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Plant–pollinator metanetworks in fragmented landscapes: a simulation study

Ehsan Rahimi¹ and Chuleui Jung^{1,2*}

Abstract

Background The topology of the plant–pollinator network can be explained by the species' abundance and their random interactions. Plant–pollinator networks can be studied in the context of a landscape, because each patch can accommodate a certain local network. Local populations of pollinators in the landscape can be connected through migration and then constitute a metanetwork that is known as a combination of spatial and ecological networks. In this regard, habitat fragmentation can affect the topology of plant–pollinator metanetworks through changes in the species abundance and limiting their interactions. However, it is not clear what pattern (fragmented or aggregated) of the landscape structure can accommodate networks with a higher degree of specialization.

Methods we created simulated landscapes with different forest proportions scenarios (from 5% to 50% of the total landscape) and degrees of fragmentation. Then, for each landscape, we limited the proportion of pollinators to the forest patch. We assumed that plants and pollinators are randomly distributed around the landscape and interact randomly. We used landscape metrics to measure different aspects of landscape structure and bipartite metrics for calculating the degree of specialization in plant–pollinator networks.

Results The statistical relationship between bipartite and landscape metrics showed that the relationship between the topology of plant–pollinator networks and the landscape structure is affected by the forest amount in the landscape and the degree of forest fragmentation. We also found that according to the nestedness and H2 (a measure of specialization) metrics, fragmented landscapes contain more general plant–pollinator networks.

Conclusions Our findings suggest that fragmented landscapes, characterized by scattered forest patches, can promote higher levels of interaction between limited pollinators and diverse flowers, leading to more general plant–pollinator networks.

Keywords Plant–pollinator metanetwork, Habitat fragmentation, Simulated landscape, Landscape metrics, Bipartite metrics

Introduction

Pollination by insects, known as entomophilous pollination, emerged in angiosperms approximately 120 million years ago (Schatz et al. 2017). Nowadays, more than 80%

of angiosperms exhibit adaptations specifically tailored for insect pollination (Ollerton et al. 2011). Insects contribute significantly to angiosperm pollination, accounting for 82% of the interactions, while vertebrates and wind play smaller roles at 6% and 11%, respectively (Ollerton et al. 2011). A considerable portion of angiosperms (33%) rely on pollinators for seed production, with 80% of their seed production being dependent on these interactions in half of the species (Rodger et al. 2021). The association between pollinators and flowering plants forms a mutualistic relationship crucial for the survival and stability of both communities. Unrelated plants

*Correspondence:

Chuleui Jung
cjung@andong.ac.kr

¹ Agricultural Science and Technology Institute, Andong National University, Andong City 36729, Republic of Korea

² Department of Plant Medicals, Andong National University, Andong City, Republic of Korea

that share common pollinators often display similar sets of floral traits, termed pollination syndromes. Pollinators can be categorized into functional groups, such as long-tongued flies or small, nectar-collecting bees, which exhibit similar behaviors and impose similar selective pressures (Song et al. 2017). This convergence in floral traits arises as a result of the mutual interactions between plants and pollinators, giving rise to coevolutionary patterns known as pollination syndromes. These syndromes represent a collection of phenological characteristics that highlight the coevolutionary dynamics between plants and their pollinators.

Previously, it was believed that there existed a symmetrical pattern in plant–pollinator interactions, where specialists interacted exclusively with specialists and generalists with other generalists (Vizentin-Bugoni et al. 2018). However, it has been discovered that only a small fraction of specialists interact with one another, while the majority interact with generalist pollinators (CaraDonna et al. 2017). In contradiction to previous expectations, other studies have emphasized the prevalence of generalization in floral traits (Bascompte and Scheffer 2023). Ollerton (1996) introduced a paradox, where many flowers exhibit specialized floral traits but are visited by a diverse range of pollinators. Earlier, Stebbins (1970) also attempted to explain the paradox between floral diversity resulting from pollination syndrome convergence (evolutionary specialization) and the observation that flowers are visited by numerous pollinators (ecological specialization). Waser et al. (1996), based on their examination of 39 European and 73 North American species, similarly assert that most plants exhibit moderate to high levels of generalization in their pollination systems.

