**Anthropogenic induced beta diversity in plant-pollinator networks: dissimilarity, turnover, and predictive power.**

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# Abstract

Biogeography has traditionally focused on the distribution of species, while community ecology has sought to explain the patterns of community composition. Species interactions networks have rarely been subjected to such analyses, as modelling tools have only recently been developed for interaction networks. Here, we examine β-diversity of ecological networks using pollination networks sampled along an urbanisation and agricultural intensification gradient in east Leinster, Ireland. We showed that communities and networks in similar anthropogenic landscapes were more similar in their composition of plants, pollinators and interactions than expected from null distributions. We further showed that species turnover, especially of plants, is the major driver of interaction turnover, and that this contribution increased with anthropogenic induced environmental dissimilarity, but not spatial distance. Finally, we built models to predict each of the drivers of interaction turnover, and compared the performance of models that included site characteristics and interaction properties to models that contained species level effects. We show that if we are to accurately predict interaction turnover, data are required on the species-specific responses to environmental gradients. This study highlights the importance of anthropogenic disturbances when considering the biogeography of interaction networks, especially in human dominated landscapes where geographical effects can be secondary sources of variation. Yet, to build a predictive science of the biogeography of interaction networks, further species-specific responses need to be incorporated into interaction distribution modelling approaches.

# Introduction

As human dominance of the biosphere continues to grow, two landscape types are continuing to expand: agricultural and urban systems (Foley et al. 2005; Seto, Sánchez-Rodríguez & Fragkias 2010). While agricultural ecosystems have been extensively studied, and the negative effects of agricultural intensification on species and ecological processes are relatively well known (IPBES 2018), it is only in the last two decades that attention has turned to urban ecosystems (McPhearson et al. 2016).

Urban landscapes can negatively affect many species, with species richness tending to be lower in urban landscapes (Shochat et al. 2006, Grimm et al. 2008, McKinney 2008). Yet, urban adapted species can thrive, occurring at high abundance levels (Shochat et al. 2010), with accumulating evidence that the urban landscape is already driving conserved phenotypic changes (Alberti et al. 2017, Alberti Marzluff & Hunt 2017). Urban areas can potentially act as a refuge for species (Carrier & Beebee 2003, Menke et al. 2011, Hall et al. 2017), with gardens and public space recognised as important conservation arenas (Goddard, Dougill & Benton 2010). Furthermore, effects are not uniform across either urban or agricultural landscapes but vary with intensity. While previous reviews of urban gradients have indicated that species richness follows a hump shaped curve along an urban gradient, with species richness peaking at medium levels of urban intensity (Blair 1999, McKinney 2002, Germaine & Wakeling 2001, Shochat et al. 2006), more recent global meta-analyses have indicated that increasing intensity of urbanisation continually erodes species richness when compared to natural habitats (Newbold et al. 2015). Newbold et al. (2015) found a similar pattern and magnitude of species loss for increasing intensity of crop and pastoral agriculture and plantation silviculture, indicating that land use intensification in general reduces local species richness (Gerstner 2014, Beckmann et al. 2019). Yet, the response of any species to increasing land use intensity can be specific to the land use and the species’ functional traits (Rader et al. 2014). For example, urban landscapes have been suggested as a potential refuge for bees, but not other insect pollinator groups, from the surrounding agricultural matrix (Hall et al. 2017).

Moving beyond local species richness, there is building consensus that β‐diversity, the turnover of species among communities, declines with agricultural intensification in temperate regions, although the trend is not universal and depends on the species studied (Vellend et al. 2007, Ekroos, Heliölä & Kuussaari 2010, Flohre et al 2011, Karp et al. 2012). Urban landscapes have the most homogenised communities of any studied land use types in a global meta-analysis, (Newbold et al. 2015), providing evidence for the claim that urbanisation results in biotic homogenisation (McKinney 2006). Yet the impacts of land use change and intensification, particularly urbanisation, on ecosystem processes such as species interactions are less well understood (Shochat et al. 2006, Alberti 2010 Elmqvist et al 2015, but see Baldock et al. 2015). Pollination is emerging as a model system for studying the effects of global change on species interactions due to a large literature on mechanistic aspects of pollination (Harrison & Winfree 2015) and well-developed network science tools to visualise and parameterise interaction webs (Bascompte & Jordano 2013). Pollinators have been extensively studied in agricultural systems and natural habitats (Kremen, Williams & Thorpe 2002, Ricketts et al. 2008, Potts et al. 2010), and while there is a growing literature on pollinators in urban landscapes (Cane et al. 2006; Bates et al. 2011; Geslin et al. 2013; Fortel et al. 2014; Baldock et al. 2015; Theodorou et al. 2017), it remains an under-studied area, particularly in term of interactions between flowers and their insect visitors (although see Baldock et al. 2015, Theodorou et al. 2017). Agricultural intensification and urbanisation are both associated with decreases in pollinating species α-diversity (Le Féon et al. 2010; Bates et al. 2011), although more recently there has been evidence accumulating that urban landscapes could play an important role in the conservation of bees (Banaszak-Cibicka & Żmihorski 2012; Hall et al. 2017). Yet, to our knowledge, no study has explored the β‐diversity patterns of pollinator interaction networks in anthropogenic landscapes.

