



Scale-dependent species–area and species–isolation relationships: a review and a test study from a fragmented semi-arid agro-ecosystem

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ABSTRACT

Aim Patterns that relate species richness with fragment area (the species–area relationship, SAR) and with isolation (the species–isolation relationship, SIR) are well documented. However, those that relate species density – the number of species within a standardized area – with fragment area (D-SAR) or isolation (D-SIR) have not been sufficiently explored, despite the potential for such an analysis to disentangle the underlying mechanisms of SARs and SIRs. Previous spatial theory predicts that a significant D-SAR or D-SIR is unlikely to emerge in taxa with high dispersal limitation, such as plants. Furthermore, a recent model predicts that the detection and the significance of D-SARs or D-SIRs may decrease with grain size. We combined a literature review with grain size-dependent sampling in a fragmented landscape to evaluate the prevalence and grain size-dependent nature of D-SARs and D-SIRs in plants.

Location Worldwide (review) and a semi-arid agro-ecosystem in Israel (case study).

Methods We combined an extensive literature review of 31 D-SAR studies of plants in fragmented landscapes with an empirical study in which we analysed grain size-dependent D-SARs and D-SIRs using a grain size-dependent hierarchical sampling of species density and species richness in a fragmented, semi-arid agro-ecosystem.

Results We found that significantly increasing D-SARs are rare in plant studies. Furthermore, we found that the detection of a significant D-SAR is often possible only after the data have been stratified by species, habitat or landscape characteristics. The results from our case study indicated that the significance and the slopes of both D-SARs and D-SIRs increase as grain size decreases.

Main conclusions These results call for a careful consideration of scale while analysing and interpreting the responses of species richness and species density to fragmentation. Our results suggest that grain size-dependent analyses of D-SARs and D-SIRs may help to disentangle the mechanisms that generate SARs and SIRs and may enable early detection of the effects of fragmentation on plant biodiversity.

Keywords

Conservation biogeography, extinction debt, habitat fragmentation, habitat islands, island biogeography theory, island ecology, isolation, scale-dependence, species–area relationship, species density.

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INTRODUCTION

The island biogeography theory (IBT; MacArthur & Wilson, 1967) is based on two fundamental premises: a decrease in extinction rate with island area and a decrease in colonization rate with island isolation. These premises underlie two important ecological patterns: an increase in species richness with island area (species–area relationship, SAR) and a decrease in species richness with island isolation (species–isolation relationship, SIR) (Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007). Inspired by the IBT and driven by growing interest in and concern about the effects of habitat loss and habitat fragmentation on biodiversity, many studies have focused on SARs, SIRs and their underlying mechanisms in fragmented (patch-matrix) landscapes (Lindborg & Eriksson, 2004; Adriaens *et al.*, 2006; Cousins, 2006; Vellend *et al.*, 2006; Watling & Donnelly, 2006; Cousins *et al.*, 2007; Laurance, 2008; Prevedello & Vieira, 2010; Fahrig, 2013; Hanski *et al.*, 2013).

Evidence for decreasing SIRs in fragmented landscapes is scarce (Fahrig, 2003; Watling & Donnelly, 2006). One explanation for the lack of evidence is the slow response of organisms to fragmentation that may conceal SIRs in recently fragmented landscapes, an effect known as the extinction debt (Helm *et al.*, 2006; Vellend *et al.*, 2006; Cousins, 2009). In contrast, the evidence for increasing SARs in fragmented landscapes is overwhelming (Fahrig, 2003; Watling & Donnelly, 2006). But whereas a decreasing SIR is attributed exclusively to the decrease in the colonization rate with the increase in isolation as proposed by the IBT, an increasing SAR in fragmented systems can be attributed to one or more non-mutually exclusive mechanisms that may operate simultaneously. Those mechanisms are often classified into five main categories (Table 1; Hill *et al.*, 1994; Turner & Tjørve, 2005; see also Scheiner *et al.*, 2011, for a comprehensive list of potential mechanisms). Three of these mechanisms are related to sampling, which may refer to the allocation and distribution of sampling efforts by the researchers (random sampling) or to the natural ‘sampling’ process of a larger species pool by natural sampling units, such as islands or fragments (random placement and the target area). The two

other mechanisms, which are ecological in nature, relate to the habitat heterogeneity and the equilibrium hypotheses. As these mechanisms can act either individually or in concert, the mere documentation of a significantly increasing SAR does not constitute a rigorous test of any of them, instead dictating the need for additional measures to distinguish the potential contribution of each mechanism (Hill *et al.*, 1994; Lomolino, 2001; Cook *et al.*, 2002; Turner & Tjørve, 2005; Laurance, 2008; Matias *et al.*, 2010; Hanski *et al.*, 2013).

One proposed approach for disentangling the effects of various mechanisms on SARs is to test the relationship between the number of species within a standardized sampling unit located within a fragment and the area of that fragment (Kelly *et al.*, 1989; Holt, 1992, 1993; Hill *et al.*, 1994; Gotelli & Graves, 1996; Hoyle, 2004; Schoereder *et al.*, 2004; Helm *et al.*, 2006). In the following we will refer (1) to the number of species in a standardized area as ‘species density’, acknowledging that the terms ‘point-diversity’, ‘local species richness’ and ‘ α -diversity’ have been used in the same sense (Gray, 2000; Cousins & Vanhoenacker, 2011; Giladi *et al.*, 2011), (2) to the relationship between fragment area and species density as D-SAR, and (3) to the relationship between fragment isolation and species density as D-SIR.

Species density is often highly correlated with and used as a proxy for fragment-level species richness (Cook *et al.*, 2002; Lindborg & Eriksson, 2004). Consequently, D-SARs and D-SIRs are sometimes analysed and interpreted as SARs and SIRs, respectively. Patterns based on species density (D-SARs and D-SIRs) can be understood to be the results of processes operating at two levels, the first of which links large-scale species richness (e.g. landscape species pool) with fragment-level species richness, and the second of which links fragment-level species richness with species density (Pärtel *et al.*, 1996; Stiles & Scheiner, 2010). This conceptualization, however, does not necessarily mean that the two sets of processes are independent of each other. Specifically, the existence and strength of a correlation between fragment-level species richness and species density may depend strongly on determinants of the fragment-level species pool (Pärtel *et al.*, 1996) and on the grain size at which species density is measured (Stiles & Scheiner, 2010).

Table 1 Processes and mechanisms hypothesized to contribute to the generation of an increasing species–area relationship (SAR), the rationale underlying each proposed mechanism, and references to early classical works that developed these ideas.

Hypothesis	Rationale	References
Random sampling	(a) Number of individuals sampled increases with sampling effort. (b) Species richness increases with sample size.	Preston (1962), Connor & McCoy (1979), Coleman (1981)
Random placement	(a) Total number of individuals increases with area. (b) Species richness increases with number of individuals.	Connor & McCoy (1979), Coleman (1981)
Habitat diversity hypothesis	(a) Habitat diversity increases with area. (b) The contribution of different habitats to species richness is complementary.	Williams (1943, 1964), MacArthur (1972)
Target area effect	Colonization rate increases with area	Connor & McCoy (1979, 2001) Gilpin & Diamond (1976)
Equilibrium hypothesis	Extinction rate decreases with area	Preston (1962), MacArthur & Wilson (1967)

The construction of the D-SAR is based on uniform sampling that controls for random sampling and random placement effects and that may also control for habitat heterogeneity. Therefore, some authors have suggested that the only mechanisms capable of generating a D-SAR are those proposed by the equilibrium hypothesis and by the target area effect, which some authors have merged into a single hypothesis (Kelly *et al.*, 1989; Holt, 1992, 1993; Hill *et al.*, 1994; Gotelli & Graves, 1996; Hoyle, 2004; Schoereder *et al.*, 2004; Helm *et al.*, 2006). In two influential papers on analysing and interpreting D-SARs, Holt (1992, 1993) emphasized that an increasing D-SAR is compatible with the habitat heterogeneity hypothesis (Table 1), arguing that the exchange of transient species among habitats within a fragment, called the ‘spillover effect’, augments species density within each habitat. Thus, larger and more heterogeneous fragments, which have higher species richness, will also have higher species density, leading to an increasing D-SAR. As these among-habitat enrichment processes are linked to dispersal ability, Holt (1992) predicted that increasing D-SARs are unlikely to be found for organisms with limited dispersal capabilities, such as plants. To the best of our knowledge, however, that prediction has not been tested.

The lack of evidence for increasing D-SARs in plants may also be the result of the slow response of plants to habitat fragmentation (Eriksson *et al.*, 2002; Helm *et al.*, 2006; but see Körner & Jeltsch, 2008). Recently, Cousins & Vanhoenacker (2011) presented a model predicting that the response of plant species to fragmentation will occur faster the smaller the grain size. The rationale behind this model is that local extinction caused by the negative effects of the post-fragmentation increase in extinction and decrease in re-colonization is most pronounced at the smaller scales and is buffered by the within-fragment movement of individuals at larger scales. Thus, during the transitional periods that follow fragmentation events, only small-scale (but not larger-scale) species density is expected to correlate with fragment area and with fragment isolation.

