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RESEARCH ARTICLE

Evaluating the restoration of plant ecological interactions in gypsum mines with species co-occurrences analyses

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Abstract

1. Ecological interactions are a crucial component of biodiversity, and their loss can disrupt ecosystem functions. Therefore, restoring these interactions is essential for effective ecological restoration. Although positive interactions between plants (i.e. plant facilitation) have gained attention in restoration ecology, most research has concentrated on population and community outcomes, with limited focus on the restoration of plant–plant interactions.
2. We used Markov network models to evaluate pairwise and higher-order plant interactions in gypsum shrublands in southern Spain and compared them with interactions in adjacent areas restored after mining activities. Restoration efforts, involving seed-based and seedling-based approaches from 13 years ago, were assessed to determine whether positive (facilitation) and negative (competition) interactions had been restored within each community. Given the stressful conditions of gypsum soils, we hypothesize that facilitation is the main force shaping the interactions in both reference and restored areas.
3. Positive interactions between the most abundant species dominated over negative ones in both natural and restored areas. In both the seed-based and the seedling-based restorations, about half of the observed pairwise interactions in the natural area were restored with the same sign. Generally, facilitation interactions that were not restored became neutral, but rarely turned negative.
4. *Synthesis and applications*. These case studies suggest that both seed-based and seedling-based approaches can restore pairwise species interactions to a similar extent. The seedling-based method, although more expensive, provides immediate visual impact by directly introducing canopy-forming species into the system. In

contrast, the seed-based approach, which is more cost-effective, can establish highly dense plant communities, enhancing soil protection, though it may also lead to increased emergent competition through third-order interactions.

KEYWORDS

competition, facilitation, gypsum mines, nurse plants, plant–plant interactions, seed-based restoration, seedling-based restoration

1 | INTRODUCTION

Despite the Convention on Biological Diversity officially recognizing the role of biodiversity for human wellbeing (United Nations, 1992), biodiversity loss continues to accelerate (Cardinale et al., 2012; Dornelas et al., 2014). In response, restoration efforts aim to reverse biodiversity changes and recover ecosystem functions in degraded ecosystems (Benayas et al., 2009). Biodiversity relies on intricate networks of ecological interactions (Hagen et al., 2012), which are often lost before species disappear (Janzen, 1974). An unintended consequence of losing these interactions is that ecosystem functions can be lost even if the species remain present in the community (Valiente-Banuet et al., 2015). Therefore, restoring ecological interactions should be fundamental to all restoration initiatives (Montoya et al., 2012). Consequently, recent restoration efforts have shifted their focus from recovering individual species to restoring functional groups, given their key role in maintaining essential ecosystem functions such as pollination and seed dispersal (Montoya et al., 2012) or plant facilitation (Gómez-Aparicio, 2009). While the restoration of plant–animal interactions has gained attention (Forup et al., 2008; Genes & Dirzo, 2022), the restoration of plant facilitation interactions remains largely overlooked, despite its documented relevance (Galindo et al., 2017; Garrote et al., 2022; Gómez-Aparicio, 2009; Gómez-Aparicio et al., 2004; Gómez-Ruiz et al., 2013; Padilla & Pugnaire, 2006; Pueyo et al., 2009; Siles et al., 2008). When facilitation is considered in restoration contexts, success is typically measured at the population level (i.e. focal plants enhance certain fitness components when interactions are present; Gómez-Aparicio et al., 2004) or at the community level (i.e. the community's taxonomic, functional, or phylogenetic plant diversity is restored; Navarro-Cano et al., 2016). However, few studies directly assess whether facilitative interactions themselves are effectively restored compared to reference systems.

Ecological models typically focus on pairwise interactions between species, but in the wild, species often engage in higher-order interactions, where the relationship between two species is influenced by the presence of other species (Bairey et al., 2016; Levine, 1999). In Mediterranean ecosystems, experimental and observational studies have documented both direct and indirect interactions underscoring the importance of capturing interaction complexity to understand community composition (Michalet et al., 2015). Incorporating higher-order interactions is crucial for understanding pairwise interactions because evidence indicates that competition among perennial plants in multi-species assemblages is often weaker than in pairwise settings. In these communities, higher-order interactions can mitigate the direct competitive effects observed between pairs of species (Aschehoug & Callaway, 2015). For this reason, it is essential to assess the sign and strength of pairwise interactions in the presence of third-party species in natural ecosystems to determine if they are being effectively restored.

Ultimately, every restored interaction can affect the structure of the resulting community through a cascade of direct and indirect effects, potentially leading to changes in its resilience to disturbances (García-Callejas & Torres, 2019). For example, restoring a positive or negative interaction between two species can indirectly affect the ability of multiple species to persist together by reshaping competitive relationships or influencing the population dynamics of other species (García-Callejas & Torres, 2019; Losapio et al., 2021). In this context, most restoration ecologists now recognize that the non-equilibrium, alternative states framework provides a more realistic approach to predicting and explaining the trajectory of a restored ecosystem (Perring et al., 2015). In this way, our interactions-based restoration approach could help to elucidate why many restoration projects do not reach the reference community. As far as we know, no study has evaluated the extent to which the pairwise plant interactions lost due to habitat degradation have been adequately restored. To this end, Markov network models can assess pairwise ecological interactions by fitting regularized logistic models for each species using the presence of other species to infer conditional associations while controlling for indirect effects (Harris, 2016). This framework can also incorporate higher-order interactions among three species.

Using this approach, we assessed the restoration of plant–plant interactions in gypsum mines taking into account third-order interactions and hypothesized that positive interactions (facilitation) dominate over negative interactions (competition) not only in reference shrublands but also in restored areas. In these stressful habitats, facilitation is expected to govern community assembly and reassembly through processes such as succession and nurse plant effects (Escudero et al., 2015; Foronda et al., 2019, 2020; Navarro-Cano et al., 2016). Pairwise and third-order interactions were analysed in reference communities and compared with those in adjacent habitats restored 13 years ago using seed-based and seedling-based approaches. Seed-based restoration allowed evaluation of whether facilitation is re-established from early successional stages, while seedling-based restoration addressed the role of nurse plants in restoring both interactions between nurse and recruit species and interactions among recruits themselves. Long-term monitoring provides a perspective rarely captured in restoration ecology, where outcomes are typically assessed only 1–2 years after intervention. Gypsum shrublands are recognized as a priority habitat under European legislation, emphasizing the importance of effective restoration for the persistence and stability of ecological interactions in these slow-recovering ecosystems (Mota et al., 2011).

