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Decoupling Fragmentation from Habitat Loss for Spiders in Patchy Agricultural Landscapes

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Abstract: *Habitat loss reduces species diversity, but the effect of habitat fragmentation on number of species is less clear because fragmentation generally accompanies loss of habitat. We compared four methods that aim to decouple the effects of fragmentation from the effects of habitat loss. Two methods are based on species-area relations, one on Fisher's alpha index of diversity, and one on plots of cumulative number of species detected against cumulative area sampled. We used these methods to analyze the species diversity of spiders in 2, 3.2 × 4 km agricultural landscapes in Southern Judea Lowlands, Israel. Spider diversity increased as fragmentation increased with all four methods, probably not because of the additive within-patch processes, such as edge effect and heterogeneity. The positive relation between fragmentation and species diversity might reflect that most species can disperse through the fields during the wheat-growing season. We suggest that if a given area was designated for the conservation of spiders in Southern Judea Lowlands, Israel, a set of several small patches may maximize species diversity over time.*

Keywords: arthropods, landscape, SLOSS, species diversity, species-area relation

Separando la Fragmentación de la Pérdida de Hábitat para Arañas en Paisajes Agrícolas Heterogéneos

Resumen: *La pérdida de hábitat reduce la diversidad de especies, pero el efecto de la fragmentación del hábitat sobre muchas especies es menos claro porque la fragmentación generalmente es acompañada por la pérdida de hábitat. Comparamos cuatro métodos que tratan de separar los efectos de la fragmentación sobre los efectos de la pérdida de hábitat. Dos métodos se basan en las relaciones especies-área, uno en el índice de diversidad alfa de Fisher, y uno en gráficos del número acumulativo de especies detectadas versus el área muestreada acumulada. Utilizamos estos métodos para analizar la diversidad de arañas en 2 paisajes agrícolas de 3.2 × 4 km en las Tierras Bajas de Judea del Sur, Israel. La diversidad de arañas incrementó a medida que incrementó la fragmentación con los cuatro métodos, probablemente no debido a los procesos aditivos intra-parche, como el efecto de borde y la heterogeneidad. La relación positiva entre la fragmentación y la diversidad de especies puede ser reflejo de que la mayoría de las especies se pueden dispersar en los campos durante la época de siembra de trigo. Sugerimos que si un área determinada fuera designada para la conservación de arañas en las Tierras Bajas de Judea del Sur, Israel, un conjunto de parches muy pequeños puede maximizar la diversidad de especies en el tiempo.*

Palabras Clave: artrópodos, diversidad de especies, paisaje, relación especies-área, SLOSS

Introduction

When human activities reduce the area of species' natural habitats, what remains is usually fragmented into distinct patches. It has long been known that loss of area reduces species diversity (Rosenzweig 1995). However, Fahrig (2003) emphasizes the distinction between the effects of habitat loss and fragmentation.

The question of effects of fragmentation is similar to the single large or several small (SLOSS) question (Diamond 1975): If area is held constant, all else being equal, does one large patch or do several small patches hold

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more species (Ovaskainen 2002)? Results of empirical studies of the SLOSS question have been inconsistent (Boecklen 1997; Ovaskainen 2002; Rosenzweig 2005). In most cases, a fragmented landscape supports more species than an unfragmented one. For example, the single large patch supports more species than the set of several small patches in 10% of 148 data sets (Boecklen 1997). Results of other studies reveal no statistically significant difference between the number of species in a single large area and several small patches (e.g., two beetle families and plants [Yaacobi et al. 2007]).

We used four published methods to decouple the effects of fragmentation from the effects of habitat loss within a given landscape. All four methods compare the number of species in a set of several small patches with a single large patch whose area equals the cumulative area of the several small patches. The methods differ in how the number of species is measured. Number of species can be the observed number of species in samples or species diversity (an estimate of the number of species corrected for sampling effort or abundance). This distinction between the observed number and an estimated number of species is important because a difference in sampling intensity between the small patches and the large patch could increase the apparent number of species of the more intensively sampled patch or set of patches.

We used and compared the results of all four methods in an examination of the species diversity of spiders in two fragmented landscapes (here a heterogeneous area in which nonlocal processes, such as dispersal and regional extinction, may contribute strongly to the focal species' diversity and composition) in the Southern Judea Lowlands, Israel.

Methods

Study Site and Sampling

The Southern Judea Lowlands lies at the transition zone between Israel's Mediterranean ecosystem in the north and the Negev desert in the south. We focused on 2, 3.2 × 4 km landscapes, Lachish and Dvir, in which remnant patches of natural vegetation are embedded in a matrix of agricultural fields, mainly wheat. The wheat starts growing at the beginning of the rainy season (January) and is harvested in May. Thereafter, the remaining straw is collected and the soil is exposed until the next growing season. We sampled between June and early September in 2007, when the fields were dominated by exposed soil.

