandi and Gatto, 2002; Hanski, 2013). Levins (1969, 1970) introduced the metapopulation model consisting of geographically isolated patches of suitable habitat interspersed throughout a matrix of unsuitable habitat to simulate the effect of habitat destruction. In this model populations in each patch can go extinct independently of other patches, while empty patches can be colonized by populated patches.

The Levins model has been criticised as an oversimplification, as it assumes that patches are equally sized and that the distance between any two patches is equal. Accordingly, it has been modified to accommodate variance in patch sizes and metapopulation structure (Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2001). Hanski and Ovaskainen (2000) defined the metapopulation capacity as the contribution that each particular landscape structure has on the probability of extinction, which can be used as a proxy for the probability of species' persistence in a given landscape.

Very few studies have compared the effect of different types of habitat loss on a species persistence in a metapopulation (Lande, 1993; Casagrandi and Gatto, 2002). Although Casagrandi and Gatto (2002) used the Levins model to compare the effect of patch destruction to patch erosion, they assumed that patch erosion would decrease the carrying capacity of a patch to zero. This may not be the most realistic model for real populations though, as a patch's quality may be reduced without becoming completely unsuitable for a species. They also used the Levins model, which assumes that patches are equally sized and separated. Here, we use the model presented by Hanski and Ovaskainen (2000) to compare the effects of patch destruction, where patches are removed; habitat degradation, where the carrying capacity of the entire metapopulation is reduced; and island degradation, where the size of each patch is decreased.

Model

Metapopulation landscapes were simulated in R by placing 100 circular patches in a 100 by 100 unit square block. We used every possible combination of the following spatial and size patch distributions to create twenty replicates of each of the twelve possible types of metapopulation landscapes. For the spatial distribution of the patches we used a uniform distribution, a random distribution, and a negative binomial clustered distribution with a dispersion parameter of 0.5 and 1. For the distribution of the patch sizes we used a random log normal distribution with log standard deviations of 0 (the uniform distribution), 0.5, and 1, which we then scaled so that the total area of habitable space was 100 units. Figure 1 shows sample landscapes for each spatial and size distribution.

Within each landscape, we simulated 1) patch destruction by removing one patch at a time, until there was only one patch left. We used the fraction of habitat remaining in the patch destruction simulation to simulate corresponding levels of habitat degradation to simulate 2) habitat degradation, where we scale the carrying capacity of each island by the fraction of habitat remaining and 3) island degradation where we scale the size of each island by the fraction of habitat remaining. We repeated these simulations ten times for each landscape.

The metapopulation capacity for each landscape was calculated as the leading eigenvalue of the matrix created with the elements $m_{ij} = exp^{-\alpha^{-1} d_{ij}} A_i A_j$ for $i \neq j$, and $m_{ii}=0$, where α is the average migration distance, d_{ij} is the minimum distance between the edges of patches i and j, and A_i is the area of patch i

(Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2001; Hanski and Ovaskainen, 2002). In our model, patches are either occupied or empty. We repeated the simulations on each landscape with the the average migration distance values of 0.5, 1, and 2.

For each type of landscape (N=20) we calculated the first intersection point at which patch destruction has a larger impact on the metapopulation capacity than habitat or island degradation. To accomplish this, we grouped the trials for each simulation into segments of 2% habitat loss. We defined the intersection points as the largest segmented proportion of habitat remaining where in more than 50% of the trials for patch destruction have a lower metapopulation capacity than their corresponding habitat or island degradation trials. In the simulations did not have an intersection point, we set the intersection point to zero habitat remaining.

Results:

By the setup of the model, the metapopulation capacity response curve for both types of degradation are convex, with the island degradation curve having a stronger convexity than the habitat degradation curve. These two curves converged as the average migration distance increased. The patch destruction curve tended to be S shaped, with the majority of the curve falling above both of the degradation curves (figure 2). The patch destruction curves had a lot of noise, with the amount of noise increasing for more spatially or patch size clustered landscapes (figure 2).