Anthropogenic disturbances affect β‐diversity through multiple processes. First, when disturbances decrease species richness, β‐diversity can increase. This is because the probability that sites do not share species increases when fewer species occupy each site (Chase et al. 2011). Second, disturbances can impose similar ecological filters over vast areas (Keddy 1992), thereby homogenizing communities (Karp et al. 2012), or create environmental heterogeneity, thereby diversifying communities (Hawkins et al. 2015). Increasing community dissimilarity with increasing geographical distance, known as distance decay, is well documented for single trophic communities (e.g. Nekola & White 1999). More recently, distance decay has been shown to occur at both local and regional scales for plant-pollinator interaction networks (Carstensen et al. 2014, Simanonok & Burkle 2014, Trøjelsgaard et al. 2015). Here, we quantify the spatial and anthropogenic induced turnover in plant-pollinator interaction networks by examining the β‐diversity of species and interactions between network pairs across twenty-one sites.We assume that the environment is composed of both its landscape context (agricultural vs urban) and the intensity of the land use (high, medium or low). At the spatial scale of this study (50km), we predict that anthropogenic gradient dissimilarities (hereon environmental dissimilarity) will produce stronger community and interaction dissimilarity than distance decay effects.Species turnover represents the most obvious source of variation in ecological networks along environmental gradients, as interactions between species are primarily conditioned by their co‐occurrence (Pellissier *et al*., 2018). There are many processes governing species co‐occurrence, such as environmental filtering, ecological interactions, dispersal limitations and historical contingencies (Peres-Neto, 2004; Wisz *et al*., 2013). Rewiring, the reassembly of interactions among co-occurring species, is the other major source of variation in ecological networks (Novotny 2009). Here, we use the method proposed by Novotny (2009) to partition network dissimilarity into additive components of rewiring and species driven interaction turnover, as the method proposed by Poisot *et al.* (2012) can underestimate species turnover and underestimate rewiring (Fründ 2021). The overwhelming importance of species turnover for pollination network dissimilarity reported by studies using Novotny’s (2009) method (Simanonok & Burkle 2014, Trøjelsgaard et al. 2015) implies that we are likely to find that rewiring is a minority contributor to network dissimilarity across the twenty-one sites of our study region. Further, we explore the components of species driven interaction turnover by decomposing interaction turnover into plant-driven, pollinator-driven and plant-&-pollinator-driven turnover and regressing each turnover component against spatial distance and anthropogenic induced environmental dissimilarity.

Finally, we explore the factors predictive of interaction turnover to understand the extent to which ecological and geographical variables generate network β‐diversity in human dominated landscapes. To do this, we construct a dataset of site pair combinations for each unique interaction, extracting all instances of interaction constancy and turnover, classifying turnover into its various components. We train a model to predict turnover using a combination of interaction properties, relative floral abundances, spatial distance, and anthropogenic environmental dissimilarities, and then test its predictive performance, and determine what makes some interactions more likely to turnover.

Thus, our aims are threefold, sequential and complementary: explore the 1. patterns, 2. components and 3. predictive variables generating β‐diversity in interaction networks situated in anthropogenic landscapes.

# Methods

## Field Site Selection

Twenty-one sites were sampled around east Leinster, Ireland, nine occurring in an urban landscape, nine occurring in agricultural landscapes and three in ‘semi natural’ landscapes (Figure 1). The agricultural and urban sites were located along gradients of intensity; high, medium and low, with three sites to each level for replication. A minimum distance of 1km separated all sites, to ensure that a separate pollinator community was sampled at each site.

The urbanisation gradient was created using an impervious surface index, from a impervious surface status map generated by the Copernicus Pan European Land Service (available at: <https://land.copernicus.eu/pan-european/high-resolution-layers/imperviousness>, © European Union, Copernicus Land Monitoring Service 2018, European Environment Agency (EEA)), while the agricultural gradient was created using an index of average field size (Supplementary Material, Table S1). Each index was calculated over an area within a 1.5km radius circle, with this circle delimiting the boundary of a ‘site’. Over 70% impervious surface was categorised as “high” urbanisation, between 20% and 70% “medium”, and less than 20% “low” urbanisation. To calculate average field size, the number of fields in a 1.5km radius circle at likely sites was counted using Google Maps My Maps application (available at: <https://www.google.com/maps/d/>) which was then divided by the area under agriculture, obtained from the Copernicus Urban Atlas land use map (available at: https://land.copernicus.eu/local/urban-atlas © European Union, Copernicus Land Monitoring Service 2018, European Environment Agency (EEA)), to obtain the average field size at that site. An average field size of greater than 5 hectares in a 1.5km radius circle was deemed a high intensity agricultural landscape, between 3.5 ha and 5ha medium intensity and less than 3.5ha average field size a low intensity agricultural landscape.

Semi natural sites were categorised using the percentage of semi natural vegetation in a 1.5km radius circle, with greater than 10% of the site area being under semi natural meadow grassland. Semi natural vegetation was calculated by combining the Herbaceous Vegetation Associations category of land use in the Copernicus Urban Atlas land use map, plus the habitats surveyed in the Grasslands of Ireland study (available at: https://www.npws.ie/maps-and-data/habitat-and-species-data). The site characteristics are shown in Table S2 (Supplementary Material, Table S2).

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**Figure 1**. Location of the 21 sites. The 9 urban sites are in Dublin city. The 9 agricultural sites are in the surrounding agricultural landscape in counties Dublin, Kildare and Meath and the 3 semi natural sites are in landscapes with a higher proportion of semi natural meadows.

## Sampling flowers, flower-visitors and flower-visitor interactions.

Each of the twenty-one sites was sampled four times between 5 May and 20 August 2018 at monthly intervals. Plants and pollinators were sampled along a 2m x 1km transect within each 1.5km radius site, with sub-sections of the transect allocated proportionately to all land cover types comprising more than 1% of the selected site (e.g. pasture, arable, continuous urban fabric; see Figure 2 Legend). Transects in residential areas were positioned along the boundary between pavements and residential gardens, so that 1m of the transect width was located in gardens and the other 1m was located on pavements and road verges. Transect locations were chosen using a random number generator to select points, and transect sections were located as close as possible to those points. Where land cover types were particularly dominant within a site, a maximum transect section length of 250m was walked, with multiple transects of the same land cover walked across multiple locations.

Flowers were sampled by noting every flowering species on the outward walk of the transect and then counting the floral units of each species on the return walk. A floral unit was defined as an individual flower or collection of flowers that an insect of 5 mm body length could walk between (see Baldock et al. 2015, Supplementary Material Table S4) and comprised a single capitulum for Asteraceae, a secondary umbel for Apiaceae and a single flower for most other taxa. Grasses, sedges and wind-pollinated forbs were not sampled.

