



Habitat fragmentation determines diversity of annual plant communities at landscape and fine spatial scales

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Abstract

The aim of this study was to disentangle the effects of landscape configuration (i.e., fragment area, connectivity, and proximity to a busy highway) on the assembly of annual plant communities at different spatial scales. Our main hypothesis was that larger and more connected fragments would have higher species densities per plot and this may result in differences in turnover and nestedness patterns at the fine spatial scales where plants interact. Specifically, since Mediterranean annuals are known to form strong competitive hierarchies, we expected to find a nested pattern of beta diversity due to sequential species loss. The study area was a fragmented gypsum habitat in central Spain with a semiarid climate where two fragmentation drivers coexist: agricultural practices and a roadway. Larger fragments had higher species densities per plot (20 × 20 m). Nevertheless, we detected no effect on the species assembly at fine spatial scales (30 × 30 cm). However, when the fragment connectivity was high the species that appeared in poor quadrats (30 × 30 cm) comprised a subset of the species in rich quadrats. These results agree well with the establishment of strong competitive hierarchies among annual species. The distance to the highway influenced the identity of the species established in the community (i.e., species composition) at fine spatial scales, but we detected no effect on species turnover, nestedness, or species densities. The main conclusion of our study is that the effects of habitat fragmentation extend beyond the landscape scale and they determine the spatial assembly at fine spatial scales.

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Introduction

Fragmentation is considered one of the most harmful drivers of global change in plant diversity over recent decades (Tilman, May, Lehman, & Nowak 1994; Collinge 2009). A sound theoretical framework has been developed in order to

understand the effects of habitat and connectivity loss mainly at the individual (Lienert 2004; Aguilar, Ashworth, Galetto, & Aizen 2006) and population levels (Leimu, Vergeer, Angeloni, & Ouborg 2010; Matesanz, Gómez-Fernández, Alcocer, & Escudero 2015). However, the effect of fragmentation on communities appears to be much more complex because habitat fragmentation is perceived by each species in a different way depending on their dispersal capacity and other functional attributes (Santamaría et al. 2018). Consequently, the effect of fragmentation on plant species assembly

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and the resulting species composition is far from obvious and it could depend on several habitat parameters such as the amount of local habitat (Fahrig 2013), in addition to the fragment size and connectivity (Haddad et al. 2017).

Traditional agriculture usually leads to habitat fragmentation (Giladi, Ziv, May, & Jeltsch 2011; Giladi, May, Ristow, Jeltsch, & Ziv 2014). These agricultural landscapes can be crossed by longitudinal infrastructures such as busy highways. Therefore, both fragmentation drivers can exert additive, synergistic, or antagonistic effects on species diversity and species assembly by altering the properties of plant communities simultaneously. A highway may act as a physical barrier to demographic movements and genetic flow (Storfer et al. 2006), but its negative effect could be counteracted for some species due to the emergence of novel habitats at the roadsides (Hopwood 2008; García-Palacios et al. 2011; Arenas, Escudero, Mola, & Casado 2017). Furthermore, the air fluxes caused by traffic on the highway may modify current propagule movements (Bochet, García-Fayos, & Tormo 2007), thereby affecting the relative contributions of anemochorous annuals in roadside communities.

Despite the frequent spatial concurrence of multiple fragmentation drivers in most landscapes, few attempts have been made to assess their simultaneous effects on plant communities. The effects of each fragmentation driver could be scale dependent (Giladi et al. 2011, 2014) so, in this study, we employed a multi-scale spatial approach to determine the potential effects of habitat losses due to agriculture and the presence of a highway on annual plant communities growing on gypsum soils: (1) at the landscape scale, we used the landscape scale beta diversity index (LSBD, Legendre & De Caceres 2013) to evaluate the unique contribution of each sampled unit to the overall beta diversity. (2) At the fine spatial scale, we used Baselga's beta diversity index (Baselga 2010) and its partition into the turnover and nestedness components of beta diversity. The turnover component measures the replacement of some species by others at fine spatial scales, and the nestedness component measures the extent to which the species assemblages in species-poor quadrats are subsets of the species in richer ones. Mediterranean annual plant communities that occur on gypsum soils are good models for studying the assembly of plant communities for two main reasons. 1) These annual plant communities have high species densities, with around 30 species per 0.25 m² in rainy years (Luzuriaga, Sánchez, Maestre, & Escudero 2012; Luzuriaga, González, & Escudero 2015), which allows a finer and far more subtle view of the differences among species assemblages than in species poor systems. 2) Annual plant establishment restarts every year from the soil seed bank, so time lags between the moment when fragmentation occurred and the appearance of effects on community properties are shorter than for perennial communities. This allows us to be reasonably confident that the fragmentation drivers studied had enough time to exert any hypothetical effect on annual plant assemblies. The main long-lasting effects of fragmentation on annual plant communities are related to propagule

migration among fragments and the demographic stochasticity of rare species within fragments.