When sampling species density, habitat heterogeneity within a sampling unit is expected to increase and resemble fragment-level habitat heterogeneity as the size of that unit increases. Thus, if the mechanism of habitat heterogeneity is the main driver of the D-SAR, we should expect an increase in the slope and significance of the D-SAR as grain size increases (but see Scheiner *et al.*, 2000). If D-SARs were generated mainly by the processes proposed by the target area and equilibrium hypotheses, however, we would expect these effects to be most apparent when the sampling units are most homogenous, i.e. mainly at smaller grain sizes. If D-SARs and D-SIRs are indeed grain size-dependent, our ability to detect these patterns and to draw correct inference from their analyses may vary with grain size. Interestingly, although the responses of species density to its various determinants have been shown to depend on grain size, very few studies have assigned importance to the choice of grain size in the analysis of species density response to area

(D-SAR) or isolation (D-SIR) (Scheiner *et al.*, 2000; Stiles & Scheiner, 2010; Brudvig & Damschen, 2011; Giladi *et al.*, 2011; Thornton *et al.*, 2011). For D-SAR or D-SIR construction, the choice of grain size is often based on conventions or practical considerations, or it is arbitrary, and specific justification is seldom given (Kohn & Walsh, 1994; Rey Benayas *et al.*, 1999). To the best of our knowledge, ours is the first study to systematically investigate the sensitivity of D-SARs, D-SIRs and their slopes to grain size.

We combined an extensive literature review with an empirical study to address several predictions about the prevalence, detectability and interpretation of D-SARs and D-SIRs in studies of plants in fragmented landscapes. If D-SARs are attributed mainly to the spillover effect among habitats within fragments, which necessitates considerable dispersal for colonization to take place [Holt’s (1992, 1993) prediction], then D-SARs in plant studies will have a slope of zero (P1). We therefore assessed the prevalence of statistically significant D-SARs in plant studies and compared it with the prevalence of statistically significant SARs. If habitat heterogeneity is the main mechanism driving D-SARs, we would expect stronger correlations between species density and fragment area as grain size increases (P2). Alternatively, if D-SARs are mainly attributable to the target area effect and the equilibrium hypothesis, then both D-SARs and D-SIRs should be most evident when species density is measured at small grain size (P3) (Cousins & Vanhoenacker, 2011). Finally, we expect D-SARs, and especially D-SIRs, to be more pronounced when historical rather than current landscape configurations are used (P4). We evaluated these predictions against the existing literature where these patterns were tested. Predictions P2 and P3 were also tested within our study system in a species-rich fragmented Mediterranean landscape where species density was simultaneously measured at different grain sizes.

MATERIALS AND METHODS

Literature search

We reviewed the evidence in the literature for D-SARs and D-SIRs in plant studies by searching the literature for studies that correlated species density of plants with fragment area and/or with fragment isolation. In November 2012, we searched the ISI Web of Science for candidate manuscripts using two search chains – one focused on the D-SAR and the other on the D-SIR. The first chain included (species density OR local species richness OR alpha diversity) AND (species–area OR SAR) AND plants. The second chain included (species density OR local species richness OR alpha diversity) AND fragmentation AND isolation AND plants. We also employed a forward citation search of some early papers on the subject (Kelly *et al.*, 1989; Hill *et al.*, 1994) and evaluated those included in a recent review on a related topic (Lindborg *et al.*, 2012). We then read the abstract of each candidate manuscript to determine whether it included data and analyses relevant to D-SARs and/or D-SIRs. When-

ever an abstract was not sufficiently informative, we carefully read the methods and results sections to decide which papers to include in our analysis. For each manuscript included in our analysis, we recorded the main vegetation type, which pattern – SAR, SIR, D-SAR or D-SIR – was tested, which patterns had a non-zero slope, the grain size used in species density measurements, the method for calculating connectivity/isolation, stratification of the data, and the functional form used to model each pattern.

Grain size-dependent D-SARs and D-SIRs in a fragmented semi-arid agro-ecosystem

Study area

The study area is a 3.2 km × 4 km landscape in central Israel (31°31'20"–31°33'40" N, 34°46'50"–34°50'20" E) located within a transition zone between Mediterranean and desert ecosystems (Fig. 1). The climate is a typical semi-arid with short mild winters and long, dry, hot summers. Average annual temperature is 19 °C (12 °C in January, and 26 °C in August; Goldreich, 2003). Average annual rainfall is 376 mm (average for 1998–2009, measured within 3 km of the study area boundaries; Data from the Ministry of Agriculture, Israel). Soil types in the study area are mainly light-brown loessial soils and light-brown rendzina (Dan *et al.*, 1976). The area has experienced grazing by sheep and goats and small-scale agriculture for thousands of years (Naveh & Dan, 1973; Ackermann *et al.*, 2008). Intensified agricultural practices over the past 60 years have reshaped the landscape, such that today it comprises a mosaic of fragments of natural vegetation within a predominately agricultural matrix (Mazor, 2006; Svoray *et al.*, 2007; Yaacobi *et al.*, 2007).

At the time of the research, the study area contained 76 fragments of natural vegetation. These vary in size from

continuous (> 100 ha) to very small (< 100 m²) fragments, the main vegetation types of which comprise semi-steppe low scrubland and grassland with a decreasing shrub cover from east to west. The most dominant perennial species are the dwarf shrub *Sarcopoterium spinosum* among the scrubland vegetation, and the tussock grasses *Hyparrhenia hirta* and *Hordeum bulbosum* in the grassland. The region's flora is species rich, including 415 vascular plant species observed within the study area alone (I.G. and M.R., pers. obs.). The percentage cover of the dominant shrubs in a plot varies from 0 to 53% (mean ± SD, 0.066 ± 0.136) for *Sarcopoterium spinosum* and 0 to 28% for *Hyparrhenia hirta* (0.064 ± 0.066). Plant density (measured at a grain size of 0.0625 m²) varies from 253 to 624 individuals m⁻² (mean ± SD, 423 ± 109) (Giladi *et al.*, 2011).

Vegetation sampling

Vegetation sampling was conducted in 39 fragments chosen to represent wide ranges of fragment area and fragment isolation (Fig. 1). About half of these fragments (20) were sampled using uniform size, hierarchically nested sampling plots. An initial set of 14 fragments were sampled using 225-m² plots (which included 25-m² subplots; details below and in Giladi *et al.*, 2011). This set was supplemented with six additional fragments that were sampled using 25-m² plots to represent combinations of fragment area and isolation that were absent from the initial set. The number of plots placed within each fragment varied correlatively with fragment area and ranged from 1 to 7 (see Appendix S1 in the Supporting Information). Such a proportional sampling was chosen to ensure that fragments of different sizes were adequately represented and as a first approximation for fragment-level species richness (Schoereder *et al.*, 2004). However, as such proportionality entails a strong sampling

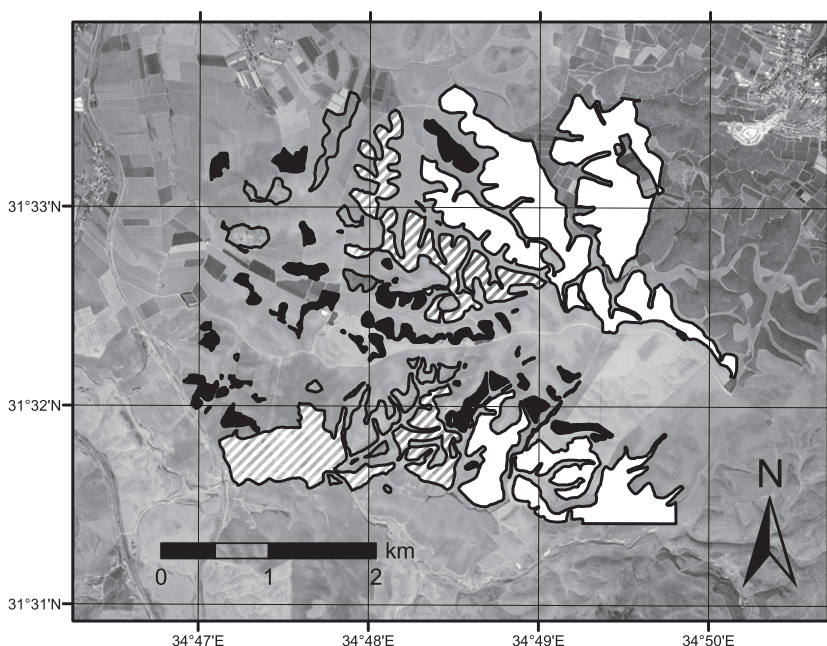


Figure 1 Map of the study area in the Lachish region of central Israel. Fragments of semi-natural vegetation that are within the study area are marked with black lines. Fragments that were sampled for species richness are shaded black. Fragments that are currently larger than 15 ha (current 'mainland') are shaded white and fragments that were mainland 20 years ago but have since been either fragmented or disturbed (historical 'mainland') are marked with stripes.

bias, sampling of fragment-level species richness of all 39 fragments was completed by a thorough survey of all plant species by experienced botanists (M.R. and I.G.) very familiar with the local flora.