As expected, the intersection point between patch destruction and island degradation was much lower than between patch destruction and habitat degradation (0.0272 and 0.0596 respectively; Chi-Square, N=720, $p \ll 0.01$). We grouped the island intersection results for each category (patch size distribution, alpha, and spatial distribution) to test for significance (Two tailed, Chi-Square, $p<0.05$). The intersection point increased as patch size distribution, average migration distance, and the level of spatial clustering increased (table 1). We also tested for two-tailed significance between every pair of simulations that differed by just one variable (figure 3), and all but one (island intersection, alpha=0.5, size clustering=0.5, between spatial random and clustering=1, figure 3b) agree with the grouped results.

Conclusion:

An integral part of conservation biology is predicting a species' response to habitat loss, as it often plays a large role in extinctions (Hanski, 2013). In this paper we compare the effect of three different types of habitat loss on the metapopulation capacity: patch destruction, habitat degradation, and island degradation. We use the metapopulation capacity, as defined by Hanski and Ovaskainen (2000), to quantify how suitable a metapopulation is for a species after sustaining habitat loss.

The metapopulation capacity curves for habitat and island degradation can be completely determined by the average migration distance and the undisturbed habitat, so they have smooth monotone increasing curves. The island degradation curve always falls below the habitat degradation curve because while the carrying capacities are reduced equally in both cases, but the island degradation curve also causes the distance between any two patches to increase.

In comparison, the patch destruction curve is highly stochastic, since it depends on which combination of patches are removed. Although patch destruction tends to preserve the metapopulation capacity better than degradation, this trend is reversed when a large proportion of the habitat is lost. This reversal occurs approximately at 94% and 97% habitat lost for habitat and island degradation, respectively (Chi-Square, $N=720$, $p<<0.01$). There are also rare cases when habitat destruction is more damaging than degradation for a low proportion of area lost. These cases are more common in clustered landscapes.

The intersection point between the metapopulation capacity curves for habitat destruction and degradation increases as the patches in the original undisturbed landscape become more clustered, either spatially or by patch size (table 1). However, this could occur purely by chance, as clustering also increases the noise of the patch destruction curve, so this intersection point may not accurately reflect the actual crossing point at which habitat destruction becomes more damaging.

We also found that the intersection point increases with average migration distance (table 1). This similar to the results of Casagrandi and Gatto (2002), who concluded that habitat destruction becomes more damaging than habitat degradation sooner for better dispersers.

References

Bender, D., T. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* 79:517–533.

Casagrandi R., and M. Gatto. 2002. Habitat destruction, environmental catastrophes, and metapopulation extinction. *Theoretical Population Biology* 61:127–140.

Hanski, I. 2013. Extinction debt at different spatial scales. *Animal Conservation* 16:12-13.

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404:755–758.

Hanski, I., and O. Ovaskainen. 2002. Extinction debt at extinction threshold. *Conservation Biology* 16(3):666-673.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* 142:911–927.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.

Levins, R. 1970. Extinction. *Lecture Notes in Mathematics* 2:75–107.

Ovaskainen, O., and I. Hanski. 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. *Theoretical Population Biology* 60(4):281–302.