Flower-visitor interactions were quantified by walking along each transect and recording every insect on flowers up to 1m either side of the transect line to a height of 2m, where appropriate, e.g. along hedgerows. An attempt was made to net all bees and hoverflies (Syrphidae), which were frozen and later identified to species. All other flower visiting insects were recorded at the family level (Coleoptera, Diptera, Lepidoptera). Bees and hoverflies were identified using Falk (2015) and Stubbs & Falk (2002) respectively, with identifications checked by taxonomists (See Acknowledgements). Plants were identified using Rose & O’Reilly (2006) and the phone application Plantnet (available at: <https://identify.plantnet-project.org/>), 85% to species and the rest to genus or morpho species. Sampling for flower visitors and their interactions took place between 09:00 and 19:00 hours on dry, warm, non-windy days.

## Community and Network Dissimilarity

The level of pairwise dissimilarity between networks was calculated using the recently developed network diversity indices that take advantage of Hill numbers (Ohlmann et al. 2019). An advantage of using Hill numbers is that the frequency of interactions can be used in assessing network similarity, as opposed to binary network β-diversity measures that consider presences and absences of interactions (Poisot *et al.* 2012), capturing a fuller representation of network similarity. Pairwise network β-diversity was calculated using the disPairwise function of the R package econetwork (Dray et al. 2020) associated with Ohlmann et al. (2019). To ensure comparability between network β-diversity measures and plant and pollinator community β-diversity measures, Hill numbers were used to calculate the plant and pollinator community pairwise β-diversity (see function hill\_taxa\_parti\_pairwise in package hillR (Li 2018)). The Hill number derived β-diversity produces the same pattern as that derived using the Bray-Curtis indices of β-diversity (see supplementary Figure S5 for Bray-Curtis derived dissimilarities).

Communities differing in species or interaction richness are likely to be less similar than communities of equal richness (Anderson et al. 2011, Burkle, Myers & Belote 2016). This influence of different α-diversities was mitigated by using a null model based on 1000 random assignments of species and interactions to our networks according to a probability distribution derived from their actual occurrences across the sites (Trøjelsgaard et al. 2015, Pellissier et al. 2018). That is, widespread species were more likely to be drawn and assigned to a network during the random assortments, and numbers of species and interactions assigned to a random network were constrained to equal empirical numbers. Across all pairwise combinations, we calculated the empirical similarity in plant, pollinator and interaction composition (βemperical). The deviation from randomness was measured using z-scores given as (βemperical −mean(βresampled))/SDresampled, where mean(βresampled) and SDresampled are the mean and standard deviation of the similarities achieved from the 1000 random assortments of species and interactions. Hence, a positive z-score suggests that two communities are more similar than expected if species or interactions were distributed randomly across the region, and vice versa for a negative z-score. The significance level of each βemperical value was obtained using the resampled values as a benchmark and all βemperical values having z-scores larger than 1.96 or smaller than −1.96, respectively, were deemed significantly different (p < 0.05) from random.

To assess the level of spatial autocorrelation in the response of the β-diversity metrics to the environmental dissimilarity metric, a variance partitioning exercise was performed on the plant and pollinator communities and the interaction networks. Variation in communities and interaction networks was partitioned into the purely spatial, purely environmental and the spatially structured environment components. To our knowledge, this is the first-time variation partitioning has been carried out on interaction networks.

Both the empirical β-diversity similarity values and the derived z-scores were compared to geographical and environmental distance using Mantel tests with 1000 permutations performed with the vegan v. 2.0-8 package for R (Oksanen et al. 2019). Multi-scale moran eigen vector maps were created using the adespatial package (Dray et al. 2020) and variation partitioning was carried out using vegan.

## Drivers of Interaction Turnover

If A and B are two ecological networks, then let *I*rewired be the number of interactions that change between the shared species of A and B, and let *I*species be the number of interactions that change due to changes in species composition (Figure 2). The total number of interactions that differ between A and B is then given by *I*rewired + *I*species, and the proportion of turnover that is due to rewiring and species-driven interaction turnover are rewiring = *I*rewired/(*I*rewired + *I*species) and species-driven = *I*species/(*I*rewired + *I*species).

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**Figure 2**. **A)** Interaction turnover between two ecological networks can be partitioned into contributions from rewiring (i.e. when shared species alter their interactions; *I*rewired) and species-driven turnover (i.e. when changing species composition change interactions; *I*species), with the latter being further partitioned into pollinator-driven (*I*pol), plant-driven (*I*pla) and pollinator + plant-driven (*I*pol*+*pla) interaction turnover. **B)** Matrices A and B represent ecological networks, with pollinator species arranged in rows and plant species in columns, which are artificially merged into one large matrix in order to identify interactions contributing to the different categories of interaction turnover. Region 1 contains interactions between shared species, and *I*common denotes interactions found in both A and B, whereas *I*rewired is the sum of interactions only observed in either matrix A or B, but between shared species. Shaded areas contain interactions contributing to species-driven interaction turnover. Interactions located in regions 2 and 3 are between shared pollinators and non-shared plants (i.e. the plants are found in either matrix A or B) and represent plant-driven interaction turnover. Interactions located in regions 4 and 7 are between shared plants and non-shared pollinators comprising the pollinator-driven interaction turnover. Finally, regions 5 and 9 contain interactions between non-shared pollinators and non-shared plants and comprise the pollinator + plant-driven interaction turnover. Regions marked with n.a. do not contain any interactions due to the artificial merging of matrices A and B. **C)** Interaction specific site-pair combinations. This (hypothetical) interaction is observed at sites 1 and 6 (filled squares) while the species pair is also present at site 5, however without interacting (open square). The plant species is absent from site 2 (green square), the pollinator species absent from site 3 (red square) and both species absent from site 4 (yellow square) allowing a dataset to be created to document all the ways in which interaction networks differ. Six site-pair combinations are possible in this case; 1↔5 rewiring, 1↔2: plant driven interaction turnover, 1↔3 pollinator driven interaction turnover, 1↔4 plant & pollinator driven interaction turnover and 1↔6: no interaction turnover (interaction constancy). Figure adapted from Trøjelsgaard et al. (2015).