In line with similar studies, the time spent surveying each fragment was adjusted relative to fragment size and habitat diversity (Öster *et al.*, 2007; Reitalu *et al.*, 2012). Surveying continued until a sharp decrease in the discovery rate of new species was noticed by the surveyors. Fragment survey time varied from approximately half an hour for the smallest and most uniform fragments to a full day for the largest and most diverse fragments. The uniform sampling was done according to a hierarchical nested design modified after Kalkhan *et al.* (2007). It yielded estimates of mean species density at three grain sizes (0.0625, 1 and 25 m²) for 20 fragments, for 14 of which the mean species density were also estimated at the 225-m² grain size (for details see Giladi *et al.*, 2011). All vascular plant species within the sampling units were recorded at the height of the growing season between early March and early April, in either 2009 or 2010, and whole fragment species lists were completed in 2010 and 2011. Plant identification followed Feinbrun-Dothan & Danin (1991).

Fragment size and isolation measurements

We used rectified aerial photographs (Ofek Aerial PhotoTM, Netanya, Israel, 2005, pixel size = 1 m²) to identify fragments of natural vegetation within the study area. We then demarcated their boundaries on a digitized map and stored the information as vector-based coverage in a geographical information system (GIS) platform (ArcInfoTM; ESRI, Redlands, CA, USA). The data were converted to a raster-based layer (grid cell size = 5 m × 5 m) and exported to FRAGSTATS[©] (McGarigal *et al.*, 2002) to calculate fragment area, distance to nearest neighbour, fragment proximity index and distance to the ‘mainland’. The proximity index is a measure of fragment isolation that quantifies the spatial context of a fragment in relation to neighbouring fragments. For each fragment *i*, the proximity index (PI_{*i*}) is given by:

$$PI = \sum_{j=1}^n \frac{a_j}{h_{ij}^2} \quad (1)$$

where a_{ij} is the area of fragment *j*, h_{ij} the distance (edge-to-edge) between fragment *i* and fragment *j*, and the summation is done over all *n* fragments that are within a certain search radius r_s of the focal fragment *i*. We present the data analysis conducted with a proximity index calculated using an r_s of 1000 m (different radii yield similar proximity values; Giladi *et al.*, 2011).

In line with similar studies, the fragmented landscape in our study does not contain a single, well-defined mainland. Therefore, we defined each fragment of natural vegetation larger than 15 ha as a mainland. Some of the fragments that would have met our criteria for ‘mainland’ status 20 years ago have since been further divided by the construction of a road two years prior to the onset of the study or have been

drastically altered by landscaping activities and the planting of exotic trees. Therefore, we calculated distance to the mainland for two mainland scenarios: one (DistM1) only considered fragments that met mainland criteria at the time of the study, and the second (DistM2) considered fragments that met these criteria 20 years ago (Fig. 1).

Data analysis and statistics

The total number of species recorded in each fragment (SR_{fragment}) and the mean species density at each of the smaller grain sizes (SpD_{0.0625}, SpD₁, SpD₂₅, SpD₂₂₅ at 0.0625, 1, 25 and 225 m², respectively) were treated as the main response variables. Fragment area, proximity index, Euclidean nearest neighbour distance (ENN) and distance to the mainland (for both scenarios DistM1 and DistM2) were initially treated as candidate explanatory variables. Prior to any statistical analysis, fragment area, proximity index and distances to mainland were all log₁₀-transformed. This was done mainly to concur with two of the most common models of SAR used in plant studies, the power model and the exponential (semi-log) model (Tjørve, 2003; Dengler, 2009; Triantis *et al.*, 2012). Because the data analysis in the main text of this manuscript was based on assuming a power model, we log-transformed species richness and species density prior to data analysis. However, we tested the robustness of our main conclusions by repeating the analyses using an exponential model.

After testing for correlation among independent variables, a set of uncorrelated explanatory variables was then used in a series of linear models to test for their effects on species richness and species density at each of the sampling scales. We conducted all of the above mentioned analyses separately for each sampling scale using the R statistical platform (R Development Core Team, 2012). We used the ‘lm’ and the ‘anova’ functions in R for the construction and analyses of the linear models, respectively. The analysis of species richness and species density at each sampling scale was performed with all the available data for that scale.

RESULTS

Literature search

We found 31 studies of plants in fragmented landscapes that tested for D-SARs, D-SIRs or both. About half of the studies (18) were conducted in grasslands, less than a third (nine studies) in forests or woodlands, and the rest in other, mainly open, habitats (Appendix S2). Twenty-eight of these studies tested D-SARs, 24 tested D-SIRs, 15 of them tested SARs and only 10 tested SIRs.

Of the 15 studies that tested SARs the pattern was found to be significantly increasing in most (87%), whereas only 36% of the 28 studies that tested for D-SARs found statistical significance. Of the 10 and 24 studies that tested SIRs or

D-SIRs, 40% or 58%, respectively, found significantly decreasing relationships (Table 2). Among the 15 studies that tested for both SARs and D-SARs, four supported both patterns, neither pattern was significant in two studies, and in nine studies only the SAR was significantly increasing. Of the nine studies that tested for both SIRs and D-SIRs, four found full or partial support (i.e. for particular subsets of the data) for both patterns, another four studies found that neither of the isolation patterns was significant, and one study supported a significantly increasing D-SIR, but in that case SIR had a slope of zero. All of the studies that found a significantly positive SAR used direct measures of fragment-level species richness and of the explanatory factors, but without data stratification. Much of the support for the other three patterns, however, was obtained only after the data were stratified by plant characteristics, habitat or landscape characteristics, or when historical landscape configuration was used to calculate fragment area and fragment isolation (Table 2).

The grain size used to measure species density in plant studies that tested for D-SARs and/or D-SIRs ranged from 0.025 to 2800 m², but most studies used a single grain size. The plot sizes used in studies in which D-SARs and/or D-SIRs were found to be significant ranged from 0.25 to 2800 m². The grain size used in studies in which the D-SAR was significant was similar to that used in studies in which the D-SAR was not significant (median = 4 and 16 m², respectively, Wilcoxon test, $W = 107$, $P = 0.93$). The grain size used in studies in which the D-SIR was significant was somewhat smaller than in studies in which the D-SIR was not significant (median = 4 and 100 m², respectively), but this difference was only marginally significant (Wilcoxon test, $W = 47$, $P = 0.06$).

Only seven of the studies used the power model, 10 studies used the exponential model, 10 others used the linear model, and the remainder used other models (e.g. categorical or nonlinear relationships; Appendix S2). Most studies that tested more than one relationship used the same functional form for all the relationships tested within the study. The analysis of the SAR was consistent across the functional forms, with 4 vs. 1, 6 vs. 0, and 3 vs. 1 significant and non-significant SAR for power, exponential and linear models, respectively. The D-SAR gained little support in studies that used the power or linear model (1 significant vs. 6 n.s. and 2 significant vs. 4 n.s., respectively) and an equal amount of support (5 significant vs. 5 n.s.) when the exponential model was used. Interestingly, support for the D-SIR was the weakest when the power model was used (0 significant vs. 2 n.s.), equivocal for the exponential model (3 significant vs. 3 n.s.) and most evident when the linear model was used (7 significant vs. 3 n.s.). Similar findings were observed for SIR, although the low number of studies that tested this relationship precludes drawing any strong conclusions. In general, the results of our analysis were sensitive to the models chosen by the researchers, an observation that should be considered in future studies.

Table 2 Summarized results of the literature review. The table shows the numbers of independent studies that tested for a species–area relationship (SAR), species density–area relationship (D-SAR), species–isolation relationship (SIR), and species density–isolation relationship (D-SIR) of plants in fragmented systems. The table includes the number of studies that found support for each of these four patterns (as reported in the original papers or deduced from the results), of studies supporting each pattern where data were stratified by plant characteristics, habitat or landscape characteristics and of studies in which only historical landscape configuration significantly explained species richness or species density. A list of studies and more detail can be found in Appendix S2.

	SAR	D-SAR	SIR	D-SIR
Number of independent tests	15	28	10	24
Total number of studies where a pattern is significant	13	10	4	14
Number of studies where pattern is significant only after stratifying data by plant characteristics	0	2	1	4
Number of studies where pattern is significant only after stratifying data by habitat or landscape characteristics	0	3	0	1
Number of studies where pattern is significant only when historical landscape configuration is used	0	1	3	4
% support	87	36	40	58
% support when data are not stratified and current landscape configuration is used	87	14	0	25

Grain size-dependent D-SARs and D-SIRs in a fragmented semi-arid agro-ecosystem

Initial examination of the explanatory variables indicated that fragment proximity was negatively correlated with all other measures of connectivity (ENN and distance to mainland) and that the two measurements of distance to mainland were highly correlated (with many fragments having the same value for both; Table 3). Therefore, we conducted the rest of the analysis with fragment area, DistM1 and ENN as uncorrelated candidate explanatory variables.