In this study, we investigated beyond the effects of these fragmentation parameters on species density. We aimed to understand the extent to which the landscape configuration affects community assembly at both the landscape and fine spatial scales. To address this objective, we evaluated the effects of fragment size, connectivity, and the distance to a highway on the annual plant species density, species composition, and the among- and within-fragment beta diversity. Our working hypothesis was that larger and more connected fragments would have higher species densities per unit area because of their lower population extinction risk and greater likelihood of species arrival. In addition, we expected that because connectivity affects the colonization dynamics of many species (Hanski 1999; Fahrig 2002), then it may determine species coexistence at fine spatial scales (Del Castillo 2015). Mediterranean annuals are known to form strong competitive hierarchies (Ben-Hur & Kadmon 2015; Kraft, Godoy, & Levine 2015), so we expected to find a nested pattern of beta diversity due to sequential species loss. Finally, community assembly processes are not driven exclusively by fragmentation but they may also be related to habitat quality, so we selected several variables in order to account for this local effect. Thus, we measured the potential solar radiation level, soil properties, and cover by perennials in each sampled unit, which allowed us to statistically control for local habitat conditions and to statistically exclude their effect from that potentially exerted by fragmentation.

Materials and methods

Study area

This study was conducted in a fragmented gypsum habitat in central Spain, where the habitat remnants were immersed in a cropland matrix (Fig. 1). This area had a semiarid Mediterranean climate with a mean annual rainfall of 525 mm m⁻² year⁻¹ and average annual temperature of 13.7 °C (at the nearest weather station in Belinchón, Cuenca 30T 495735X; 4433384Y). The precipitation distribution comprised major rainfall periods in late autumn and early spring, and extremely intense summer droughts. The soil was classified as typical Gypsiorthid with a gypsum content >80%. The vegetation comprised a gypsiferous shrubby community dominated by specialized gypsophytes, such as *Helianthemum squamatum* (L.) Dum.-Cours., *Lepidium subulatum* L., *Centaurea hyssopifolia* Vahl., *Gypsophila struthium* L. and the tussock-forming grass *Stipa tenacissima* L. The mean perennial plant cover in our study system was 36% (between 10% and 68%) and open areas had a well-developed biological soil crust (BSC) dominated by lichens (e.g., *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamaria lentigera* (G.H. Weber) Poelt, *Fulgensia subbracteata* (Nyl.) Poelt, and *Psora decipiens* (Hedw.) Hoffm.). In these open

