Structure knows best: predicting ecological interactions across space through pairwise integration of latent network patterns

Kesem Abramov [1], Barry Biton [1], Geut Galai [1], Rami Puzis [2], and Shai Pilosof [1,3]

[1] *Department of Life Sciences, Ben-Gurion University of the Negev, Be'er Sheva, Israel*
[2] *Department of Systems Information and Software Engineering, Ben-Gurion University of the Negev, Be'er Sheva, Israel*
[3] *The Goldman Sonnenfeldt School of Sustainability and Climate Change, Ben-Gurion University of the Negev, Be'er Sheva, Israel*

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Abstract

1. Ecological communities are complex and exhibit considerable spatial variability, presenting challenges in accurately understanding these systems. A primary obstacle in ecological research is the existence of 'missing links' between species: inevitable unobserved interactions that limit our comprehension of ecological networks and their response to change. While link prediction methods have been developed to address this challenge, most approaches overlook the intrinsic spatial variability of ecological systems.
2. We introduce a flexible, spatially explicit framework based on matrix decomposition that leverages latent structural patterns to predict missing interactions and their strength, without requiring species traits or environmental data. The framework integrates information from paired auxiliary and target networks (locations) using thresholded SVD for link prediction. We applied it to plant–pollinator networks across the Canary Islands, performing pairwise predictions between locations, comparing them to within-location predictions (as a control), and quantifying how spatial variability influences predictive performance.
3. Predictions revealed that latent network structure contains substantial predictive information, with F1 scores consistently exceeding a random baseline (mean F1 = 0.68 ± 0.04 SD), while being less sensitive to interaction strength. The method enabled identifying plausible gaps in the data and producing ecologically coherent predictions. Incorporating information from auxiliary locations enhanced predictive accuracy in certain cases, but success depended critically on spatial context: predictions were most reliable when derived from nearby, ecologically similar sites or islands with larger networks, and declined with increasing geographic and ecological distance, demonstrating a clear distance-decay effect.
4. We conclude that the predictability of missing links is spatially variable, reflecting both network and species-level heterogeneity. These patterns provide insights into network structure and the ecological processes shaping it, complementing trait-based approaches. While network structure offers rich predictive information, spatial context is essential for applying it effectively: ignoring spatial variability can obscure ecological signals and inflate predictive error. Our framework is computationally efficient, transferable, and readily applicable to any system with spatial or temporal replication. It can be used for a variety of across ecological contexts, including island systems, fragmented landscapes, and environmental gradients, making it a practical and scalable tool for advancing link prediction in ecology.

Keywords: ecological networks, island biogeography, link prediction, network embedding, pollination, spatial variability

1 Introduction

What we observe in nature is never the full picture. Ecological interaction data are inherently incomplete, limited by sampling effort, methodological biases, and the cryptic nature of many interactions (Chacoff *et al.*, 2012; Souza *et al.*, 2022; Jordano, 2016; Llopis-Belenguer *et al.*, 2023). Missing links between species can obscure key patterns and processes, hindering our understanding of the structure, function, and dynamics of ecological communities (Peralta *et al.*, 2024). Given the central role of species interactions in ecosystem functioning and human wellbeing, from crop pollination to disease transmission and biodiversity conservation (Derocles *et al.*, 2018; Poisot *et al.*, 2023), completing interaction networks can improve predictions of community responses to environmental change (Tylianakis *et al.*, 2008; Pearse & Altermatt, 2013). Consequently, there is growing interest in predicting missing links (Peralta *et al.*, 2024; Desjardins-Proulx *et al.*, 2017; Rohr *et al.*, 2016; Terry & Lewis, 2020; Strydom *et al.*, 2021; Pichler *et al.*, 2020; Biton *et al.*, 2025). Notably, spatial heterogeneity, a key driver of ecological variability (Poisot *et al.*, 2012; Dupont *et al.*, 2009), has rarely been explicitly incorporated into link prediction models (Sydenham *et al.*, 2022; Dormann *et al.*, 2025). Yet incorporating spatial context offers a promising path forward, as it enables the use of variation across networks to inform predictions. Despite this potential, the influence of spatial variability on the accuracy and generalisability of link prediction remains poorly understood.

Spatial variability in interactions is driven by several ecological processes, including changes in species abundance (Vázquez *et al.*, 2007), community composition (species turnover) (Vázquez *et al.*, 2009), and interaction rewiring (Tylianakis & Morris, 2017; Trøjelsgaard *et al.*, 2015). For instance, co-occurring species may interact in one location but not another due to factors such as spatial differences in phenology (Carstensen *et al.*, 2014; Olesen *et al.*, 2011). Moreover, the degree of interaction turnover varies among species, depending on their tendency to maintain consistent partners across sites (Trøjelsgaard *et al.*, 2015; Fortuna *et al.*, 2020; Galai *et al.*, 2024). These processes often result in distance decay, whereby increasing geographical distance leads to growing dissimilarity in species and interaction composition (Baselga, 2010; Trøjelsgaard *et al.*, 2015; Vitali *et al.*, 2024; Soininen *et al.*, 2007).

Recently, several pioneering attempts have been made to incorporate spatial context into link prediction, aiming to better understand how spatial patterns, such as distance decay, can influence and inform predictive models. Sydenham et al. (2022) used scale-dependent environmental descriptors to predict plant–pollinator interactions in habitat patches. Dormann et al. (2025) integrated abundances, traits, and phylogeny to predict interaction frequencies across replicated networks, revealing that predictability declined with compositional distance. The promising approach of Dansereau et al. (2024) advanced this direction by downscaling a regional metaweb to predict local networks through probabilistic inference, based on species distributions and co-occurrence probabilities. An important consideration arising from these insightful studies is whether data pooling across sites could obscure spatial signals and lead to unrealistic predictions. Such aggregation limits the ability to assess the location-specific informativeness of data. In parallel, several additional studies have shown how information from one network can be "transferred" to inform predictions in other networks (Strydom *et al.*, 2023; Caron *et al.*, 2024; Nunes Martinez & Mistretta Pires, 2024; Biton *et al.*, 2025), considerably advancing the ability to predict interactions in target locations based on data from other areas. However, these methods often rely on traits or phylogeny, which are not always accessible.

An alternative approach is to predict links based solely on network structure, i.e., existing linkage patterns between species. Currently, the extent to which structural information from one site can enhance predictions at another within the same spatial system, and how between-site variation in network structure influences predictive success, remain poorly understood.

We introduce a framework that explicitly incorporates spatial variability by predicting interactions and their strength from one site to another, leveraging network structure. Our aim is twofold: (1) to quantify how predictions based solely on local information differ from those that incorporate non-local information, and (2) to identify the processes (e.g., species and interaction turnover) that contribute to predictive success. Specifically, we evaluate whether ecologically meaningful predictions about missing links at a target location can be made using only the structure of interaction networks from an auxiliary location, without relying on trait data. To this end, we develop a spatial prediction pipeline based on singular value decomposition (SVD)—a graph embedding technique that captures latent structural patterns in networks. Recent work has demonstrated the potential of SVD for predicting unobserved links in ecological networks (Strydom *et al.*, 2021, 2022; Nunes Martinez & Mistretta Pires, 2024), but it has not been used for spatial analysis. Moreover, prior studies combined it with additional information such as traits or phylogeny (Strydom *et al.*, 2022; Nunes Martinez & Mistretta Pires, 2024), which are not always available. In contrast, we rely exclusively on the network structure of the auxiliary and target locations.

We apply our pipeline to an empirical pollination dataset from the Canary Islands, where each island represents a distinct network. This is an ideal model system due to the clear spatial separation between the communities (networks). Because the data set contains weighted links, we are also able to perform both binary and weighted predictions. This is crucial because there have been only a few attempts to predict link weights, with limited success (Terry & Lewis, 2020; Dormann *et al.*, 2025). Additionally, because two sites were sampled within each island, we can assess the effect of spatial scale by comparing predictions based on site-level versus island-level (i.e., pooled-site) networks.

We show that predictive accuracy can be enhanced by supplementing focal network data with information from external locations, especially when networks are large and ecologically or geographically close. Our pipeline produced ecologically coherent predictions that reflected well-documented patterns, despite relying solely on structural information, highlighting the value of accounting for spatial variability for link prediction.

2 Method description

2.1 Data set used for case study

We used a plant-pollinator data set collected by Trøjelsgaard *et al.* (2015) in the Canary Islands, which are volcanic-origin islands in the Atlantic Ocean. A full description of the data set is provided in the original publication. Briefly: the data were collected in five major islands of the archipelago: El Hierro (27.804 N, 17.895 W), La Gomera (28.039 N, 17.226 W), Fuerteventura (28.564 N, 13.891 W), Gran Canaria (27.904 N, 15.433 W) and Tenerife (28.353 N, 16.912 W). Additionally, the data set included a mainland location in Western Sahara (26.161 N, 14.422 W). Owing to its complex geological history, Tenerife was sampled at two distinct locations (Trøjelsgaard *et al.*, 2013). Pairwise distances between sampling locations ranged from 52 to 455 km (Trøjelsgaard *et al.*, 2015; Vitali *et al.*,

2024). At each location, interactions were recorded at two replicate sites situated 50–194 m apart. The sites were selected based on the presence of a large population of the endemic shrub *Euphorbia balsamifera*, and shared additional perennial plant species. Sampling occurred twice between January and March 2010 by conducting 15-minute censuses for every flowering perennial species present. Sites were equally sampled according to accumulation curves and Chao2 estimates (Trøjelsgaard *et al.*, 2015). This comparability in sampling completeness allowed us to attribute differences in prediction quality to ecological variation, rather than to inconsistencies in sampling intensity (Vitali *et al.*, 2024). The data set contained a total of 249 pollinator species and 39 plant species.