Figures

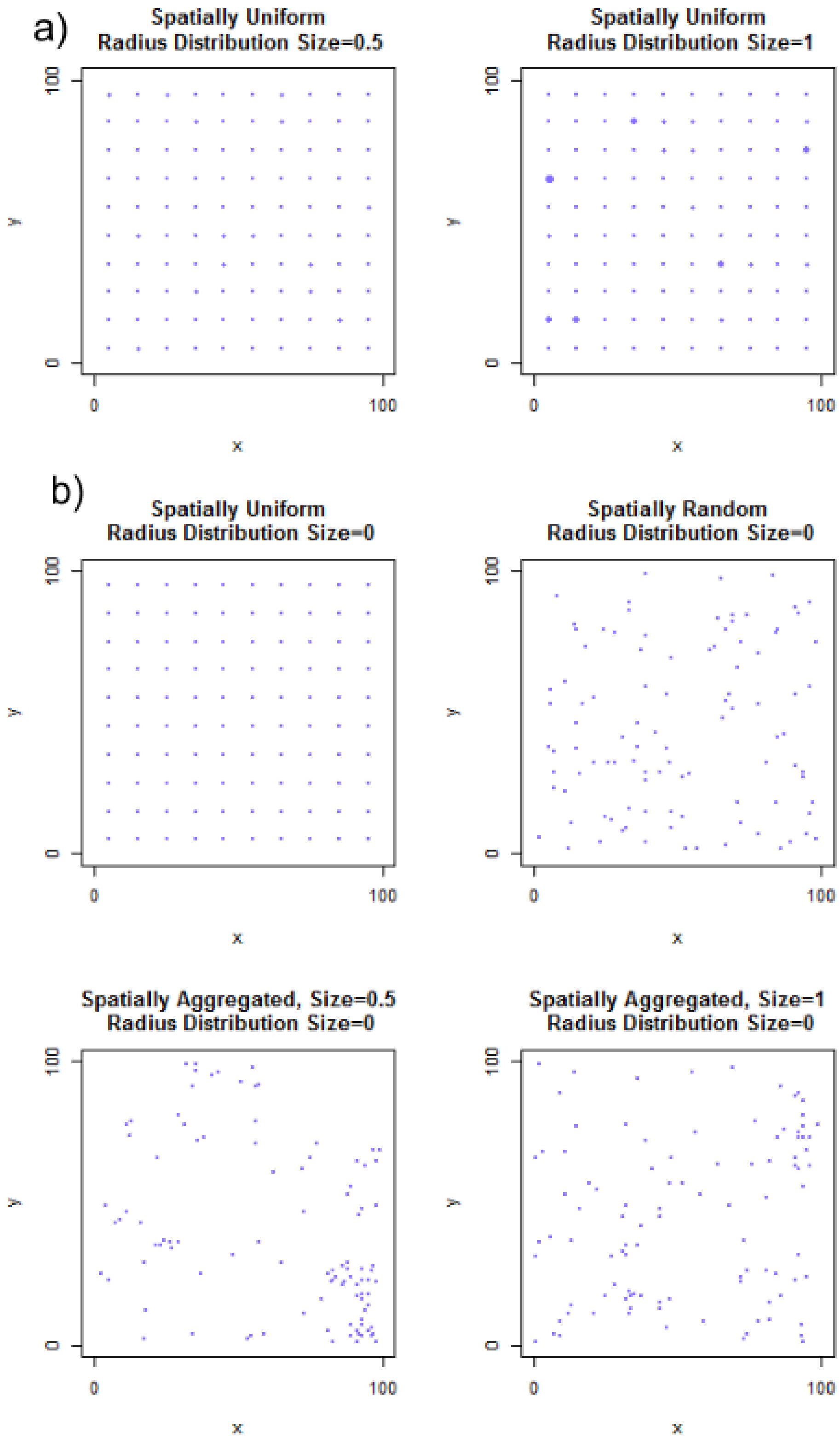