In general, we found a positive relationship between fragment area and species richness (SAR) and between fragment area and species density (D-SAR) at different grain sizes (Fig. 2). However, the D-SAR was significant for the three smaller grain sizes, but was not significant for the 225-m² grain size (Fig. 2). Most importantly, the slope of the D-SAR in the linearized power model (z) decreased linearly with log (grain size), with the slope of the D-SAR at the smallest grain sizes comparable to that of the SAR [$F_{1,2} = 128$, $P = 0.008$, linear regression of slope against log(grain size); Fig. 3].

Table 3 Correlation matrix for explanatory variables – fragment area, proximity index (PI), distance to the nearest fragment (ENN), and distance to current or historical mainland (DistM1 and DistM2, respectively) measured for 39 fragments of semi-natural vegetation in the Lachish fragmented agro-ecosystem in central Israel. All variables were \log_{10} -transformed prior to the calculation of correlation coefficients (Pearson's r). Numbers in bold represent significant correlations ($n = 39$ for all the correlation tests).

	Area	PI	ENN	DistM1
PI	0.05			
ENN	−0.16	−0.68		
DistM1	−0.02	−0.63	0.32	
DistM2	0.03	−0.87	0.44	0.71

Apart from fragment area, the only other explanatory variable that showed a significant effect on species density was distance to the mainland (DistM1) (Table 4a). Its effect on species density was significant when species density was measured using smaller grain sizes (SpD_{0.0625}, SpD₁, SpD₂₅), but significant effect of distance to the mainland was not observed for either large grain size species density (SpD₂₂₅) or species richness (SR_{fragment}) (Fig. 4). When significant, the effect of DistM1 was negative, such that fragments situated far from the mainland exhibited lower species density than those near the mainland (Table 4a). The slope of the D-SIR became flatter with increasing grain size, although this trend

was not statistically significant [$F_{1,2} = 3.07$, $P = 0.22$, linear regression of slope against $\log(\text{grain size})$; Fig. 5].

The lack of significance of the D-SAR or D-SIR at the 225-m² scale may have been a result of the smaller sample size available at this scale (14 fragments) as opposed to the larger sample sizes (20 fragments) used at the other sampling scales (Appendix S1). We tested this possibility by repeating our grain size-dependent analysis, this time eliminating from the analysis all fragments for which data were not available for all grain sizes. The results were qualitatively similar to those obtained with the full data set for the effect of area, but the effect of distance to mainland remained significant only at the smallest grain size (Table 4b). Repeating the analysis using the exponential model yielded qualitatively similar results, with significantly increasing D-SARs and significantly decreasing D-SIRs at all grain sizes except 225 m² (Appendix S3). The changes in the slopes of D-SARs and D-SIRs with grain size did not follow the same pattern as in the power model and always intensified with grain size. However, the slope of the exponential model has a different meaning than the z -value of the power model and is inherently sensitive to the measurement scale, and as such, in contrast to the slope of the power model, it cannot be used for comparison (Tjørve & Tjørve, 2008).

DISCUSSION

Overall, our review of the literature on plant studies in fragmented landscapes confirms the well-established ubiquity of

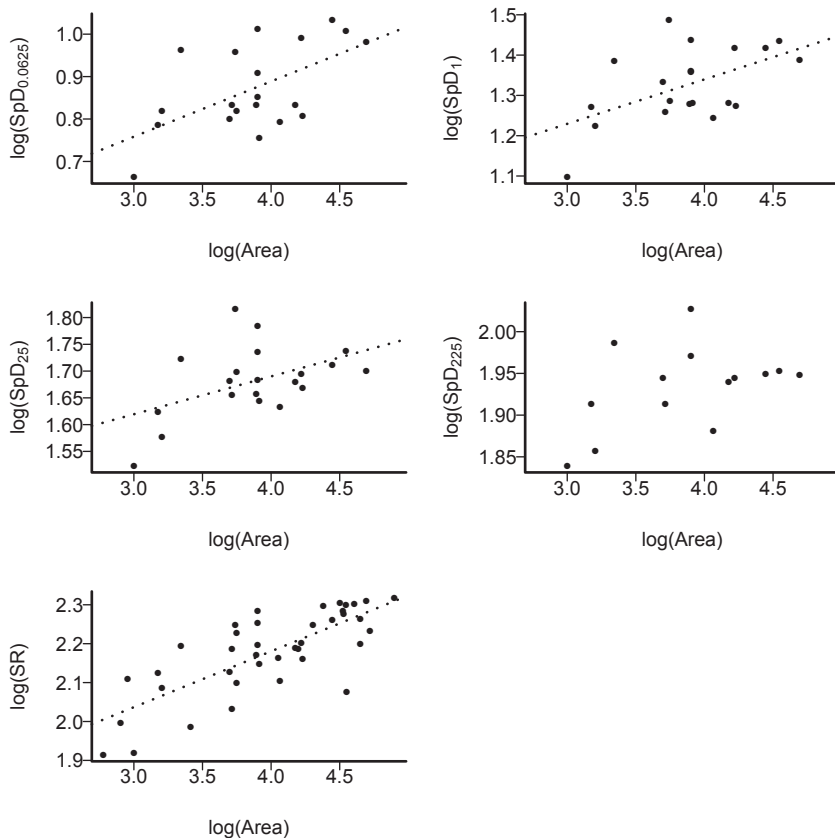


Figure 2 The relationship between plant species density (measured at different grain sizes) and fragment area (D-SAR) and between plant species richness (SR – measured at the whole fragment level) and fragment area (SAR) in the Lachish fragmented agro-ecosystem in central Israel. Trend lines were added whenever the slope was significantly different from zero ($P < 0.05$). $n = 20$ for the D-SARs at 0.0625, 1 and 25 m² grain-size, $n = 14$ for the D-SAR at the 225 m² grain size and $n = 39$ for the SAR.

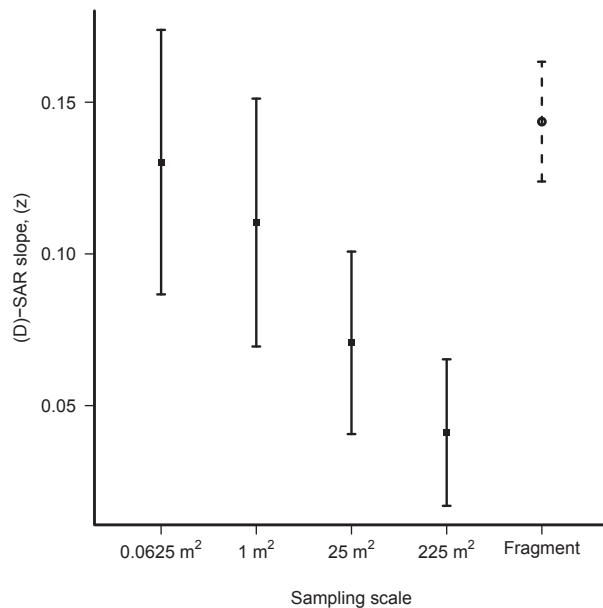


Figure 3 The slopes of species–area relationship (SAR), species density–area relationship (D-SAR) for plant species in the Lachish fragmented agro-ecosystem in central Israel, as a function of the sampling scale used. Symbols (squares and solid lines for D-SAR, circle and dashed line for SAR) represent estimates of the slope of a log–log species richness (density)–area relationship with error bars representing standard errors of the slope estimates.

SARs in general. Evidence of the other three patterns that we tested for (D-SAR, SIR and D-SIR) is weaker, suggesting that these patterns are not affected by the entire suite of mechanisms that generate SARs. In addition, the literature review suggests that, when comparing across studies, D-SARs are independent of grain size whereas D-SIRs become more pronounced with the decrease in grain size. Our case study analysis, however, clearly shows that the detection of both relationships is grain size-dependent. The relatively weak support for an increasing D-SAR found in the literature review agrees with our first prediction (P1), which is based on that by Holt (1992), who stated that species density of poorly dispersed taxa (e.g. plants) will be unrelated to fragment area. However, our detailed literature review, together with the results of our field study in a semi-arid agro-ecosystem, suggest that limited dispersal is not the only reason for the observed weak support for an increasing D-SAR in plants. Specifically, increasing D-SARs (within a study) and decreasing D-SIRs (both among and within studies) are more likely to be detected when species density is measured at smaller grain sizes. This scale-dependency of D-SARs and D-SIRs is not predicted by the habitat heterogeneity hypothesis (P2), but it is in agreement with the patterns predicted by the equilibrium hypothesis and the target area effect (P3) and with the model by Cousins & Vanhoenacker (2011), which assumes a slow response of plants to fragmentation.