2.2 Interaction network construction

Following the original publication (Trøjelsgaard *et al.*, 2015), we constructed a plant-pollinator interaction network for each site (14 in total), with rows representing plant species and columns representing pollinator species. In the weighted version of the networks, link weights (matrix cells) were calculated based on flower visitation frequencies and species relative abundances: for each pollinator, a link weight represents the species-specific number of visits paid to a specific plant species multiplied by the relative abundance of the visited plant species (Trøjelsgaard *et al.*, 2015). In the binary version, every link whose value is > 0 is considered as 1, while a 0 signifies an unobserved interaction. One potential factor that could affect our analysis is the scale at which the data are aggregated (site vs. island). Pooling data across locations is a common strategy to address ecological data sparsity, but it can also introduce spurious interactions (Poisot *et al.*, 2015; Blüthgen & Staab, 2024). While the effect of scale on link prediction is a question by itself, which is beyond the scope of this work, pooling data could affect our predictions. Hence, we repeated our analysis at two scales: site and island. For the island scale, we pooled data across the two sites within each island, summing interaction strengths, resulting in 7 island-level networks. We found that scale did not qualitatively affect the patterns we found nor the study's conclusions. We present this analysis in Appendix S1 (Fig. S1–S7), and proceed throughout the paper with the island scale since this level best addresses the questions we posed and produced better quality predictions (Fig. S1).

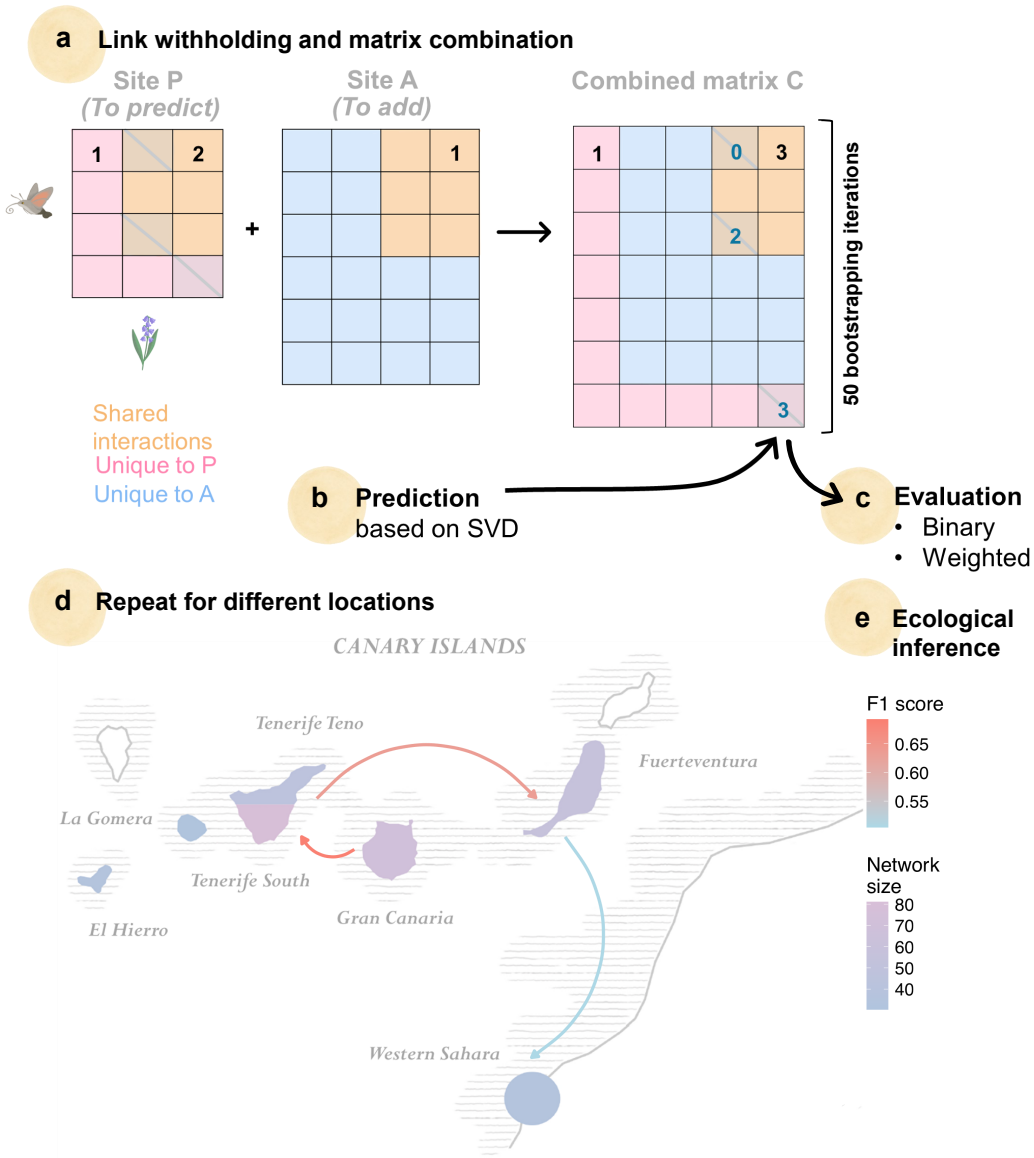

Fig. 1: Schematic overview of the spatial link prediction pipeline. (a) In each target network (whose links we predict), $\mathbf{P}$, we randomly remove 20% of observed links and an equal number of non-links (0s) by setting them to NA. This allows us to simultaneously identify potential missing links and evaluate predictive performance. We then integrate data from an auxiliary location, $\mathbf{A}$, to $\mathbf{P}$, creating a combined interaction matrix, $\mathbf{C}$. To do so, we sum the interaction strength from both locations. **(b)** SVD is applied to predict the missing values (NA). **(c)** Predictions are evaluated using both binarised and weighted values. **(d)** The entire process is repeated 50 times for each location pair in the Canary Islands. **(e)** For ecological interpretation, we relate predictive performance to potential relevant explanatory variables, including network size and similarity in species composition.

2.3 Link prediction pipeline

2.3.1 SVD algorithm

We inferred missing interactions using a matrix-completion approach based on Singular Value Decomposition (SVD), a widely used dimensionality-reduction technique, which is also commonly applied for link prediction in other fields of network science (Martínez *et al.*, 2017). SVD decomposes the observed interaction matrix into a set of latent factors that capture the underlying structure of the network in a

reduced space. Specifically, it expresses the original bipartite network as the product of two low-rank matrices, one representing rows (e.g., plants) and the other columns (e.g., pollinators). Each low rank matrix represents species embedded in a shared low-dimensional trait space. Ecologically, the axes of this space can be interpreted as latent interaction traits: unobserved gradients or affinities that influence how species interact. Species with similar interaction profiles are positioned close together along these axes, effectively clustered by their ecological roles or preferences (Strydom *et al.*, 2022, 2023).

A standard workflow for link prediction using SVD is to decompose the (possibly partially observed) matrix into its singular vectors and singular values, truncate the decomposition to the top k dimensions (latent features), and reconstruct the matrix from these k dimensions to obtain predicted values for missing entries (Strydom *et al.*, 2023). In a standard SVD workflow, the matrix must be complete (i.e., no NAs); any missing entries (including uncertain non-links, i.e. 0s in ecological networks) must be pre-filled and are then treated as true data in the factorisation. Therefore, a standard SVD cannot exclude selected 0-entries from fitting.

To overcome this limitation, we used the softImpute algorithm (R package softImpute) (Mazumder *et al.*, 2010; Hastie, 2022; Hastie *et al.*, 2015), which performs regularised matrix completion via iterative soft-thresholded SVD. In contrast to a standard SVD, softImpute works directly with matrices containing missing values (NAs), fitting only to observed entries and iteratively estimating the rest. This makes it possible to withhold both observed links (1s) and non-links (0s) for evaluation. By combining low-rank structure learnt via singular-value optimisation and the ability to exclude both presences and absences during fitting, softImpute avoids biases from arbitrary imputations and handles sparsity naturally, making it particularly well suited for ecological network applications.

softImpute seeks a low-rank approximation M that minimises the observed-entry reconstruction error while penalising complexity:

$$\min \ \|X - M\|_{\mathrm{o}}^2 + \lambda \|M\|_*, \tag{1}$$

where $\|X - M\|_{\mathrm{o}}^2$ is the sum of squared differences only over observed entries of X (the observed network), $\|M\|_*$ is the nuclear norm (sum of singular values), and λ is a nuclear-norm regularisation parameter. At each step, the algorithm iterates between (i) imputing the missing cells with the current low-rank approximation and (ii) applying a soft-thresholded SVD (shrinking small singular values toward zero) to filter out noise, and the process repeats until convergence.

Two parameters control the complexity of the imputed matrix. The first is the maximum rank (k), which sets the upper bound on the number of latent features retained in the decomposition. Smaller k values produce a simpler model capturing only dominant interaction patterns, whereas larger k values allow more nuanced structure but increase the risk of overfitting. We set $k = 2$, after sensitivity checks across a wider grid ($k = 2, 5, 10$) showed no meaningful differences in predictive performance. The second parameter is the regularisation parameter λ, which penalises complexity. Larger λ values produce more conservative predictions by applying stronger shrinkage to the singular values, reducing their magnitudes and diminishing the smaller ones most strongly. We set λ to the data-derived threshold λ_0 which is the largest value at which the solution does not collapse to an all-zero matrix (Hastie *et al.*, 2015; Hastie, 2022). Before applying matrix completion, we centered the interaction

matrix, resulting in a matrix with row and column means of zero, to improve numerical stability.

2.3.2 Matrix aggregation and link withholding

Our goal was to predict interactions in a target location matrix **P** using additional information from an auxiliary location matrix **A**. Performing SVD on **P** and **A** separately would yield different latent spaces, making it impossible to directly infer links in **P** from patterns in **A**. To ensure both matrices are represented in the same latent space, we first combined them into an aggregated matrix **C** (Fig. 1). Aggregating data is a common strategy for representing interactions at broader spatial scales, typically applied to binary presence/absence data (Strydom *et al.*, 2023). Since our data contained weighted interactions, we extended this idea to a quantitative setting: for interactions present in both locations (i.e., the same species pair), we summed their weights, while for interactions unique to one location, we retained their recorded values. This fusion preserves both shared and complementary interaction information across locations while providing a consistent basis for decomposition. The resulting matrix **C** can be viewed as a small-scale analogue of the metaweb concept (Dunne, 2006; Poisot *et al.*, 2012; Strydom *et al.*, 2023), equivalent to a quantitative gamma network encompassing all of the potential interactions occurring in a pair of locations.