Species-driven interaction turnover (*I*species) can be further partitioned into that caused by (i) pollinators only present in one of the networks but interacting with plants present in both (i.e. pollinator-driven interaction turnover), (ii) plants only present in one of the networks but interacting with pollinators present in both (i.e. plant-driven interaction turnover) or (iii) plants and pollinators only occurring in one of the communities and interacting together (i.e. a complete turnover of species and hence interactions) (Figure 2). Therefore, if *I*pla is number of interactions between non-shared plants and shared pollinators (regions 2 and 3 in Figure 2), *I*pol is number of interactions between non-shared pollinators and shared plant species (regions 4 and 7 in Figure 2), and *I*pol*+*pla is number of interactions between non-shared pollinators and non-shared plants (regions 5 and 9 in Figure 2), then *I*species = *I*pol + *I*pla + *I*pol*+*pla, and the fractions of the species-driven interaction turnover that can be explained by replacement of pollinators, plants or both are *T*pol = *I*pol/*I*species; *T*pla = *I*pla/*I*species and *T*pol+pla = *I*pol+pla/*I*species, respectively. Custom R functions to partition interaction turnover into the various components are available on GitHub at:

Owing to nonlinearity between plant driven (*Tpla*)and pollinator driven (*Tpol*) turnover, and both geographical distance and anthropogenic environmental distance, we used Local Regression (loess) which was evaluated with confidence intervals calculated using bootstrap with replacement (Wehrens et al. 2000). First, we estimated a local regression for the empirical data and local regressions for each of 10 000 permutations of the data. Second, ‘basic bootstrap confidence intervals’ (Wehrens et al. 2000) were calculated.

## Predicting Interaction Turnover

For each unique interaction between a plant and a pollinator species observed, we isolated the site pairs where rewiring and each of the components of species driven interaction turnover occurred. Thus, for each unique interaction, we obtained twenty events of interaction turnover or interaction constancy between site pairs, with interaction turnover being split into its constituent drivers. Each data entry is therefore an interaction-specific site-pair combination.

We tested an interaction property (average interaction frequency), four site characteristics (the geographical distance between sites, anthropogenic induced environmental dissimilarity between sites, the average impervious index of the site pair and the average agricultural index of the site pair) and two ecological characteristics (difference in flower abundance of the focal plant species between sites and whether the plant species was native or introduced) in their relation to the binary response variable of whether the interaction would turnover or not between site-pairs. Average interaction frequency, relative difference in floral abundance, spatial distance between site pairs and anthropogenic induced environmental dissimilarity were scaled and centred around 0 to ensure that the GLMM would converge. The absolute value of the relative difference in floral abundance was used.

For each of the drivers of interaction turnover (rewiring and species driven turnover decomposed into pollinator driven turnover, plant driven turnover and both plant and pollinator driven turnover), we fitted binomial generalised mixed effects (GLMM) regression models to predict when an interaction turns over or stays constant. The purpose is twofold: 1) to compare and contrast the predictor variables that are correlated with each driver of interaction turnover and 2) to assess the importance of these predictor variables by carrying out a prediction exercise. The random effects in the GLMMs were the site pair being compared, the pollinator species and the plant species involved in the interaction. To assess the importance of the fixed predictor variables in predicting when an interaction turns over, we split the data into training and test datasets and calculate the area under the receiver operating curve (AUC) in a binomial GLMM containing the predictors variables with a GLMM containing just the random effects. The receiver operating curve was created by plotting the true positive rate (TPR) against the false positive rate (FPR) at various threshold settings. For a given threshold value, the closer the corresponding point in the ROC space is to the upper left angle (FPR = 0, TPR = 1), the more accurate the model can be considered to be. Thus, an indication of the overall model performance is given by the Area Under Curve (AUC) index (Hanley and McNeil, 1982). AUC is computed by numerical integration of the curve f = TPR(FPR). Finally, a binomial GLM was fitted to assess the predictive performance of the fixed effects in the absence of the random effects. By comparing the AUC values generated from the three models it is possible to assess the importance of the fixed and random effects in predicting each driver of interaction turnover. (See Prediction of Interaction Turnover of the Supplementary Materials for further information on model development, validation and fitting.)

Average interaction frequency is the average of how frequently a given pairwise interaction is observed when both species are present at a site. This measure is therefore a property of the given interaction. Each unique interaction of the entire system (the metaweb, *sensu* (Dunne 2006)) thus has an average interaction frequency. It was calculated as the sum of all the interaction frequencies registered between two focal species (i.e. the interaction frequency in the metaweb) divided by the number of sites where both species occur (interacting or not). For a given interaction specific site-pair combination we calculated the difference in flower abundance between sites by subtracting the flower abundance of the one site from that of the other. This was then standardized by the total number of flowers for both sites for that species in order to get a measure of the relative change in flower abundance. This relative difference was used as an explanatory variable in the model. Anthropogenic induced environmental dissimilarity was measured by creating a dissimilarity matrix for each site pair based on the percentage cover of impervious surface (degree of urbanisation), percentage cover of semi-natural grassland (degree of naturalness), and average field size (degree of agricultural intensification). The anthropogenic environmental dissimilarity index thus represents how different the site pairs are in their land use, however, by using a dissimilarity matrix it does not distinguish the type of land use being contrasted between site pairs. Thus, we included the average impervious index and the average agricultural index of the site pair to measure the impact of each of these gradients. As many of the plant species in the Dublin region are introduced, a plant origin (native versus introduced) factor was included in the model to determine whether the co-evolutionary history of plant-pollinator interactions impacted the likelihood of interaction turnover. Geographical distance was calculated as the Euclidean distance between a site-pair.