In each landscape we sampled 12 small patches and one relatively large unfragmented area. We quantified the internal heterogeneity of patches on the basis of the proportional cover of nine vegetation cover types. Four of the cover types were structurally simple: exposed soil, annual plants <15 cm tall; annual plants ≥15 cm tall; and rosette plants (mainly *Asphodelus ramosus*). The three latter cover types were dry at the time of sampling. Conditions (e.g., plant cover and stoniness) of exposed soil in patches were similar to conditions in the wheat fields during the sampling season. Therefore, we used samples from the exposed-soil cover type to explore species' associations with wheat fields during the sampling season. Five of the cover types were more structurally complex: cover dominated by the perennial plants *Sarcopoterium spinosum* and *Hyparrhenia hirta*, respectively, by perennial bushes ≥35 cm tall, by perennial shrubs <35 cm tall, and by thistles (mainly *Silybum marianum* and *Notobasis syriaca*). We measured cover along 20-m line transects (Supporting Information).

We used a stratified random sampling scheme to establish 0.5 × 0.5 m quadrats in which we sampled spiders. Each quadrat was located at least 5 m from the edge of the patch. Each quadrat contained a single-cover type, and there was ≥1 quadrat of each complex cover type observed in each patch. We were careful to sample complex cover types in each patch because preliminary sampling revealed that spider abundance and number of species in the structurally complex cover types was significantly higher than in the structurally simple cover types. Each patch contained ≥7 quadrats (Supporting Information). We established 248 quadrats in Dvir and 245 in Lachish.

To obtain samples, we used the vacuum option on a leaf blower with a mesh (0.5 mm) sleeve inserted within the suction tube (Stewart & Wright 1995). For annual plants and exposed soil, we moved the suction tube above the quadrat for 1 min. For perennials, during the 1 min of sampling we first placed the suction tube above the external parts of the plants and then inserted the suction tube into the internal sections of the plant and into the debris under the plant. We identified all spiders >0.5 mm in total length to the lowest possible taxonomic level. If we could not determine the species of an individual, we classified it as a morphospecies. We identified arthropods other than spiders to order and considered them potential spider prey.

Analyses

We applied three analytical methods to data from both Dvir and Lachish and a fourth method (SLOSS index) only to data from Lachish.

Method 1: Quinn and Harrison (1988) Saturation Index

Following Quinn and Harrison (1988), we analyzed data from the 12 patches in each landscape, but not the two large unfragmented patches. We plotted the cumulative observed number of species against the cumulative area sampled in increasing order of patch size (small to large) and in decreasing order of patch size (large to small). We expected that if the set of several small patches contained more species than the single large patch, that the small-to-large curve would have a stepper rate of species accumulation and vice versa. The ratio between the areas under the two curves is therefore a measure of the effectiveness of the small-to-large curves relative to the large-to-small curves. We calculated the area under the curves by connecting the data points with straight lines (but see Cook 1995) because this calculation provided good estimates and it was relatively easy to carry out.

However, sampling intensity (number of samples relative to patch area) decreased as patch area increased. Therefore, comparing the cumulative observed number of species with cumulative area for increasing patch size involved steeper rates of accumulation of samples. For example, in Dvir, the area of the largest patch (of the 12 fragments) was similar to the total area of the nine smallest patches. We observed 57 species in the largest patch and 97 species in the nine smallest patches. However, we observed the 57 species in 25 samples, whereas we observed the 97 species in 83 samples. To explore the effect of this sampling bias on the method, we repeated the accumulation of samples process for both the small-to-large and large-to-small curves and replaced the cumulative patch areas with the cumulative number of samples.

Method 2: SLOSS Index

Boecklen (1997) simultaneously applied several species-area relations (SAR; McGill 2011), each to a different level of fragmentation, and used the difference between the SARs to decouple fragmentation from loss of habitat. We define *fragmentation level* as the number of small patches into which a focal patch is divided. Our objective was to explore how the expected number of species changes as total area and fragmentation level change.

We calculated SLOSS indices only with data from the 12 small patches. We reduced bias in the estimated number of species in each of the 12 small patches. As mentioned above, sampling intensity usually decreases as patch size increases. Boecklen (1997) did not reduce bias. We reduced bias by calculating species diversity with the F5 estimator (Rosenzweig et al. 2003) of ws2m (Turner et al. 2003), a bias-reduction software package. We used the power-model SAR, not the semilogarithmic SAR used by Boecklen (1997), because its fit to the data was greater ($R^2 = 0.48$ and 0.39, respectively). The expected number of species for a given area A according to the power-law SAR (S_{A_1}) is used as the base level of fragmentation level 1, to which SARs of other fragmentation levels are compared.