Evidence for SARs and D-SARs of plants in fragmented landscapes

In contrast to the overwhelming support for the existence of an increasing SAR, evidence for an increasing D-SAR was only found in 40% of the studies that tested for it (Table 2, Appendix S2). Furthermore, the detection of an increasing D-SAR was rarely straightforward. For example, for half of the cases in which D-SARs increased significantly, detection of that change required that the data be stratified according to characteristics of landscape (e.g. land use, management practices, habitat type) and/or of species (taxonomic or ecological) prior to the analysis. Cousins (2006) tested for D-SARs in two types of landscapes that differed in terms of agricultural practice used (modern versus traditional) and found an increasing D-SAR in the former only. Kelly *et al.* (1989) stratified their data by habitat and found a significant D-SAR for only one out of five habitat types (a north-facing slope in beech forest). The variance in species density explained by the D-SAR increased when the analysis was restricted to one habitat type (dry pasture; Kohn & Walsh, 1994), or to plants that are rare at the local and landscape scales (Cagnolo *et al.*, 2009). Helm *et al.* (2006), Petit *et al.* (2004), Rodríguez-Loinaz *et al.* (2012) and Brueckmann *et al.* (2010) found increasing D-SARs only when the analysis was restricted to specialists (or indicator species) of habitat types that can only be found in the fragments. Lobel *et al.* (2006) found significant D-SARs for bryophytes and lichens but not for vascular plants, and Rodríguez-Loinaz *et al.* (2012) found stronger patterns for ferns than for vascular plants.

Overall, the literature review indicates that the D-SAR pattern in plants is often masked by sources of variation, some of which can be controlled for by stratification of the data. As such, exposing a significant D-SAR may require data stratification by habitat, thereby controlling for variation in habitat heterogeneity within the sampling unit, which may significantly affect species density (Giladi *et al.*, 2011). Stratification by species habitat affinity may enhance D-SARs by focusing on those species that are most sensitive to area-dependent extinction and isolation-dependent colonization (Cook *et al.*, 2002; Dupré & Ehrlén, 2002; Cousins & Vanhoenacker, 2011).

Evidence for SIRs and D-SIRs of plants in fragmented landscapes

The proportion of studies that found that habitat isolation significantly affects fragment-level species richness (SIR) is lower than that indicating an effect of fragment area (SAR; Table 2, Appendix S2). Similar to the observed support for D-SARs, evidence of D-SIRs was often apparent only when the species lists were stratified by species affinity to habitat (specialist versus generalists; Cook *et al.*, 2002; Petit *et al.*, 2004; Brueckmann *et al.*, 2010; Reitalu *et al.*, 2012) or by taxonomic group (Lobel *et al.*, 2006). In general, more support was found when the species analysed were specialists of

Table 4 Summary of linear models analysing the effects of fragment area, distance to mainland (DistM1), proximity index and distance to nearest neighbour (NND) on plant species density (at different grain sizes) and plant species richness in the Lachish agro-ecosystem in central Israel. Estimates and standard errors of significant coefficients are in bold. In one set of analyses (a) we used all the available data for each sampling scale [therefore, the degrees of freedom (d.f.) differ among scales]. Another set of analyses (b) was restricted to those fragments that had measurements at all sampling scales.

Response variable	Scale [m ²]	d.f. _{res}	Explanatory variables	Coefficient estimate ± SD	F	P
(a)						
Species density	0.0625	15	Area	0.138 ± 0.03	21.80	<0.001
			DistM1	−0.09 ± 0.03	10.02	0.006
			Proximity		0.08	n.s.
			NND		0.03	n.s.
Species density	1	15	Area	0.117 ± 0.032	12.21	0.003
			DistM1	−0.092 ± 0.034	7.41	0.016
			Proximity		0.034	n.s.
			NND		0.079	n.s.
Species density	25	15	Area	0.076 ± 0.027	8.08	0.01
			DistM1	0.064 ± 0.027	5.75	0.03
			Proximity		0.52	n.s.
			NND		0.08	n.s.
Species density	225	9	Area		2.73	n.s.
			DistM1		1.81	n.s.
			Proximity		0.02	n.s.
			NND		0.36	n.s.
Species richness	Fragment	34	Area	0.141 ± 0.020	49.69	<0.001
			DistM1		2.07	n.s.
			Proximity		0.18	n.s.
			NND		0.23	n.s.
(b)						
Species density	0.0625	9	Area	0.136 ± 0.03	16.99	0.003
			DistM1	−0.08 ± 0.03	5.82	0.04
			Proximity		0.33	n.s.
			NND		0.04	n.s.
Species density	1	9	Area	0.124 ± 0.038	10.44	0.01
			DistM1	−0.073 ± 0.040	3.25	0.10
			Proximity		0.18	n.s.
			NND		0.16	n.s.
Species density	25	9	Area	0.080 ± 0.027	8.98	0.015
			DistM1	−0.052 ± 0.028	3.34	0.1
			Proximity		0.68	n.s.
			NND		0.02	n.s.
Species density	225	9	Area		2.73	n.s.
			DistM1		1.81	n.s.
			Proximity		0.02	n.s.
			NND		0.36	n.s.
Species richness	Fragment	9	Area	0.158 ± 0.038	17.31	0.002
			DistM1		3.42	n.s.
			Proximity		0.018	n.s.
			NND		0.23	n.s.

n.s., not significant.

habitat types that can only be found in the fragments and/or when the analysis was restricted to ‘lower plants’ (bryophytes, lichens and ferns).

The relatively weak support found for the isolation effect on species richness in fragmented landscapes has several possible explanations (Kochy & Rydin, 1997; Watling & Donnelly, 2006). First, both the magnitude and the variance of fragment isolation in many plant studies may not be sufficient to generate statistically detectable patterns, even if such

effects exist (Watling & Donnelly, 2006; Cousins, 2009). Second, functional connectivity in many fragmented landscapes may be higher than what is initially presumed due to the permeability of the apparently ‘hostile’ matrix (Cook *et al.*, 2002; Prevedello & Vieira, 2010). Third, the slow dynamics of plants, which often lead to the accumulation of an extinction debt, tend to obscure isolation effects unless an appropriate time lag in the response of plant communities to fragmentation is taken into account (Lindborg & Eriksson,

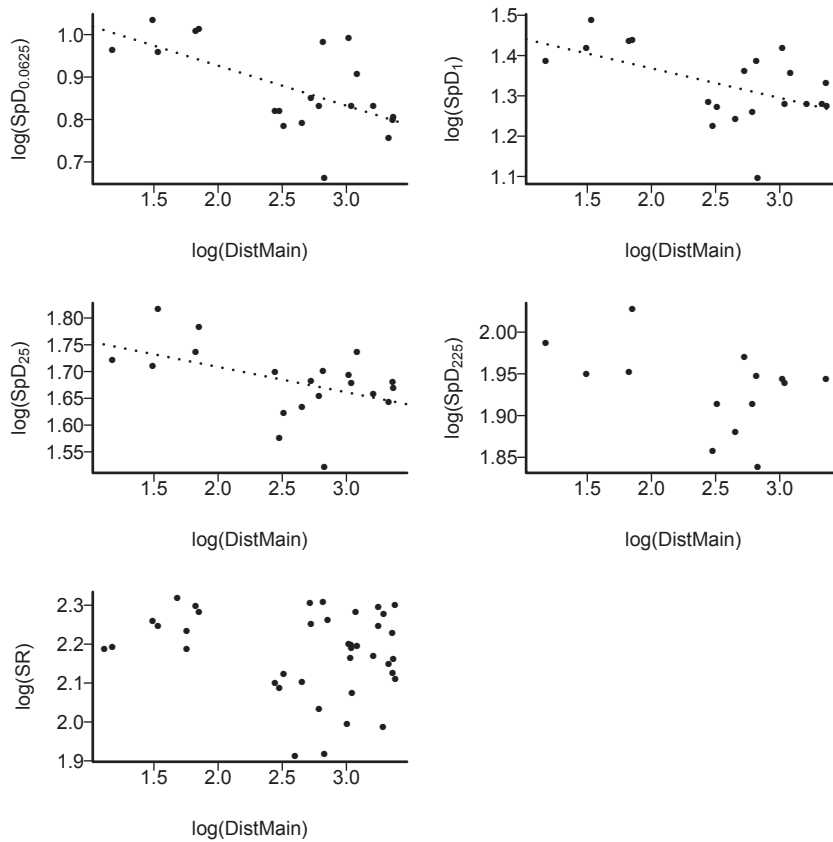


Figure 4 The relationship between plant species density (measured at different grain sizes) and fragment isolation (D-SIR) and between plant species richness (SR – measured at a whole fragment level) and fragment isolation (SIR) in the Lachish fragmented agro-ecosystem in central Israel. Fragment isolation is represented here as the edge to edge distance of a target fragment from the nearest current ‘mainland’. Trend lines were added whenever the slope was significantly different from zero ($P < 0.05$). $n = 20$ for the D-SIRs at 0.0625, 1 and 25 m² grain-size, $n = 14$ for the D-SIR at the 225 m² grain size and $n = 39$ for the SIR.

2004; Helm *et al.*, 2006; Vellend *et al.*, 2006; Cousins, 2009; Kuussaari *et al.*, 2009).

Evidence for SAR, D-SARs, SIR and D-SIRs in a fragmented semi-arid agro-ecosystem

In general, our empirical results are congruent with the two patterns predicted by island biogeography theory, e.g. decreasing species–isolation relationships (SIR/D-SIR) and increasing species–area relationships (SAR/D-SAR). Furthermore, the increasing D-SARs that we detected in our data suggest that the increasing SAR can be at least partially attributed to area-dependent colonization and/or extinction rates, as proposed by the equilibrium and the target area effect hypotheses. However, our scale-dependent sampling and analysis also suggest that the presence and/or the detection of an increasing D-SAR and a decreasing D-SIR and their slopes are grain size-dependent and become more pronounced as grain size decreases.