During the GLMM model validation procedure, the residuals were checked for overdispersion with respect to each model predictor and the discretised response using the DHARMa package (Hartig 2020). It was found that the model was over dispersed with respect to the discretised model predictions. As such, the model behaves differently as the probability of an interaction turning over increases: the model predictions have a higher variance at high probability of interaction turnover while having a lower variance at low probability of interaction turnover. Such overdispersion is likely due to the model missing an informative predictor that was not measured in this study. The simpler binomial GLM without random effect variables did behave better in terms of overdispersion, but the simpler model’s fit prediction performance tended to be much lower than the more complex binomial GLMM. We choose to present the results of the binomial GLMM, noting that the overdispersion with respect to the discretised predictions is likely to be caused by a missing predictor variable.

Linear binomial mixed models were performed with the packages lme4 v. 1.0-5 for R (Bates et al. 2015) and all analyses were performed using R version 4.0.2. (R Core Team 2020). We acknowledge that the linear mixed models only account for the taxonomic non-independence (i.e. the multiple entries of each species) and not necessarily the spatial non-independence (i.e. the multiple entries of the pairwise comparisons of the networks).

# Results

A total of 4,161 insect flower visitors were sampled from the 21 sites, of which 62% were Hymenoptera, 35% Diptera, 2% were Lepidoptera and 1% were Coleoptera. This comprised of 85 visitor taxa (44 Diptera, 30 Hymenoptera, 11 Lepidoptera; Coleoptera were not identified beyond order) visiting 213 plant taxa (180 identified to species, 21 to genus and 12 to morpho species). A total of 862 unique interactions were recorded, resulting in a 73% sample coverage for interactions; 86 pollinator species were recorded with a 99% sampling coverage; and 192 plant species were recorded with a 97% sampling coverage. (Figure S1).

## Community and Network Dissimilarity

Taking α diversity into account by using z-scores, geographical distance increased the pairwise dissimilarity of pollinator communities (*r*M = 0.1909, *p* = 0.036) and interaction networks (*r*M = 0.1876, *p* = 0.025) but not plant communities (Mantel test with 999 permutations: *r*M = 0.1298, *p* = 0.11; Figure 2 *a, b* & *c* respectively). Moreover, we found a stronger and significant increase in dissimilarity with the anthropogenic gradient dissimilarity for plants (Mantel test with 999 permutations: *r*M = 0.5733, *p* < 0.001) and interaction networks (*r*M = 0.5705, *p* < 0.001) but not pollinator communities (*r*M = 0.0913, *p* = 0.212; Figure 2 *d, f* & *e* respectively). The z-scores revealed that many communities and networks were more similar than expected under the null assortment of species and interactions (dark circles below -1.96 in Figure 2), while only a few plant communities were more different than expected (dark circles below +1.96 in Figure 2). The gradient dissimilarity was a particularly strong driver of plant community and network composition, resulting in plant communities and networks more similar than expected under null assumptions, with the gradient dissimilarity driving plant communities in very different landscapes to be more different than expected in their composition.

Disaggregating the pollinator community shows that it was the bee community responded neither to environmental dissimilarity nor spatial distance, while hoverfly composition did respond to spatial distance (Mantel test with 999 permutations: *r*M = 0.148, *p* = 0.039) but not environmental dissimilarity (Figure S6). Disaggregating the plant community into introduced and native plant species revealed that the native plant community responded to both environmental dissimilarity (Mantel test with 999 permutations: *r*M = 0.2643, *p* = 0.002) and geographical distance (Mantel test with 999 permutations: *r*M = 0.3486, *p* = 0.001; Figure S7 a-b), while the introduced plant community composition responded to environmental dissimilarity (Mantel test with 999 permutations: *r*M = 0.1989, *p* = 0.027) but not to geographical distance (Figure S7 c-d).

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Figure 3. Dissimilarity in the composition of plants (a, d), pollinators (b, e) and their interactions (c, f) networks as a function of spatial (a-c) and environmental distance (d-f). To reduce the effect of differing α diversities, we calculated z-scores as a measure of deviation from randomness. *z*-scores were given as (*β*emperical – mean(*β*resampled))/SDresampled, where *β*emperical is the empirical similarity between two networks, mean(*β*resampled) and SDresampled are the mean and standard deviation of the similarities when performing 1000 random assortments of species and interactions, respectively. Positive and negative *z*-scores signify higher and lower similarity, respectively, than expected from null distributions of species and interactions. Dark circles indicate that a given empirical pairwise comparison differed significantly from the resampled values, and grey dashed lines mark the boundary between 1.96 and −1.96.

Variation partitioning produced qualitatively similar results (see Figure S8), where the pure environmental component explained more variation than the pure spatial component in each community and the interaction networks, confirming that in a heavily modified region it was the anthropogenic environmental variables that structured communities more than spatial distance. Adding the plant and pollinator community change as explanatory matrices to the network variation partitioning explained additional interaction variation (Figure S8 c *- f*), yet there were still large proportions of explained variation related to the purely environmental or spatial data indicating that interaction networks have biogeographic patterns not determined solely by their respective communities.

## Drivers of Interaction Turnover

Interaction turnover was dominated by species-driven interaction turnover (*Ispecies > Irewire*), which accounted for ~80% of interaction turnover (Figure 4 *a*). Species-driven turnover and rewiring varied inversely with environmental dissimilarity; with species-driven turnover increasing with increasing environmental dissimilarity (Mantel test with 999 permutations: *r*M = 0.5277, *p* < 0.001), while rewiring decreased (-0.5277, p < 0.001; Figure 4 *d*). There was no significant effect of spatial distance on the contribution of species-driven turnover (Mantel test with 999 permutations: *rM* = 0.1504, p = 0.072) or rewiring (Mantel test with 999 permutations: *rM* = -0.1504, p = 0.072; Figure 4 *a*)

The species driven turnover (*Ispecies*) was further partitioned into plant (*Tpla*), pollinator (*Tpol*)and plant + pollinator (*Tpla+pol*) driven turnover (Figure 4 *b-c, e-f*). Along both the spatial and environmental dissimilarity gradient, plant driven interaction turnover contributed more to species driven interaction turnover than pollinator driven (*Tpla > Tpol*,Figure 4 *b,e*), accounting for ~70% of species driven interaction turnover. While spatial distance did not have much impact on proportional contributions (the bootstrap limits did not show a trend, Figure *4 b*; see Table S5 for non-significant mantel test), the proportion of plant and pollinator turnover varied as a function of enviromental dissimilarity (Figure 4 *e*). The effect was most pronounced at small environmental dissimilarities, where pollinator driven turnover peaked and plant driven turnover reached its minimum. For pollinator driven turnover, this was significant as the lower limits of the bootstrap confidence bands at environemtnal dissimilarity score of 15 were higher than the upper limits at other dissimilarities, while for plant driven turnover, the peak occurred at a score of 45, where the lower confidence band is higher than the upper limits at other landscape dissimilarities.

