Species-area relationships emerge from multiple coexistence mechanisms

David García-Callejas[1,2,*], Ignasi Bartomeus[1], and Oscar Godoy[2]

[1]Estación Biologica de Doñana (EBD-CSIC), Seville, Spain.
[2]Departamento de Biología, Instituto Universitario de Ciencias del Mar (INMAR),Universidad de Cádiz, E-11510, Puerto Real, Spain.
[*]correspondence: david.garcia.callejas@gmail.com

The increase of species richness with area is a universal phenomenon on Earth. However, this observation contrasts with our poor understanding of how these species-area relationships (SARs) emerge from the collective effects of area, spatial heterogeneity, and local interactions. By combining a structuralist approach with five years of empirical observations in a highly-diverse grassland, we show that, contrary to expectations, spatial heterogeneity plays a little role in the accumulation of species richness with area in our system. Instead, as we increase the sampled area more species combinations are realized, and they coexist mainly due to direct pairwise interactions rather than by changes in single-species dominance or by indirect interactions. We also identify a small set of transient species with small population sizes that are consistently found across spatial scales. These findings empirically support the importance of the architecture of species interactions together with demographic stochasticity for driving SARs.

Introduction

One of the few general patterns observed in nature is the positive relationship between species richness and spatial extent, formalized as the species-area relationship (SAR) (Arrhenius, 1921; Rosenzweig, 1995). The universality of these positive relationships and their canonical form across taxa and habitats suggest that there are common processes shaping the spatial distribution of biodiversity (Chase *et al.*, 2019). After almost a century of studies on SARs since the first formalizations by Arrhenius Arrhenius (1921) and Gleason Gleason (1922), different branches in ecology and biogeography have explored several specific mechanisms potentially shaping SARs (e.g. niche differentiation, colonization-competition trade-offs, dispersal limitation). These deterministic processes overall maintain species with different environmental niches thanks to the increase in environmental heterogeneity with spatial extent (Connor & McCoy, 1979; Liu *et al.*, 2020; Shen *et al.*, 2009). Likewise, SARs are modulated by the simple fact that larger areas harbor higher species richness and population densities, or larger areas have by definition a higher probability of receiving immigrants by dispersal or stochastic events (Lomolino, 2001). The relative importance of deterministic processes and stochastic/sampling events in driving SARs has been explored in different contexts with contrasting results (Ben-Hur & Kadmon, 2020; Chase *et al.*, 2019; Gooriah & Chase, 2020). Despite these recent efforts, we still poorly understand how SARs emerge in a more general way from integrating the collective effects from multiple deterministic processes and stochastic factors.

A straightforward way to make solid progress into this aim would be to explicitly account for each of all potential deterministic and stochastic sources of SARs. However, such an approach is so far lacking due to theoretical and practical reasons. As an alternative, it has been recently suggested that this integration can be summarized by understanding how variation in local patterns of species coexistence across scales determine the shape of SARs (Hart *et al.*, 2017). The underlying argument is that multiple deterministic processes and stochastic events jointly modulate the spatial location and relative abundance of species across space, through their influence on species interactions and coexistence patterns. Although there are multiple available methods to study coexistence patterns, we focus on a structuralist approach because it provides theory and associated toolboxes that unify the deterministic nature of ecological processes and the intrinsic variability of real-word systems (Saavedra *et al.*, 2020; Song *et al.*, 2020). Specifically, we define coexistence as the ability of two or more species to persist (i.e. maintain positive abundances in the long term) within ecological communities despite showing contrasting population dynamics. Following a structuralist approach, this coexistence condition is met when the architecture of species interactions creates a domain of opportunities for species to coexist (i.e. feasibility domain) that is able to accommodate differences in their intrinsic growth rates (Godoy *et al.*, 2018; Saavedra *et al.*, 2017). In multispecies communities, intra and interspecific (both direct and indirect) interactions can increase or decrease the size of the feasibility domain with the general prediction that the larger this domain is, the larger the probability of persistence of individual species and of the entire community. The empirical study of SARs through the lens of a structuralist approach provides a platform for quantifying two assessments that remain unexplored. First, it allows quanti-

fying the relative importance of passive sampling and stochastic events coming from increases in spatial extent versus environmental heterogeneity in shaping the increase of the number of coexisting species with area. Second, the possibility to distinguish which species coexist at increasing spatial scales from those which do not (i.e. transient species defined as sink species with a viable population source elsewhere) allows exploring the role of sink-source dynamics for shaping SARs.

Here, we experimentally assess the effects of species persistence on driving SARs (Fig. 1). We specifically ask three questions: 1) How important are increases in environmental heterogeneity versus increases in the spatial extent for determining species persistence? 2) What is the relative contribution of direct and indirect interactions to species persistence across spatial scales? and finally, 3) How do SARs emerge from the balance between persisting and transient species? To address these questions, we performed detailed field observations of fecundity and neighborhood composition of 9130 individuals for 19 annual plant species during 5 years (2015-2019) and across different spatial scales (9 plots of 72 m^2, giving a total sampling area of 650 m^2) in a grassland system in which we know that the performance and spatial location of these annual plant species is strongly affected by a marked gradient in soil salinity (Lanuza *et al.*, 2018). With this empirical information, we estimated the strength of species interactions (both competition and facilitation) and their intrinsic ability to grow following mathematical models that describe reasonably well the population dynamics of interacting species. Finally, we assessed which species are predicted to persist, that is, which species or combinations of species (if any) possess a configuration of interactions that accommodate differences in their intrinsic growth rates. To answer the first question, model parameterization and predictions of species persistence were done for two contrasted environmental scenarios, namely homogeneous or heterogeneous environments, by allowing models to account for spatial variability at the plot scale. To answer the second question, we computed which is the simplest community (defined by the number of species) allowing the persistence of each individual species. To answer the third question, SARs were built by accounting for the number of species predicted to persist across spatial scales (see Fig. 1 for a schematic diagram).