2 | METHODS

2.1 | Study sites and restoration activities

We analysed two restoration activities in abandoned gypsum mines in the Iberian Peninsula, one in the south (Escúzar, Granada, 37°3′50.5″ N, 3°50′36.9″ W; 830 m a.s.l.) and the other in the southeast (Sorbas, Almería, 37°4′54.7″ N, 2°5′47.9″ W; 400 m a.s.l.) (see Figures S1 and S2 in Supporting Information). These sites used different restoration techniques: seed-based in Escúzar and seedling-based in Sorbas. The choice between using seeds or seedlings in restoration efforts at the two sites was driven by different constraints and practical considerations. In Escúzar, the use of seeds was chosen for economic and ecological reasons. Seeds were easily collectible, had high viability, and the species involved had short life cycles with rapid reproductive maturity—some individuals began reproducing within 1–3 months, and by the following year, up to 100% of survivors were reproductive. Direct seeding allowed higher initial plant densities and lower costs, while producing a more heterogeneous plant distribution by broadcasting seeds rather than planting seedlings in rows, better mimicking natural establishment patterns. In contrast, in Sorbas, the mining company determined the use of 1-year-old seedlings in order to obtain immediate coverage results, while the researchers provided technical support. This method may produce faster initial establishment but often results in less natural spatial distribution and higher operational costs compared to direct seeding. The restoration process and monitoring were carried out under collaboration agreements between the mining concessionaire companies and the Universities of Almería and Granada, ensuring that the authors held all necessary permissions for fieldwork throughout the entire study period.

Based on the Köppen–Geiger climate classification, Escúzar is categorized as a Hot-Summer Mediterranean climate (Csa), with a mean annual temperature of 15.8°C and an average annual precipitation of 421 mm (Figure S3, left). In the second site, Sorbas, the climate is classified as a Cold Semi-Arid climate (BSk), with a mean annual temperature of 17.1°C and an annual precipitation of 250 mm (Figure S3, right). In both areas, the natural shrubland surrounding the mine served as the reference community, consisting of gypsum-adapted small sub-shrubs predominantly growing in patches and leaving over 50% of the ground bare. A patch refers to a discrete aggregation of vegetation, typically dominated by one or more gypsum-adapted small sub-shrubs, surrounded by areas of bare soil. These patches reflect the natural spatial heterogeneity of vegetation that is typical of ecosystems shaped by facilitative interactions (Kéfi et al., 2007; Scanlon et al., 2007). In Escúzar (Granada), these communities are dominated by *Helianthemum squamatum*, *Helianthemum syriacum*, *Thymus zygis*, *Ulex parviflorus*, *Lepidium subulatum* and *Ononis tridentata*, whereas in Sorbas (Almería) the dominant species include *H. squamatum*, *Santolina viscosa*, *Coris hispánica*, *Gypsophila struthium*, *Sedum sediforme*, *H. syriacum*, *Teucrium turredanum* and *Stipa tenacissima*.

2.1.1 | Seed-based restoration (Escúzar)

The seed-based restoration of the abandoned gypsum quarry took place in November 2011, by hydroseeding of 1.53 ha. The mixture consisted of water, cellulose mulch (200 g/m^2), soil stabilizer (1–1.6 g/m^2) and fertilizer (30 g/m^2 NPK 15-10-10 + 3MgO + 6S), together with a mixture of native seeds (1104 seeds/m^2) consisting of three gypsophytes (i.e. species specialist to gypsum; *H. squamatum*, *L. subulatum* and *O. tridentata* ssp. *crassifolia*) and four gypsovags (i.e. species living on gypsum, and limestone, marls, etc.; *H. syriacum*, *T. zygis* ssp. *gracilis*, *Salvia rosmarinus*, *S. tenacissima*). Plants were watered the first summer once a month (three times, 50 L/m^2 each). Further details on the sequence of restoration activities can be found in Figure S1 and in Lorite et al. (2021).

The emerging interactions among all the species were evaluated 13 years later in both the natural and the restored area. In the natural area, 12 transects of 60 m^2 (i.e. 20 × 3 m) each were sampled, totalling 720 m^2. In the restored area, we sampled 14 transects of 60 m^2 each, totalling 840 m^2. We recorded every species detected, whether represented by a single individual or by multiple individuals forming a vegetation patch, to ensure that all occurrences contributed to the calculation of the ecological interaction coefficients. In total, our dataset for Escúzar thus consists of 5345 patches in the natural area and 2644 patches in the restoration. The restoration was heavily seeded with *S. rosmarinus*, which was not detected in our sampling of the natural area but was included in the hydroseeding mixture due to its high abundance on gypsum outcrops at the regional scale. Therefore, this species was excluded from the focal species, as no meaningful comparison could be made for them between the two areas.

2.1.2 | Seedling-based restoration (Sorbas)

The seedling-based restoration was performed in April 2011. To approximate the substrate to the characteristics of gypsum soils, fines extracted from the gypsum mine were reused and spread over the restored areas. On this layer, species grown in nurseries were planted either by creating furrows or through manual digging. Irrigation was applied weekly from the time of planting until the first autumn rain. Seedling survival after the first year was close to 100%. A total of 25 species were planted, eight of which can be considered gypsophytes (Figure S1 and Mota et al. (2023) for more details). Among these species, two (*G. struthium* and *S. viscosa*) were selected for their ability to colonize barren gypsum substrates and for their nurse plant characteristics (Merlo et al., 2009; Mota et al., 2023). In 2024, we evaluated the interactions promoted by these two nurse species. Since one of our objectives was to assess nurse–recruit interactions, it is important to note that these species are expected to exert facilitative effects, aiding the establishment of other plants in the harsh gypsum environments.

In this site, sampling focused specifically on two target species and therefore large plots instead of transect surveys were conducted. Four distinct plots in the natural area where these species were abundant were sampled. The sizes of these areas varied, measuring 500, 1000, 2500 and 5000 m^2, respectively. In the restoration area, all individuals of the two target species planted were sampled within three plots of different sizes: 500, 1000 and 2000 m^2. The species established on open ground in an adjacent area, equal in surface area to that occupied by the corresponding nurse plant and located 1–2 m away, were also recorded.

In the natural area, we sampled all plants growing beneath 404 nurse individuals of *G. struthium* and beneath 594 nurse individuals of *S. viscosa*, as well as in adjacent open areas of the same size as each nurse plant. In the restored area, we sampled all the plants established beneath 265 individuals of *G. struthium* and 166 individuals of *S. viscosa* nurse plants and in open areas. Our dataset for Sorbas consisted of 1996 patches in the natural area, and 862 in the restoration.

2.2 | Fitting procedure

A central challenge when inferring plant–plant interactions from field data is distinguishing true biotic interactions from environmentally driven species co-occurrence, as emphasized by Steinbauer et al. (2016). Apparent associations may arise from shared habitat preferences rather than direct ecological effects. In our study, this potential bias is minimized through the sampling design: in Sorbas, microsites were spatially paired immediately adjacent to nurse plants to reduce environmental heterogeneity, and in Escúzar, species occurrences were exhaustively recorded within fixed transects rather than selectively comparing under-canopy and randomly located open plots. By combining this design with statistical models that explicitly estimate interaction coefficients from co-occurrence patterns, we aim to infer structured biotic associations while limiting confounding effects due to habitat sharing. We followed the procedure used in Harris (2016) to fit the coefficient of interactions, with some modifications. This author suggested extracting the interaction coefficients between species using generalized linear models, as a computationally efficient approximation to the full Markov Network. In practice, Harris (2016) demonstrated a reliable approach: fitting regularized logistic models for each species, using the other species as predictors. This is the approach we follow here, and illustrate with a toy example involving only three species. Our main modification on top of the work of Harris (2016) is to introduce direct interaction coefficients involving three species.