To evaluate predictive performance, we withheld interactions from the target matrix **P** prior to constructing **C**. Specifically, we randomly removed 20% of observed links (Biton *et al.*, 2025) in **P** by replacing them with NA. If a withheld link also occurred in **A**, it was still set to NA in the combined matrix. While this method assumes that a link that was not observed in **P** was also not observed in **A**, it is crucial and necessary to set it to NA to prevent leakage of withheld information from the auxiliary site. Simultaneously, we withheld an equal number of randomly chosen non-links (0s) from **P**. Unlike standard link prediction evaluation in ecological applications, this approach evaluates the model's ability to predict both presences and absences, acknowledging that 0s may reflect incomplete sampling rather than true absences. Importantly, we evaluated predictions only for species present in the target location, even though completion was performed on the combined matrix **C**, which also included species from the auxiliary location **A**. Predictions for **P** were therefore informed by structural patterns in **A**, including interactions involving species absent from the target location. The rationale behind this choice is further explained in the Experimental design.

2.3.3 Model evaluation

We generated predictions from the weighted interaction data and then evaluated the algorithm's performance in both binary and weighted frameworks. For binary evaluation, raw SVD predictions were transformed to the interval [0,1] using a logistic function ($1/(1+e^{-x})$). Each transformed value was then classified as a predicted link (1) or non-link (0) using a probability threshold. We fixed the threshold at 0.6, chosen in preliminary analysis to balance two performance metrics: the F1 score and balanced accuracy (Fig. S8). The F1 score, our primary evaluation metric, is the harmonic mean of recall (the proportion of true interactions correctly predicted) and precision (the proportion of predicted interactions that are actually true). F1 reflects the quality of predicting existing links, with a higher score representing higher quality predictions. Because the withheld evaluation set contained equal numbers of interactions and non-interactions (balanced withholding data set), random guessing yields an expected F1 score of 0.5. Balanced accuracy is the average of recall and specificity (the proportion of non-interactions correctly identified), and complements the F1 score by also accounting

for non-interactions. In addition to threshold-based evaluations, we evaluated predictive performance across classification thresholds by calculating the area under the precision–recall curve (PR-AUC) and the area under the receiver operating characteristic curve (ROC-AUC), which are standard measures of predictive performance across all thresholds.

The SVD procedure decomposes the interaction matrix and reconstructs it using a reduced number of dimensions (k, see Link prediction pipeline). Because some information is lost in this reduction, the reconstructed matrix is not identical to the original and may contain negative values, particularly for cells corresponding to zeros. For evaluating weighted predictions, we first set negative predicted values to zero. We then quantified how closely the predicted interaction strengths ($\hat{y}_i$) matched the observed strengths (y_i) using the normalised Nash–Sutcliffe Efficiency (NNSE) (Dormann *et al.*, 2025):

$$\mathrm{NSE} = 1 - \frac{\sum_{i=1}^{n} \left(y_i - \hat{y}_i\right)^2}{\sum_{i=1}^{n} \left(y_i - \bar{y}\right)^2}, \tag{2}$$

where $\bar{y}$ is the mean of the observed values. NSE measures predictive skill relative to simply predicting the mean of the observations. To facilitate comparison across networks, we normalised NSE to the interval [0,1]:

$$\mathrm{NNSE} = \frac{1}{2 - \mathrm{NSE}} \tag{3}$$

An NNSE of 0.5 indicates no predictive skill (equivalent to predicting $\bar{y}$), and values closer to 1 indicate higher predictive accuracy. Unlike metrics such as RMSE, NNSE is scale-independent, allowing comparisons between networks with different ranges of interaction strengths.

2.4 Experimental design

We applied the prediction–evaluation pipeline to all 42 pairwise combinations of target (**P**) and auxiliary (**A**) island networks, as well as to the 7 cases of self-prediction (target network predicted using only its own data, with no auxiliary location). This yielded 49 prediction cases. For each case, we performed 50 independent iterations of random link withholding, analogous in spirit to repeated cross-validation, to reduce the influence of single withholding configuration on the performance estimates.

While predictions were evaluated only for species present in the target network **P**, the imputation procedure was performed on the combined matrix **C**, which also included species from the auxiliary community **A**. This design allows predictions for **P** to be informed by additional interaction patterns observed in the auxiliary location, providing indirect evidence that can compensate for missing data. At the same time, incorporating species absent from **P** may introduce noise if their interactions in **A** reflect ecological dynamics irrelevant to the target community. To assess this trade-off, we repeated the analysis using only the subset of species shared between the target and auxiliary locations.

2.5 Ecological correlates of predictive performance

To explore how predictions vary across space and community structure, we related the average of each evaluation metric (F1 for binary predictions, NNSE for weighted predictions) to ecological and network-level variables.

2.5.1 Compositional and geographical distance decay

We tested for distance decay in predictive quality by correlating the evaluation metrics with geographic distance between network pairs, using Pearson's correlation. Additionally, we applied multiple regression on distance matrices (MRM), to account for spatial autocorrelation via permutation-based inference (Legendre *et al.*, 1994; Lichstein, 2007), following the approach of Vitali *et al.* (2024) applied to the same data set. The slope of the MRM indicates the magnitude of distance decay. Analyses were carried out in R using the vegan and ecodist packages (Goslee & Urban, 2007; Oksanen *et al.*, 2013). As geographical distance decay emanates from species and interaction turnover, we further correlated the Jaccard similarity (between every pair of networks) in pollinator and plant species and interactions with evaluation metrics.

2.5.2 Network size and connectance

The variables described earlier are candidate ecological variables that may influence predictability. However, variability in predictive capacity may also partially result from a mathematical reason. In particular, the size (i.e., the total number of plant and pollinator species) and connectance (proportion of realised links, or network density) of the matrix are known to correlate with multiple network properties (Delmas *et al.*, 2019) and may therefore influence model performance (Farrell *et al.*, 2022). We correlated the size and connectance of $\mathbf{P}$ and $\mathbf{C}$ (which is larger and sparser than $\mathbf{P}$) with our evaluation metrics, using Pearson's correlation.

3 Results

The Canary Islands pollination system consisted of seven networks with sizes ranging from 62 to 84 species and mean connectance of 0.15 ± 0.02 SD (Supplementary Table S1).

Predictive performance was higher when including all species present on both (auxiliary and target) islands, compared to restricting analyses to the subset of species shared between them (Fig. 2a,b). Thus, retaining the full species assemblage across spatial contexts provides more informative predictions. Given this finding, we hereafter present results of predictions made with the species of both locations.

Overall, the binary predictive performance of the algorithm was strong, with an F1 consistently exceeding 0.5 (the value expected under random guessing) (Fig. 2). The average F1 across the 49 test cases was 0.68 ± 0.04 SD, with a maximum value of 0.74. Results for non-thresholded evaluators followed similar trends (Fig. S9). In contrast, weighted predictions were not significantly different than random (Fig. 2b), despite a significant correlation between the observed and predicted link weights (Fig. S10). The low predictive power of weights was primarily due to the tendency of the algorithm to assign a wide range of predicted values to the weak observed interactions (Fig. S10).

3.1 Evaluating the importance of auxiliary information for predictions

There was no statistical difference in F1 between self-predictions (matrix diagonal values in Fig. 2c) and predictions made using auxiliary locations (off-diagonal values in Fig. 2c) (Wilcoxon test: $P = 0.56$). The lack of statistical difference partly reflected the higher variability in F1 for auxiliary predictions (0.57 − 0.74) compared to single-location predictions (0.64–0.71). However, this variation indicates

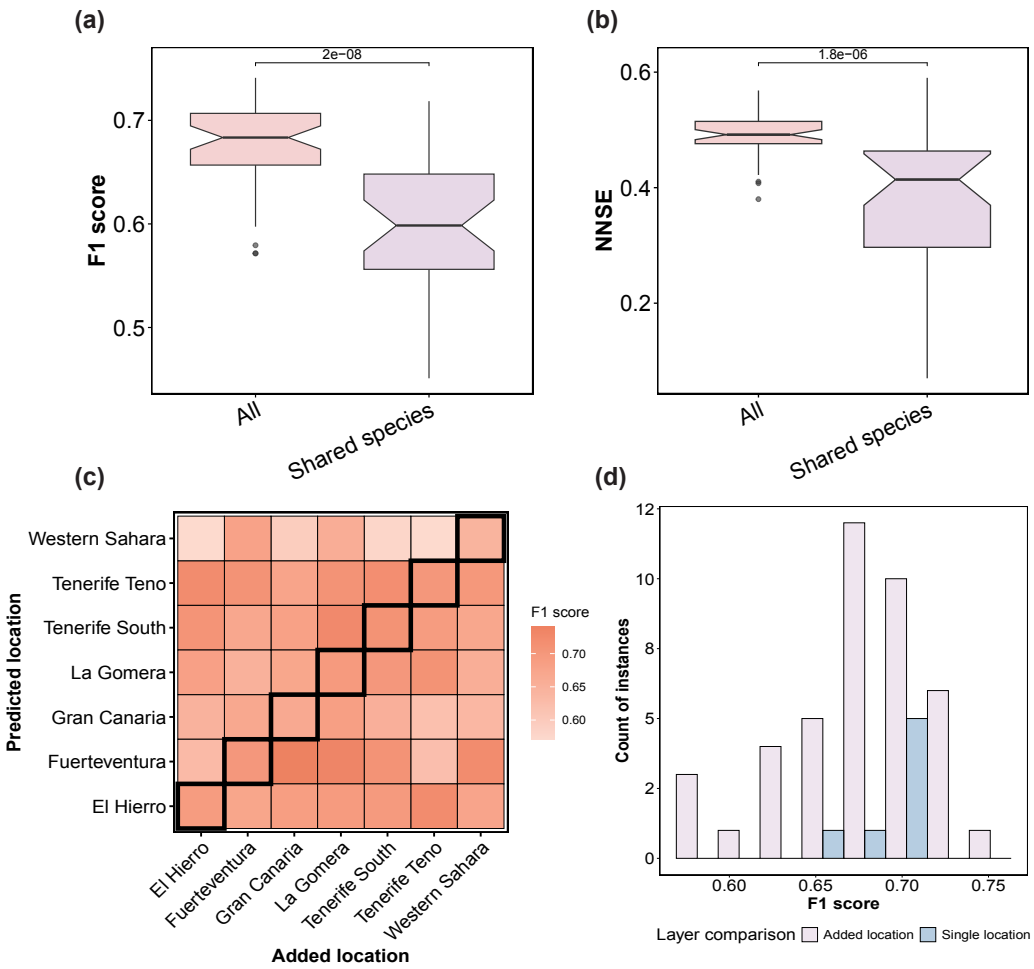

Fig. 2: Predictive performance depends on the spatial context. Comparison of predictive performance for binary **(a)** and weighted **(b)** networks using either all species pooled across auxiliary and predicted locations or only overlapping species between locations. P-values correspond to Wilcoxon test for F1 scores and t-test for NNSE. **(c)** Predictive performance of 42 auxiliary-location predictions (off-diagonal values) versus 7 self-predictions (diagonal values, highlighted in a black frame), showing location-specific variability in the predictive power provided by auxiliary information. **(d)** Histogram of values from panel **(c)**, illustrating that the highest F1 scores were generally achieved when incorporating data from auxiliary locations rather than single locations, which also produced large variability in F1.