Contrary to the dearth of similar findings in the literature, we successfully detected increasing D-SARs and decreasing D-SIRs without stratifying the data and while using current landscape configuration rather than incorporating a time lag into the analysis. There are several possible reasons for these findings. First, the flora in the study regions is characterized by an exceptionally high (67%) percentage of annuals, which, relative to perennials, are considered more prone to extinction and respond to fragmentation more rapidly (Lindborg,

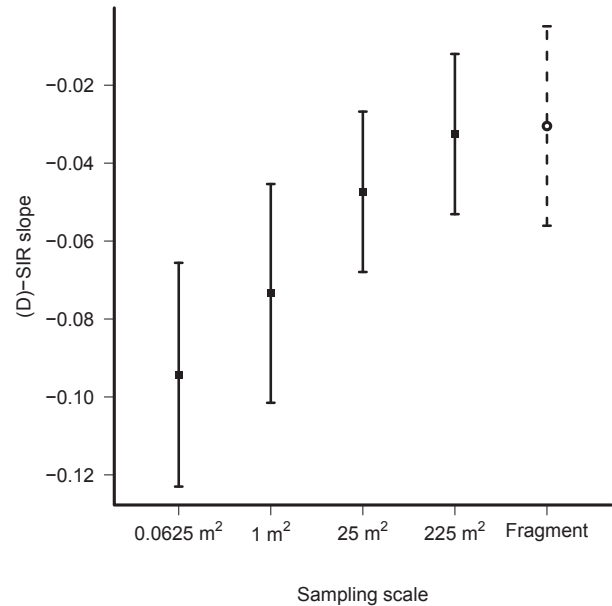


Figure 5 The slopes of species–isolation relationship (SIR), species density–isolation relationship (D-SIR) for plant species in the Lachish fragmented agro-ecosystem in central Israel, as a function of the sampling scale used. Symbols (squares and solid lines for D-SIR, circle and dashed line for SIR) represent estimates of the slopes of species richness (density)–isolation relationship with error bars representing standard errors of the slope estimates.

2007; Johansson *et al.*, 2011; cf. Adriaens *et al.*, 2006). The community dynamics in the study landscape have been shown to fit a regional model of isolated communities that are dominated by extinction events and in which colonization events are extremely rare (May *et al.*, 2013). Second, a series of historical aerial photographs of the study site indicate that the landscape's configuration, and consequently its level of habitat fragmentation, has changed little over the past 60 years (I. Giladi, unpublished). Third, our multi-scale sampling of species density increased the chance that we would detect significant D-SARs and D-SIRs at scale(s) where area and isolation effects are least obscured by other determinants of species density.

Grain size-dependent D-SARs and D-SIRs

A model suggested by Cousins & Vanhoenacker (2011) presumes that the response of plant species to fragmentation occurs faster at smaller grain sizes than at larger ones. According to the model, during the transition phase that follows fragmentation, fine grain, but not large grain, species density will be correlated with fragmentation effects. Previous analysis of our study system showed that it is currently in such a transition phase and that it carries an extinction debt that has not been fully paid yet (May *et al.*, 2013). Thus, our analysis supports the predictions of the Cousins & Vanhoenacker (2011) model. Furthermore, to the best of our knowledge, ours is the first study to demonstrate a decrease in the positive slope of the D-SAR and a mirroring attenuation of the negative slope of the D-SIR with increasing grain size. Interestingly, with the exception of the analysis by Tangney *et al.* (1990), the significance of D-SARs in the literature is scale-independent.

The lack of evidence in the literature of D-SAR grain size-dependency is intriguing given that the response of species density to other determinants, such as climatic gradient, habitat heterogeneity, management practices and distance from edge, has been shown to vary with grain size (Kiviniemi & Eriksson, 2002; Cousins *et al.*, 2007; Brudvig & Damschen, 2011; Giladi *et al.*, 2011; Thornton *et al.*, 2011). While the influence of habitat heterogeneity on species density may increase with grain size (Giladi *et al.*, 2011), the effects of the other determinants may diminish with grain size, especially when small grain size also entails habitat homogeneity (Stiles & Scheiner, 2010; Giladi *et al.*, 2011). The evidence for grain size-dependent D-SARs in the literature may be limited because most studies that tested for D-SARs used only one grain size. Indeed, only seven of the studies that we reviewed conducted grain size-dependent analyses of D-SARs, and five of these studies also investigated grain size-dependent D-SIRs. Of the seven studies that incorporated grain size-dependent analyses, three (Kiviniemi & Eriksson, 2002; Stiles & Scheiner, 2010; Brudvig & Damschen, 2011) reported insignificant D-SARs at all grain sizes. Tangney *et al.* (1990) found significant D-SARs at two grain sizes (4 m² and 10 m²).

The three other studies, which can be classified as testing scale-dependent D-SARs, actually tested D-SARs at one grain

size and then contrasted those results with another type of species–area relationship, in which the cumulative number of species from a fixed number of sampling plots within a fragment is regressed against fragment size (Lindborg & Eriksson, 2004; Öster *et al.*, 2007; Cousins & Vanhoenacker, 2011). This 'cumulative' SAR maintains equal sampling effort (i.e. total sampling area) across fragments (as a 'regular' D-SAR), but the extent of the sampling usually increases with fragment size. Although the effects of sampling effort and extent on species richness reflect different processes and thus are not interchangeable (Azovsky, 2011), cumulative 'SARs' are sometimes treated as controlling for both sampling and extent or for neither. This duality is reflected in the terminology, analysis and interpretation that different studies ascribe to these cumulative (D)-SARs. For example, relying on previous analysis showing that their cumulative sampling is sufficient to represent fragment-level species richness, Lindborg & Eriksson (2004) referred to their cumulative SAR as a 'regular' SAR, and found that both this pattern and regular D-SAR (at the 1-m² scale) were insignificant. In contrast, Öster *et al.* (2007) constructed a D-SAR (at the 1-m² scale) and two cumulative SARs (for ten 1-m² plots, total area = 10 m², and for fifty 0.01-m² subplots, total area = 0.5 m²) and referred to all of these patterns as D-SARs. They found that the cumulative (D)-SARs were both significantly increasing whereas the 'regular' D-SAR was not. Cousins & Vanhoenacker (2011) referred to a D-SAR (at the 0.25-m² scale) and a cumulative (D)-SAR as alpha and gamma diversity SARs, respectively. They found that alpha diversity was correlated with current fragment area whereas gamma diversity was correlated with historical fragment area. The placement of sampling plots for cumulative (D)-SARs is often either randomly selected, equally spaced or specifically chosen to represent various sections/habitats of a fragment. Therefore, although cumulative (D)-SARs control for total sampling area, the extent, the aggregation and the representation of habitat heterogeneity in each fragment in cumulative (D)-SARs are correlated with fragment size, and therefore, they are expected to be affected by mechanisms similar to those that generate fragment-level SARs. For that reason, interpreting the difference between cumulative (D)-SARs and D-SARs as simply a matter of scale-dependency (as, for example, by Öster *et al.*, 2007) neglects some important discrepancies between the methods that may also point to fundamental differences in the mechanisms that generate these patterns (Azovsky, 2011).

The discussion in the literature about the theoretical, ecological and statistical properties of the functional forms used to model SARs is ongoing and lively (Tjørve, 2003, 2009; Dengler, 2009; Scheiner, 2009; Triantis *et al.*, 2012). However, little effort has been devoted to delineating the functions that best describe either D-SARs or D-SIRs. In most of the studies that we reviewed, the function used to model the SAR (mainly either power or exponential) was also used to model the D-SAR. We found that the degree of support for both D-SARs and D-SIRs varied depending on the functional

form used, but we could not detect any systematic change. In our case study, both the D-SAR and the D-SIR were similarly sensitive to grain size, regardless of whether we used the power or the exponential model. Nevertheless, questions about which functional form is the most appropriate for modelling D-SARs and D-SIRs and the possibility that the dependence of these patterns on grain size varies with functional form across and within studies are still unresolved issues that require further research.

Mechanisms explaining the patterns

The variation observed in the degrees of support for the relationships we examined may reflect differences in the relative importance of the mechanisms underlying each pattern. In general, species density is often highly correlated with, and thus can be reasonably explained by, fragment-level species richness (Pärtel *et al.*, 1996). However, even when local and fragment-level species richness are highly correlated (Table 5 for this study), each may be explained by different determinants (Stiles & Scheiner, 2010; Reitalu *et al.*, 2012). In any case, the two patterns of species–isolation (SIR and D-SIR) and D-SAR are thought to be generated by a subset of the mechanisms that generate significantly increasing SARs (Hill *et al.*, 1994; Turner & Tjørve, 2005).