Differences between sites were not considered in the analysis, as the objective of the study was not to compare sites, but rather to assess how ecological interactions are recovered and to provide a methodological framework for doing so. The two sites were selected because they apply different restoration techniques, offering useful case examples for illustrating the method. Since there are no replicates for either the restoration methods or the sites themselves, we cannot determine the relative contribution of each. However, the proposed methodology could be used in future studies to evaluate restoration success across sites and restoration strategies.

2.2.1 | Toy model with only three species

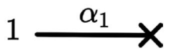
We focus on a toy model with three plant species, numbered 1, 2 and 3. As a matter of example, let us focus on species 1, and denote by $y_1 = 0$ its absence, and $y_1 = 1$ its presence in a given patch. We can write the conditional probability of finding this species as a function of the presence/absence of the other species, as follows:

$$P(y_1 = 1 | y_2, y_3) = \text{logistic}(\alpha_1 + \beta_{1,2} y_2 + \beta_{1,3} y_3 + \gamma_{1,2,3} y_2 y_3),$$

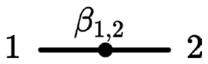
where $\text{logistic}(x) = 1/(1 + \exp(-x))$.

The ecological interpretation of the α_i, β_{ij}, γ_{ijk} coefficients is as follows:

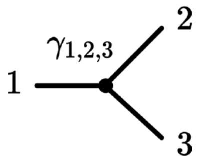
The coefficient α_1 determines the prevalence of species 1 in absence of other species or interactions. In statistical physics, it would correspond to the chemical potential, while here it describes the suitability of the species in this environment. We represent this term by a cross:



The next term in the expansion, $\beta_{1,2}$ represents the direct effect of species 2 on the probability of finding species 1: if it is positive, the presence of species 2 increases the chances of finding species 1 in that same patch, if it is negative, that same probability is decreased. In our theoretical framework, one can show that $\beta_{1,2} = \beta_{2,1}$. This holds even if one species functions as a nurse and the other as a recruit, and is simply a consequence of the assumption that the system has reached statistical equilibrium. This permutation symmetry would be lost if a Lotka–Volterra model were used to describe temporal population dynamics; in that case, one could distinguish the effect of a nurse on a recruit from the effect of a recruit on a nurse (Levine et al., 2017). For instance, $\beta_{1,2}$ can be represented as:



The interpretation is that, if $\gamma_{1,2,3}$ is positive, the presence of species 2 and 3 increases the probability of finding species 1, and decreases it if the coefficient is negative. The internal consistency of our theoretical framework forces γ to be symmetric under permutation of the indices. This interaction term is represented graphically as:



Further details on the three-species model are provided in Appendix S2, and the generalization to more than three species is presented in Appendix S3.

2.2.2 | Relative importance of interaction coefficients

Ecologically, we expect the main filter for the suitability of a species to be abiotic, as represented by the linear/background terms α, corrected by a leading order biotic filter represented by pairwise interactions β. While we expect the α coefficient for each species to depend on the location, we want to check whether the β coefficients are fixed for each pair of species, independently of the location. In other words, we seek to determine to what extent biotic interactions modify species abundances that are largely shaped by abiotic factors.

Also, for our approximation of limiting ourselves to direct interactions between few (namely 2 or 3) species to be self-consistent, we expect the higher-order interactions to be less important than the lower-order ones. In our case, we can test how much the introduction of γ coefficients impact the determination of β pairwise interactions.

When performing fits of the conditional probabilities, we are thus particularly interested in two aspects:

1. Does the inclusion of γ terms improve the goodness-of-fit? If so, it provides evidence for the role of higher-order interactions beyond simple pairwise effects (β). In this case, species co-occurrence patterns are better explained by complex multi-species interactions rather than by direct pairwise relationships alone.
2. Are the pairwise interaction coefficients β significantly different between a restored area and its neighbouring natural area? If so, we can conclude that restoration has successfully recovered ecological interactions; if not, we can assess how far the system still is from achieving that goal.

We focused on three possible models to fit the interaction coefficients order-by-order in the Taylor expansion described above:

- Fit coefficients up to order 1: fitting only the α coefficients, while setting all interactions between species to zero, whether pairwise (β) or three-species interactions (γ);
- Fit up to order 2: fitting the α and β coefficients while setting all three-species interactions γ to zero;
- Fit up to order 3: fitting all coefficients α, β and γ.

2.2.3 | Extracting interaction coefficients

In addition to limiting ourselves to direct interactions involving up to three species, we focused on the most common species occurring in our study systems. Six species were included in the seed-based restoration site (*H. squamatum*, *H. syriacum*, *T. zygis*, *U. parviflorus*, *L. subulatum* and *O. tridentata*). In the seedling-based restoration site, four species were selected (*S. viscosa*, *G. struthium*, *H. squamatum* and *Coris hispanica*), with the first two acting as both nurse and recruit. In both sites, the other species were considered only through their average effect on the focal species (we also consider different numbers of focal species in Figures S4 and S5). When interactions involve fewer species than those available, the number of interaction coefficients is lower than the number of data points. In this situation, the conditional probabilities cannot be directly inverted to recover the interaction coefficients, as in the three-species case, and a statistical analysis is therefore used to obtain the best fit.

While Harris (2016) started from a full Markov Network to compare different methods for extracting interaction coefficients, that paper also showed that it was possible to speed up calculations by using generalized linear models to fit the presence/absence pattern for each species depending on all the others, that is all conditional probabilities. This is the method we describe below.

As we represented the data as a matrix y of ones and zeroes, and used the column index i to represent the species and the row index p to identify patches, we can denote each entry in the matrix by $y_i^{(p)}$. The probability of finding a 1 in that entry is written $P\left(y_i^{(p)} = 1\right)$, while the probability of finding this same value knowing the values of all $y_j^{(p)}$'s for all $j \neq i$ in the same patch p is the conditional probability for the presence of species i conditioned on all other species, denoted by $P\left(y_i^{(p)} = 1 | y_j^{(p)}\right)$.

These are the conditional probabilities we fit, using the standard formalism of a logistic regression, that is performing a linear regression for the log-odds of the presence/absence y_i of a given species i (dependent variable) as a function of the presence/absence y_j of other species j (independent variables):

$$P(y_i = 1 | y_j) = \text{logistic}\left(\alpha_i + \sum_{j \neq i} \beta_{ij} y_j + \sum_{j,k \neq i} \gamma_{ijk} y_j y_k\right)$$

We did not necessarily have to include every single species present in the right-hand side of this equation, and in fact, we used a compromise for infrequent species or species that are not present in either the natural area or the restored one. Specifically, we lumped all such species into a single column of the matrix y: when any of these species is present in patch p, we will count $y_i^{(p)} = 1$ for j = other species, and $y_i^{(p)} = 0$ otherwise.