that a fine-detailed look at pairwise predictions is insightful since predictive performance varied across locations (Fig. 2c). In some cases, incorporating data from auxiliary locations produced the highest quality predictions, but in others it reduced accuracy (Fig. 2d). Notably, Western Sahara, which was the only mainland location, produced the lowest F1 scores for predictions made using auxiliary island data (mean 0.61 ± 0.05 SD). Together, these results indicate that the benefits of using information from auxiliary locations are location-specific.

3.2 Interaction-level spatial transferability

Until now, we have analysed predictive power at the location level. Spatial replicability allows us to extend this analysis to variability at the interaction level. We visualised the set of 1,161 predicted but unobserved links across the Canary Islands pollination system, positioning them alongside the empirically-observed links (Fig. 3a, Fig. S11). Most of these interactions (835, 72%) were obtained through either self-prediction or auxiliary analyses (Fig. 3b). As expected, these interactions fre-

quently involved the most generalist species, which also occurred on most islands (Fig. S11, Fig. S12). Nevertheless, 66 interactions (6%) of predicted interactions could only be recovered using information from auxiliary locations. Finally, 260 predicted interactions (22%) were recovered exclusively through location-specific information and not with auxiliary data (Fig. 3b). These belonged mainly to species with intermediate or low degree (Fig. S11), indicating that some interactions can only be detected within their specific spatial contexts.

It is important to note that some predicted links may represent false positives. Typically, validation of such predictions relies on external datasets (e.g., Stock *et al.* (2021); Strydom *et al.* (2022)), but the presence of an interaction in a completely different system does not guarantee its occurrence in the system at hand. Our spatial framework presents an opportunity to overcome this issue because it enables validation within the system itself, thereby increasing confidence in the predicted links. We recalculated the proportions focusing only on the 496 *within-system validated links*, which are the predicted interactions that were observed at least once in the system. Of these, most (428 links, 86%) were recovered by both approaches, 60 (12%) were predicted only from within-island data, and 8 (2%) were identified exclusively when incorporating information from other islands.

A noticeable trend was the tendency of the algorithm to assign more missing links to generalists (species with high degree), such as the shrub *E. balsamifera* (Fig. 3a). This trend was reflected in a strong correlation between the number of predicted links assigned to each species and the total number of observed partners it had across all islands (Fig. 3c). Nonetheless, there were notable exceptions to this pattern. Several highly generalist species, such as *Launaea arborescens*, received only few additional predicted links. Closer inspection of the prediction patterns revealed more nuanced spatial variability (Fig. S11). For instance, missing interactions involving male *E. balsamifera* were consistently recovered regardless of whether local or external data were used. In contrast, female individuals of the same species displayed a different pattern, with certain missing links predicted only when information from other islands was included (Fig. S11).

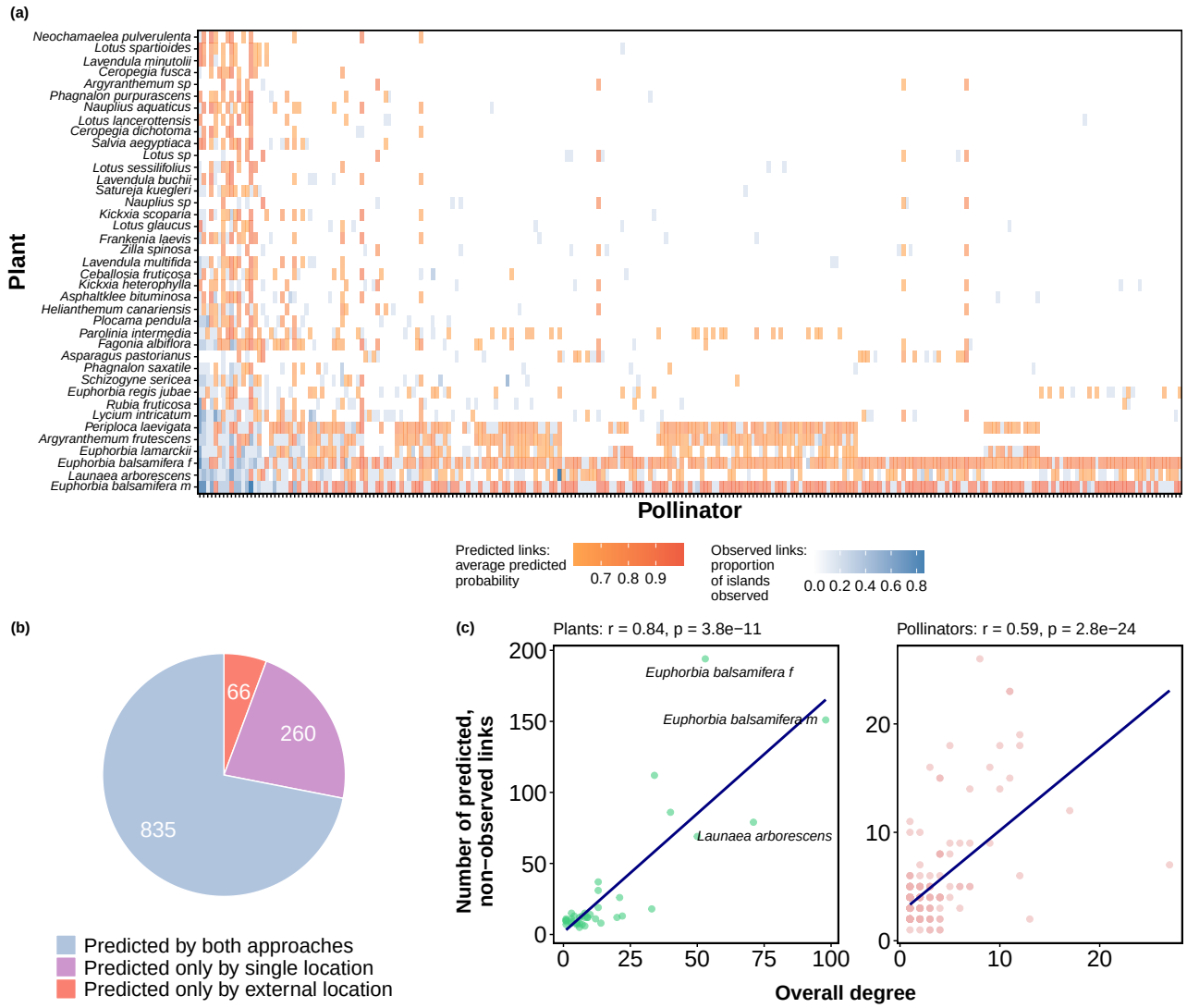

Fig. 3: Mapping potential missing interactions in the Canary Islands pollination system. (a) Blue cells represent observed interactions; darker shades indicate a higher proportion of islands in which the interaction was recorded. Orange cells indicate unobserved interactions (interactions never observed in the data), that were predicted to exist based on an average predicted probability above the classification threshold across withholding instances within 49 prediction cases (including auxiliary and self-predictions). The intensity of orange reflects this average predicted probability. Species are ordered according to their overall observed degree (total number of unique interaction partners across islands). **(b)** Amount of unobserved interactions that were predicted using only self-prediction, only using auxiliary islands, or by either of these approaches. The counts correspond to the interactions detailed in Fig. S11. **(c)** The number of unobserved yet predicted links per species (orange cells in **(a)**) is strongly correlated with the species' overall degree across locations (Pearson's correlation). The two most generalist plants in the system are noted.

3.3 Assessing the correlates of spatial predictability

Predictive quality significantly improved with increasing similarity in species composition (Fig. 4a,b) and in interactions (Fig. 4c) between the target and added locations. We expected that the positive effect of similarity on predictive power will mirror a distance decay in predictive capacity such that the ability to correctly identify links will decline with increasing geographic distance between locations. We indeed detected the expected pattern (MRM, $a = -0.00015$, $P = 0.01$ and corresponding correlation trend in Fig. 4d). However, these patterns were not apparent when predicting interaction strength

($P > 0.05$ for correlations of NNSE with geographical distance or species and interaction turnover).