To create the SAR for fragmentation level 2, we listed all combinations of two patches, except where a combination's total area exceeded the area of the largest patch. Thus, we avoided extrapolation problems. We estimated the number of species for each combination by again reducing the bias by calculating the F5 species diversity. For example, if four patches have areas of A_1, A_2, A_3, and A_4, one possible combination of fragmentation level 2 is $A_1 + A_2$. If the combined area of the two patches ($A_1 + A_2$) was greater than the largest patch (A_4), we removed this combination from the list. If not, we pooled the samples of the two patches and estimated the combination's species diversity with F5. We repeated these steps for all possible combinations of two patches and used the list to build the SAR for fragmentation level 2. We fitted a least-squares linear regression in a log-log space to the estimated species diversity against $A_i + A_j$. Substituting **A** in the regression yielded the expected number of species (**S**) in two patches with the same total area: S_{A_2}.

We then calculated the SLOSS index for a given area **A** (represented as the proportion of the area of the largest patch) as $100 \times (S_{A_2} - S_{A_1})/S_{\text{pool}}$, where S_{pool} is the size of the species pool (i.e., estimated species diversity for all the patches together). The SLOSS index indicates the proportional change in species diversity of a pair of fragments relative to a large patch of the combined area of the fragments. For example, an index of 20% indicates that the two fragments contain 20% more species from the species pool than a single patch of the same total area. We calculated the SLOSS index from 10% to 100% of the area of the largest patch at 10% intervals.

We fitted a power model to the relation between SLOSS index values and percent area with linear regression on logarithmic axes. We extrapolated the regression equation to the cumulative area of all patches. We repeated the method for all possible combinations of three patches.

Method 3: Extrapolation of SAR

To obtain the SAR extrapolation, we calculated species diversity to estimate the number of species in each of the 12 small patches. Then, we applied a log–log least-squares linear regression to the area and estimated species diversity of the 12 patches. We substituted the cumulative area of the 12 patches into the regression equation and solved for the expected number of species (S) in a hypothetical patch of the same cumulative area, which was the estimated result of using a single large area (S_{sl}). To reduce the bias in the cumulative number of species in the 12 patches (i.e., species diversity [S_{ss}]), we calculated S_{ss} by pooling all samples from the 12 patches. Because S_{ss} is derived from a set of small patches, it is the empirical result of using several-small strategy. The SLOSS index is $100 \times (S_{\text{ss}} - S_{\text{sl}})/S_{\text{ss}}$.

To ensure that the extrapolation process would yield a reliable estimate, we further extrapolated the SAR equation to the area of the large unfragmented area, which was not included in the SAR data. We considered the extrapolation yielded a reliable estimate if the estimated number of species in the unfragmented area was close to the SAR extrapolation.

Method 4: Fisher's Alpha Index of Diversity

We generalized the method used by Yaacobi et al. (2007). In each landscape, we calculated an area range for each patch (±5% of the patch area). We then listed all the possible combinations of patches for fragmentation levels of 2–11. We chose, for each patch, all the combinations that were within its area range.

For each patch combination, we calculated Fisher's alpha (Fisher et al. 1943). Fisher's alpha is a reliable index of species diversity that is independent of sample size (Hubbel 2001). We also calculated the Fisher's alpha of each patch (fragmentation level 1) and of the large unfragmented area. Because the number of combinations within the area range increased as patch area increased, we calculated the weighted mean and SE of Fisher's alpha for fragmentation level 1. The weight of each patch was the ratio between the number of combinations found for that patch and the total number of combinations found for all patches. We then calculated the mean Fisher's alpha for fragmentation levels 2–8.

Results

We sampled 11,501 individual spiders from 30 families and 180 species or morphospecies (Supporting Information). We recorded three species (25 individuals) from the two main families of agrobiont spiders (Linyphiidae and Corinnidae) that occur in wheat fields in the region (Pluess et al. 2008; Opatovsky et al. 2010). One of these species, *Trachelas minor* (Corinnidae), which was not detected in the wheat fields by Pluess et al. (2008), accounted for 22 of the 25 individuals.

The samples within our patches with exposed-soil cover type contained significantly fewer spider species (t test, $p < 0.001$) and had lower abundances of spiders ($p < 0.001$) and potential prey per sample than the five structurally complex cover types (Table 1). Only three species, each represented by one individual, were observed only on exposed soil (Table 1); thus, our data mainly include species whose obligatory habitat appears to be the natural area.