The analysis of D-SARs is often advocated as a test of the mechanisms associated with the equilibrium hypothesis after controlling for the effects of sampling and habitat heterogeneity (Bruun, 2000; Krauss *et al.*, 2004). Alternatively, an increasing D-SAR can be explained by the habitat heterogeneity hypothesis of SAR, which can generate an increasing D-SAR via two different pathways. First, if habitat diversity within a standardized area (e.g. sampling plot) is positively correlated with fragment area, then an increasing D-SAR may be evident. However, in our study system, habitat heterogeneity within a standardized plot (measured either at the 1, 25 or 225-m² grain sizes) is not correlated with fragment area (see Giladi *et al.*, 2011, for details). Second, D-SARs may still be found to be increasing if the diverse habitats that constitute the entire fragment contribute to species density (a spillover effect; Holt, 1992, 1993). However, it is not yet clear at which spatial scale(s) the spillover effect should be most prominent (Rosenzweig, 1995; Cook *et al.*, 2002; Kadmon & Allouche, 2007; Whittaker & Fernández-Palacios, 2007; Lundholm, 2009; Matias *et al.*, 2010; Tamme *et al.*, 2010). The contribution of the spillover effect to D-SARs is often linked with a graphical representation of parallel within-island species–area curves, the ‘elevations’ of which increase with fragment size (e.g. Cook *et al.*, 2002). Interestingly, in our study system the slope of these curves actually decreases with fragment area (Appendix S1). Furthermore, as both theoretical considerations and empirical results suggest that the effect of habitat heterogeneity on species density is expected to increase with grain size (P2) (Kadmon & Allouche, 2007; Tamme *et al.*, 2010; Giladi *et al.*, 2011, and references herein), habitat heterogeneity is unlikely to explain the

Table 5 Correlation matrix for plant species density (SpD, measured at different grain sizes given in m²) and species richness (SR) in semi-natural fragments in the Lachish agro-ecosystem in central Israel. The correlation coefficients (Pearson’s *r*) were calculated using the subset of fragments that had full sets of measurements of SR and SpD at all grain sizes (*n* = 14). All the correlation coefficients are significantly positive.

	SpD _{0.0625}	SpD ₁	SpD ₂₅	SpD ₂₂₅	SR
SpD _{0.0625}	1	0.93	0.84	0.71	0.84
SpD ₁		1	0.92	0.85	0.89
SpD ₂₅			1	0.94	0.84
SpD ₂₂₅				1	0.77
SR					1

pattern of grain size-dependency that we observed. Therefore, a grain size-dependent study of D-SARs combined with scale-sensitive quantification and/or scale-sensitive modelling of the spillover effect is needed to understand if and how the habitat heterogeneity hypothesis explains increasing and grain size-dependent D-SARs.

CONCLUSIONS

Understanding the response of biodiversity to habitat loss and fragmentation, an issue that is of immense importance for conservation, is a hotly discussed topic in the literature. The challenges created by apparent inconsistencies in the responses of plants to fragmentation were recently addressed by proposing and testing several interesting ideas that were partially successful in reconciling apparent contradictions. Among these proposed explanations are the slow response of plant communities to fragmentation (which creates an extinction debt), the partial connectivity that intervening matrices provide, and the differential responses of plant groups representing different traits. The elucidation of these issues will help to better understand and potentially predict plant response to fragmentation. Our study points to two additional criteria that should be considered. First, a clear distinction must be made between patterns that are based on species density, accumulated number of species and fragment-level species richness. Because these different patterns point to different mechanisms, a useful synthesis of our common knowledge necessitates that information concerning this distinction will be clearly presented and easy to extract from publications. Second, in using species density to study fragmentation effects, one should be aware that the results and the derived conclusion are grain size-dependent. Although a positive correlation between species density and fragment-level species richness may be common, the SAR and the D-SAR are not the same pattern, are not generated by the same mechanisms, and the detection of one cannot be inferred as evidence for the other. As our results show, the link between these patterns may be scale dependent, although the generality of this dependence can only be verified by additional studies that will examine grain size-dependent

D-SARs and D-SIRs using different functional forms within the same study system.

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REFERENCES

- Ackermann, O., Svoray, T. & Haiman, M. (2008) Nari (calcrete) outcrop contribution to ancient agricultural terraces in the Southern Shephelah, Israel: insights from digital terrain analysis and a ge archaeological field survey. *Journal of Archaeological Science*, **35**, 930–941.
- Adriaens, D., Honnay, O. & Hermy, M. (2006) No evidence of a plant extinction debt in highly fragmented calcareous grasslands in Belgium. *Biological Conservation*, **133**, 212–224.
- Azovsky, A.I. (2011) Species–area and species–sampling effort relationships: disentangling the effects. *Ecography*, **34**, 18–30.
- Brudvig, L.A. & Damschen, E.I. (2011) Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. *Ecography*, **34**, 257–266.
- Brueckmann, S.V., Krauss, J. & Steffan-Dewenter, I. (2010) Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *Journal of Applied Ecology*, **47**, 799–809.
- Bruun, H.H. (2000) Patterns of species richness in dry grassland patches in an agricultural landscape. *Ecography*, **23**, 641–650.
- Cagnolo, L., Valladares, G., Salvo, A., Cabido, M. & Zak, M. (2009) Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conservation Biology*, **23**, 1167–1175.
- Coleman, B.D. (1981) On random placement and species–area relations. *Mathematical Biosciences*, **54**, 191–215.
- Connor, E.F. & McCoy, E.D. (1979) Statistics and biology of the species–area relationship. *The American Naturalist*, **113**, 791–833.
- Connor, E.F. & McCoy, E.D. (2001) Species–area relationships. *Encyclopedia of biodiversity* (ed. by S.A. Levin), pp. 397–412. Academic Press, New York.
- Cook, W.M., Lane, K.T., Foster, B.L. & Holt, R.D. (2002) Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters*, **5**, 619–623.
- Cousins, S.A.O. (2006) Plant species richness in midfield islets and road verges – The effect of landscape fragmentation. *Biological Conservation*, **127**, 500–509.
- Cousins, S.A.O. (2009) Extinction debt in fragmented grasslands: paid or not? *Journal of Vegetation Science*, **20**, 3–7.
- Cousins, S.A.O. & Vanhoenacker, D. (2011) Detection of extinction debt depends on scale and specialisation. *Biological Conservation*, **144**, 782–787.
- Cousins, S.A.O., Ohlson, H. & Eriksson, O. (2007) Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. *Landscape Ecology*, **22**, 723–730.
- Dan, J., Yaalon, D.H., Koyumdjisky, H. & Raz, Z. (1976) *The soils of Israel*. Ministry of Agriculture, Volcani Center, Bet Dagan.
- Dengler, J. (2009) Which function describes the species–area relationship best? A review and empirical evaluation. *Journal of Biogeography*, **36**, 728–744.
- Dupré, C. & Ehrlén, J. (2002) Habitat configuration, species traits and plant distributions. *Journal of Ecology*, **90**, 796–805.
- Eriksson, O., Cousins, S.A.O. & Bruun, H.H. (2002) Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. *Journal of Vegetation Science*, **13**, 743–748.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.
- Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, **40**, 1649–1663.
- Feinbrun-Dothan, N. & Danin, A. (1991) *Analytical flora of Eretz-Israel*. Cana Publishing House, Jerusalem, Israel.
- Giladi, I., Ziv, Y., May, F. & Jeltsch, F. (2011) Scale-dependent determinants of plant species richness in a semi-arid fragmented agro-ecosystem. *Journal of Vegetation Science*, **22**, 983–996.
- Gilpin, M.E. & Diamond, J.M. (1976) Calculation of immigration and extinction curves from the species–area–distance relation. *Proceedings of the National Academy of Sciences USA*, **73**, 4130–4134.
- Goldreich, Y. (2003) *The climate of Israel: observations, research and applications*. Kluwer Academic, New York.
- Gotelli, N.J. & Graves, G.R. (1996) *Null models in ecology*. Smithsonian Institution Press, Washington, DC.
- Gray, J.S. (2000) The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *Journal of Experimental Marine Biology and Ecology*, **250**, 23–49.
- Hanski, I., Zurita, G.A., Bellocq, M.I. & Rybicki, J. (2013) Species-fragmented area relationship. *Proceedings of the National Academy of Sciences USA*, **110**, 12715–12720.
- Helm, A., Hanski, I. & Pärtel, M. (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters*, **9**, 72–77.