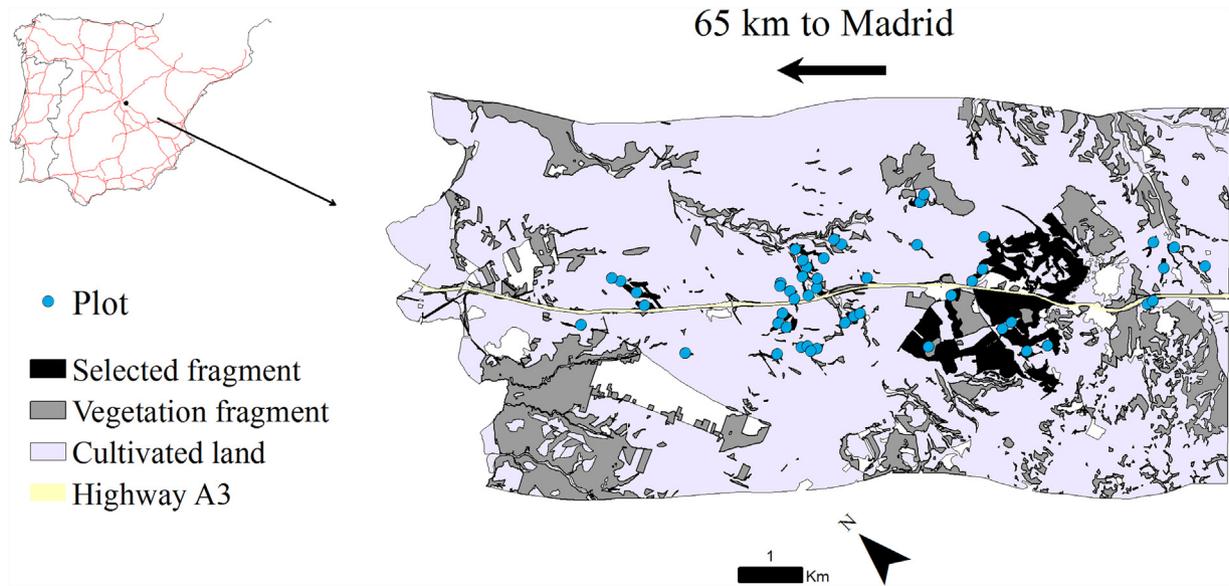


Fig. 1. Study area. Locations of the 49 fragments (in black) along a 13 km × 6 km band in the agricultural landscape on both sides of the A3 highway (Madrid–Valencia). Vegetation fragment: habitat fragments covered with gypsum vegetation. Cultivated land: agricultural matrix. Selected fragments: study sites.

areas, the BSCs coexisted with a highly diverse plant community comprising annual ephemerals, with a regional species pool of nearly 120 species and up to 30 species per 0.25 m² in rainy years (Luzuriaga et al. 2012, 2015).

This fragmented habitat was crossed by a major roadway (A3 Madrid–Valencia) built 60 years previously, which was transformed into a highway 30 years ago. Our study area comprised a zone measuring 13 km × 6 km located 60–70 km from Madrid on both sides of this highway (Fig. 1). This stretch of road had very heavy traffic (more than 35,000 vehicles per day; Ministerio de Fomento 2015) and it was 50 m wide. We selected 49 random habitat fragments embedded in an agricultural matrix at 4.3–1085 m from the highway to the border of the fragment. The areas of the selected fragments ranged from 0.05 to 102 ha.

Sampling design

In each fragment, we established a 20 m × 20 m plot within a homogenous area without evidence of recent disturbance and at least 20 m from the fragment border except for the smallest fragment where only 2–3 m could be left from the plot border to the fragment. The total cover of perennial plants was visually estimated at the quadrat level in five 2.4 m × 2.4 m subplots, one in each corner inside the plot, and the fifth in the center of the plot. The latter subplot was regularly divided into 64 quadrats measuring 30 × 30 cm. Ten of these 64 quadrats in the central subplot were selected randomly and the presence of every annual plant species was recorded during the phenological peak of the community in April 2013, which was an average season in terms of precipitation and temperature (AEMET 2016). In this study, the subplot level characteristics represented the properties

at a large spatial scale and the quadrat level characteristics represented the patterns at a fine spatial scale.

To evaluate whether the sampling design and sample size were adequate for annual communities, we employed a bootstrap function to estimate unseen species in each plot, which was implemented with the *specpool* function of the *vegan* package in R 3.4.1 (also see Palmer 1990; Colwell & Coddington 1994):

$$Ex_{sp} = Obs_{sp} + \sum_{i=1}^n (1 - p_i)^Q,$$

where Ex_{sp} is the number of species extrapolated for each subplot, Obs_{sp} is the observed species number, p_i is the frequency of species i , and Q is the number of quadrats ($Q = 10$ in this study).

According to the estimated bootstrap values, the observed number of species in each subplot, which was our operative sample for the large scale, was always above 85.6% of the extrapolated values, and we recorded more than the 90% of the extrapolated species in 35/49 subplots (see Appendix A: Table 1 in Supplementary material).

Three soil samples (5 cm in diameter and 10 cm deep) were collected per plot in the bare ground zones where the ephemeral communities thrived. The soil samples were air-dried for one month and sieved through a 2-mm mesh.