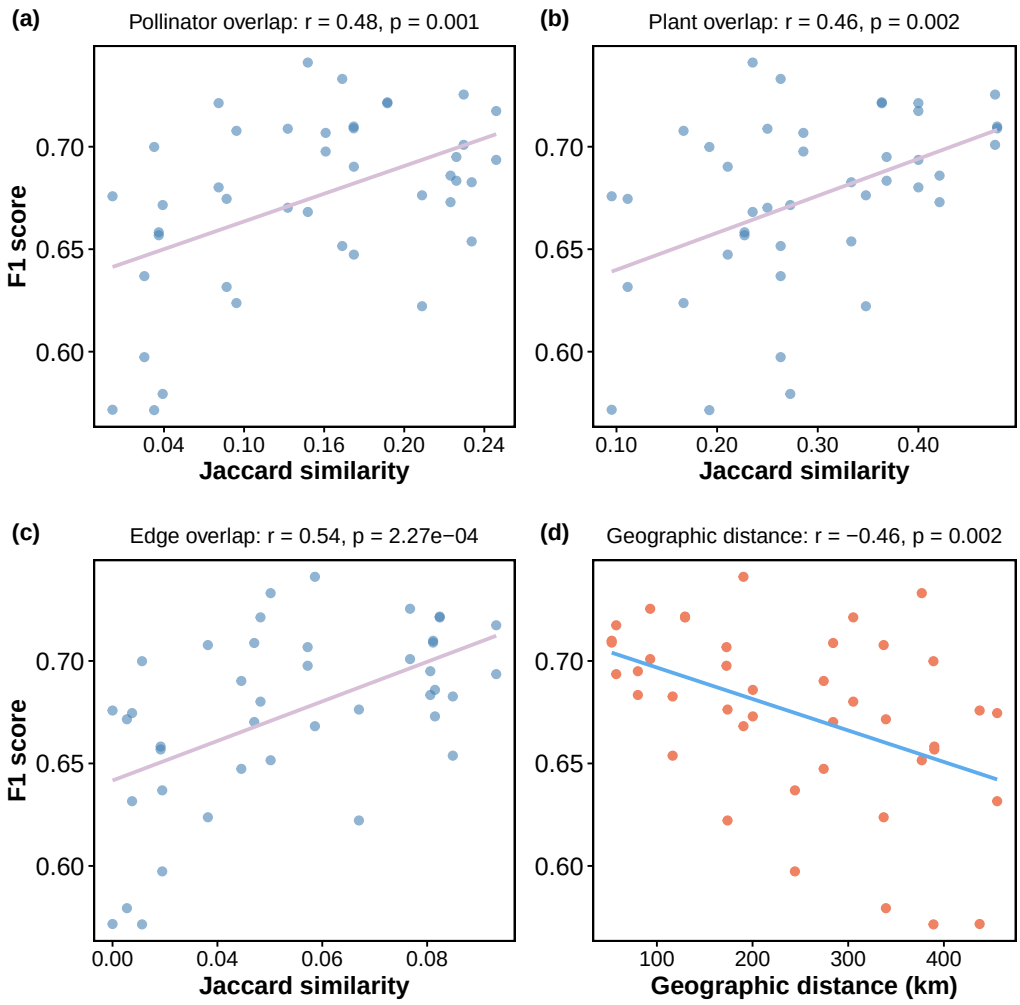

Fig. 4: Compositional similarity and interaction consistency enhance predictive accuracy. Predictive ability (F1 scores) increases with greater similarity in pollinator composition **(a)**, in plant composition **(b)** and in interactions **(c)** between predicted and added locations. **(d)** Predictive accuracy declines with increasing geographical distance between predicted and added locations.

An important question is whether predictive ability results solely from ecological variability or also from network properties, which are known to correlate with structure (Delmas *et al.*, 2019). Binary predictions were not correlated with the connectance of the target or combined matrices, although a trend was apparent (Fig. 5a,b). In contrast, predictive performance of link weights significantly decreased as the target networks became denser (Fig. 5c,d). As expected, these trends were generally opposite to the correlation with network size (Fig. S13).

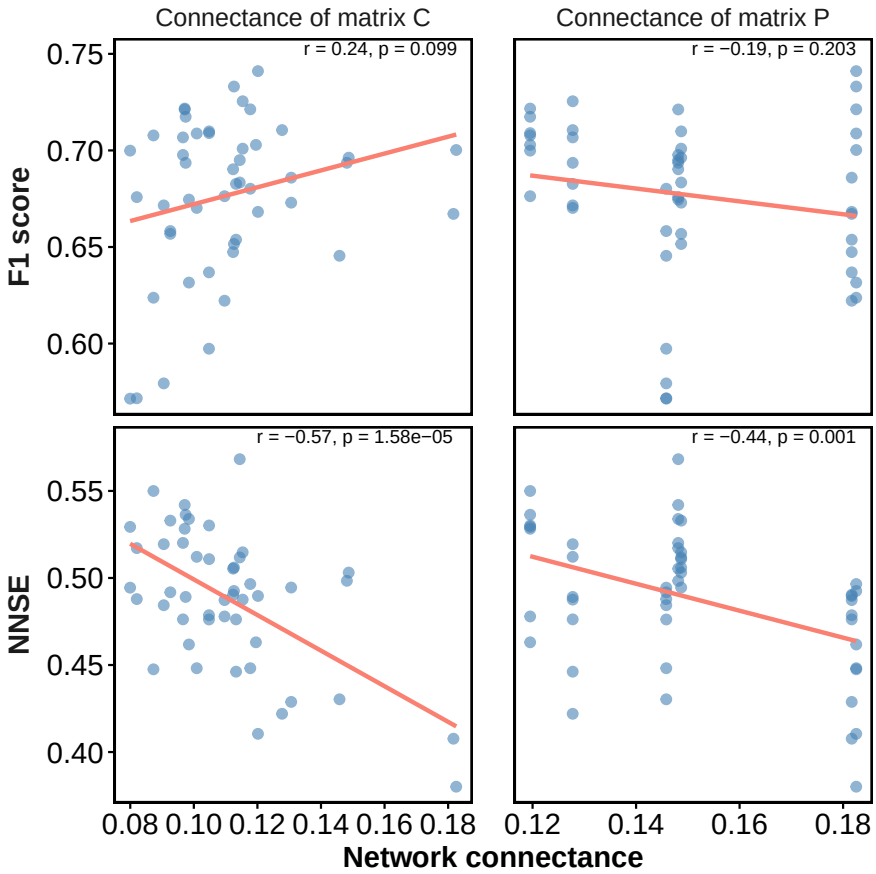

Fig. 5: Effect of network connectance on predictive performance. Binary prediction quality was not related to the connectance of the predicted matrix $\mathbf{P}$ nor to the matrix combining interactions from the predicted and added locations ($\mathbf{C}$) (upper panels). Weighted prediction quality significantly decreased as the networks became denser (lower panels). Nevertheless, we note that for this data set weighted predictions were generally not better than random.

4 Discussion

A substantial proportion of ecological interactions remain undetected, even with extensive sampling efforts (Chacoff *et al.*, 2012; Jordano, 2016). We developed and tested a spatially explicit framework for link prediction that addresses the long-standing methodological gap of how spatially replicated networks can be leveraged for inference. By leveraging latent structural information from paired auxiliary and target networks, our method accurately predicts missing links and identifies potential data gaps. Our pairwise-location approach represents the opposite end of the spatial aggregation spectrum from the metaweb: rather than aggregating all networks in the system (Strydom *et al.*, 2023), we combine only two at a time. While metawebs can be downscaled to local predictions (Dansereau *et al.*, 2024) or networks upscaled by aggregation, our method captures the most localized form of cross-site inference.

We found that spatial variability exerts a measurable influence on our capacity to uncover missing interactions, and that integrating external information with focal data can enhance predictive performance. However, predictive ability depends on the ecological compatibility of the added data (e.g., poor prediction of the mainland Western Sahara using additional information from islands). Combining larger and ecologically similar networks yields better predictions, with adjacent locations providing the most compatible data, supporting distance-decay expectations (Soininen *et al.*, 2007; Vitali *et al.*,

2024; Trøjelsgaard *et al.*, 2015). Therefore, aggregating data from dissimilar, distant locations, which is done when predicting links in metawebs (Strydom *et al.*, 2023) or multi-site aggregations (Dormann *et al.*, 2025), could reduce predictive power.

Our results indicate that network structure encapsulates substantial information for predicting interactions, consistent with previous studies (Terry & Lewis, 2020; Strydom *et al.*, 2022, 2023; Biton *et al.*, 2025). Degree (the number of unique partners), which reflects a species' niche breadth, emerged as a key predictor of link assignment in our system. This finding echoes earlier work showing that degree often dominates as a determinant of interaction predictability (Farrell *et al.*, 2022; Biton *et al.*, 2025). In our spatial context, however, degree also carries a geographic signal, being positively correlated with species occurrence across islands (Fig. S12). Yet degree alone did not fully explain model behaviour: some highly connected species received few additional predicted links, and we also detected intra-specific variation in link assignments (Fig. S11). These patterns suggest that the algorithm captures structural information beyond simple partner counts, integrating subtler spatial and topological signals.

Our study shows that spatial information can be leveraged for predicting interactions, yet two main aspects should be further considered in future developments of this approach. First, as with other link-prediction methods, our framework may predict links that do not truly occur in nature. However, spatial replicability provides a means to conduct *within-system* validation. Within-system validation is advantageous because it draws on information from the same ecological context, capturing relevant spatial and ecological variability, rather than relying on external datasets that may differ in sampling design, community composition, or environmental conditions (Stock *et al.*, 2021; Farrell *et al.*, 2022). Consequently, this approach helps prioritise candidate links for targeted sampling and guides more efficient data collection. In our analysis, only 37% of the predicted links were observed at least once in the system. Given the limited spatial and temporal coverage of our dataset, some non-validated predictions may nonetheless represent ecologically valid but undetected interactions. False positives can be further reduced by integrating additional predictors beyond network structure, such as phylogenetic or trait-based information (Peralta *et al.*, 2024).

Secondly, while binary link predictions were consistently accurate and outperformed random expectations, predictions of interaction strengths performed no better than random and showed limited associations with ecological variables beyond network size and connectance. The low predictive ability of quantitative interactions aligns with previous studies highlighting the difficulty of modelling interaction weights (Terry & Lewis, 2020; Dormann *et al.*, 2025). Improving quantitative link prediction therefore remains an important methodological frontier. Future efforts could explore alternative strategies for aggregating and transferring link weights across space, for instance by integrating abundance-based scaling or probabilistic weighting schemes, and by employing other modelling approaches than matrix factorisation.

Our framework is transferable and scalable to a wide range of systems with spatial replication, requiring only moderate computation because soft-thresholded SVD operates efficiently on sparse matrices. Future extensions should consider three elements: (i) the spatial scale of the networks, and resulting similarity between them; (ii) strategies for matrix aggregation; and (iii) approaches to link withholding (for instance, varying the proportion of links and non-links withheld). Given the broad range of possible technical and ecological extensions, exploring them all is beyond the scope of this study.