Materials and Methods

Study system

We conducted our study in Caracoles Ranch, located in Doñana National Park (SW Spain 37º 04´ N, 6º 18´ W). The study area has a Mediterranean climate with mild winters and an average 50-year annual rainfall of 550-570 mm. Vegetation is dominated by annual grassland species, with no perennial species present. A subtle topographic gradient (slope 0.16%) is enough to generate vernal pools at the lower border of the ranch from winter (November-January) to spring (March-May), while upper parts do not get flooded except in exceptionally wet seasons. In our study, an extreme flooding event occurred during the growing season of 2018. A strong soil salinity-humidity gradient is structured along this topographic gradient.

In September 2014, we established nine plots of 8.5 m * 8.5 m along a 1 km * 200 m area. Three of these nine plots were located in the upper part of the topographic gradient, three at the middle, and the last three at the lower part. The average distance between these three locations was 300 m and the average distance between plots within each location was 30 m (minimum distance 20 m). In addition, each plot was divided into 36 subplots of 1 m * 1 m with aisles of 0.5 m in between to allow access to subplots where measurements were taken (total of 324 subplots). This spatial design was established to parameterize population models including an intrinsic fecundity component and the effect of intra and interspecific pairwise interactions. Specifically, the core of the observations involved measuring, for each focal individual, per germinant viable seed production as a function of the number and identity of neighbors within a radius of 7.5 cm including individuals of the same species. This radius is a standard distance used in previous studies to measure competitive interactions among annual plant species (Levine & HilleRisLambers, 2009; Mayfield & Stouffer, 2017), and has been validated to capture the outcome of competition interactions at larger scales (1 m^2) under locally homogeneous environmental conditions (Godoy & Levine, 2014). From November 2014 to September 2019, we sampled 19 species present in the study area each year and obtained independent estimates of seed germination rate (see Lanuza *et al.* (2018) for details on obtaining germination rates). We sampled one individual per subplot for widespread species and several individuals per subplot when species were rare (max. 324 individuals/species). These 19 species belong to disparate taxonomic families and exhibit contrasted functional profiles along the growing season (S1). The earliest species with small size and open flowers such as *Chamaemulum fuscatum* (Asteraceae) peak at beginning of the growing season (February) while late species with succulent leaves such as *Salsola soda* (Amaranthaceae) and *Suaeda splendens* (Amaranthaceae) grow during summer and peak at the end of the growing season (September-October). All these species represent up to 99% of plant cover in the study area.

Estimating species interaction networks and intrinsic growth rates

We estimated the effect of nearby individuals on individual fecundity via a Ricker model of population dynamics, which allowed us to estimate the strength of positive or negative interactions among pair of species, and therefore, to build a matrix of interactions among species. This approach has recently been shown to have several advantages compared to other formulations (Mayfield &

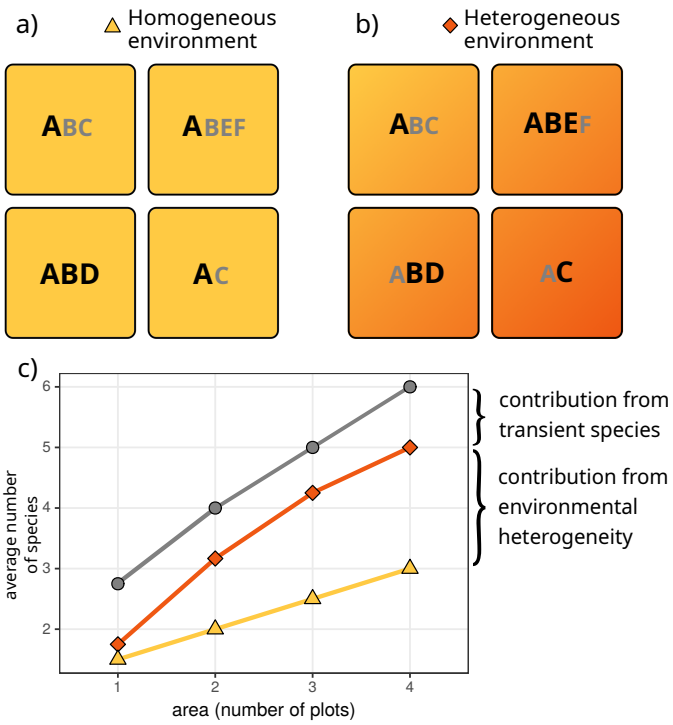

Fig. 1. A schematic dissection of Species Area Relationships (SARs) and their relation to species persistence in homogeneous and heterogeneous environments. In the upper panels (a and b), each square represents a sampling area. In a) we assume species experience the environment in a homogeneous way, meaning that their intrinsic growth rates and direct and indirect interactions do not change across squares. In b) we consider that species are sensitive to changes in environmental heterogeneity to the extent that it promotes variation in both intrinsic growth rates and their network of interactions across the sampling area. Considering both scenarios allow testing the additional contribution of environmental heterogeneity to the increase in the number of coexisting species with area compared to the homogeneous environment that promote species coexistence by increasing their chances to interact (see panel c, differences between yellow and orange curves). The condition to know which species coexist (represented by bold letters) according to a structural stability approach is met when species interaction strengths are able to accommodate differences in their intrinsic growth rates (Saavedra *et al.*, 2017). The classical coexistence example occurs when niche differences overcome competitive differences between pairs of species (Chesson, 200). On the other hand, grey letters in panels a and b represent transient species. These are species not predicted to persist at any sampled area, yet they are present mostly likely due to dispersion from external areas. Accounting for these transient species is important as it serves to quantify the importance of sink-source dynamics in the community, which can be done by comparing the increase of the total number of species found (grey line, panel c) with those stably coexisting under heterogeneous environments (red line, panel c). Finally, note that species-area relationships are built by taking the average of all combinations of plots for a given area (i.e. a Type B relationship (Scheiner *et al.*, 2011), thus resulting in non-integer values at intermediate areas.