Characterization of habitat fragments

Aspect and slope values were measured in each subplot in order to calculate Gandullo's potential solar radiation coefficient (Gandullo 1974):

$$GS_1 = \text{sen } i \cdot \cos p - \cos \alpha \cdot \cos i \cdot \text{sen } p$$

$$GS_2 = \sin i \cdot \cos p + \cos \alpha \cdot \cos i \cdot \sin p,$$

where GS_1 is the sunshine calculated in north-facing sites and GS_2 is that in south-facing sites, i is the solar incidence angle (i.e., latitude 90°), p is the slope, α is the angle formed by the aspect, where 0° for GS_1 and the aspect, and 180° for GS_2 . The subplot slopes ranged from 4% to 18% and the orientation ranged from 47° to 280° . This surrogate for evapotranspiration estimates the solar radiation in clear mid-day conditions and it ranges from 0 to 1 (shade and maximum sunshine, respectively). The fragment size and minimum distance to the highway were measured using aerial photographs and with *Conefor* software (Saura & Torné 2009). To quantify the connectivity of each fragment, we used a proximity index that considers the number of surrounding fragments weighted by their distance to the target fragment (Tremlová & Münzbergová 2007; Matesanz et al. 2015):

$$C_j = \log_{10} \sum_{z=1}^n A_z / d_{jz}^2, j \neq z,$$

where C_j is the connectivity of fragment j , z is the total number of fragments around the target fragment j within a 500-m buffer zone because the annual plant species rarely had primary dispersal events beyond that distance in our study system (Luzuriaga et al. in prep.), A_z is the area of fragment z , and d_{jz} is the minimum edge-to-edge distance between fragment j and z . Negative values of C_j were changed to zero. Connectivity was calculated for the 49 selected fragments.

Soil properties

Six soil properties were evaluated in each subplot. Total organic carbon (C), total nitrogen (N), total phosphorus (P), and potassium (K) comprised “slow variables” (sensu Reynolds et al. 2007), which are related to the primary productivity and soil resource stocks (see Maestre et al. 2012). In addition, two soil enzyme activities related to the C (β -glucosidase) and phosphorus (phosphatase) cycles were measured as estimates of “rapid variables” (Reynolds et al. 2007), which are highly dependent on the current soil microbial diversity and functionality (see Appendix B for more details). We calculated the z-scores for the six soil parameters at the plot scale and we then averaged the z-scores for all the variables to obtain a multifunctionality index as a surrogate of soil productivity for each subplot (Maestre et al. 2012).

Species density and beta diversity measures of the annual plant community

The annual species density was calculated at two spatial scales. The species density per quadrat was the number of species recorded at the fine scale (30×30 cm). The species density per subplot was the cumulative number of species in the 10 quadrats surveyed (0.9 m^2).

Beta diversity among subplots (landscape spatial scale)

The landscape level beta diversity was calculated using the abundance-based Sorensen index with the *beta.div* function in the *betapart* package in R. This index represents the contribution of each subplot to Landscape Scale Beta Diversity (LSBD), thereby estimating the uniqueness of each subplot in terms of the species composition and it ranges from 0 to 1 (Legendre & De Cáceres 2013). The null hypothesis that species were randomly distributed among quadrats in each subplot was tested by using random permutations with fixed species abundances for each quadrat.

Beta diversity within subplots (fine spatial scale)

We estimated fine spatial scale beta diversity by computing Baselga's beta diversity (Baselga 2010) with the *beta.multi* function in the *betapart* package (Baselga 2013) in R 3.4.1. Total beta diversity within subplots was partitioned into its two additive components: species turnover and nestedness. Turnover was the replacement of some species by others from quadrat to quadrat within a subplot, and nestedness occurred when species assemblages of species-poor quadrats were subsets of the species present in richer quadrats.

Statistical analyses

We employed a generalized linear mixed model (GLMM) to analyze species density at the quadrat scale. In this case, subplot was considered a random factor with quadrats nested within subplot in order to account for the lack of independence of the data. Generalized linear models (GLMs) were used to analyze the diversity estimates at the subplot level. The dependent variables for the GLMs were species density per subplot, LSBD, and Baselga's turnover and nestedness components of beta diversity within subplots (Baselga 2010). We tested the correlations among the explanatory variables to avoid multicollinearity and six uncorrelated predictors were employed as fixed variables to build the GLMs: distance to the highway, fragment size, fragment connectivity, sunshine index, edaphic multifunctionality, and perennial plant cover. The best error distribution and link functions adjusted for each model are shown in Table 1.