Nonetheless, one of the strengths of this framework is its flexibility, and we look forward to seeing how future work will adapt and expand it across diverse ecological systems. We tested our approach on an island system with a clear separation between locations and in which differences between islands are expected due to geological history (Trøjelsgaard *et al.*, 2013, 2015). Natural next steps include extending the approach to inland mosaics, such as natural habitat patches within agricultural landscapes, to evaluate how spatial signals vary with habitat connectivity or compared to island systems. Less evident extensions are applications to temporal networks or to gradients such as elevation and climate, which unlike space represent directional systems. In such cases, source–target predictions would need to be constrained to move forward in time or along gradient direction.

In conclusion, our study shows that latent patterns in network structure can effectively capture spatial signals, enabling the evaluation of how external data can improve the prediction of missing ecological interactions. Our results demonstrate that our ability to predict these missing links is spatially variable. Therefore, while network structure is highly informative for prediction, incorporating spatial context is essential to determine when and where this information can be reliably applied. The flexible framework we introduce offers an opportunity to integrate spatial variability into link prediction, supporting more realistic and ecologically informed predictions across diverse replicable systems.

5 Code and data availability

The data are available in the repository set up in the original publication by Trøjelsgaard *et al.* (2015): `https://datadryad.org/dataset/doi:10.5061/dryad.76173`. The full code and technical descriptions on how to run our pipeline are available on the GitHub repository `https://github.com/Ecological-Complexity-Lab/svd_based_spatial_prediction/tree/clean_for_publish`.

6 Acknowledgments

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8 Author contribution statements

Kesem Abramov conceptualized the study, developed the methodology, conducted the investigation, performed formal analysis, developed and implemented software, prepared visualizations and wrote the original draft; **Barry Biton** developed the software and provided validation; **Geut Galai** developed and implemented software, performed formal analysis, prepared visualizations and conducted validation; **Rami Puzis** developed the methodology and reviewed the original draft; **Shai Pilosof** conceptualized the study, secured funding and resources, conducted investigation, developed the methodology, developed software, provided supervision and wrote the original draft. All authors contributed critically to the drafts and gave final approval for publication.

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9 Supplementary information

9.1 Appendix S1: Scale analysis

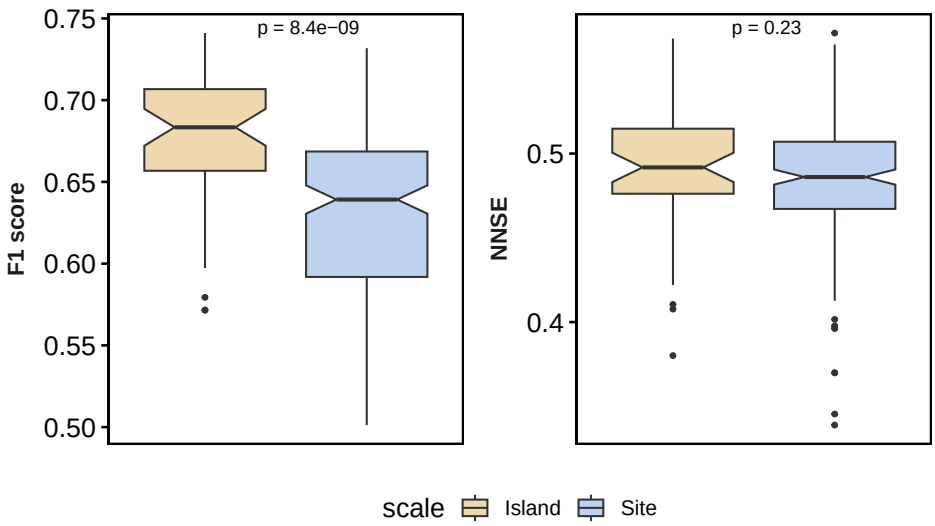

Fig. S1: Effects of spatial scale on predictive performance. Binary link prediction capacity, measured by F1 scores, is higher when site scale data are aggregated into island scale. However, weighted predictive power (NNSE) is similar at the site and island scales. P values denote Wilcoxon test results.

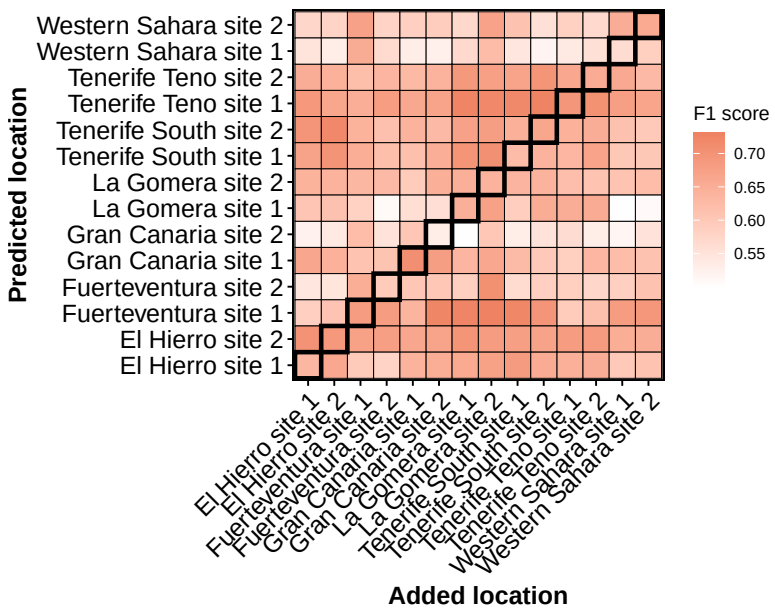

Fig. S2: Site-scale variation in predictive capacity. F1 scores vary according to the pair of predicted and added sites.

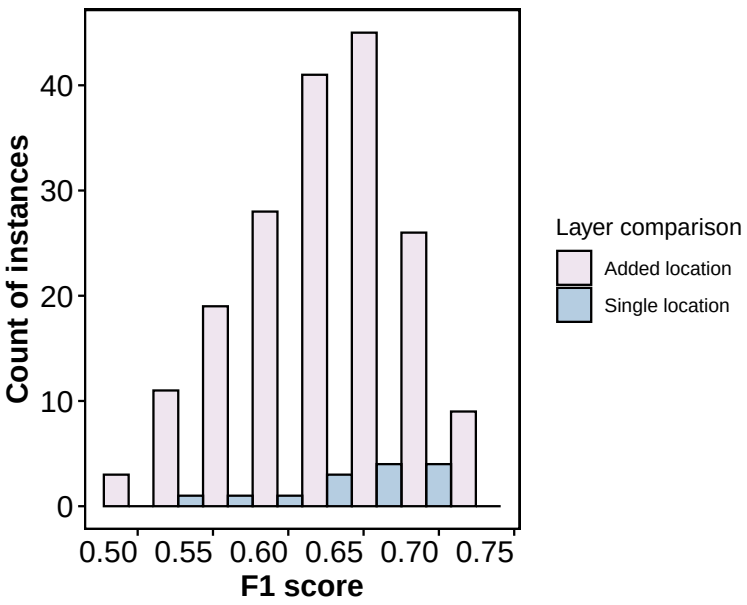

Fig. S3: Distribution of site-scale prediction quality. Quality of binary predictions according to the F1 scores when incorporating data from other sites compared to using single-site data.

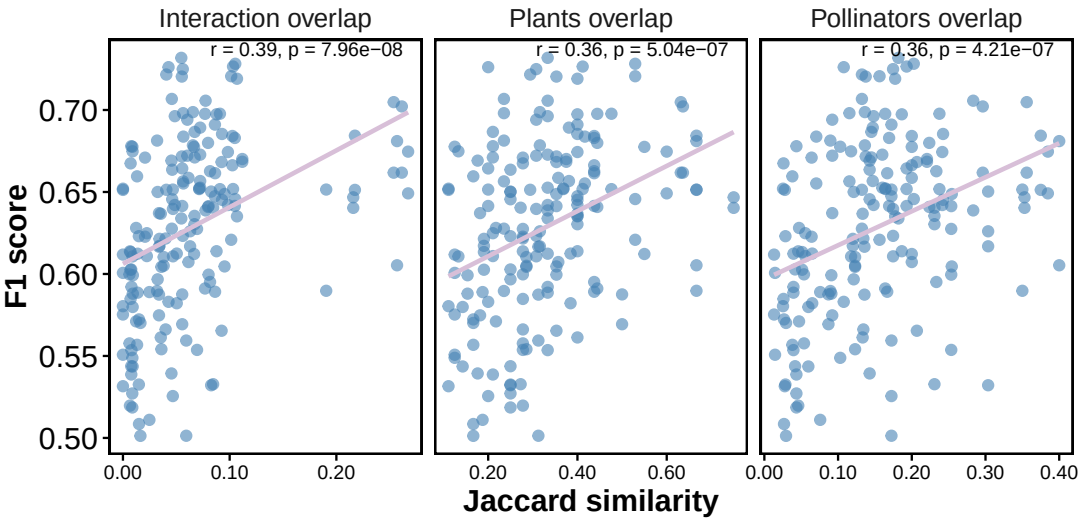

Fig. S4: Site-scale predictive quality is correlated with ecological similarity between sites. Predictive ability (F1 scores) increases with greater similarity in interaction and species composition between predicted and added sites.

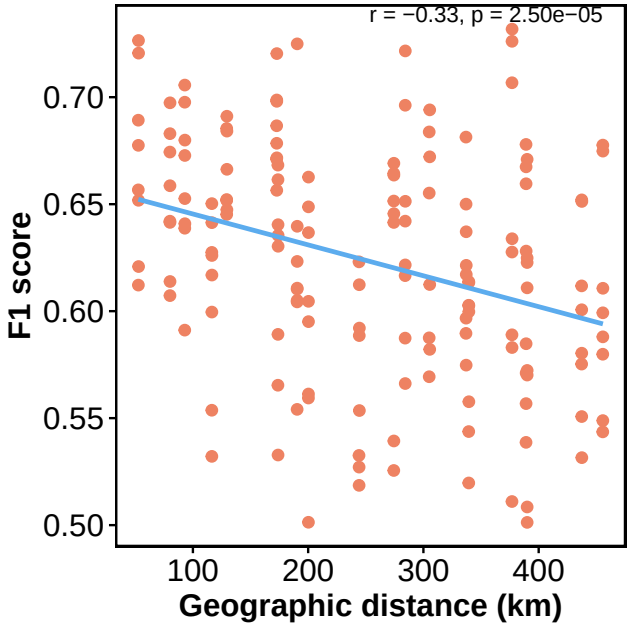

Fig. S5: Distance decay in site-scale predictive performance. Predictive accuracy declines with increasing geographical distance between predicted and added sites, aligned with MRM test results ($a = -0.00015$, $P = 0.003$).