The plant and pollinator driven turnover (*Tpla+pol*) contributed 15% to all interaction turnover (Figure 4 *c*), meaning in any given network comparision, 15% of interactions will be between plant and pollinator species unique to either network. Spatial distance had a non-significant postive effect on the contribution of unique interaction to interaction turnover (Mantel test with 999 permutations: *rM* = 0.1274, p = 0.103; Figure 4 *c*), while the unique interaction contribution to interaction turnover increased linearly with gradient dissimilarity ((Mantel test with 999 permutations: *rM* = 0.2256, p = 0.027; Figure 4 *f*).



Figure 4. The proportion of the total interaction turnover that can be labelled as either species-driven interaction turnover (yellow points and yellow line) or rewiring (purple points and purple line) change in relation to geographical distance (a) or the environmental dissimilarity (d) between paired networks. The proportion of the species-driven interaction turnover that can be ascribed as pollinator-driven (blue points and blue line) and plant-driven (orange points and orange line) as a function of spatial distance (c) or environmental dissimilarity (e). Proportion of species-driven interaction turnover that is caused by a combined turnover of both plants and pollinators (pollinator + plant-driven) in relation to geographical distance (c) and environmental dissimilarity (f).

## C) Predicting Interaction Turnover

The prediction performance of the mixed effects model and the random effects model was similar for each driver of interaction turnover, indicating that the fixed effects added little useful information for predicting interaction turnover (see AUC values in Table 1). The good predictive performance of the random effects models indicates that most of the variation in whether an interaction would turnover or not is contained in the species and site pair under comparison. The prediction performance of the GLM was poor for pollinator driven turnover (AUC = 0.62), plant driven turnover (AUC = 0.65) and plant & pollinator driven turnover (AUC = 0.58), yet performed reasonably well for rewiring (AUC = 0.83, Table 1), meaning that the fixed effects, composed of site variables (gradient dissimilarity, average impervious index and average impervious index) and interaction properties (average interaction frequency), can be used to predict interaction rewiring (Figure 5). Yet, this predictive performance is lower compared to the random effects model (random effects model AUC = 0.93), meaning that much of the variance in whether an interaction would rewire or not is dependent on the species in question and less so on the surrounding environment. For pollinator driven, plant driven and plant & pollinator driven interaction turnover the GLMs performed very poorly in comparison to the random effects GLMMs (see Table 1 for comparison of AUC values), illustrating that whether an interaction turned over due to species driven turnover is dependent on the species in question and not on the measured site variables or interaction properties.

Table 1. Model specification and area under the receiver operating curve (AUC) estimates for each driver of interaction turnover. A mixed effects GLMM, a random effects GLMM and GLM was fit to explore the importance of the predictor variables in predicting when an interaction turns over. Models with high AUC have high predictive performance. See supplementary material section *Predicting Interaction Rewiring* for the parameter estimates of the mixed models.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Rewiring** |  | |  | |
| Mixed Model |  | | AUC: 0.97 | |
|  | | | | |
| Random Effects Model | | | AUC: 0.93 | |
|  | | | | |
| Binomial GLM | | | | AUC: 0.83 |
|  | | | | |
|  | | | | |
| **Pollinator Driven Interaction Turnover** | | | | |
| Mixed Model | |  | | AUC: 0.826 |
|  | | | | |
| Random Effects Model | |  | | AUC: 0.828 |
|  | | | | |
| Binomial GLM | |  | | AUC: 0.62 |
|  | | | | |
|  | | | | |
| **Plant Driven Interaction Turnover** | | | | |
| Mixed Model | |  | | AUC: 0.913 |
|  | | | | |
| Random Effects Model | |  | | AUC: 0.913 |
|  | | | | |
| Binomial GLM | |  | | AUC: 0.65 |
|  | | | | |
|  | | | | |
| **Plant & Pollinator Driven Interaction Turnover** | | | | |
| Mixed Model | |  | | AUC:0.86 |
|  | | | | |
| Random Effects Model | |  | | AUC: 0.87 |
|  | | | | |
| Binomial GLM | |  | | AUC: 0.58 |
|  | | | | |

The binomial GLM for rewiring performed reasonably well (AUC = 0.83) indicating that the covariates are useful for predicting when an interaction will rewire or stay constant. The effect of average interaction frequency on interaction turnover was negative (Figure 5 *a*), while the average agricultural index, the average impervious index and the environmental dissimilarity (Figure 5 *b-d*) were positively correlated with interaction turnover. Plant origin, whether native or introduced, affected the probability of interaction turnover, with native plants having a lower mean turnover probability (Figure e). See Table S7 for model outputs and summaries of the binomial GLM.



Figure 5. Probability of interaction turnover and model predictors based on a binomial GLM predicting rewiring (a–e) and a sample of individual pollinator responses from a binomial GLMM (f). a) Average interaction frequency is negatively related to the probability of interaction turnover. The more frequent interactions show lower probabilities of turnover between sites. b) The larger the average agricultural index of the site pair, the higher the probability that an interaction turns over. c) The larger the average impervious index of the site pair, the higher the probability that an interaction turns over. d) The more dissimilar the environmental gradient is between site pairs, the higher the probability that an interaction turns over. e) Probability of interaction turnover for native and introduced plant species. f) Large variance in how the interaction turnover of individual pollinator species changes with average interaction frequency. Superimposed residuals result in darker marks (a-e). See Table S7 for binomial GLM parameter estimates and Table S6 for mixed effects GLMM parameter estimates and random effect variances.