We performed permutational multivariate analysis of variance (PERMANOVA) to evaluate differences in species compositions among subplots and among quadrats (Anderson & Willis 2003). Species frequency data were square-root transformed at the subplot scale in order to minimize the effects of dominant species. At the quadrat scale, the species data comprised presence/absence values, and thus transformation was not required. The Bray–Curtis index was used to construct the similarity matrices. Six independent descriptors of habitat fragments were used (i.e., distance to the highway, fragment area, fragment connectivity, sunshine index, edaphic multifunctionality, and perennial plant cover) and they were standardized before performing the PERMANOVA

Table 1. Results obtained using the generalized linear mixed model (GLMM) for species density at the quadrat scale (30 × 30 cm) and with the generalized linear models (GLMs) to test the effects of distance to the highway, fragment area, connectivity, sunshine intensity, edaphic multifunctionality, and perennial plant cover on the species density per plot (20 × 20 m). Among-fragment beta diversity, and within-fragment beta diversity in terms of its turnover and nestedness components are shown. The likelihood ratio tests and associated Chi-square based *p*-values are shown. Error distributions (Distr.) and link functions assumed in each model are indicated. N: normal. Id.: identity link function. Log: logarithmic link function. The signs of the significant coefficients are shown. LSBD: landscape scale beta diversity as the contribution of each plot to the landscape beta diversity (*sensu* Legendre & De Cáceres 2013).

	Species density		Among-fragment beta diversity	Within-fragment beta diversity	
	Quadrat scale	Plot scale	LSBD	Turnover	Nestedness
Distr.	Poisson	Poisson	<i>N</i>	<i>N</i>	<i>N</i>
Link	Log	Log	<i>Id</i>	<i>Id</i>	<i>Id</i>
Distance	2.0	0.02	0.3	1.0	0.1
Fragment area	1.5	+4.0*	0.1	1.7	0.25
Connectivity	−6.4*	−4.8*	+9.3**	3.6	+5.4*
Sunshine	−8.8**	−10.3**	2.4	1.5	+6.5*
Multifunctionality	+7.9**	+7.6**	0.5	−4.3*	0.6
Perennials	0.1	2.6	0.3	2.4	1.1

* 0.01 < *p* < 0.05.

** 0.001 < *p* < 0.01.

analyses with 999 permutations. Analyses were performed using the *vegan* statistical package in R 3.4.1.

Results

Species composition and diversity

We recorded 99 annual plant species (see Appendix A: Table 2 in Supplementary material). The mean species density per subplot was 29.3 (±6.1 SD per 0.9 m², cumulative value for the 10 quadrats) ranging from 16 to 41 species. The species density per quadrat (0.09 m²) ranged from 1 to 28 species with a mean of 12.7 species (±4.3 SD). In larger fragments, we found higher species density per subplot and there was less species density in more connected fragments, both per subplot and per quadrat, than that in more isolated ones (Table 1). The sunshine index was negatively related to species density at both spatial scales. The habitat productivity estimated as the edaphic multifunctionality index was related to an increase in the species number at the quadrat and subplot scales. Fragment area and connectivity affected the species composition at both the subplot and quadrat scales (Fig. 2, Table 2), but distance to the highway only had a significant effect on the species composition at the quadrat scale.

Beta diversity among subplots (landscape scale)

LSBD had a limited range of values (from 0 to 0.1) and it was only significantly different from random in 6/49 subplots, and thus most subplots did not make a unique contribution to the overall species density. Nevertheless, the low variability among subplots indicated a significant relationship with connectivity. In particular, the subplots made higher contributions to LSBD in more connected fragments, i.e., the subplot

Table 2. PERMANOVA analysis results for the species composition at the plot (20 × 20 m) and quadrat (30 × 30 cm) scales. The plot species composition was square root-transformed and explanatory matrices were standardized. Quadrats were nested in the plot for the quadrat scale models. Type III sums of squares were estimated.

Source	Quadrat F-model	Plot F-model
Distance	6.3***	1.0
Connectivity	16.7***	2.8**
Fragment area	10.1***	1.9*
Sunshine	10.8***	1.6
Multifunctionality	26.3***	4.1***
Perennials	2.1*	1.8*

contributed more unique species to the overall species density in the fragments that were more connected (Table 1).