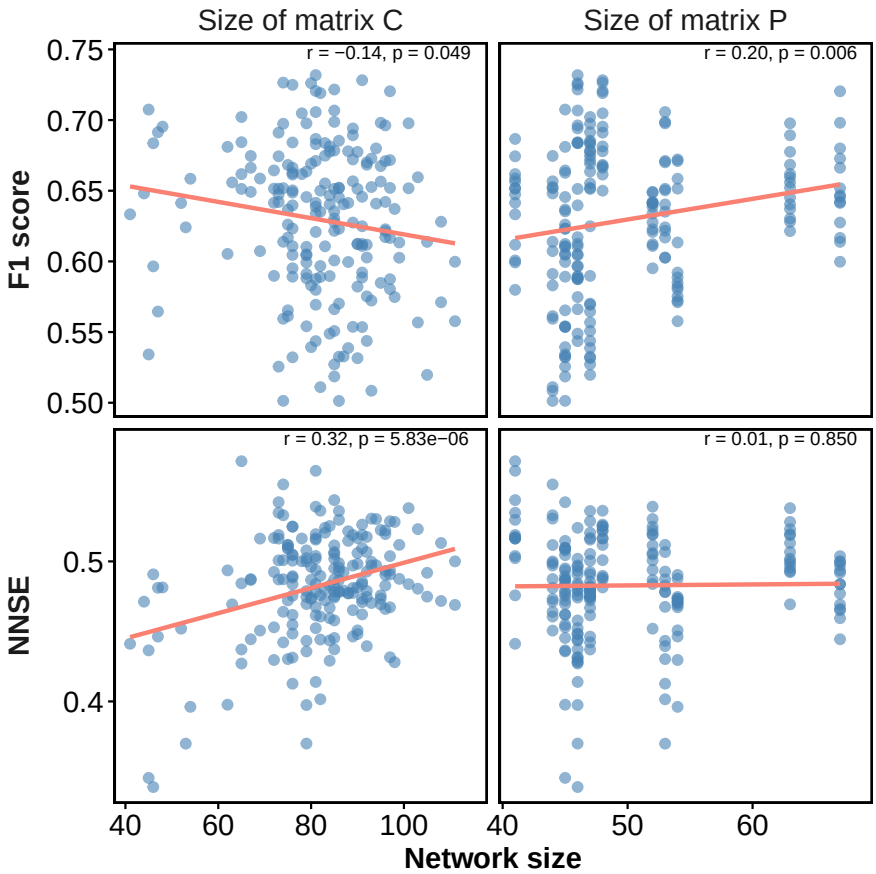

Fig. S6: Effect of site-scale network size on predictive ability. Binary prediction quality (upper panels) tends to improve as the size of the predicted network increases. Weighted prediction quality, on the other hand, increases as the size of the matrix combining interactions from the predicted and added sites increases (lower panels).

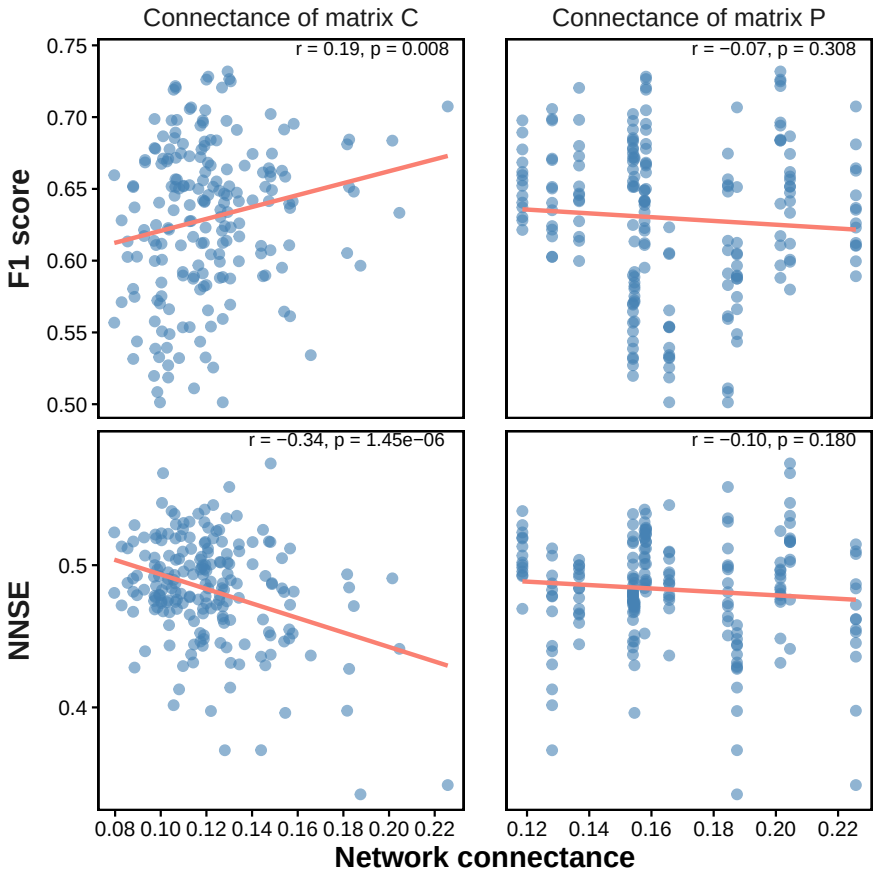

Fig. S7: Effect of site-scale network connectance on predictive performance. Binary prediction quality increases with greater combined matrix density (upper left), whereas weighted prediction accuracy declines under the same conditions (lower left). By contrast, prediction quality shows no clear relationship with the connectance of the target matrix (right panels).

9.2 Appendix S2

Table S1: Network size and connectance (density) for each location in the data set.

Island	Size	Connectance
Tenerife South	84	0.128
Tenerife Teno	78	0.120
Western Sahara	72	0.146
La Gomera	67	0.149
El Hierro	65	0.148
Fuerteventura	65	0.183
Gran Canaria	62	0.182

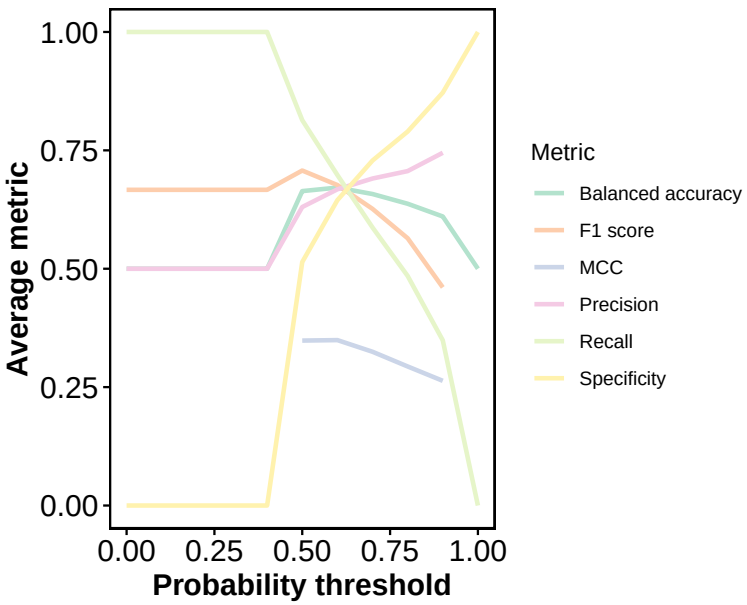

Fig. S8: Selecting the optimal threshold for classifying binary predictions. The classification threshold was defined as the point where mean F1 score and balanced accuracy across location pairs intersect, based on thresholds ranging from 0 to 1 and intervals of 0.1 .

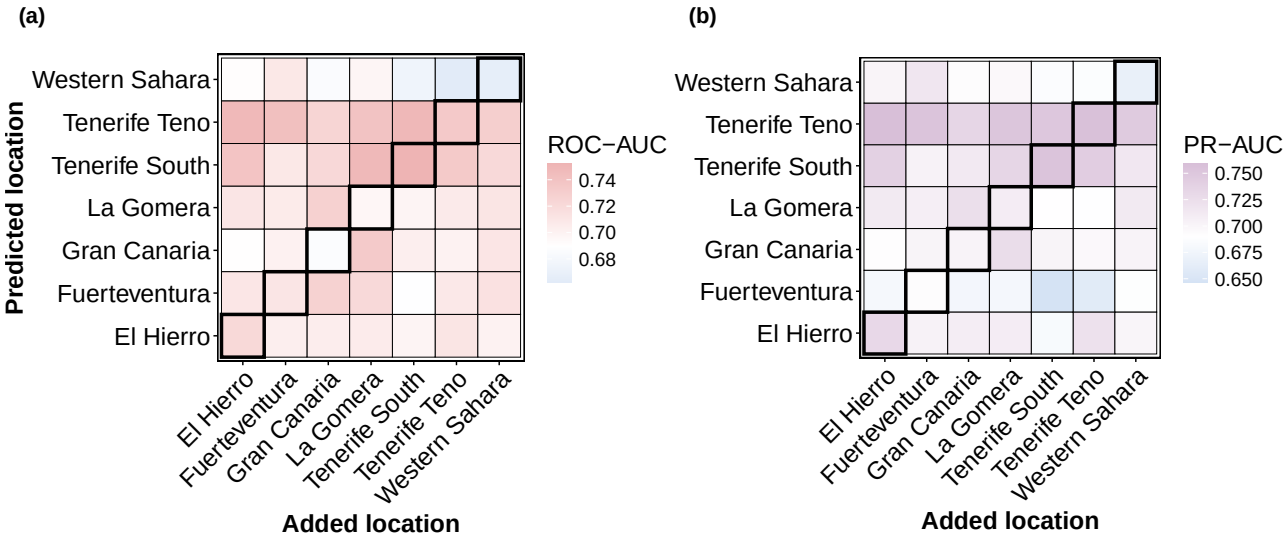

Fig. S9: Spatial variability in non-thresholded binary predictive performance. (a) ROC-AUC values and **(b)** PR-AUC values vary according to the combination of predicted and added locations.