# Discussion

## Community Dissimilarity

Community and interaction network beta diversity was structured mostly by anthropogenic environments, rather than their geographical proximity. Previous studies have shown distance decay effects for plant-pollinator interaction networks across a variety of spatial scales (Carstensen et al. 2014, Trøjelsgaard et al. 2015), yet to our knowledge, this is the first evidence that environmental gradients (in this case, urbanisation and agricultural intensification) structure interaction beta diversity, and indeed can exert a greater structuring force. In fact, neither the plant nor pollinator community was structured purely due to spatial distance, suggesting that dispersal limitation plays no role in driving species assemblages in the study region at this scale. Rather the spatially structured anthropogenic environment was the largest measured structuring force, implying that anthropogenic environmental filtering is likely a significant driver of community composition in the study region.

Interestingly, the interaction networks show a degree of spatial structure independent of the measured environmental variables. The purely spatial component was similar to the variation explained by the purely environmental (approximately 5%). This demonstrates that interactions are subject to processes that do not operate for their constituent organisms. Additionally, when the plant and pollinator community dissimilarity measures were included in the network variation partitioning procedure, further variation was explained, yet a significant proportion of interaction variation was still correlated purely with environmental or spatial variables. This provides evidence that interactions have their own biogeographic patterns not determined exclusively by their respective communities: the realisation of an interaction is influenced by the interacting organisms’ surroundings. Using a different method, Poisot et al. (2012) found a similar pattern, the dissimilarity of interactions formed by species shared between sites shows no correlation with the dissimilarity of species composition, implying that environmental filtering of species and interactions are different. Thus, if we are to build a predictive biogeography of ecological interactions, we are required to not only model species co-occurrence as influenced by environmental and spatial data but also model the influence of such variables on the likelihood of interactions occurring, essentially condition interaction probabilities on the environment and space distance (Gravel *et al.* 2019).

Networks and communities that occur in sites with similar environmental characteristics were more similar than expected by the null model distribution. This suggests a local environmental filtering effect was occurring, where species and interactions in similar landscapes were selected for. We can rule out the effect of human preferences for garden and agricultural plant species in generating this pattern as it is the native plant community, rather than the non-native, that corelate with environmental dissimilarity. Likewise, both the pollinator community and the interaction networks, which humans have little intentional influence over, were more similar than expected in similar landscapes, thus suggesting that it is the environmental context, the degree of urbanisation or intensity of agriculture, filtering community composition. Interestingly, there were no communities or networks more dissimilar than expected by the null model distribution, meaning that both spatial distance and the environmental dissimilarity between sites were not great enough to create communities and networks significantly different in their composition. Studies have found that networks that are far apart (~450 km) are more different than expected (Trøjelsgaard et al. 2015), suggesting that the spatial distance of this study (50 km) was not large enough for dispersal limitation to have an effect. Yet, it is surprising that the relatively large differences in the anthropogenic gradient, comparing sites in an urban centre to sites with a significant proportion of semi-natural habitat to sites in intensive agriculture, did not produce communities or interaction networks that were significantly different from each other than expected by chance. Overall, that communities and networks are more similar than expected in similar landscapes is suggestive of homogenisation within anthropogenic land use classes, a finding similar to studies that show intense agriculture erodes β-diversity (Karp et al. 2012) or that residential lawns homogenise urban plant communities (Wheeler et al. 2017), while the finding that no communities or networks were more dissimilar than expected suggests that even a diversity of anthropogenic landscapes in a region may not assist in maintaining β-diversity in the face of landscape intensification.

It should be noted that most of the variation in the plant and pollinator communities and in interaction networks could not be explained by either the measured environmental variables or spatial distance, indicating that while urbanisation and agricultural intensification do structure communities and interaction networks, they account for a relatively small proportion of the total dissimilarity. Thus, while we conclude that landscape scale anthropogenic environmental filtering is contributing to structuring community assembly and interaction formation in our study region, the major structuring processes have not been elucidated. A potential reason for the low explanatory power is that by aggregating communities and interaction networks collected in different habitats at a site into landscape level communities and networks that the local habitat filtering effects remain unaccounted for in this analysis.

## Drivers of Interaction Turnover

We found that species driven interaction turnover was the major driver of interaction turnover, accounting for ~80% of the difference in interactions. Increasing spatial distance had no effect on the proportion of rewiring, or species driven interaction turnover, in contrast to a previous study conducted a study at a larger spatial scale (Trøjelsgaard et al. 2015), again suggesting that geographical effects occur at larger spatial scales than the 50km scale of the present study. However, increasing environmental dissimilarity had a strong effect, increasing the proportion of species driven turnover and decreasing the rewiring contribution. The contribution of rewiring more than halves across the anthropogenic dissimilarity gradient: rewiring contributes ~25% at low anthropogenic dissimilarity but less than 10% at high anthropogenic dissimilarity. Disaggregating species driven interaction turnover into its respective components reveals that plant species turnover accounts for 70% of all species driven interaction turnover, the reverse of previous studies in more natural areas (Trøjelsgaard et al. 2015), suggesting that in urban and agricultural environments, where the native plant species pool is supplemented with non-natives, plant driven turnover is the dominant driver of network β-diversity.

Plants and pollinators appear to be affected differently by anthropogenic dissimilarity, with a peak for pollinator driven interaction turnover at low gradient dissimilarity while the peak for plant driven interaction turnover occurred at medium levels of gradient dissimilarity. This is consistent with the respective responses of the plant and pollinator communities to anthropogenic dissimilarity. Plant community dissimilarity is more strongly correlated to anthropogenic dissimilarity than the pollinator community is, and thus we should expect the proportion of plant driven interaction turnover to increase as anthropogenic dissimilarity increases. A weak positive effect of environmental dissimilarity on plant & pollinator driven interaction turnover existed, meaning a complete substitution of both plants and pollinators accounted for an increasing fraction of species driven turnover in landscapes with increasingly different compositions. In the Canary Islands, Trøjelsgaard et al (2015) found that these entirely novel interactions dominate interaction turnover at regional spatial scales, yet in strongly contrasting anthropogenic landscapes complete substitution only account for ~25% of interaction turnover. Thus, while the anthropogenic gradients likely impose habitat filtering effects resulting in complete substitution and novel interactions, the strength of the anthropogenic filtering effect is not as strong as island biogeographic dispersal limitation and habitat filtering.