Beta diversity within subplots (fine scale)

Nestedness increased in subplots of more connected fragments, i.e., the species that appeared in poor quadrats comprised a subset of the species in rich quadrats when the connectivity was high (Table 1). In addition, the nestedness increased under high sunshine conditions (Table 1). The species assemblies were more similar from quadrat to quadrat in high habitat quality fragments than those in low habitat quality fragments (i.e., a lower turnover of species was related to higher multifunctionality) (Table 1).

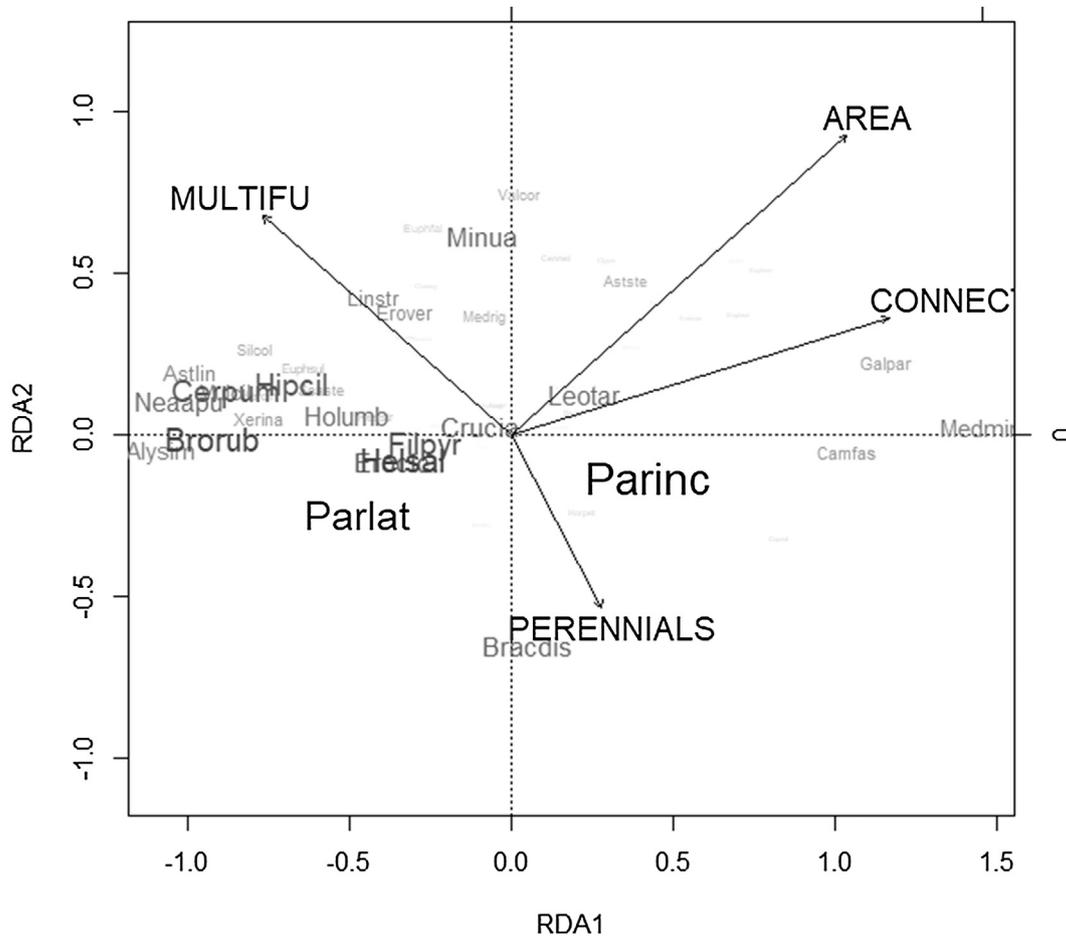


Fig. 2. RDA biplot with the 58 species that appeared in more than four plots. Only the 20 most abundant species are shown in this figure. Species data were square root-transformed and explanatory variables were standardized. The size of each species name is proportional to its relative abundance. See Appendix A: Table 2 in Supplementary material for abbreviations of species names. Explanatory variables with significant effects on species composition are shown ($p < 0.05$; see Table 2). CONNEC: connectivity index. MULTIFU: Multifunctionality index. PERENNIALS: perennial plant cover. AREA: fragment size.