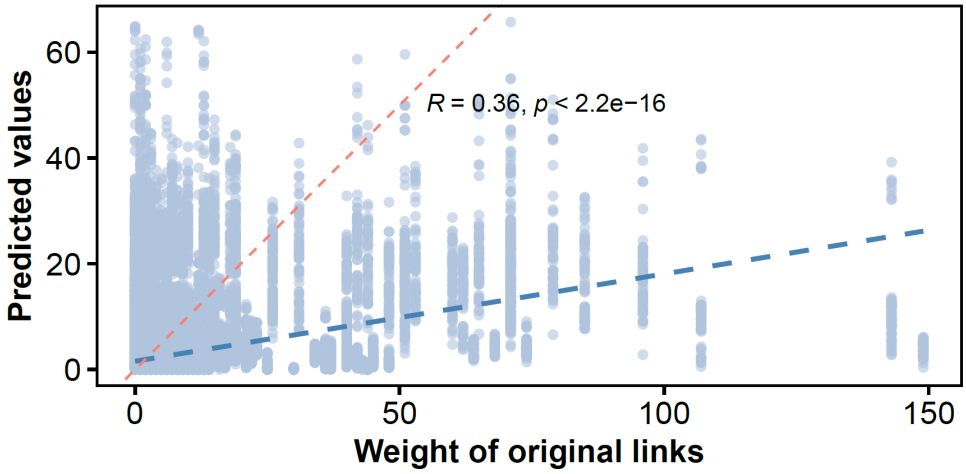

Fig. S10: Range of predictions for observed link weights. Pearson's correlation between predicted values and original link weights. Empiric trend line is in blue. For comparison, a trend line denoting perfect correlation is in red.

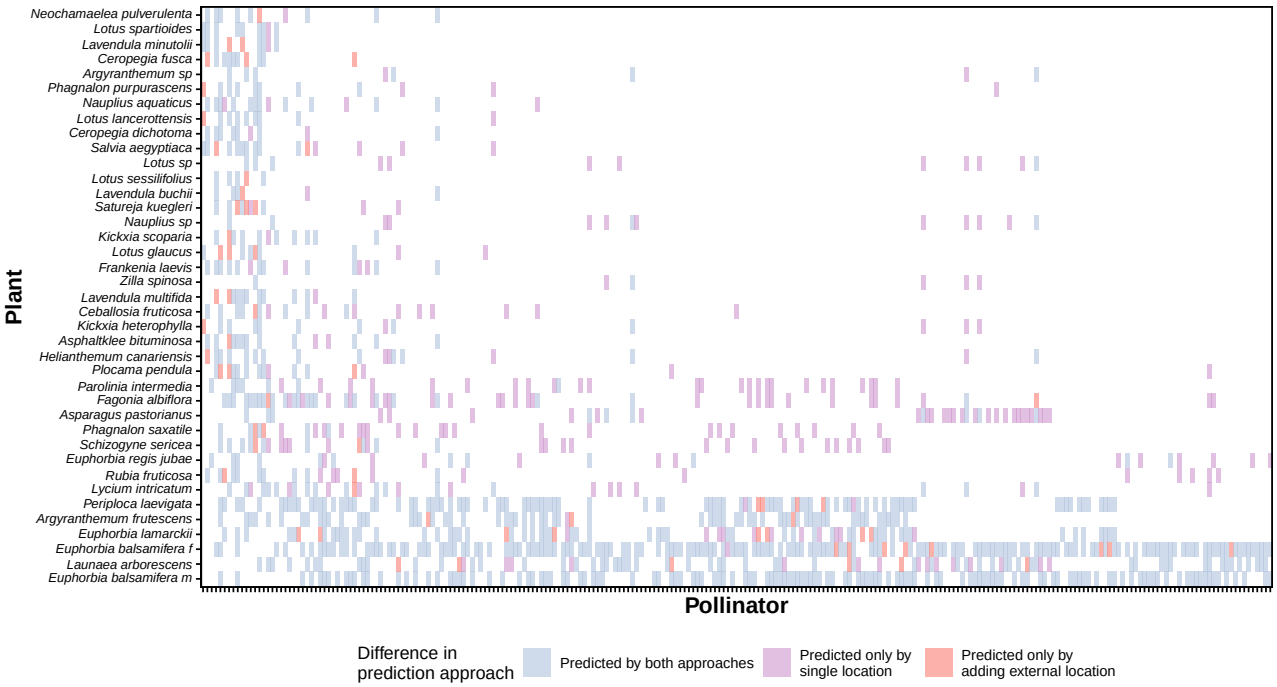

Fig. S11: Predicted missing interactions with and without additional spatial information. The heatmap breaks down the missing interactions predicted in the data set (shown in Fig. 3a,b) based on whether they were predicted when incorporating data from other locations or using data from the target location alone. Interactions predicted only when using external data are shown in orange; those predicted using only information from the island itself (single location) are shown in purple; and those predicted by either approach are shown in blue. Predictions are based on a classification threshold of 0.6.

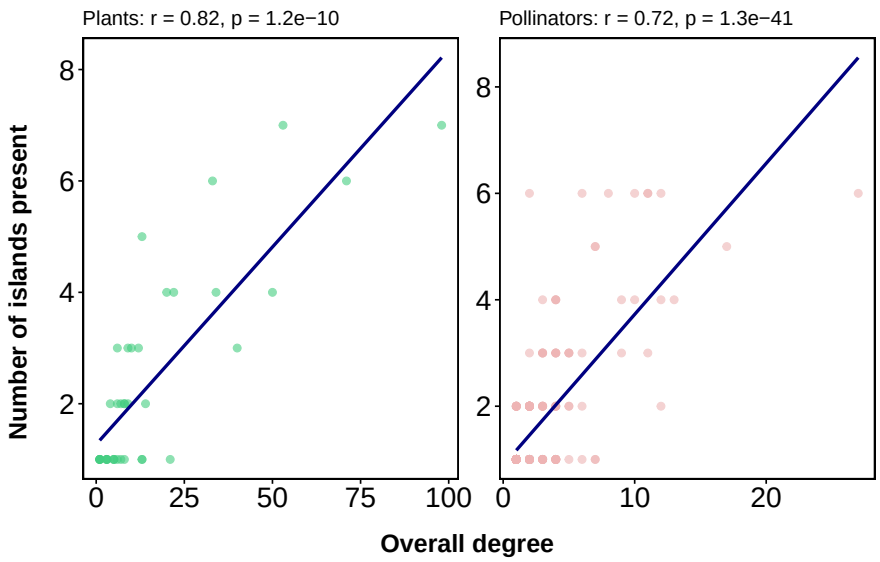

Fig. S12: Correlation between species degree and occurrence. For each plant and pollinator species, degree (the number of unique partners across the Canary Islands, representing generalisation level) is plotted against the number of islands where the species occurs. Values denote Pearson's correlation.

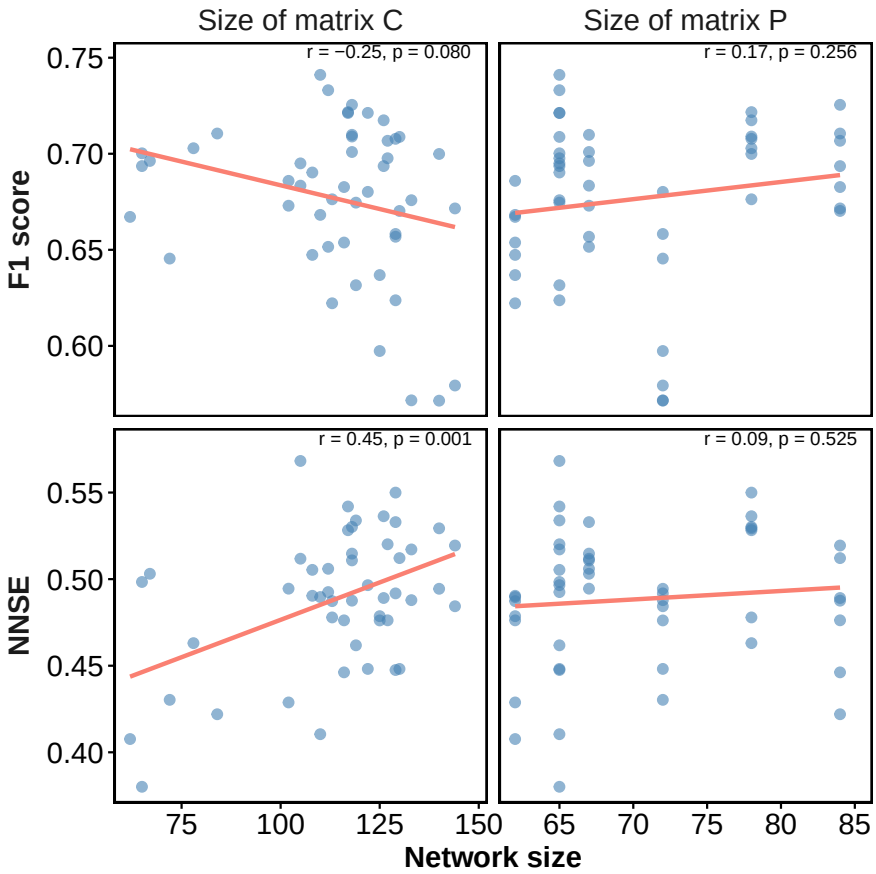

Fig. S13: Effect of network size on predictive ability. While binary prediction quality (upper panels) does not improve as the size of the predicted or combined network increases, weighted prediction quality improved with the expansion of the combined matrix (lower left).