Networks can only be different due to interaction turnover, so when studying network β-diversity, it is useful to explore the components of interaction turnover to understand the reasons that networks are dissimilar. Trøjelsgaard et al (2015) documented how spatial distance correlates with the components of interaction turnover and here we added to the biogeographical network beta diversity literature by exploring how anthropogenic induced environmental gradients structure the drivers of interaction turnover.

## Predicting Interaction Turnover

Pairwise interactions have proven difficult to predict (Burkle & Alacron 2011). Efforts in the last decade have moved towards probabilistic models that generate both interactions and networks, moving the field beyond descriptions of network structure (Strydom et al. 2021). Here, our aim was to explore which variables (species-level, environmental, spatial) influence the turnover of interactions to highlight the data required by probabilistic models to accurately predict patterns of network β-diversity.

We found that species driven interaction turnover, as opposed to rewiring, is difficult to predict without species level information. The site variables and interaction properties that we measured provided little useful information for predicting species driven interaction turnover. The inclusion of the species identities and the site pair combination as random effects drastically improved prediction performances, indicating that species specific variables are required to accurately predict species driven interaction turnover. As species driven turnover is the dominant driver of interaction turnover in spatially separated networks, further work building probabilistic models to predict network β-diversity would benefit from adopting species distribution modelling practices, in particular joint species distribution models (Tikhonov et al. 2017) and interaction distribution modelling (Gravel et al. 2019). As the local species pool forms the basis of interaction networks, building probabilistic species pools based on spatially explicit distribution models is essential to predict networks across space (Strydom et al. 2021).

In contrast to species driven interaction turnover, it was possible to predict interaction rewiring to a reasonable degree of accuracy with site characteristics and interaction properties. Average interaction frequency was the most significant predictor of rewiring, with interactions that occurred frequently between co-occurring species much less likely to rewire. Interactions with high interaction frequency can be interpreted as linking species with high mutual affinity, it is likely that such species would interact with high frequency if no temporal or spatial constraints are imposed (Carstensen et al. 2014). These interactions were likely a result of both niche and neutral processes: at a minimum, these interactions were not forbidden due to trait mismatches and were likely heavily influenced by the relative abundances of the respective species (Poisot, Stouffer & Gravel 2014). Additionally, the relative difference in plant abundance between a site pair showed a positive relationship with rewiring, meaning that increasing the difference in plant floral abundance between a site pair increased the likelihood of interaction turnover, underscoring how important neutral processes are to interaction formation. Yet, interaction frequency in pollination systems is difficult to predict (Strydom et al. 2021) and, to the best of our knowledge, models predicting floral abundance for each species within a community do not exist. Thus, the more useful variables for predicting rewiring are currently unavailable to probabilistic network modellers interested in exploring network dissimilarity across space and time. The long-standing assumption that co-occurrence is equivalent to meaningful interaction strength has been shown to be false (Blanchet, Cazelles & Gravel 2020), and thus to predict rewiring, a significant component of network dissimilarity accounting for ~20% of interaction turnover in our study, species level information on abundance and traits are particularly important in constraining the set of possible networks generated from probabilistic models. The proliferation of open access databases, such as those on plant functional traits (TRY <https://www.try-db.org/TryWeb/About.php> ), species interaction data (Mangal <https://mangal.io/#/> and GloBI <https://www.globalbioticinteractions.org/about> ) and metacommunity ecology and species trait data (<https://icestes.github.io/>) could facilitate the development of predictive models of interaction strength and floral abundance.

Landscape level variables were predictive of rewiring, particularly agricultural intensity which increased the likelihood of rewiring strongly. Interestingly, this would increase the beta diversity of interaction networks in intensive agricultural landscapes, contrasting with the homogenisation of the plant communities in such landscapes (Karp et al. 2012). A much weaker positive effect of the impervious gradient was found, indicating that urbanisation also increases the probability of interaction rewiring. However, the urbanisation effect was not retained in the mixed effects model, and so we can conclude that while agricultural intensification shows a strong and consistent effect of increased rewiring probability, the evidence for urbanisation is mixed and needs further exploration. Additionally, the gradient dissimilarity between site pairs increased the probability of an interaction rewiring, indicating an effect of landscape composition. That these landscape variables impact rewiring probabilities highlights that remote sensing can be a useful data source for models seeking to enhance predictive power. Yet, the random effects GLMM still outperformed the binomial GLM to such a degree that if we are to build predictive models of interaction rewiring, and more generally of interaction turnover, it would be more fruitful to build predictive models using species level information. Gravel *et al.* (2019) proposes to build probabilistic models of species interactions which combines species distribution modelling and species level trait data to model the probability of interactions between species. The probabilistic approach is data intensive, yet this study has shown that to accurately predict interaction turnover, species level data are required.

# Conclusion

Using methods and tools developed to make interaction networks amenable to community ecology analysis, we have shown that an anthropogenic environmental gradient structures the composition of interaction networks while geographical distance exerts a weaker effect, to our knowledge the first study to do so. A similar pattern is observed with the components of interaction turnover, demonstrating that the anthropogenic gradient moderates the components of interaction turnover and not geographical distance, highlighting the importance of considering anthropogenic disturbances in studying the biogeography of interaction networks. Yet, when it comes to predicting when an interaction turns over, site characteristics and interaction properties perform poorly**,** showing that if we are to build a more predictive science of the biogeography of interaction networks, there is still much work to be done to integrate species specific responses. Given that species driven interaction turnover is the main driver of the patterns observed in this study, extending species distribution modelling to interaction distribution modelling is a promising avenue of further research.

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