Discussion

As hypothesized, fragmentation affected the assembly of ephemeral plant communities. In particular, connectivity affected plant assembly at the fine spatial scales where plant-to-plant interactions occur, at least in an average climatic year. We found that in more connected fragments, the annual plants that assembled in species-poor quadrats comprised a subset of those in the species-rich quadrats. This fine spatial pattern may conform well to processes related to the strong competitive hierarchies that operate among annual plant species in semiarid systems. These findings support our hypothesis and the results obtained by Ben-Hur and Kadmon (2015) who showed that 25 species of annual plants in Mediterranean systems formed a clear hierarchy in terms of their competitive ability. It should be noted that strong competitive hierarchies may explain why the species density per subplot was lower in isolated fragments than that in more connected fragments, which most species are likely to colonize, i.e., stronger competitive hierarchies are likely to form

in more connected fragments, thereby resulting in the local competitive exclusion of rare species. Nevertheless, we cannot exclude the possibility that the greater plant abundance in more connected fragments might have resulted in the nested patterns detected simply because of sampling effects.

The species densities per subplot were greater in larger fragments, but the annual plant communities did not differ significantly in terms of their beta diversity at the landscape or fine spatial scales. These results agree with those obtained in previous studies of perennial plant communities in semiarid systems (Pueyo, Alados, Barrantes, Komac, & Rietkerk 2008; Giladi et al. 2011, 2014). Annual species may be able to maintain viable populations in a wide range of fragment sizes (from 0.05 to 102 ha in our study) due to the small plant size of most species (<15 cm height), which ensures that a sufficiently large carrying capacity is present to sustain viable populations even in the smallest fragments. In addition, most annual species in semiarid environments form persistent soil seed banks (Caballero, Olano, Loidi, & Escudero 2008; Martínez-Duro, Luzuriaga, Ferrandis, Escudero, &

Herranz 2012; Peralta, Sánchez, Luzuriaga, & Escudero 2016), which together with specific environmental germination cues (Sánchez, Luzuriaga, Peralta, & Escudero 2014) may allow annual species to reduce the risk of failure during establishment in unfavorable conditions (Piessens, Honnay, Nackaerts, & Hermy 2004).

We detected a clear effect of the distance to the highway on the annual plant species composition at fine spatial scales, but there were no effects on the beta diversity or the species density. Some previous studies have connected this lack of effects on diversity with time lags in the appearance of these effects, i.e., the so-called “extinction debt” (Tilman et al. 1994). This effect has usually been detected in perennial plant communities (Ewers & Didham 2006; Helm, Hanski, & Partel 2006) and the time lags have been estimated at around 50 to 90 years until the communities reach a dynamic equilibrium (Renjifo 1999). However, annual plant communities complete their life-cycle within a year, so we can assume that the extinction debt would be negligible after 60 years since the construction of the highway. Thus, the effect of this highway on the annual plant communities involved the establishment of different species in the surroundings of the highway at fine spatial scales. These results suggest that high density traffic movements create air flows parallel to the highway, which is known as the “the wind tunnel effect,” and they may have modified the relative contributions of species with anemochorous fruit/seed traits in the vicinity of the highway.

In summary, we demonstrated that the effects of habitat fragmentation on diversity in terms of species density, turnover, and nestedness extended to the landscape scale but also to fine spatial scales. We showed that the connectivity among fragments determined the species assembly at the fine spatial scales where annual plants coexist. We suggest that more connected fragments allowed the arrival of more annual plants, which may have resulted in stronger competitive hierarchies forming among species, and finally leading to a reduction in the species densities per plot. Our results suggest that evaluating habitat fragmentation at different spatial scales may provide the insights needed to obtain a global perspective on the effects of fragmentation on diversity (Giladi et al. 2011, 2014; Del Castillo 2015). Similar to Fahrig (2017), we showed that greater isolation among fragments did not necessarily decrease the species density per area, at least within the range of connectivity values observed in our study area; indeed, we found greater species densities in the subplots of more isolated fragments. However, isolation had a meaningful effect on the structure of the community at fine spatial scales, and the distance to the highway determined the identity of the species that established in the final assemblies. The ephemeral communities in this semiarid region are priority habitats in the EU context and they give shelter to some rare species, and thus we consider that the maintenance of well-conserved fragments is of greater importance in terms of biological conservation. This is much more relevant than the effects of fragmentation drivers per se (agricultural habi-

tat destruction and highway use), at least within the range of connectivity values measured in our study.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.baae.2018.03.008>.

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