Coming back to the point of the symmetry of the β and γ coefficients, one can show that they have to be symmetric for consistency of the various conditional probabilities. This is evident in the case of the Markov Network, as shown in the following expression, which gives the probability of observing a specific configuration of the network:

$$P(y_i) \propto \exp\left(\sum_{i} \alpha_i y_i + \frac{1}{2!} \sum_{i,j} \beta_{ij} y_i y_j + \frac{1}{3!} \sum_{i,j,k} \gamma_{ijk} y_i y_j y_k \right).$$

in which only the symmetric part contributes. As noted before, in order to speed up computations, we directly fitted the conditional probabilities instead of the Markov Network, and we thus extract values for β_{ij} and for β_{ji} separately, which usually turn out to be numerically close to each other, as was the case for Harris (2016). We therefore followed the same procedure of averaging the two values into a single, symmetric one. As for the γ_{ijk} coefficients, from the six possible orderings of each set of three species, we only consider the mean value after performing the fits.

2.2.4 | Goodness of fits

To check the agreement between a given model and the real observations, we computed a goodness-of-fit metric (specifically the G-statistic) between a validation subset of the data and the predictions from the model fit on a training subset of the data. We used 70%–30% training-validation splits of the data and repeated the procedure on 100 random such splits to estimate the error on the goodness-of-fit due to finite dataset size.

For each of these splits, we first extracted coefficients from a fit to the training subset, then used the obtained coefficients in a Monte-Carlo simulation to generate a synthetic distribution of data produced by these parameters. We then compared the predicted frequencies of occurrence with those observed in the validation subset. While this is equivalent to comparing the number of observed counts in bins with those of a multinomial distribution, we did not use Chi-squared as our metric, since it is not reliable when we have bins with only a few counts, which is the case for our observational data. Instead, we used the G-statistic (or log-likelihood ratio) as advocated by McDonald (2014), which would reduce to the Chi-squared statistic in the appropriate limit, but has the advantage that it still applies with low bin counts.

As an extra complication, note that our expected distribution is calculated after fitting coefficients to the training dataset, and then using these coefficients to generate large synthetic datasets via a Monte-Carlo. Because of this, we sometimes find fit models that generate an expected distribution where a given unique patch composition does not occur (empty bin). This would give a divergent result for the G-statistic (and for the Chi-squared statistic as well). We therefore regulate our estimate for the predicted distribution with a James-Stein shrinkage using the R package 'entropy' (Hausser & Strimmer, 2009).

2.2.5 | Proportion of bare soil and 'empty' patches

Our datasets record the presence and absence of plants in patches or clusters separated by bare soil, but did not record the proportion of the latter, that is the area covered by bare soil. Yet, the above formalism implicitly considers these areas of bare soil: in fact, it predicts a number of patches that turn out to be empty unless some species happen to have probability 1.

One could thus hope to estimate the number of such empty patches by dividing the area of bare soil by the average area covered by a real patch. However, different patches do not actually cover the same area, so these approximations would inevitably introduce a degree of arbitrariness in our procedure, as well as extra steps and parameters such as the number of such empty patches.

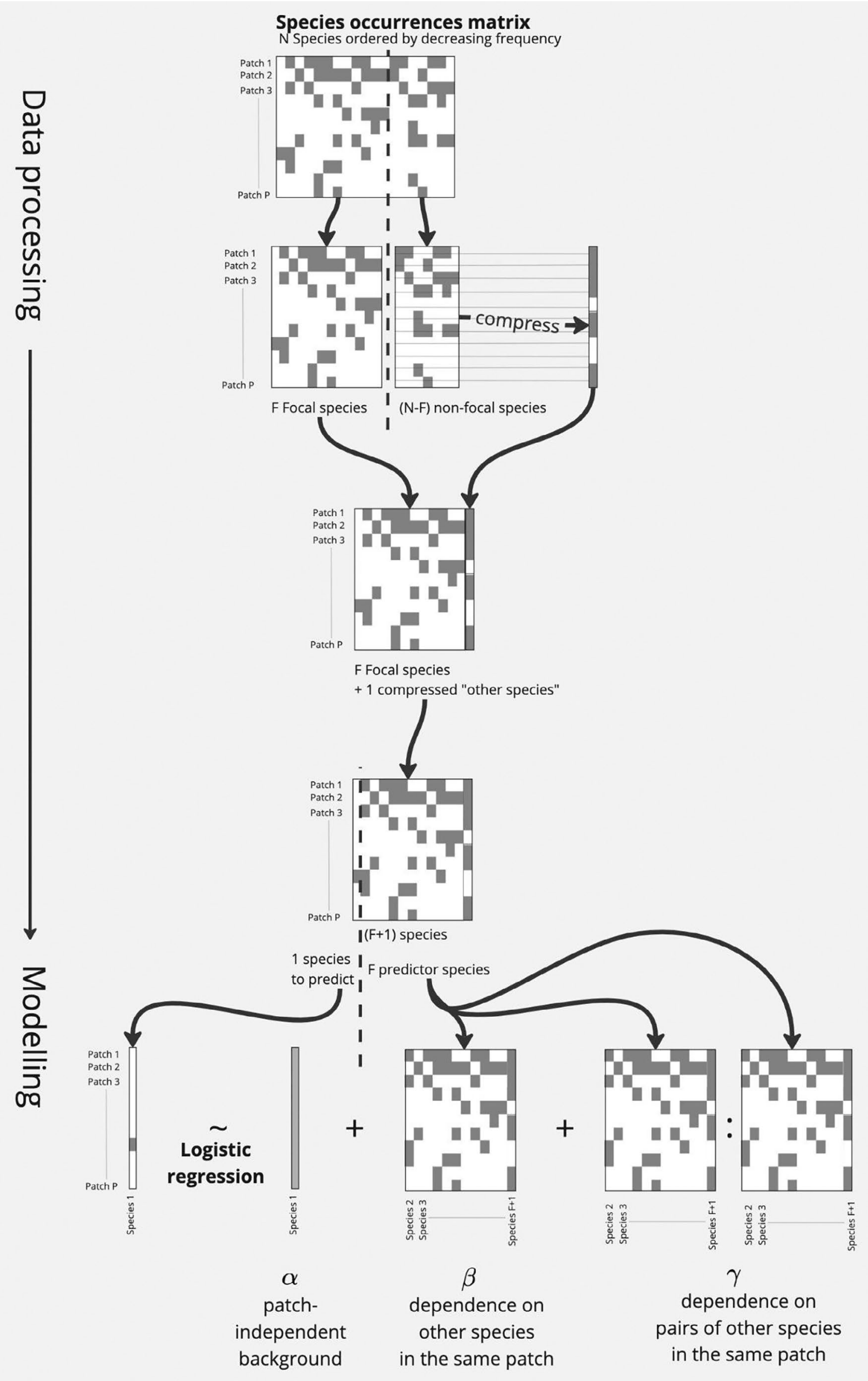
To avoid introducing such an extra parameter to adjust or marginalize over, we adopt the following method in the present paper: We perform the fit only on actual (non-empty) patches, that is, when fitting the conditional probability for species i, we perform the fit only on a subset of data where there is always at least one other (j) species present. While it might naively seem that this shortcut would introduce larger statistical uncertainties by reducing the data available for the fit, it turns out that the same uncertainties would reappear in another way in the alternative procedure. We relegate a discussion of these technicalities and of an alternative method to Appendix S4.

2.3 | Data processing

The approximations described in the previous sections are outlined together with the data-processing steps, which are also shown in Figure 1.