Stouffer, 2017). For example, this model implemented using a negative-binomial distribution for individual fecundities is more flexible in terms of modelling overdispersion than a Poisson model, while maintaining predictions as positive integers. The model is of the form:

$$F_{i,t} = \lambda_i e^{-(\sum \alpha_{i,j} N_j)} \quad \textbf{(1)}$$

where λ_i is the number of seeds produced by species i in the absence of interactions, $\alpha_{i,j}$ is the per-capita effect of species j over species i (which can be positive or negative, thus allowing both competitive and facilitative effects), and N_j is the number of individuals of species j within 7.5 cm of the focal individual at timestep t. We fitted this model to the empirical data using Bayesian multilevel models with a negative binomial distribution (Mayfield & Stouffer, 2017). For model fitting, we used non-informative priors with MCMC settings of 5000 iterations (of which 2500 were warm-up) and 6 chains. The model was implemented using the *brms* R package (Bürkner, 2017). The effect of changes in environmental conditions on species persistence can be phenomenologically evaluated by allowing models to vary in their estimates of species´ intrinsic growth rates and the reorganization of species interactions (Cenci *et al.*, 2018). In our case, to evaluate the effect of environmental heterogeneity on species persistence (Question 1), we developed two complementary models. In both cases, we modelled the observed viable seed production per individual as a function of the identity and abundance of neighboring species. For the model assuming that plant species interact within a homogeneous environment across plots, we pooled together observations from the whole study area, and allowed the intercept and slope of the relationships to vary across years by including year as a random effect. Thus, the λ_i and $\alpha_{i,j}$ values in Eq. 1 vary across years, but are homogeneous for the whole study area. We used the means from the obtained posterior distributions as estimates in the sub-

sequent analyses. For the model that assumes that heterogeneous environments across space and time impact species population dynamics, we included an additional crossed random effect 'plot', thus obtaining spatially and temporally differentiated seed production in the absence of neighbors (λ_i) and interaction coefficients ($\alpha_{i,j}$) Importantly, our modelling approach does not evaluate the magnitude per se of the spatiotemporal variability in our system. It rather evaluates the response of plant species to changes in environmental conditions through their effects on vital rates and interaction coefficients (see Bimler *et al.* (2018); Hallett *et al.* (2019); Matías *et al.* (2018)). In the following, we refer to these two models as "homogeneous parameterization" and "heterogeneous parameterization", respectively (Fig. 1).

Analyzing species persistence

To analyze which species are predicted to persist and coexist with others in our system, we built communities based on the species' spatial location. At the smallest spatial scale, given a community of S species observed in the field in a given plot and a given year, we calculated the persistence of each species within every community combination, from 2 species to S. Thus we obtained, for each species, plot, and year, two estimates of persistence, one from the homogeneous and another from the heterogeneous parameterization. To scale-up our predictions of species persistence at increasingly large areas, we aggregated species composition and persistence patterns from increasing numbers of plots. We consistently evaluated species persistence using a structuralist approach because prior work has shown it is compatible with the model used to estimate interaction coefficients (Eq. 1) (Saavedra *et al.*, 2017). Specifically, for a given community we first used the strength of sign of intra- and interspecific interactions to compute its feasibility domain. Broadly speaking the feasibility domain is the structural analog of niche differences, and it represents the possible range of intrinsic species growth rates compatible with the persistence of individual species and of the entire community (Saavedra *et al.*, 2017). Indeed, the larger the feasibility domain, the larger the likelihood of species to persist. Yet, computing the feasibility domain does not tell us which species can persist. To obtain such information, we need to check whether the vector containing the observed differences intrinsic growth rates between species fits within the limits of the feasibility domain. If so, then all species are predicted to coexist. If not, then one or more particular species is predicted to be excluded (see Saavedra *et al.* (2017) for a graphical representation).

This methodology further allowed us to dissect which specific configuration of species interactions is behind species persistence in our system (Question 2), among three possibilities: first, a given species may be able to persist by itself, and hinder the long-term persistence of neighboring species (category dominant). Second, pairs of species may be able to coexist through direct interactions (category pairwise coexistence). The classic example of pairwise coexistence is when the stabilizing effect of niche differences that arise because intraspecific competition exceeds interspecific competition overcome fitness differences (Chesson, 2000). Lastly, species may only be able to coexist in more complex communities (category multispecies coexistence) (Allesina & Levine, 2011) thanks to the effect of indirect interactions on increasing the feasible domain of the community (Saavedra *et al.*, 2017). A classic example of multispecies coexistence is a rock-paper-scissors configuration in which the three species coexist because no species is best at competing for all resources (Laird & Schamp, 2015; Soliveres *et al.*, 2015). Because species may be predicted to persist under different configurations in a given community, we assigned their persistence category to the simplest community configuration. For instance, if we predicted that a three-species combination coexists as well as each of the three pairs separately, we assigned these species to the pairwise coexistence category (Gallien *et al.*, 2017; Godoy *et al.*, 2017).

Finally, if a species is not predicted to persist but it is observed in the system, we classify it as naturally transient, that is, it will tend to become locally extinct no matter its surrounding community. In order to ascertain our classification of species as transient, we further analyzed whether these species shared ecological traits known to be common to transient species. In particular, a pervasive characteristic of transient species is their comparatively small population sizes. We explored the relationship between our classification as transient and species abundance through a logistic regression with logit link (Table S3).