Method 1: Quinn and Harrison (1988) Saturation Index

When plotting the cumulative observed number of species against the cumulative area, the small-to-large (increasing patch size) curve lay considerably above the large-to-small (decreasing patch size) curve. The ratios of the areas under the curves were 1.48 and 1.46 for Dvir and Lachish, respectively (Fig. 1a-b). However, when plotting the cumulative observed number of species against cumulative number of samples, the small-to-large and large-to-small curves were extremely close to each other (Fig. 1c-d). This indicates a sample-size bias influenced the results obtained from this method.

Method 2: SLOSS Index

There were 52 and 119 combinations of two and three patches, respectively, with total area less than the area of the largest patch. The linear regressions of the SARs of fragmentation levels 1, 2, and 3 were statistically significant ($p < 0.05$). The values of the SLOSS index for

Table 1. Results of arthropod sampling in two landscapes, Dvir and Lachish, in exposed soil and other cover types.

	Landscape	
Variable	*Dvir*	*Lachish*
Total number of arthropods (excluding spiders)	9779	10,425
Total number of spiders	4047	7454
Total number of spider species	147	144
Number of spider species in 12 patches[a]	114	115
Number of species found only on exposed soil[b]	2	1
Number of species not found on exposed soil	96	103
Number of species found on exposed soil and on other cover types[c]	16	11
Mean (SE) number of spider species/sample		
exposed soil	0.69 (0.15)	0.96 (0.20)
complex cover type[d]	8.77 (0.34)	10.22 (0.44)
Mean (SE) number of spider individuals/sample		
exposed soil	0.74 (0.16)	1.22 (0.26)
complex cover type[d]	19.68 (1.29)	32.24 (2.78)
Mean (SE) number of prey/sample		
exposed soil	2.69 (0.56)	2.70 (0.82)
complex cover type[d]	60.95 (8.25)	51.5 (5.16)

[a] *Twelve patches in each landscape, excluding the two large, unfragmented areas.*
[b] *One individual of each species was observed.*
[c] *All species had lower abundances on the exposed soil relative to the other cover types (sampling effort corrected).*
[d] *Complex cover types as described in text (e.g.,* S. spinosum*).*

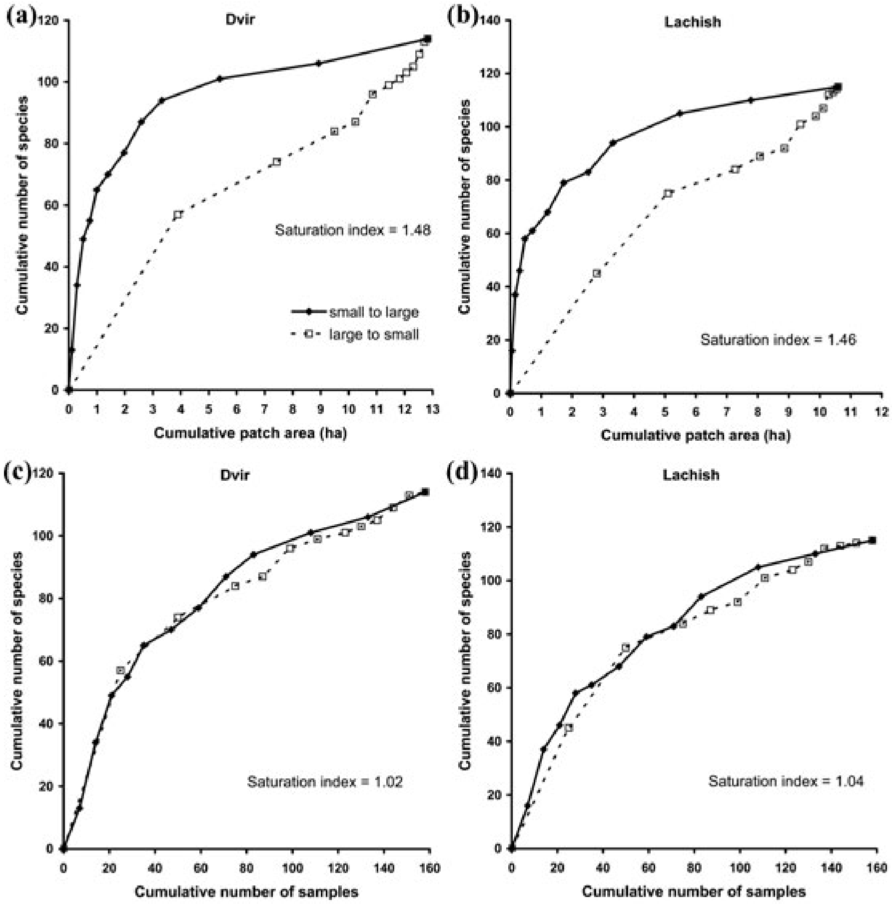

Figure 1. Cumulative observed number of species relative to (a, b) the cumulative area sampled and (c, d) cumulative number of samples from Dvir and Lachish used in the saturation-index method. Accumulation of species occurs in two directions, from the smallest patch to the largest (small to large) and from the largest patch to the smallest (large to small).