In order to simplify the statistical analysis, we work with presence/absence for each species instead of abundance per patch, that is matrices of ones and zeros instead of integers. In most of this paper we focus on six species that occur frequently both in the natural and restored area (for the cases of 5, 7 and 8 focal species, see Figures S4 and S5), and we always include all patches in the dataset. This is motivated by our main goal of checking how well

FIGURE 1 Workflow for compressing species occurrence matrices and modelling species co-occurrence. Species occurrence data are first split into *focal* and *non-focal* species based on frequency of occurrence. Non-focal species are compressed into a single aggregated 'other species' variable, which is then combined with focal species into a reduced matrix of $(F+1)$ species. For each focal species, logistic regression models are fitted to quantify (α) baseline occurrence probability, (β) dependence on other focal species in the same patch, and (γ) dependence on interactions among focal species.


Data processing
Modelling
Species occurrences matrix
N Species ordered by decreasing frequency
Patch 1
Patch 2
Patch 3
Patch P
compress
F Focal species
(N-F) non-focal species
F Focal species
+ 1 compressed "other species"
(F+1) species
1 species
to predict
F predictor species
~
Logistic
regression
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Species 1
Species 2
Species 3
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dependence on
pairs of other species
in the same patch

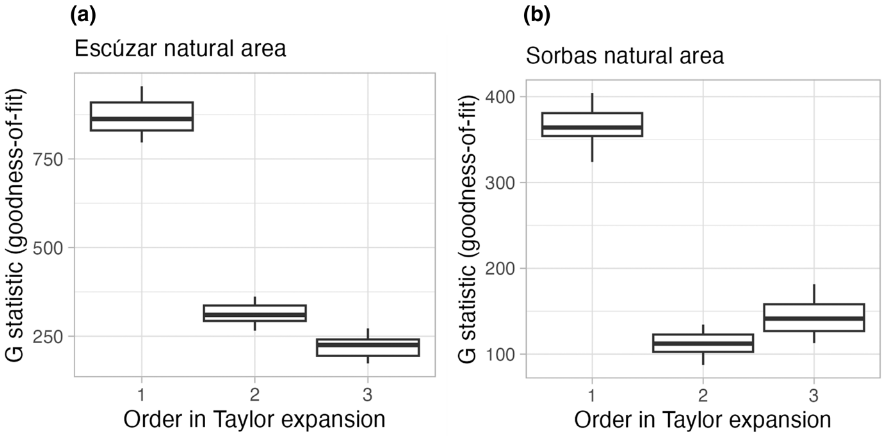


FIGURE 2 Model performance (less is better, as in a Chi-squared statistic), as a function of the order of interactions included, for the Escúzar community (panel a) and the Sorbas community (panel b). The variability comes from performing bootstrap resamplings.

the interactions between species are reproduced in a restored area compared to the nearby undisturbed natural area: we can only hope to compare coefficients for those species that are sufficiently frequent in both areas. Instead of discarding entirely the non-focal species, we treat those species as if they were different individuals of the same 'Other species' category with its own presence/absence data (see Table S1). This enables us to maintain a degree of freedom that describes the averaged effect of the other (non-focal) species that would otherwise have been discarded in step 2.

3 | RESULTS

At the seed-based restoration site (Escúzar), we recorded 12,778 plants of 28 species in the natural area and 6962 plants of 26 species in the restored area, with 17 species shared between the two. The seven-seeded species, along with *U. parviflorus*, appeared abundant in the restoration 13 years later (Table S1), indicating the success of the restoration effort. The most abundant species in the natural area were *Teucrium capitatum*, *T. zygis*, *U. parviflorus*, *H. syriacum*, *H. squamatum* and *L. subulatum*, while in the restored area they were *L. subulatum*, *U. parviflorus*, *H. squamatum*, *S. rosmarinus*, *H. syriacum*, and *T. zygis*. Five species were shared between both areas, with *T. capitatum* found only in the natural area and *S. rosmarinus* only in the restored area.

In the natural area of the seedling-based restoration site (Sorbas), we recorded 7067 plants belonging to 43 species beneath *G. struthium* and *S. viscosa* nurse plants, and in their adjacent open areas. In the restored area, we registered 2467 plants of 32 species (25 being common with the natural area) beneath *G. struthium* and *S. viscosa* nurse plants, and in their adjacent open areas. The natural area was dominated by *T. turredanum*, *H. squamatum*, *S. viscosa*, *C. hispanica*, *S. sediforme*, and *H. syriacum*, while the restored area was dominated by *S. sediforme*, *G. struthium*, *S. viscosa*, *Helichrysum stoechas*, *Helianthemum alypoides*, and *Thymus hyemalis*. Only *S. viscosa* and *S. sediforme* were abundant in both areas.

We present results for six focal species in Escúzar and four species in Sorbas (two of which can act as both nurse and recruit, see Table S1). Similar patterns are observed when including a larger number of species; however, the coefficients for these additional species tend to have greater uncertainty due to smaller sample sizes and are often indistinguishable from zero, as reflected by wider bootstrap percentile intervals (see Figures S4 and S5 for results with varying numbers of focal species).

The model setting all interactions β and γ to zero consistently yielded a worse goodness-of-fit than the model setting only the three-species interactions γ to zero, demonstrating conclusively that the occurrence of a given species depends on interactions with other species (Figure 2).

The results of the comparison between the fit of order 3 (which includes three-species γ interactions), and the fit of order 2 (which assumes $\gamma = 0$) lead to a different conclusion for each site: in the case of Escúzar, allowing non-zero direct γ interactions between three species improved the fit, whereas in Sorbas it led to overfitting. We therefore use the fit of order 3 (fitting α, β and γ) for Escúzar in the remainder of this article, and the fit of order 2 (setting $\gamma = 0$ before fitting α and β) for Sorbas (except in Figure S6 where we display extracted γ coefficients).

3.1 | Seed-based restoration

Of the seven species most frequently found in the natural area, all except *T. capitatum* were also found in the restored area. Some species, such as *T. zygis*, were overrepresented in the restored area but were included, as long as there was enough data to allow meaningful analysis in the natural area (Figure 3a).

Of the 15 pairwise interactions (β) observed in the natural area which served as the reference shrubland for the seed-based restoration, 93% were significantly positive, 7% were neutral, and none were negative (blue dots in Figure 4a). In the restored area, the positive pairwise interactions were 40%, the neutral interactions 53%, and the negative interactions (7%) (red circles in Figure 4a). About half (7 out of 15) of the pairwise interactions observed in the natural area were restored with the same sign (diagonal values in Figure 4a). The interactions that were not restored with the same sign were most of the time (7 out of 8) positive interactions in the natural area that were neutral in the restored area (off-diagonal