Species-area and coexistence-area relationships

To answer question 3, we obtained standard species-area relationships (SARs) for each year, by calculating the average diversity observed when moving from 1 plot (72 m^2) to the 9 plots (650 m^2) of our system. In the classification of SAR types proposed by Scheiner *et al.* (2011), the curves from our system are thus of type III-B, i.e. plots in a non-contiguous grid, with diversity values obtained using averages from all possible combinations of plots. Likewise, the yearly coexistence-area relationships (CARs) were built taking the average number of coexisting species in each combination from 1 to 9 plots. In this case, a species was taken to persist in a given area if it was persisting alone or if it was part of at least one coexisting community within that area. We obtained CARs for the two parameterizations, i.e. assuming homogeneous interaction coefficients and individual fecundity throughout the study area, or explicitly including spatial variability in these terms. We fitted the coexistence-area relationships from Fig. 2 to power-law functions and obtained their associated parameters (Table S2) using the "mmSAR" package in R (Guilhaumon *et al.*, 2010). In the last step of the analyses, to evaluate the role of species identity in driving these empirical fits

of CARs, we compared them to two complementary null models that reshuffle the strengths of per capita interactions between species pairs across the interaction matrix. In particular, we took as baseline the coexistence-area relationships from the homogeneous parameterization, in order to have a unique interaction strength value per species pair. In the first null model, and taking the inferred interaction matrix from a given plot and year, we redistributed the pairwise interaction coefficients randomly. That is, we fixed the number of species observed in a certain plot and year as well as the structure of the interaction matrix, but randomized the magnitude of observed pairwise interactions (both intra and interspecific interactions) in that community. The second null model is similar, but keeping the diagonal coefficients of the interaction matrix, i.e. the intraspecific terms, fixed. While the first null model accounted for the effect of interspecific competitive responses as well as self-limiting processes on driving CARs, the second null maintained self-limiting processes fixed by avoiding changes in the diagonal elements of our interaction matrices. We ran 100 replicates of each model for each year, and obtained the average coexistence-area relationships across replicates.

Results

In line with theoretical expectations, the relationship between the predicted number of coexisting species with area, the coexistence-area relationship (CAR) (Hart *et al.*, 2017), matches the shape of classic species-area relationships (Fig. 2), with power-law relationships whose exponents (z = 0.21 to 0.45, Table S2) are well within the range of slopes observed for standard SARs (Drakare *et al.*, 2006). But contrary to these expectations, we find that despite the marked soil salinity gradient present in the study area, increases in spatial extent without accounting for environmental heterogeneity explain most of the coexistence predicted in our system (Fig. 2). In particular, the contribution of spatial heterogeneity to species coexistence is 12% when averaged across all years and spatial scales.

On average, between 70-100% of the species predicted to persist in our system reach coexistence via direct pairwise interactions, whereas coexistence by indirect interactions in multispecies combinations and by switches in local dominance was much less prevalent (Fig. 3). Moreover, the relative importance of coexistence mediated by pairwise direct interactions increased with area and was relatively robust across years, with the exception of 2018, where an extreme flooding event effectively knocked out from March to May almost all plant individuals in the study area. Despite most of the species being predicted to persist in the system, we still identified across spatial scales a small set of transient species that represents on average 13.5% of the plant community (Fig. 3). Although the identity of transient species is variable across years, they all share characteristics commonly attributed to transient species in the literature (Snell Taylor *et al.*, 2018). In particular, species systematically classified as transient (e.g. *Suaeda splendens* and *Lythrum tribracteatum*, which show strong preferences for very high soil salinity conditions) were more likely to be comparatively rare (Table S3), reinforcing the evidence from our classification based on the ability of species to persist by its local interactions.

Despite the predominant role of direct interactions among species for predicting species coexistence, we interestingly found no significant differences between the coexistence-area relationships (CARs) derived from the null models and the empirical parameterizations (Fig. 4), In 2016, 2017, and 2019, the observed coexistence is only marginally higher than that expected from both null models, whereas in 2015 and in 2018 the observed coexistence is similar or marginally lower than in the null models. Both null models displayed almost identical average coexistence-area curves in most years, not being able to differentiate between rearranging all coefficients or only the interspecific ones. Overall, these null model analyses suggest that CARs in our system arise independently from species identity.

Discussion

Our findings provide strong empirical evidence that SARs emerge from how local species interactions scale up to generate coexistence patterns across spatial scales. In particular, we have shown that coexistence-area relationships (CARs) in a highly-diverse Mediterranean grassland are consistently similar in shape to classic species-area relationships. But contrary to expectations, we also show that the contribution of spatial heterogeneity to species coexistence is remarkably lower than the contribution from purely spatial processes. Although these results are sensitive to the study system here considered, they provide the first empirical evaluation supporting recent hypothesis that there is a scale dependence of diversity maintenance (Hart *et al.*, 2017).