fragmentation level 2 were between 9.3% and 12.1% and increased as the proportional area of the largest patch increased (Fig. 2). The values of the SLOSS index for fragmentation level 3 ranged from 12.8% to 18.9% and exhibited a similar increase as the proportion of the largest patch area increased (Fig. 2).

The regression between the SLOSS index and percent area of largest patch (both log transformed) was significant ($p < 0.001$) for fragmentation levels 2 and 3 ($y = 7.136x^{0.116}$ for fragmentation level 2 and $y = 8.851x^{0.167}$ for fragmentation level 3; Fig. 2). The total area of all the patches in Lachish was 377% of the area of the largest patch. With an x of 377%, the expected value of the SLOSS index was 14.2% and 23.8% for fragmentation levels 2 and 3, respectively. For comparison, the value of the SLOSS index for Lachish for fragmentation level 12 (all patches) was 41.2% (see below), which indicates the increase in species diversity as fragmentation level increases may depend on the number of small patches.

Method 3: Extrapolation of SAR

The SARs of Dvir and Lachish were statistically significant ($p < 0.05$; Fig. 3a-b). The estimated number of species in the 12 patches was greater than the expected number for a hypothetical patch with the combined area of all 12 patches (Fig. 3a-b). The values of the SLOSS indices were 35.7% and 41.2% for Dvir and Lachish, respectively (Fig. 3). That is, the 12 patches contained 35.7% and 41.2%, respectively, more species than expected in a single patch of equal area. In both the landscapes, the estimated number of species in the unfragmented area (not included in the calculation of the SAR) was very close to the extrapolated regression line of the SAR, even though the unfragmented area was 40 times the area of the largest of the 12 patches (Supporting Information). This suggests the extrapolation itself had little effect on results.

Method 4: Fisher's Alpha Index of Diversity

A total of 311 and 208 combinations from all fragmentation levels were within the area range of patches in Dvir and Lachish, respectively (Supporting Information). In both Dvir and Lachish, mean Fisher's alpha increased as fragmentation level increased (Fig. 4a-b). Whereas Fisher's alpha did not increase in fragmentation levels 2 (Dvir and Lachish) and 3 (Dvir) relative to fragmentation level 1, it increased in fragmentation level 4–8 relative to fragmentation level 1. As expected, in Dvir and Lachish,

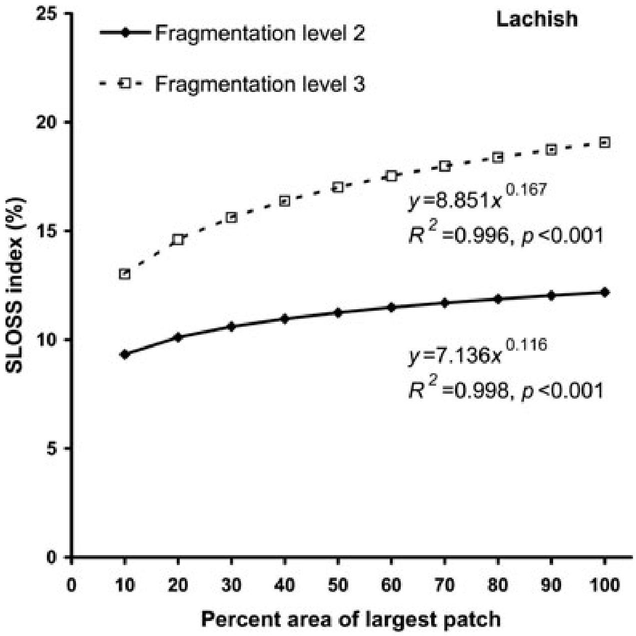

Figure 2. The change in area as the number of species increases (SLOSS index) in sets of two (fragmentation level 2) and three patches (fragmentation level 3) relative to a single large patch. The values of the x-axis are percent of the area of the largest of the 12 patches.

the mean Fisher's alpha did not reach the bias-reduced estimated value in the larger, unfragmented area. We found a similar pattern of increased mean Fisher's alpha as fragmentation level increased when we compared separately each focal patch with its valid combinations of different fragmentation levels.