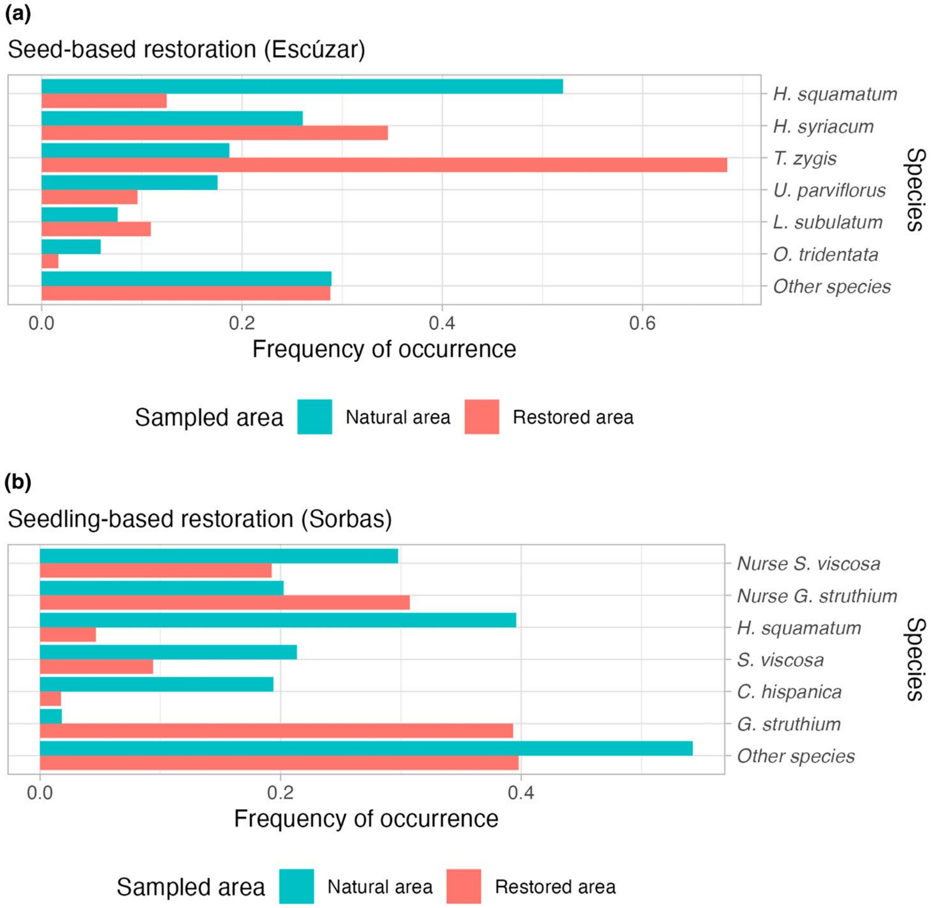


FIGURE 3 Frequency of the selected species occurring in the natural and restored areas in (a) the seed-based restoration in Escúzar. *Other species* include the remaining 22 species (in the natural area) or 20 species (in the restored area) and (b) the seedling-based restoration in Sorbas. *Other species* considered together (39 species in the natural area, 28 in the restored area). Note that *Santolina viscosa* and *Gypsophila struthium* are considered as both nurses and recruits.

values in Figure 5a), although one interaction (*H. squamatum*-*O. tridentata*) that was positive in the natural area came out negative in the restoration.

Regarding the magnitude of the pairwise interactions, most estimates in the restored and natural areas had overlapping 95% bootstrap confidence intervals, indicating similar magnitudes. However, 4 out of 15 interactions showed reduced magnitudes in the restoration area compared to the natural area.

3.2 | Seedling-based restoration

In the seedling-based restoration performed in Sorbas, one of the common species in the natural area (*T. turredanum*) was nearly absent from the restored area, and thus was not included in the focal species. However, other species present at higher frequencies in the restored area (e.g. *G. struthium* as a recruit), were included in the analysis (Figure 3b).

In the natural reference shrubland of the seedling-based restoration, we found that *G. struthium* and *S. viscosa* tended to reduce the recruitment of their own species (see the blue labels in Figure 4b). Regarding the effect of these canopy species on the recruitment of other plants, *G. struthium* acted as a nurse plant for two species (*H. squamatum* and *S. viscosa*) but not for *C. hispanica*, for which it had a neutral effect (blue dots in top panel in Figure 4b). On the other hand, *S. viscosa*, acting as a nurse plant, facilitated the establishment of *H. squamatum* and *C. hispanica*, although it had no effect on the recruitment of *G. struthium* (blue dots in top panel in Figure 4b). Interestingly, the recruit–recruit interactions were either positive (50%) or neutral (50%), but not negative (blue dots in bottom panel in Figure 4b).

In the restored area, the effect of the nurses on the recruitment of their own species was neutral (for *G. struthium*) or positive (for *S. viscosa*) (see Figure 4b). Regarding the rest of species, *G. struthium* as a nurse established positive interactions with only one of the three species (*H. squamatum*) and neutral interactions with the rest (*S. viscosa*, *C. hispanica*) (red dots in top panel in Figure 4b). On the other hand, *S. viscosa* facilitated the recruitment of two of the four species (*H. squamatum*, *C. hispanica*) in the restoration and had no effect on the establishment of the other one (*G. struthium*) (red dots in top panel in Figure 4b). Of the six interactions established between recruits, five were neutral and one was negative (red dots in the Recruit, Recruit panel in Figure 4b).