The overwhelming importance of direct interactions for predicting species persistence, and its increasing role at larger areas, suggests that in our system, the accumulation of species with area does not occur via changes in local dominance (e.g. species dominant at low salinity versus at high salinity). Rather, we interpret that this accumulation emerges from two complementary effects. The first one is a deterministic effect that allows species to coexist locally thanks to the structure of pairwise interactions. We know that specific mechanisms such as species differences in resource requirements, in tolerance to soil salinity, and in their mutualistic interactions with floral visitors, promote pairwise coexistence in our system via niche differences when intraspecific competition exceed interspecific competition (Lanuza *et al.*, 2018). Nevertheless, we do not discard the additional importance of other mechanisms acting in our system such as more general facilitation effects, which are accounted for in our

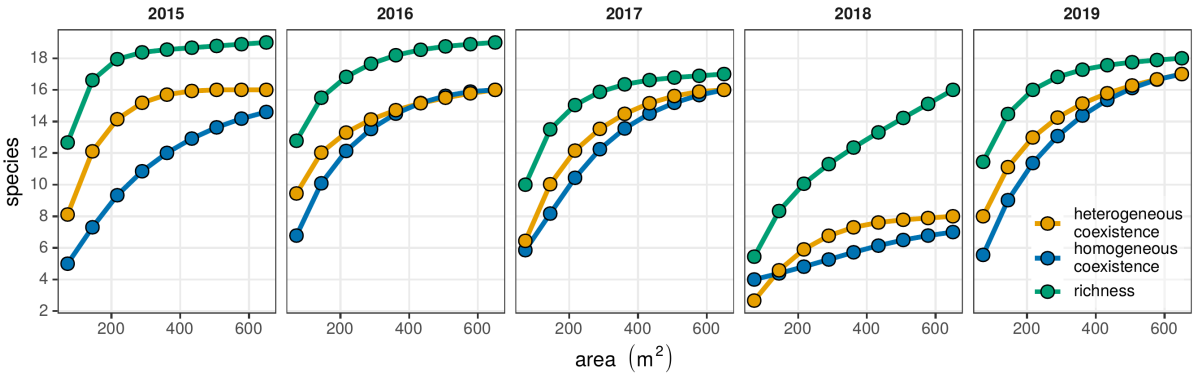

Fig. 2. Species and coexistence-area relationships in a Mediterranean grassland community across five years. Note that curves describing the contribution of homogeneous and heterogeneous environments to the number of coexisting species (blue and yellow lines, respectively), and the curve describing the overall increase of species richness with area (green lines) remain very similar across years except for 2018. That particular year a series of strong rainfall events flooded our system during two months at the peak of the growing season (March to May). This extreme event represents a unique opportunity to document how coexistence and species area relationships are perturbed and how they can recover afterwards. Points represent average values over all combinations of plots resulting in a given area, as in Fig. 1.

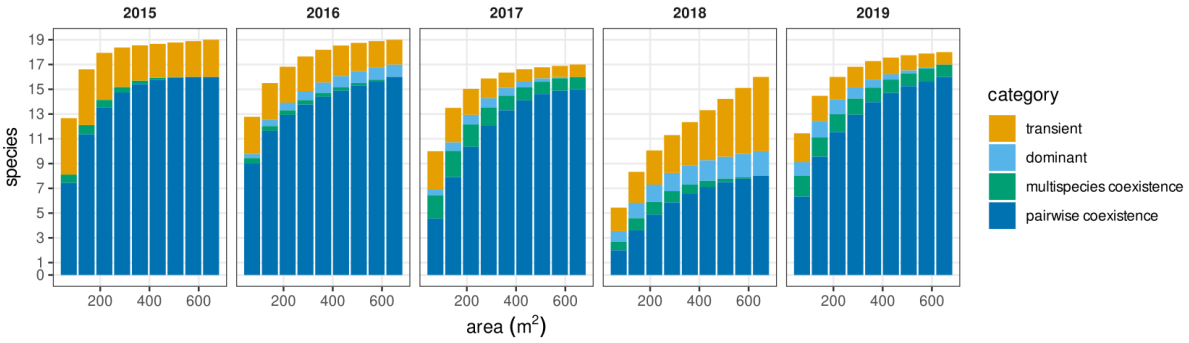

Fig. 3. Coexistence relationships and their variability with spatial extent. Relative bar height for each color represents the average number of species in each category when pooled across combinations of plots. These categories detail which specific configuration of species interactions predict their persistence. Configurations of direct interactions that promote persistence of species pairs (category pairwise coexistence, dark blue bars) show across years an overwhelming importance for shaping species area relationships. Note also that species predicted to be transient (i.e. species not predicted to persist, orange bars) is a general feature of the system, and their relative proportion increased during the year of the extreme flooding event (2018). A fully detail explanation for each category describing how species persist under different configuration of species interactions is given in Material and Methods, section "Analyzing species persistence".

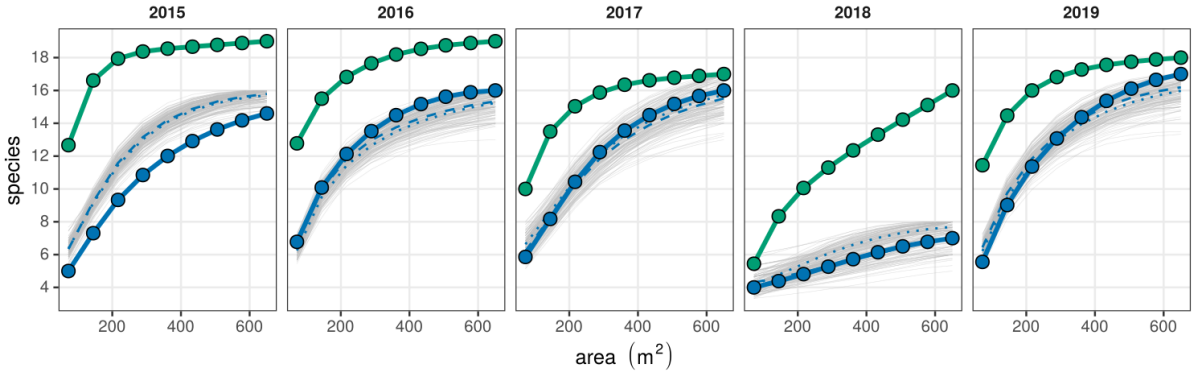

Fig. 4. Null expectations for coexistence-area curves. For reference, species-area curves (green lines and dots) and coexistence-area curves with homogeneous parameterization (blue lines and dots) are also depicted. Null replicates are shown in light grey, and averages are shown as dotted lines (null model reshuffling all interaction coefficients) and dashed lines (null model keeping intraspecific terms fixed, and reshuffling interspecific terms).