Discussion

Performance of the Four Methods

No matter which method we used, fragmentation was associated with an increase in the number of spider species. The four methods differed in their ability to correct sampling bias (Table 2). Sampling bias is an inherent property of most studies conducted at moderate and large spatial extent (i.e., extents at which environmental heterogeneity affects distribution and composition of species). Although the focus (i.e., "the inference space to which the question applies" [Scheiner et al. 2000]) increases in such studies, the sampling is still local, usually over a few meters. On one hand, a minimum number of samples must be taken in the smallest patch for the samples to represent the community. On the other hand, a larger number of samples must be taken in larger patches to account for the greater diversity within them. Therefore, if sampling intensity is defined as the proportion of patch area that was sampled, then the sampling intensity is highest in the smallest patch and tends to decrease as patch size increases. For example, if 10 samples are needed to accurately reflect the species diversity of the community in a 1-ha patch, 1000 samples will be needed in a 100-ha patch to maintain the same sampling intensity. Our data had this sampling bias and probably most data sets used to explore effects of fragmentation on species diversity have such a bias. For example, Tscharntke et al. (2002) used the Quinn and Harrison (1988) saturation index, and the intensity (time for unit area) of their sampling of butterflies on the smallest patch (15 min, patch area 300 m^2) was 63 times the sampling intensity in the largest patch (60 min, 76,000 m^2).

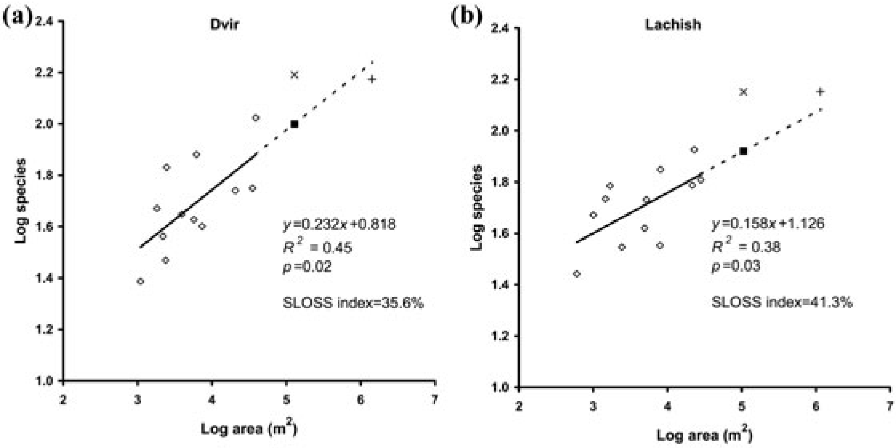

Figure 3. Relation between number of spider species and area at (a) Dvir and (b) Lachish (diamond, observed after correction for sampling bias; solid line, fitted linear regression of the log of the number of species against log area; broken line, extrapolation beyond the area of the largest patch; ×, observed number of species in a set of 12 patches; solid square, expected log of the number of species in the single large patch with similar area as the 12 patches combined; +, number of species in the large unfragmented area).

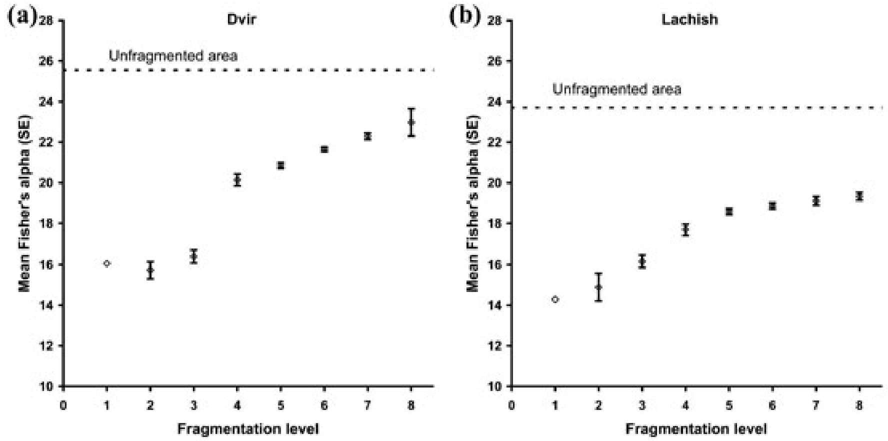

Figure 4. Mean (SE) Fisher's alpha index of diversity for different fragmentation levels in (a) Dvir and (b) Lachish. Value of fragmentation level 1 (single large patch) is the weighted mean of the patches' alpha value (see text). Dashed horizontal line shows Fisher's alpha values in the large unfragmented area.