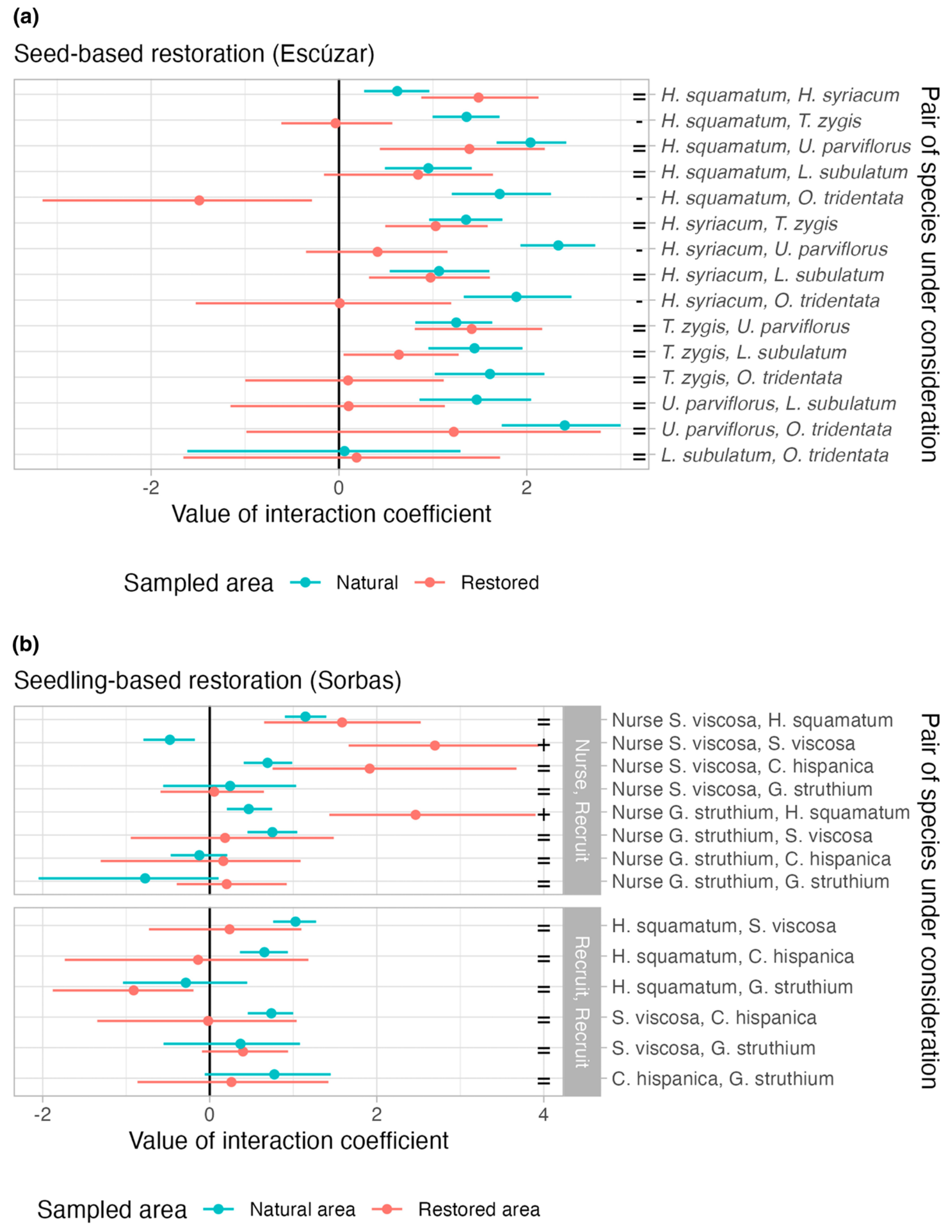


FIGURE 4 Pairwise species interaction coefficients with median values and 95% bootstrap intervals in (a) seed-based restoration (Escúzar) and (b) seedling-based restoration (Sorbas). Third-order interactions are included where relevant (see Figure 2; Figure S6). Symbols '=', '+', and '−' indicate whether restored values overlap or differ from natural areas.

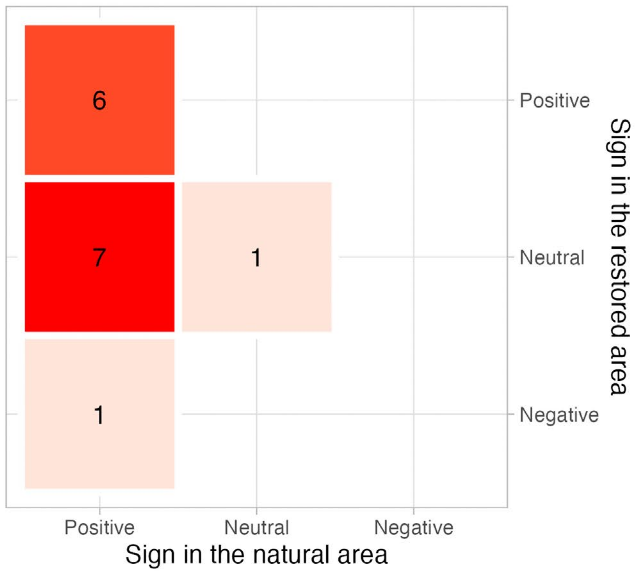
In total, of the 14 pairwise (β) interactions observed in the natural area, eight (57%) were restored with the same sign (diagonal numbers in Figure 5b). Of the interactions that were not restored with the same sign (off-diagonal values in Figure 5b), most (4 out of 6) were interactions that were positive in the natural area, but not differing from zero in the restored area. On the other hand, one interaction that was neutral in the natural zone turned out negative in the restoration, while, of the interactions that were negative in the natural area, one turned positive in the restoration.

As for the magnitude of the pairwise interactions, we found that most had overlapping 95% bootstrap confidence intervals between the natural and restored areas. However, two nurse–recruit interactions were notably stronger in the restored area: the self-interaction of *S. viscosa* (acting as both nurse and recruit) and the interaction between *G. struthium* as a nurse and *H. squamatum* as a recruit.

4 | DISCUSSION

We assessed the recovery of biotic interactions in ecological restoration, focusing on both pairwise and higher-order plant–plant interactions, using Markov Network models. We compared restored communities in abandoned gypsum mines with reference ecosystems

(a) Seed-based restoration (Escúzar)



(b) Seedling-based restoration (Sorbas)

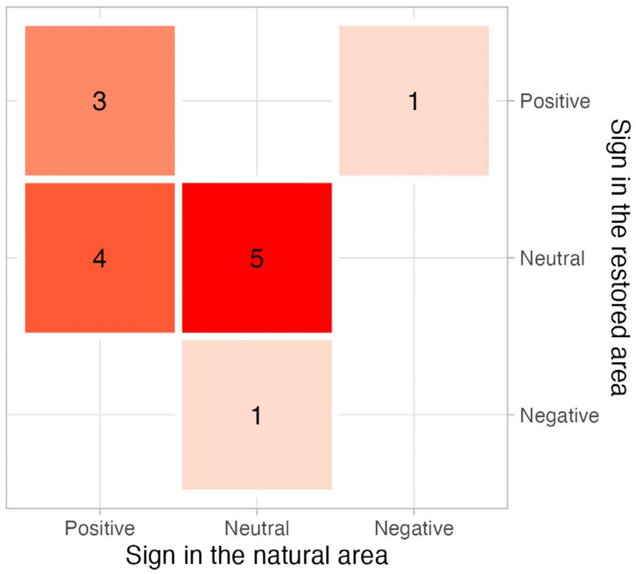


FIGURE 5 Confusion matrix with columns representing the number of pairwise (β) interactions for each sign observed in the natural area, and rows showing those in the restored area. Panel (a) shows the Escúzar community, and panel (b) shows the Sorbas community. The diagonal contains the interactions restored with the same sign, while the off-diagonals show those restored with a different sign. Note that the total possible number of pairwise interactions between six species is 15 for Escúzar, but only 14 are shown in the case of Sorbas, as the pairwise interaction between nurses is theoretically infinitely negative, as the nurses never co-occur in our data.

to evaluate whether facilitation and competition interactions are re-established after 13-year restoration efforts. Although we studied two restoration approaches—one seed-based (seeding) and one seedling-based (planting)—the objective was not to compare them, as there were no replicates for each approach, but rather to provide a theoretical framework for studying the recovery of ecological interactions. Including pairwise interactions significantly improved the model fit at both locations compared to models without interactions, providing strong evidence that the occurrence of the species is influenced by direct interactions with other species. Beyond pairwise interactions, it is ecologically relevant to incorporate higher-order interactions to capture multi-species processes, such as indirect effects, interaction chains, or context-dependent outcomes that emerge only in species assemblages. We observed a key difference when we included higher-order (third-party species) interactions. At the seed-based restoration site (Escúzar), incorporating these higher-order interactions further improved the model's accuracy, indicating that such complex interactions were likely present in the community. In contrast, at the seedling-based restoration site (Sorbas), including three-species interactions did not improve the model, suggesting that higher-order interactions were not clearly detectable under the conditions studied. These interactions may still be relevant but could depend on factors such as the species selected for evaluation, the time elapsed, and other context-specific variables, which we discuss later. Regardless of these differences, the process of testing for higher-order effects reinforces our confidence in the reliability of the pairwise interaction coefficients we extracted numerically.