modelling approach, or natural enemies (Petry *et al.*, 2018). The second effect reflects the fact that sampling larger areas increase the chance of more coexisting pairs to co-occur in different places. This latter result suggests that demographic stochasticity plays an important role in our system (Hart *et al.*, 2017). Smaller areas attain in general smaller populations that are more prone to extinction (Gilbert & Levine, 2017; Lande *et al.*, 2003). As area increases, the risk associated with demographic stochasticity in smaller areas is reduced because populations are represented by more individuals, which in turn increases the chance of species to interact. Theoretically, an increase in the number of opportunities for species to interact could either promote of hinder their persistence, but we empirically show that the structure of direct interactions between species pairs is key to maintain diversity. Related to this result, a critical question still unanswered is: Over what area do species interactions limit species diversity? (Hart *et al.*, 2017). The saturating trend observed across years (except for 2018) of the homogeneous parameterization CARs suggests that the limit to maintain species diversity in our system starts at the largest scale of analyses (650 m^2). Below that spatial scale, fewer number of species are predicted to coexist most likely due to a combination of dispersal limitation and demographic stochasticity.

Despite our results suggest a small role of abiotic heterogeneity in driving species persistence, it may still be of importance for determining their relative abundances. For instance, while some generalist species (e.g. *Hordeum marinum*, *Leontodon maroccanus*) attain high abundances across all the study area, it is also possible to observe more subtle changes in community composition and species relative abundances across the soil salinity gradient (e.g. *Scorzonera laciniata* and *Sonchus asper* being more abundant at low soil salinity versus *Chamaemelum fuscatum* and *Salsola soda* at high soil salinity). Finally, the little importance of indirect effects in granting coexistence as we increased the study area is surprising given theoretical expectations from competitive communities (Allesina & Levine, 2011; Levine *et al.*, 2017; Soliveres *et al.*, 2015), in which indirect effects are expected to play a large role in shaping coexistence. Rather, our results suggest that the large-scale network structure in our study system hardly includes new opportunities for coexistence that were not contained already in direct pairwise interactions. This aligns well with another line of theoretical and empirical evidence that highlights the critical role of self-limiting processes in stabilizing population dynamics of multiple interacting species (Barabás *et al.*, 2016; Godoy *et al.*, 2017).

We also show that despite high predicted levels of species coexistence, a small but sizable set of transient species are systematically identified even at the largest spatial scale of our study (650 m^2). Transient species can be interpreted as representing, in open systems like ours, outside contributions to the community in the form of propagules arriving via dispersal or present already in the system in the form of persistent soil seed banks. Therefore, the observed ratio between the number of coexisting species and the overall species richness can be seen as a proxy to quantify the role of source-sink dynamics in the system (Hart *et al.*, 2017), as well as the importance of the surrounding habitat in shaping its observed diversity. Specifically, comparing differences observed between CARs and SARs shapes to predictions done with a spatially explicit lottery model (see Fig. 2 from Hart *et al.* (2017)) suggests that our system is governed by short dispersal dynamics, and by species showing on average both low and high spatial autocorrelation in their response to the environmental conditions (years 2017, 2019, versus years 2015, 2016 respectively). We, unfortunately, could not distinguish which group of environmental variables were most affecting species performance. Most likely, these variables differ across species, and future work needs to develop techniques that allow distinguishing what factors drive the sensitivity of species responses to changes in environmental conditions. It has been also hypothesized that coexistence-area relationships should converge with species-area relationships (which include coexisting and non-coexisting species) for sufficiently large areas (Hart *et al.*, 2017); this is likely to occur in our system if we increased the spatial scale to include those rare hypersaline patches that would allow the persistence of halophytes (i.e. salt specialists). Regardless of the expected concordance between species-area relationships and coexistence-area relationships at large scales, our results highlight transient species as important features of local ecological communities (Snell Taylor *et al.*, 2018).

All patterns observed, i.e. the shape of the coexistence-area relationships, the greater importance of spatial extent compared to spatial heterogeneity, the prevalence of direct pairwise interactions on promoting species coexistence, and the small but consistent frequency of transient species at increasing spatial scales, are robust across years (Figs. 2 and 3). This is a surprising finding in an annual system given the fact that interaction networks are reassembled and disassembled each hydrological year, under contrasting annual precipitation patterns (ranging from 384 mm in 2019 to 625 mm in 2016). It suggests that key structural features of the system are conserved across years, despite differences in species abundances or the composition of specific plots in the system. Our null model analyses show, specifically, that the identity of pairwise interactions, which drive stabilizing effects among pairs of species, is not a key driver of the spatial coexistence patterns in our system. An explanation for these results is that most interactions, both intra and interspecific, are comparatively weak (Fig. S1). In 20-40% of the observed pairwise interactions, intraspecific interactions are nevertheless slightly stronger than interspecific ones, generating coexistence domains that can accommodate small competitive differences be-