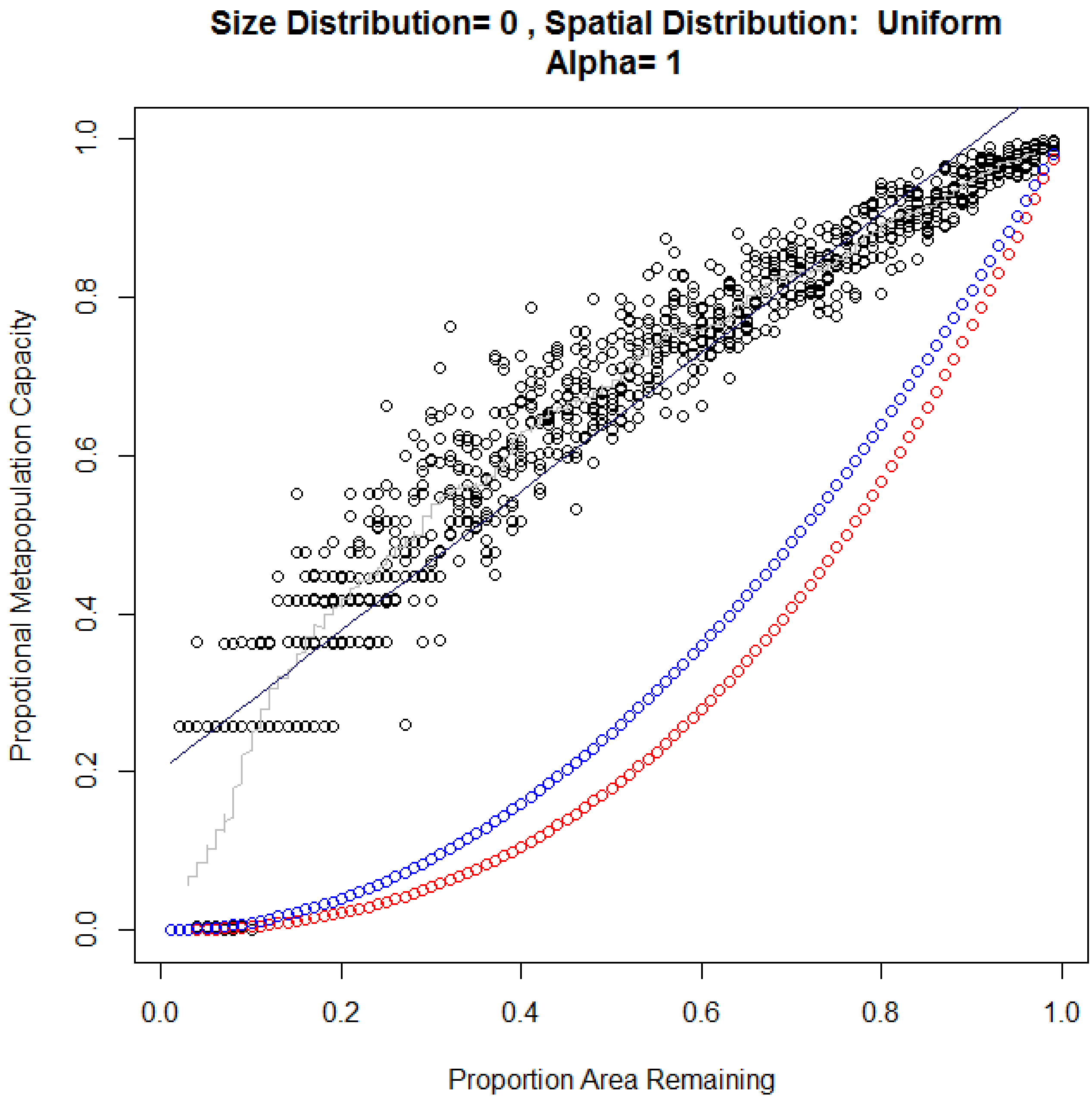