The saturation-index method could not rectify this bias (Fig. 1c-d); thus, our results with this method were biased toward detecting greater species diversity in many small patches than in one large patch. In contrast, Fisher's alpha was insensitive to sample size and needed no correction. Inferences derived from the other two methods may have been weakened by sampling bias if we had not first corrected data, with a diversity index that was independent of sample size (the F5 index [Turner et al. 2003]).

The four methods also differ in their quantitative definition of "several small" (Table 2). In the saturation index and SAR extrapolation methods *several* is the total number of patches in the landscape. In the SLOSS index and Fisher's alpha methods *several* is a flexible term because the analyses are repeated for all possible combinations of 2, 3, 4,. . .,n patches. For Lachish, the SLOSS index (Fig. 2) suggested species diversity increased even when two patches were compared with a single patch. However, for Dvir and Lachish results of the Fisher's alpha index (Fig. 4) suggest species diversity increased as fragmentation increased only with $\geq$4 patches.

Selecting the most accurate method depends on the data structure and focal taxon. We suggest avoiding the saturation-index method in all cases in which there is a known reduction in sampling intensity as patch area increases. However, sampling bias may affect this method even if an equal number of samples are taken in all patches (e.g., Fischer & Lindenmayer 2002; Arroyo-Rodriguez et al. 2009). Were we restricted to only one method, we would prefer to use Fisher's alpha.

The SLOSS-index, SAR-extrapolation, and Fisher's alpha methods should be considered complementary in the insights they provide. So we suggest using all three when possible. The SAR-extrapolation method is the extreme case of the SLOSS-index method, in which species diversity is extrapolated to the cumulative area of all patches. Because there is only one combination of all patches, the SAR of fragmentation level n, where n is the total number of patches, is compressed to a single point. Hence, SAR extrapolation may allow comparison of systems with different numbers of patches. In our system, this method revealed that species diversity in Dvir and Lachish was 35.6% and 41.3% higher, respectively, than if all patches were one continuous patch of equal area. The SLOSS index provided additional information. For Lachish it showed that species diversity increased as fragmentation level increased (Fig. 2), similar to the results with Fisher's alpha (Fig. 4b). However, it also indicates this increase in species diversity depended on the area. This was evident in the convex-shaped increase in the SLOSS index as the proportion of the area of the largest patch increased. This means two small patches supported greater species diversity than a single large patch of the same total size, but two large patches supported even greater species richness compared with a patch of their same total size. This pattern was also evident with Fisher's

Table 2. Summary of the properties of different methods for examining whether species richness is likely to be greater in a set of small patches than in one large patch when area is held constant.

Method	*Reference*	*Method for reducing sampling bias*	*Definition of several small patches*	*Requirements for species data*
Saturation index	Quinn & Harrison 1988	none	all patches in the landscape	presence–absence or abundance
SLOSS[a] index	Boecklen 1997	requires software	flexible	presence–absence or abundance
SAR[b] extrapolation	Lomolino & Weiser 2001	requires software	all patches in the landscape	presence–absence or abundance
Fisher's alpha	Yaacobi et al. 2007	automatic	flexible	abundance

[a]*Single large or several small.*
[b]*Species-area relation.*

alpha method, with which we explored the effect of fragmentation on species diversity of each patch separately. For a given fragmentation level, Fisher's alpha increased more in large patches than in small patches.

Conservation of Spiders in Southern Judea Lowlands

To conserve spiders in the Southern Judea Lowlands over the long term we suggest the following three primary steps be taken: identify the species most likely to be affected by fragmentation, determine the processes associated with the short-term pattern of fragmentation effects on species diversity, and project the long-term effect of those processes. Our results for the exposed-soil cover type (Table 1) and those of others (Pluess et al. 2008; Opatovsky et al. 2010; Pluess et al. 2010) indicate that most spider species in our study system require their natural habitat to persist over the long term.

Currently two types of processes may explain our results: those that primarily affect within-patch species diversity and have an additive effect on the cumulative species diversity of the set of small patches (i.e., edge effect and heterogeneity) and those that relate primarily to the flow of individuals among patches (i.e., extinction-colonization dynamics and rescue effects). Edges could affect species diversity because small patches have larger edge-to-core ratios than large patches, which may result in the flow of species from agricultural fields into natural habitat. This may result in an increase in the number of species within the patch. Because different agrobiont species may enter different patches, edges may increase the overall species diversity in the set of several small patches. However, we rarely observed agrobiont species in our samples. Moreover, several shape indices (Supporting Information) did not change significantly as a function of area. Therefore, we believe edges have had little or no effect on the results of our fragmentation analyses.