tween species (Fig. S2). In other cases, even if intraspecific interactions do not exceed interspecific ones, pairwise coexistence is achieved by weak interspecific facilitation. This quasi-neutral state in the annual assembly of our communities contrasts with prior work positing that the maintenance of high-levels of diversity corresponds to a situation in which large stabilizing niche differences can accommodate strong differences in competitive ability between species (Germain *et al.*, 2018; Levine & HilleRisLambers, 2009), but support more recent theoretical views of the importance of the species functional equivalence for driving self-organization patterns in ecological communities (Scheffer *et al.*, 2018). The observed quasi-neutral state surfaces even after the occurrence of extreme climatic events, as shown by the patterns observed in 2019, the year after the flooding event that wiped out most of the studied plant community. This extreme disturbance provided an unexpected and very valuable natural experiment, as it showed how in a single year the community recovered richness and coexistence levels comparable to 2015, 2016, and 2017. Similarly, fast recoveries of species-area relationships have been previously described for lizards (Schoener *et al.*, 2001) and marine fouling communities (Schoener & Schoener, 1981), highlighting the importance of dispersal and population buffers against disturbances (seed banks, in the case of annual plant communities) in recovering canonical SAR shapes. We extend these observations of rapid recovery of community properties to empirical CARs under quasi-neutral dynamics, showing that pairwise coexistence mechanisms can rapidly restore high levels of species diversity in natural communities.

For over a century, ecologists have been documenting that the increase of species richness with area follows universal rules. By taking a bottom-up approach where we combine theory and modeling with detailed empirical observations of species interactions at local scales, we highlight that spatial extent can be as important as environmental heterogeneity, and in some cases even more important, to maintain high species richness under quasi-neutral species interactions. More importantly, we provide strong empirical evidence that SARs emerge from the collective effect of multiple coexistence mechanisms arising from the architecture of species interactions together with stochastic and dispersal events.

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Acknowledgements

We thank the Radical Community Ecology group (https://github.com/RadicalCommEcol/) for fruitful discussions. OG acknowledges financial support provided by the Spanish Ministry of Economy and Competitiveness (MINECO) and by the European Social Fund through the Ramón y Cajal Program (RYC-2017-23666). This study was funded by Spanish Ministry of Science and Innovation (MICINN) and the European Social fund through the MeDiNaS project (Mechanisms of maintenance of species diversity in variable environments, RTI2018-098888-A-I00).

Supplementary Figures

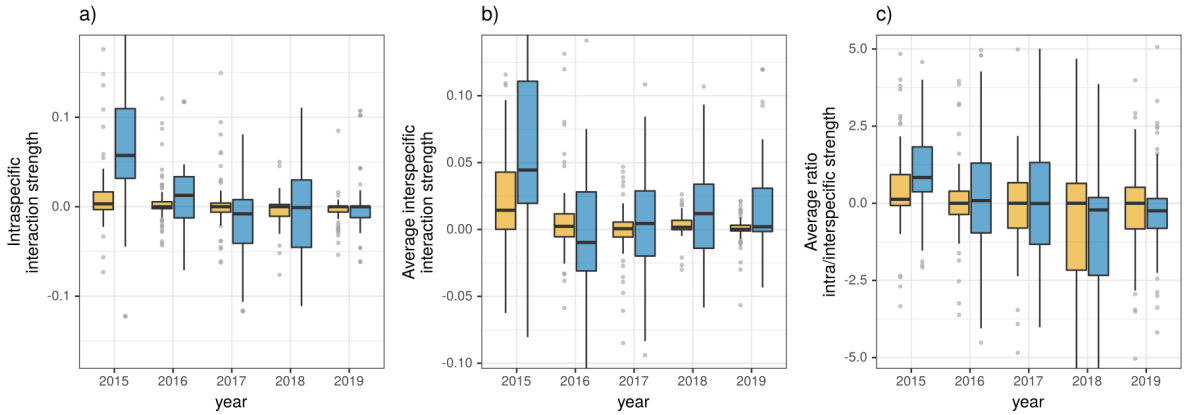

Fig. S1. Interaction strength distributions across years, for the homogeneous (blue, right-side boxplots) and heterogeneous (yellow, left-side boxplots) parameterizations: (panel a) intraspecific, panel b) average interspecific, panel c) intra/interspecific ratio).

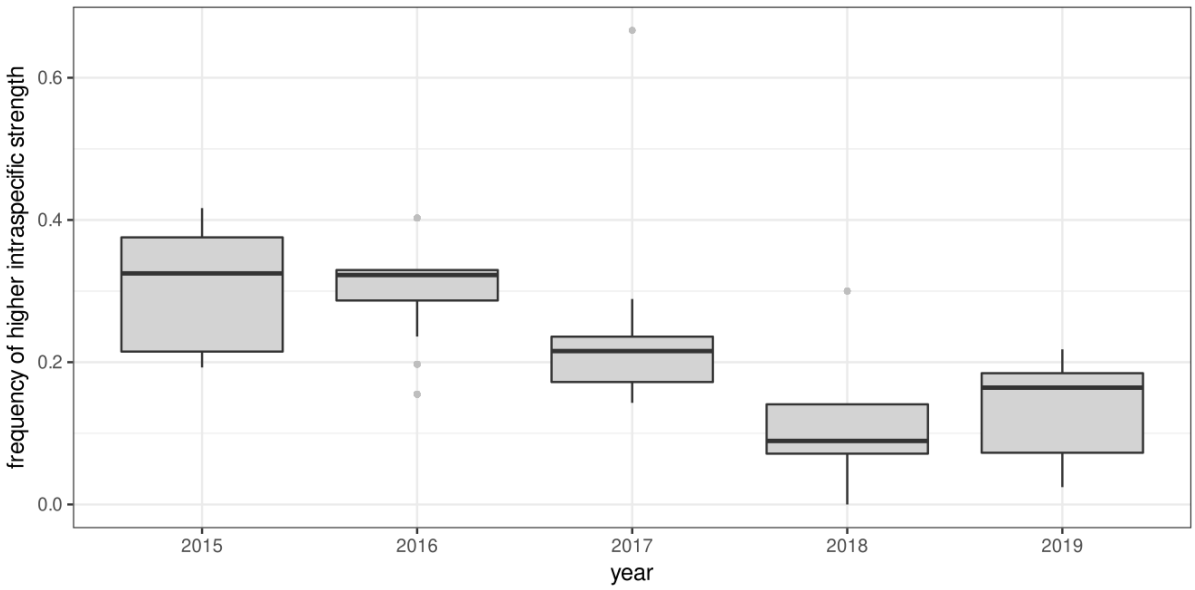

Fig. S2. Frequency of observing higher intraspecific interaction strengths than interspecific ones, for all observed pairwise combinations of species in each year. Results shown for the heterogeneous parameterization.