- Hill, J.L., Curran, P.J. & Foody, G.M. (1994) The effect of sampling on the species–area curve. *Global Ecology and Biogeography Letters*, **4**, 97–106.
- Holt, R.D. (1992) A neglected facet of island biogeography: the role of internal spatial dynamics in area effects. *Theoretical Population Biology*, **41**, 354–371.
- Holt, R.D. (1993) Ecology at the mesoscale: the influence of regional processes on local community dynamics. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 77–88. University of Chicago Press, Chicago.
- Hoyle, M. (2004) Causes of the species–area relationship by trophic level in a field-based microecosystem. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1159–1164.
- Johansson, V.A., Cousins, S.A.O. & Eriksson, E. (2011) Remnant populations and plant functional traits in abandoned semi-natural grasslands. *Folia Geobotanica*, **46**, 165–179.
- Kadmon, R. & Allouche, O. (2007) Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. *The American Naturalist*, **170**, 443–454.
- Kalkhan, M.A., Stafford, E.J. & Stohlgren, T.J. (2007) Rapid plant diversity assessment using a pixel nested plot design: a case study in Beaver Meadows, Rocky Mountain National Park, Colorado, USA. *Diversity and Distributions*, **13**, 379–388.
- Kelly, B.J., Wilson, J.B. & Mark, A.F. (1989) Causes of the species–area relation: a study of islands in Lake Manapouri, New Zealand. *Journal of Ecology*, **77**, 1021–1028.
- Kiviniemi, K. & Eriksson, E. (2002) Size-related deterioration of semi-natural grassland fragments in Sweden. *Diversity and Distribution*, **8**, 21–29.
- Kochy, M. & Rydin, H. (1997) Biogeography of vascular plants on habitat islands, peninsulas and mainlands in an east-central Swedish agricultural landscape. *Nordic Journal of Botany*, **17**, 215–223.
- Kohn, D.D. & Walsh, D.M. (1994) Plant species richness – the effect of island size and habitat diversity. *Journal of Ecology*, **82**, 367–377.
- Körner, K. & Jeltsch, F. (2008) Detecting general plant functional type responses in fragmented landscapes using spatially-explicit simulations. *Ecological Modelling*, **210**, 287–300.
- Krauss, J., Klein, A.M., Steffan-Dewenter, I. & Tscharrntke, T. (2004) Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. *Biodiversity and Conservation*, **13**, 1427–1439.
- Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Ockinger, E., Pärtel, M., Pino, J., Roda, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution*, **24**, 564–571.
- Laurance, W.F. (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation*, **141**, 1731–1744.
- Lindborg, R. (2007) Evaluating the distribution of plant life-history traits in relation to current and historical landscape configurations. *Journal of Ecology*, **95**, 555–564.
- Lindborg, R. & Eriksson, O. (2004) Historical landscape connectivity affects present plant species diversity. *Ecology*, **85**, 1840–1845.
- Lindborg, R., Helm, A., Bommarco, R., Heikkinen, R.K., Kuhn, I., Pykala, J. & Pärtel, M. (2012) Effect of habitat area and isolation on plant trait distribution in European forests and grasslands. *Ecography*, **35**, 356–363.
- Lobel, S., Dengler, J. & Hobohm, C. (2006) Species richness of vascular plants, bryophytes and lichens in dry grasslands: the effects of environment, landscape structure and competition. *Folia Geobotanica*, **41**, 377–393.
- Lomolino, M.V. (2001) The species–area relationship: new challenges for an old pattern. *Progress in Physical Geography*, **25**, 1–21.
- Lundholm, J.T. (2009) Plant species diversity and environmental heterogeneity: spatial scale and competing hypotheses. *Journal of Vegetation Science*, **20**, 377–391.
- MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. Princeton University Press, Princeton, NJ.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Matias, M.G., Underwood, A.J., Hochuli, D.F. & Coleman, R.A. (2010) Independent effects of patch size and structural complexity on diversity of benthic macroinvertebrates. *Ecology*, **91**, 1908–1915.
- May, F., Giladi, I., Ristow, M., Ziv, Y. & Jeltsch, F. (2013) Metacommunity, mainland-island system or island communities? Assessing the regional dynamics of plant communities in a fragmented landscape. *Ecography*, **36**, 842–853.
- Mazor, S. (2006) *Landscape change in the Southern Judea lowlands and the effect of patch attributes on species richness in semi-arid environment: embedding fuzzy logic in GIS*. Department of Geography and Environmental Development, Ben-Gurion University, Beer Sheva.
- McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) *FRAGSTATS: spatial pattern analysis program for categorical maps*. University of Massachusetts, Amherst, MA.
- Naveh, Z. & Dan, J. (1973) The human degradation of Mediterranean landscapes in Israel. *Mediterranean type ecosystems: origin and structure* (ed. by F. Castri and H.A. Mooney) pp. 370–390. Springer-Verlag, New York.
- Öster, M., Cousins, S.A.O. & Eriksson, O. (2007) Size and heterogeneity rather than landscape context determine plant species richness in semi-natural grasslands. *Journal of Vegetation Science*, **18**, 859–868.
- Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, **75**, 111–117.
- Petit, S., Griffiths, L., Smart, S.S., Smith, G.M., Stuart, R.C. & Wright, S.M. (2004) Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain. *Landscape Ecology*, **19**, 463–471.
- Preston, F.W. (1962) The canonical distribution of commonness and rarity: Part II. *Ecology*, **43**, 410–432.

- Prevedello, J.A. & Vieira, M.V. (2010) Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation*, **19**, 1205–1223.
- R Development Core Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reitalu, T., Purschke, O., Johansson, L.J., Hall, K., Sykes, M.T. & Prentice, H.C. (2012) Responses of grassland species richness to local and landscape factors depend on spatial scale and habitat specialization. *Journal of Vegetation Science*, **23**, 41–51.
- Rey Benayas, J.M., Colomer, M.G.S. & Levassor, C. (1999) Effects of area, environmental status and environmental variation on species richness per unit area in Mediterranean wetlands. *Journal of Vegetation Science*, **10**, 275–280.
- Rodríguez-Loinaz, G., Amazega, I. & Onaindia, M. (2012) Does forest fragmentation affect the same way all growth forms? *Journal of Environmental Management*, **94**, 125–131.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Scheiner, S.M. (2009) (2009) The terminology and use of species–area relationships: a response to Dengler. *Journal of Biogeography*, **36**, 2005–2008.
- Scheiner, S.M., Cox, S.B., Willig, M., Mittelbach, G.G., Osenberg, C. & Kaspari, M. (2000) Species richness, species–area curves and Simpson's paradox. *Evolutionary Ecology Research*, **2**, 791–802.
- Scheiner, S.M., Chiarucci, A., Fox, G.A., Helmus, M.R., McGlenn, D.J. & Willig, M.R. (2011) The underpinnings of the relationship of species richness with space and time. *Ecological Monographs*, **81**, 195–213.
- Schoereder, J.H., Galbiati, C., Ribas, C.R., Sobrinho, T.G., Sperber, C.F., DeSouza, O. & Lopes-Andrade, C. (2004) Should we use proportional sampling for species–area studies? *Journal of Biogeography*, **31**, 1219–1226.
- Stiles, A. & Scheiner, S.M. (2010) A multi-scale analysis of fragmentation effects on remnant plant species richness in Phoenix, Arizona. *Journal of Biogeography*, **37**, 1721–1729.
- Svoray, T., Mazor, S. & Pua, B. (2007) How is shrub cover related to soil moisture and patch geometry in the fragmented landscape of the Northern Negev desert? *Landscape Ecology*, **22**, 105–116.
- Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R. & Pärtel, M. (2010) Environmental heterogeneity, species diversity and co-existence at different spatial scales. *Journal of Vegetation Science*, **21**, 796–801.
- Tangney, R.S., Wilson, J.B. & Mark, A.F. (1990) Bryophyte island biogeography: a study in Lake Manapouri, New Zealand. *Oikos*, **59**, 21–26.
- Thornton, D.H., Branch, L.C. & Sunquist, M.E. (2011) The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. *Landscape Ecology*, **26**, 7–18.
- Tjørve, E. (2003) Shapes and functions of species–area curves: a review of possible models. *Journal of Biogeography*, **30**, 827–835.
- Tjørve, E. (2009) Shapes and functions of species–area curves (II): a review of new models and parameterizations. *Journal of Biogeography*, **36**, 1435–1445.
- Tjørve, E. & Tjørve, K.M.C. (2008) The species–area relationship, self-similarity, and the true meaning of the *z*-value. *Ecology*, **89**, 3528–3533.
- Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species–area relationship: biology and statistics. *Journal of Biogeography*, **39**, 215–231.
- Turner, W.R. & Tjørve, E. (2005) Scale-dependence in species–area relationships. *Ecography*, **28**, 721–730.
- Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G. & Hermy, M. (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology*, **87**, 542–548.
- Watling, J.I. & Donnelly, M.A. (2006) Fragments as islands: a synthesis of faunal responses to habitat patchiness. *Conservation Biology*, **20**, 1016–1025.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.
- Williams, C.B. (1943) Area and the number of species. *Nature*, **152**, 262–265.
- Williams, C.B. (1964) *Patterns in the balance of nature*. Academic Press, London.
- Yaacobi, G., Ziv, Y. & Rosenzweig, M.L. (2007) Effects of interactive scale-dependent variables on beetle diversity patterns in a semi-arid agricultural landscape. *Landscape Ecology*, **22**, 687–703.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of fragments sampled, their attributes, and plant species richness and species density.

Appendix S2 List of studies used in the literature review.

Appendix S3 Figures showing species–area and species–isolation relationships using an exponential model.

BIOSKETCHES

This work is part of an ongoing collaboration between the research groups of **Yaron Ziv** and **Florian Jeltsch** that combines large-scale field data and spatially explicit modelling to study plant scale-dependent biodiversity and life-history traits in a heterogeneous landscape.

Author contributions: The study was designed by I.G., F.J. and Y.Z.; I.G. and M.R. collected the data for the case study; I.G. and F.M. compiled the literature review and performed the data analysis; and I.G. wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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