Figure 1 Example landscapes for a) uniformly spatially distributed patches with size distributions of 0.5 and 1, and b) uniformly sized patches that are spatially distributed in a uniform, random, and clustered fashion.

a)


Size Distribution= 0 , Spatial Distribution: Uniform
Alpha= 1
Propotional Metapopulation Capacity
Proportion Area Remaining
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
1.0

b)

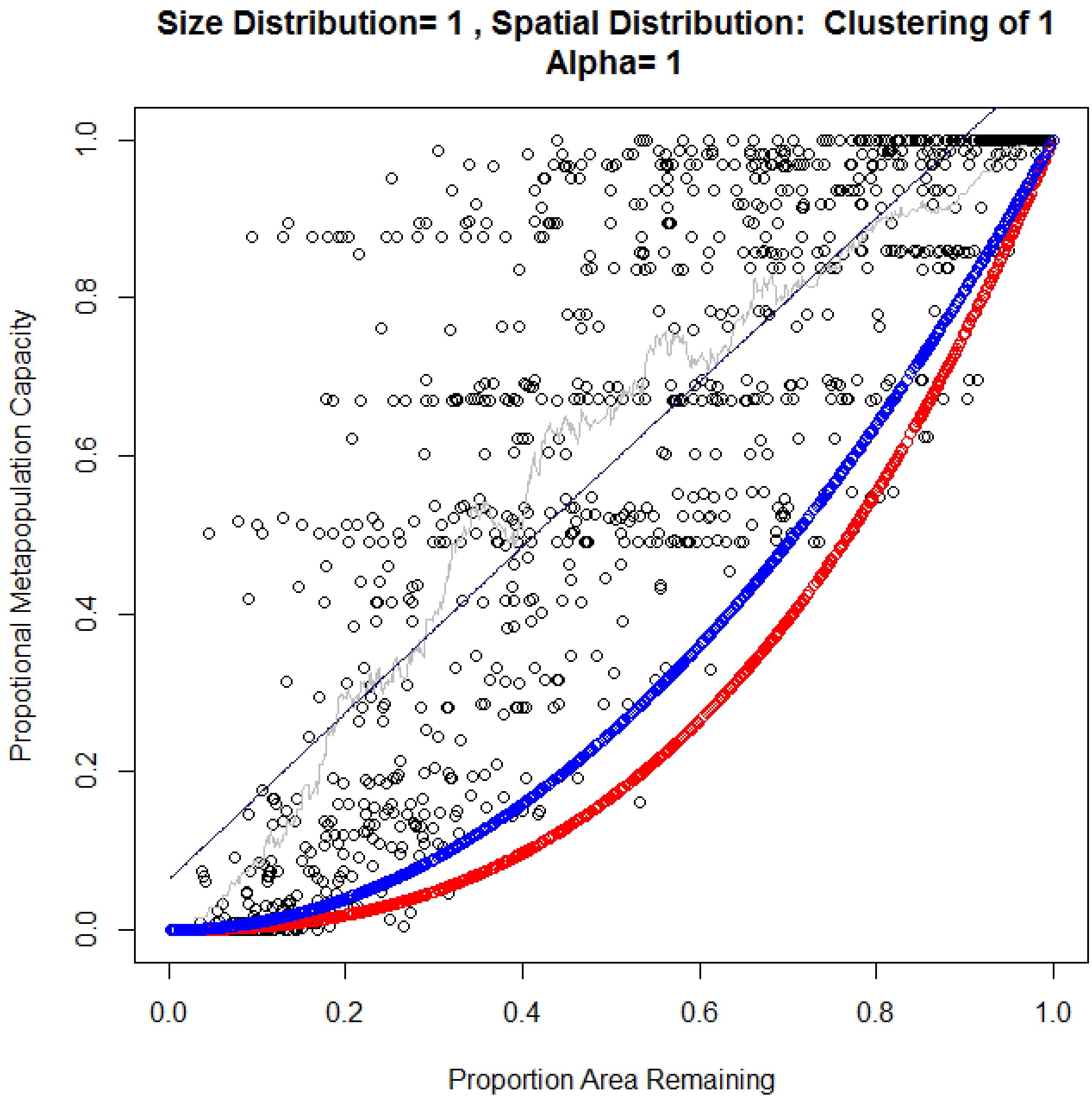


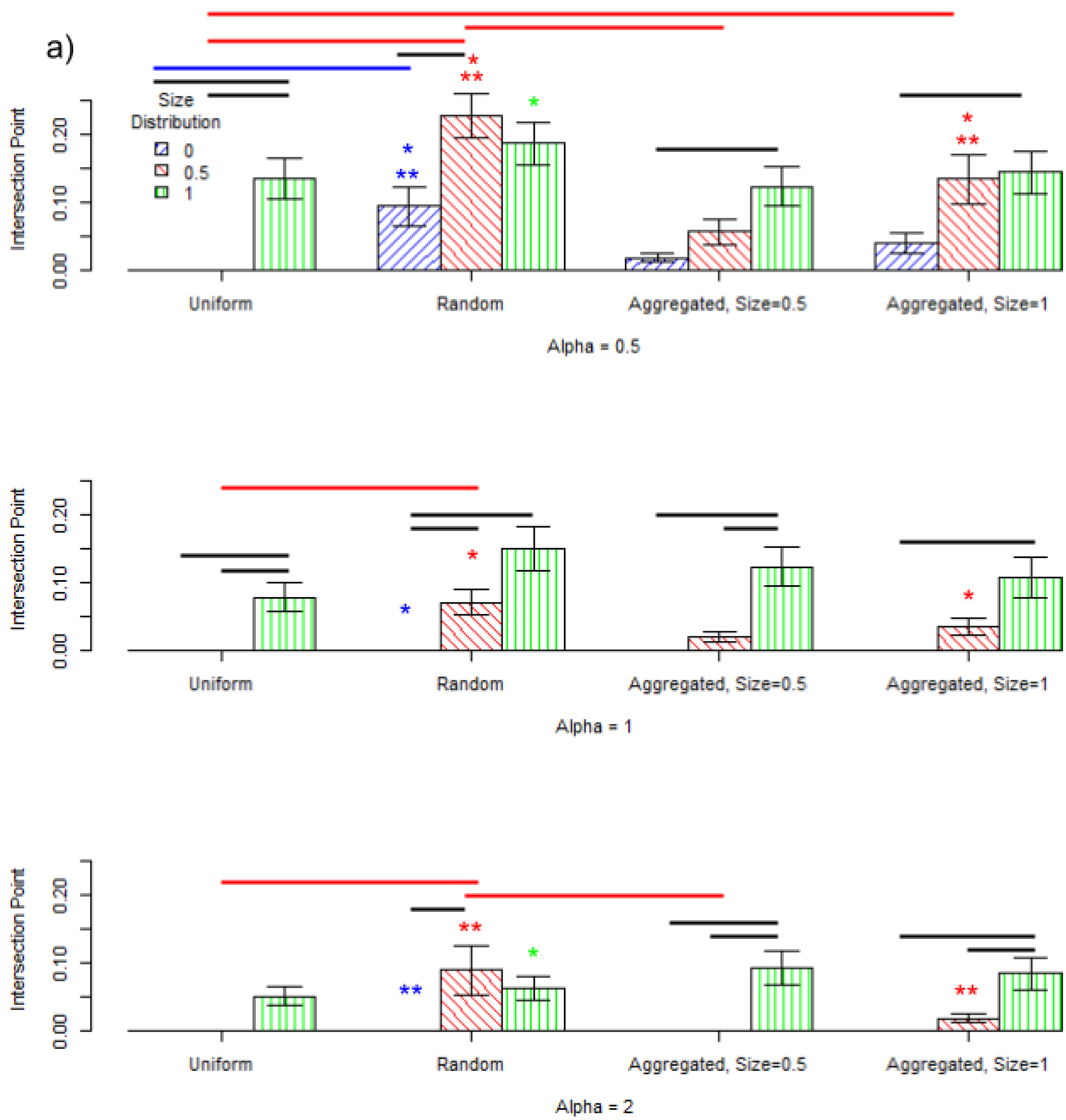
Figure 2 The metapopulation capacity response curves, scaled to the metapopulation capacity of the undisturbed landscape for one replicate of a) a spatially uniform landscape with uniform patch sizes and b) a spatially clustered landscape with clustered patch sizes for a dispersion value of 1. The metapopulation capacities are shown for patch destruction, habitat degradation, and island degradation trials are shown in black, blue, and red, respectively. A spline curve fitted to the patch destruction trials is shown in grey, while a smoothed version is shown in dark blue.

Table 1 The significance levels between a) patch size clustering, b) alpha levels representing the average migration distance, and c) spatial clustering for the habitat degradation simulation.

a) Size	0.5	1
0	2.22e-05*	2.09e-16*
0.5		2.96e-05*

b) Alpha	1	2
0.5	2.47e-04*	4.43e-07 *
1		1.33e-01

c) Spatial	Random	Clustering=0.5	Clustering=1
Uniform	1.71e-06*	1.00e-01	8.11e-03*
Random		1.12e-03*	2.73e-02*
Clustering=0.5			2.93e-01


a)
Size
Distribution
0
0.5
1
Intersection Point
0.00
0.10
0.20
Uniform
Random
Aggregated, Size=0.5
Aggregated, Size=1
Alpha = 0.5
Alpha = 1
Alpha = 2