As hypothesized, in the stressful environments characteristic of our study's natural areas, positive pairwise interactions were more common than negative ones, reinforcing the importance of facilitation in shaping plant community structure under arid conditions (Alcántara et al., 2025; Gleiser et al., 2025). Interestingly, the same pattern was found in the restored areas, where a greater number of positive interactions than negative ones were established. These findings support the widely held view that facilitation plays a crucial role in ecological restoration (Gómez-Aparicio et al., 2004; Padilla & Pugnaire, 2006), particularly in disturbed environments such as the mining sites examined in this study (Markham et al., 2011; Navarro-Cano et al., 2018, 2019).

The present study shows that facilitation can act independently when seeds of multiple species are sown together or when seedlings of nurse species are planted. We have found that after 13 years, about half of the observed pairwise interactions in the natural area were restored with the same sign in both the seed-based (47%) and seedling-based (57%) restored areas. Non-restored interactions were mostly positive in the natural area but became neutral in the restored area, losing their clear positive effects on the species involved. The shift from positive to more neutral interactions in restored areas may reflect that facilitative processes typical of natural communities have not yet fully developed after 13 years of restoration (Navarro-Cano et al., 2016). Although increasing competition could theoretically offset facilitative effects and contribute to the observed shift toward neutral interactions, this explanation is unlikely in our case, given the consistently low prevalence of competitive interactions across all studied scenarios. Alternatively, the decline of positive interactions in restored habitats may result from reduced abiotic stress due to soil preparation and initial irrigation, lessening the need for facilitation (Bertness et al., 2024). These possibilities underscore the complexity of successional dynamics and the need for long-term monitoring to clarify the balance between facilitation and competition in trajectories toward reference conditions (Brooker et al., 2008; Soliveres et al., 2015). The restored area may follow an alternative trajectory compared to the reference shrubland (Perring et al., 2015), meaning that not all ecological interactions are expected to recover. This divergence can be attributed to a range of biotic and abiotic factors that persist post-disturbance, fundamentally altering community assembly processes. Our interactions-based restoration approach offers a valuable framework for understanding these deviations, particularly for identifying which interactions are successfully restored and which are not. For example, modified soils resulting from specific planting densities or the dominance of particular species may modify abiotic filters and initial species configurations in ways that persist over time, influencing demographic processes, niche availability, and the outcome of interactions (Valladares et al., 2015). Such early alterations can constrain or redirect the assembly dynamics of plant communities, reducing the likelihood of convergence with reference states (Walker & del Moral, 2009). In any case, our results are similar to those found in studies on the restoration of plant–animal interactions, such as seed dispersal, herbivory, pollination, and seed predation, showing that habitat restoration typically increases the frequency of these interactions compared to degraded areas, although it does not reach the levels observed in reference areas (Genes & Dirzo, 2022).

Altogether, our results suggest that planting nurses tends to favour simpler, pairwise interactions rather than more complex, multi-species effects; however, this interpretation should be approached with caution due to limited replication and the need for further research to confirm these patterns. For practitioners, this implies that beyond selecting facilitative nurse species (Padilla & Pugnaire, 2006), it is also important to assess whether multi-species effects may enhance or hinder recruitment—particularly in spontaneous restoration settings. Where possible, comparing models with and without higher-order terms can help determine the appropriate level of complexity needed to guide effective species combinations and avoid unintended negative interactions. Given that both approaches restored pairwise species interactions in a similar magnitude (i.e. about 50%), other factors should be considered when selecting a restoration strategy (Lorite et al., 2021). The seedling-based method, although more expensive, provides immediate visual impact by introducing canopy species. In contrast, the seed-based approach is more cost-effective, promotes higher plant density and soil protection (see pictures in Figure S1), but may increase emergent competition through third-order interactions. Experimental evidence shows that when co-occurring species grow together over multiple generations, paired competition is further reduced in favour of facilitation (Schmutz & Schöb, 2024a). Although this effect was demonstrated over just three generations of cultivated plants, the early maturation of the species used in our seed-based restoration (Ballesteros et al., 2012; Lorite et al., 2021) suggests that the sampled individuals may already represent third or later generations. Consequently, they could already benefit from the positive effects of growing together over successive generations (sensu Schmutz & Schöb, 2024a, 2024b). Since half the interactions remain unrecovered after 13 years, monitoring over multiple generations is key to determine if restoration continues towards reference states. A critical next step for restoration ecology involves establishing comprehensive long-term monitoring programs that track facilitative interactions in restored gypsum habitats. By systematically assessing changes in the frequency, strength, and spatial patterns of these interactions across multiple generations, researchers can gain deeper insights into how facilitation contributes to ecosystem stability, species coexistence and resilience. This detailed understanding will enable the development of targeted restoration techniques that harness positive species interactions to promote recovery processes, optimize species assemblages, and improve the overall success of restoration efforts in dryland ecosystems. Such efforts will help ensure that restoration trajectories move beyond the risk of becoming, as Janzen (1974) warned, a ‘haphazard, semi-self-sustaining botanical garden,’ and instead culminate in the establishment of fully functional, resilient ecosystems where facilitation plays a central role.

AUTHOR CONTRIBUTIONS

Johannes Hirn, Verónica Sanz, and Miguel Verdú conceived the study. Verónica Sanz and Miguel Verdú provided financial support. Juan Lorite, Fabián Martínez-Hernández, Antonio Jesús Mendoza-Fernández, Juan F. Mota, Francisco Javier Pérez-García, José Antonio Navarro-Cano, Jorge Prieto-Rubio, Ricardo Sánchez-Martín, and Miguel Verdú collected the data. Johannes Hirn and Verónica Sanz ran the analyses. Johannes Hirn and Miguel Verdú wrote the first draft. All authors contributed to and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All the data and the scripts to run the analyses are available at https://github.com/johanneshirn/eco_restoration and also in the Zenodo repository at https://doi.org/10.5281/zenodo.19365102 (Hirn, 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Sequence of restoration activities based on hydroseeding (Escúzar) and planting 1-year-old seedlings (Sorbas).

Figure S2. Map of the study sites.

Figure S3. Climograms of the study sites. Monthly mean air temperature (red line, °C) and monthly total precipitation (blue bars, mm) are shown for Escúzar (left; Köppen–Geiger climate type Csa) and Sorbas (right; Köppen–Geiger climate type BSk).

Figure S4. Extracted bootstrap 95% intervals and median values for pairwise interactions β in (a) Escúzar natural area and (b) Sorbas natural area, as a function of the number of focal species.

Figure S5. Number of pairwise interactions with a given sign according to their bootstrap 95% interval, as a function of the number of focal species for (a) Escúzar natural area and (b) Sorbas natural area.

Figure S6. Values extracted for three-species interactions γ in (a) Escúzar natural area and (b) Sorbas natural area, with median and 95% percentile intervals over bootstrap resamples.

Table S1. Numbers of occurrences in (a) Escúzar and (b) Sorbas for those species that occur at least 10 times in total.

Appendix S2. Interaction coefficients with three species.

Appendix S3. Interactions involving four or more species.

Appendix S4. Number of empty patches as a hyperparameters.

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