Supplementary Tables

species	family	2015	2016	2017	2018	2019
Beta macrocarpa	Amaranthaceae	136	1230	90	20	1052
Centaurium tenuiflorum	Gentianaceae	1206	37	1057	522	705
Chamaemelum fuscatum	Asteraceae	5050	5802	2619	0	3989
Chamaemelum mixtum	Asteraceae	882	909	208	2	9
Hordeum marinum	Poaceae	6719	13159	54264	43355	71923
Leontodon maroccanus	Asteraceae	2485	3448	21657	814	4182
Lythrum tribracteatum	Lythraceae	1321	474	676	3	0
Melilotus elegans	Fabaceae	313	135	2	0	6
Melilotus sulcatus	Fabaceae	504	414	36	1	1059
Parapholis incurva	Poaceae	1239	78	2980	29	7534
Plantago coronopus	Plantaginaceae	5439	518	2427	1	118
Polypogon maritimus	Poaceae	4101	709	5085	315	7332
Polypogon monspeliensis	Poaceae	442	26	89	1	284
Pulicaria paludosa	Asteraceae	124	201	2899	746	739
Salsola soda	Amaranthaceae	7346	490	1629	4771	791
Scorzonera laciniata	Asteraceae	881	226	85	1	17
Sonchus asper	Asteraceae	237	41	0	1	366
Spergularia rubra	Caryophyllaceae	146	103	108	0	550
Suaeda splendens	Amaranthaceae	60	26	0	1	52

Table S1. Species studied and their overall abundance (individuals counted) in the whole study area for each year of observations.

year	fit.type	parameter	estimate	se	t_value	p_value	lower.bound	upper.bound
2015	heterogeneous	c	3.47	0.91	3.81	0.01	1.65	0.91
2016	heterogeneous	c	3.98	0.38	10.37	0.00	3.21	0.38
2017	heterogeneous	c	1.73	0.39	4.43	0.00	0.95	0.39
2018	heterogeneous	c	0.64	0.20	3.15	0.02	0.23	0.20
2019	heterogeneous	c	2.37	0.33	7.28	0.00	1.72	0.33
2015	homogeneous	c	0.77	0.12	6.72	0.00	0.54	0.12
2016	homogeneous	c	1.84	0.37	4.96	0.00	1.10	0.37
2017	homogeneous	c	0.97	0.17	5.88	0.00	0.64	0.17
2018	homogeneous	c	1.06	0.12	8.56	0.00	0.81	0.12
2019	homogeneous	c	1.00	0.21	4.84	0.00	0.59	0.21
2015	richness	c	7.69	1.30	5.92	0.00	5.09	1.30
2016	richness	c	6.71	0.65	10.33	0.00	5.41	0.65
2017	richness	c	4.77	0.83	5.78	0.00	3.12	0.83
2018	richness	c	0.86	0.07	12.01	0.00	0.72	0.07
2019	richness	c	5.77	0.76	7.58	0.00	4.25	0.76
2015	heterogeneous	z	0.25	0.04	5.57	0.00	0.16	0.34
2016	heterogeneous	z	0.22	0.02	13.41	0.00	0.19	0.25
2017	heterogeneous	z	0.35	0.04	9.33	0.00	0.28	0.43
2018	heterogeneous	z	0.40	0.05	7.61	0.00	0.30	0.51
2019	heterogeneous	z	0.31	0.02	13.43	0.00	0.26	0.36
2015	homogeneous	z	0.46	0.02	18.62	0.00	0.41	0.51
2016	homogeneous	z	0.34	0.03	10.16	0.00	0.28	0.41
2017	homogeneous	z	0.44	0.03	15.59	0.00	0.38	0.50
2018	homogeneous	z	0.29	0.02	14.73	0.00	0.25	0.33
2019	homogeneous	z	0.45	0.03	13.01	0.00	0.38	0.51
2015	richness	z	0.15	0.03	5.05	0.00	0.09	0.20
2016	richness	z	0.17	0.02	10.04	0.00	0.13	0.20
2017	richness	z	0.20	0.03	6.93	0.00	0.14	0.26
2018	richness	z	0.45	0.01	32.66	0.00	0.42	0.48

year	fit.type	parameter	estimate	se	t_value	p_value	lower.bound	upper.bound
2019	richness	z	0.18	0.02	8.09	0.00	0.14	0.23

Table S2. Parameter of power-law fits ($S = cA^z$) to the species-area relationships and coexistence-area relationships of Fig. 2. SE = standard error. 2.5%/97.5% = lower and upper bounds of 95% confidence interval for parameter estimates.

term	estimate	SE	z-value	p-value
intercept	0.62	0.45	1.36	0.18
log(abundance)	-0.18	0.07	-2.63	0.009

Table S3. Coefficients of a logistic regression (with logit link function and N = 171) for the relationship between species abundance (log-transformed) and the classification of species as coexisting or transient. SE = standard error.