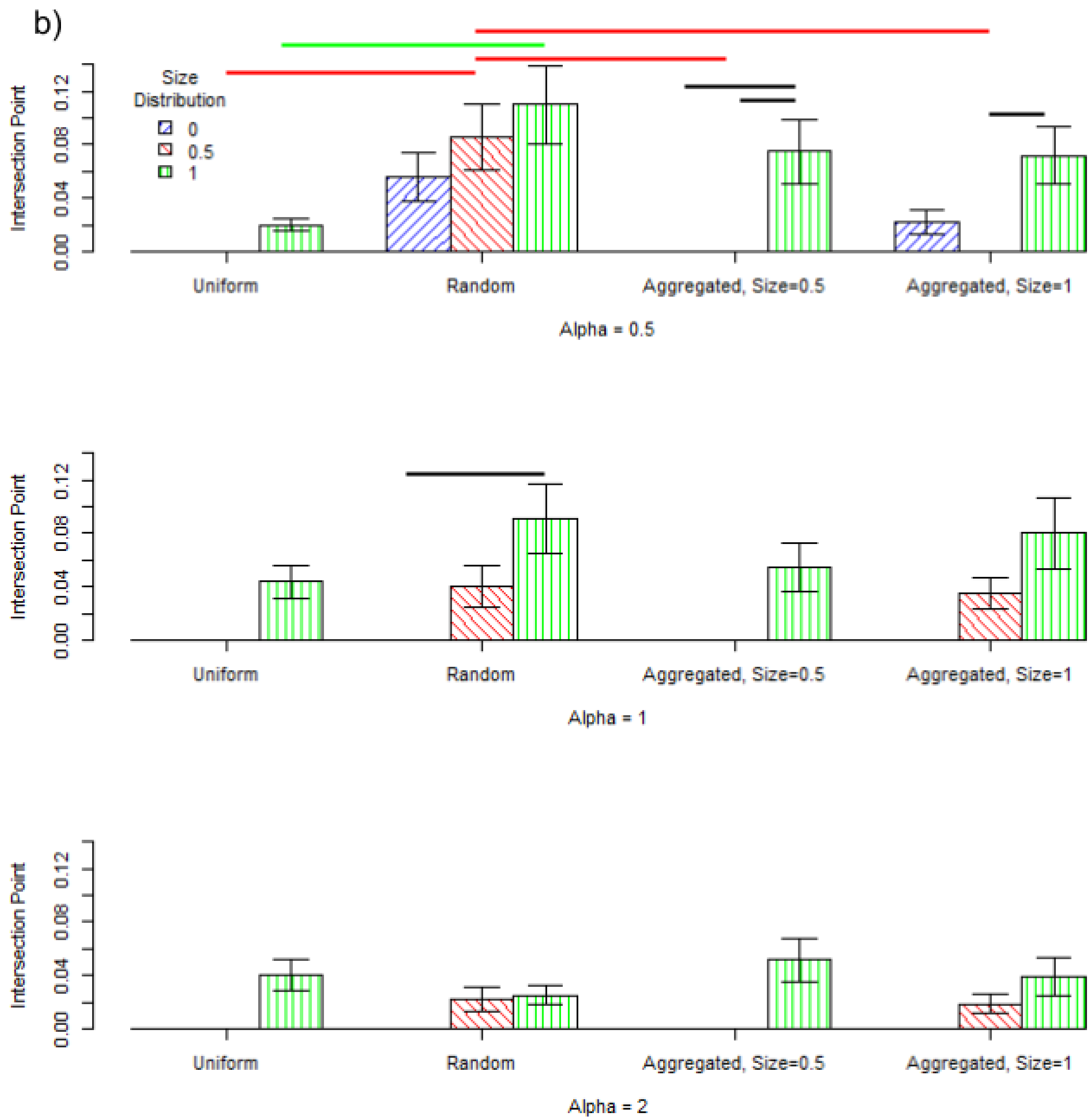


Figure 3 The means and variances of the proportion area remaining at which the median of the metapopulation capacity for the patch removal simulation first crosses that of a) the habitat degradation simulation, and b) the island degradation simulation (N=20). The intersection points are shown for the patch size distributions of 0, 0.5, and 1 in blue, red, and green, respectively. The results for each spatial distribution of patches are shown by column, while the results for the levels of dispersal are shown by row. Significance is shown between patch size distributions by black bars, between spatial distributions by coloured bars, and between dispersal levels by asterisks (Chi-Square, N=20, p<0.05).