Habitat heterogeneity usually increases as patch area increases, yet several small patches may additively hold higher overall heterogeneity. If our results arose from higher overall habitat diversity in several small patches despite lower diversity within each patch, then the most effective strategy may be to conserve one large heterogeneous patch. We found that the composition of spider species differed significantly between most pairs of cover types (analysis of similarity; Y.G., unpublished). In addition, we sampled more cover types in larger patches. In the saturation-index method, the results may have been strongly affected by faster accumulation rates of cover types in the small-to-large curve relative to the large-to-small curve. Conversely, the SLOSS index in Lachish increased as patch area increased for a given fragmentation level even though larger patches contained samples of most cover types. With SAR extrapolation, sampling more cover types in larger patches increased the slope of the relation and thereby increased the estimate of species diversity for the single large patch. However, both landscapes had positive SLOSS-index values. In the Fisher's alpha method, larger patches had more combinations of fragmentation levels that satisfied the 5% area rule (i.e., weights of larger patches were higher in the calculation of level-1 fragmentation). These larger patches also had more cover types than smaller patches. Despite this, several small patches had higher Fisher's alpha values. Hence, although heterogeneity and the amount of edge may affect the outcome of fragmentation analyses, this is probably not the case in our system.

Fragmentation increases within-patch extinction risk if fewer individuals occupy smaller patches. When a system approaches equilibrium, one expects occupancy to be significantly correlated with patch area for at least some species. However, logistic regression of species occupancy against log area was not significant for all the species in both landscapes. It is possible that not enough time passed to observe effects of fragmentation, although aerial photographs from 1945 show that the two landscapes were highly fragmented then (albeit less than at the time of sampling). It is also possible that most species are able to disperse through the wheat fields, resulting in fast recolonization rates or strong rescue effects.

Most species we observed are probably able to disperse through the wheat fields during the wheat-growing season. Some spider species may disperse aerially and thus be relatively unaffected by land cover (Marc et al. 1999). In addition, for other wheat fields in the region, the percent cover of natural area around fields increases species diversity within a field (Pluess et al. 2010), mainly reflecting presence of species with higher activity levels within the natural area (Pluess et al. 2008). These results suggest that many species use the wheat fields during the growing season for dispersal and for other activities such as foraging. That is, the fields may act as a facultative habitat for the species and thus provide supplementary resources and further reduce extinction risk within patches. However, the fields may also act as ecological traps if spiders do not return to the natural habitat before wheat harvest; mortality rates during harvest are probably high. Nonetheless, these species need the natural patches after harvest to complete their life cycle, as evident from the small number of spiders observed on exposed soil. Finally, the remaining natural habitat (40% in Dvir and 36% in Lachish) is still above suggested threshold levels, below which connectivity collapses (Andren 1994, but see below).

So, for the spiders that rely on the natural patches for their survival, several small patches are occupied by more species than a single large patch. The current diversity of spiders suggests fragmentation may not have negative effects on their extinction-colonization dynamics in Southern Judea Lowlands. If some area can be protected, distributing that area among several small patches may maximize the long-term diversity of spiders in the area.

However, conservation of the patches will not conserve spiders if surrounding land use changes to a use that is less hospitable to spiders than wheat farming.

Comparisons between Landscapes

Fragmentation is a landscape-scale process (Fahrig 2003). We focused on decoupling fragmentation from habitat loss within a given landscape and not between landscapes. Other approaches involve simultaneous sampling of many paired landscapes with similar amounts but different distributions of habitat (e.g., Radford et al. 2005). Estimating the amount of habitat within a landscape is straightforward once the borders of the landscape have been defined. However, the borders do not necessarily represent any biological or environmental barrier, so the amount of habitat within a landscape is an arbitrary value. The between-landscape approach strongly depends on this arbitrary value. That is, a slight modification of landscape location and size may alter the analyses used because the amount of habitat within each landscape would change.

The methods we explored may aid in overcoming problems associated with this arbitrary choice of landscape size and location. They provide reliable indices that decouple fragmentation from area loss. Comparisons of landscapes with indices that are based on our methods (with the exception of the saturation-index method) may allow one to identify key variables related to the effect of fragmentation on species diversity. Manipulative experiments that explore effects of fragmentation are rare and technically difficult (McGarigal & Cushman 2002), and long-term data are few. Therefore, we suggest that methods that decouple effects of fragmentation from those of habitat loss be further developed (Fahrig 2003; Laurance 2008).

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Supporting Information

Sampling effort per patch, patch characteristics (area and shape), and various measures of heterogeneity for the 12 patches (Appendix S1), presence–absence data for all 180 species of spiders from the 12 patches in each landscape (Appendix S2), and the number of patches of each fragmentation level for the Fisher's alpha method (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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