Forbidden links, which arise from niche-based processes, encompass a range of factors that prevent the occurrence of interactions between two species, such as plants and pollinators, in nature. These factors can be attributed to phenological disparities, differences in size, microhabitat preferences, nervous system characteristics, and spatial and temporal mismatches (Jordano 2016). In contrast, the neutrality hypothesis states that the topology of the plant–pollinator network is because individuals meet randomly, resulting in abundant species having a higher likelihood of interacting with one another (Vázquez et al. 2009b). Forbidden links can arise due to various reasons, including insufficient sampling, niche-related biological constraints, such as spatial and temporal mismatches and morphological barriers, as well as the neutrality hypothesis that is contingent on species abundance (Vizentin-Bugoni et al. 2018).

Vázquez (2005) and Vázquez et al. (2005) conducted research that demonstrated how the arrangement of plant–pollinator networks can be explained by the

abundance of species and their random interactions. Through the use of null models, they observed that there were no discernible differences between the patterns generated by random interactions and the actual observed patterns in these networks. In a separate study, Vázquez et al. (2007) proposed the “abundance-asymmetry hypothesis,” suggesting that if species within a community interact randomly, the abundance of each species would determine the frequency and strength of interactions, resulting in an asymmetric structure in plant–pollinator networks. However, this claim has faced criticisms from other researchers, such as Santamaría and Rodríguez-Gironés (2007). Krishna et al. (2008) conducted a quantitative analysis to estimate the relative impact of abundance and other ecological traits on the structure of plant–pollinator networks. Their findings indicated that relative abundance accounted for approximately 60–70% of the observed patterns, while the remaining 30–40% could be attributed to ecological constraints.

Within agricultural landscapes, comprising combinations of forest, agriculture, or pasture, forest patches play a crucial role as nesting habitats for pollinating insects, particularly bees, while agriculture and pasture areas provide essential floral resources. Rahimi et al. (2022a) conducted a comprehensive review of 93 articles investigating the impact of forest patches on bees in agricultural landscapes, considering factors, such as patch size, distance, and structure. The findings revealed that approximately 80% of the studies reported a strong reliance of bees on forest patches, with the abundance and diversity of bees declining as the distance from these patches increased. Therefore, plant–pollinator networks can be examined within the broader context of a landscape, where each patch can support a distinct local network. These local populations of pollinators within the landscape can connect through migration (Librán-Embid et al. 2021), resulting in metanetworks that encompass both spatial and ecological dimensions (Hagen et al. 2012). The topology of these plant–pollinator metanetworks can be influenced by habitat fragmentation, which can alter the abundance of both pollinators and angiosperms. However, there has been limited research investigating the impact of landscape structure on these metanetworks (Librán-Embid et al. 2021). Some studies have focused on the effects of habitat fragmentation on local networks. For instance, Ferreira et al. (2020) examined seven landscapes in the Brazilian Atlantic Forest and found that the reduction and isolation of forest patches led to less specialized networks. In another study of plant–pollinator networks on Mediterranean gypsum islands, Santamaría et al. (2018) observed that increased patch connectivity resulted in more visited plants, thus reducing network asymmetry.

The majority of studies in this field have primarily focused on the combined effects of habitat loss and fragmentation. However, it is important to distinguish the concept of fragmentation per se, which refers to fragmentation independent of the overall habitat amount in a landscape, where only the configuration of patches changes (Fahrig 2017). Investigating the specific effects of fragmentation per se on plant–pollinator networks through field experiments can be challenging and time-consuming. Therefore, simulation-based approaches are recommended to estimate these effects (Häussler et al. 2017; Rahimi et al. 2021a, b). Simulated models offer advantages over real-world landscapes as they provide greater control and fewer limitations, allowing for the examination of specific aspects within a landscape. For instance, utilizing the Lonsdorf model and simulated landscapes, Rahimi et al. (2021b) discovered that agricultural landscapes characterized by a high degree of fragmentation per se in forest patches yielded the highest pollination rates.

In a similar investigation, Rahimi et al. (2021a) observed that in agricultural landscapes, fragmented patterns resulted in reduced pollination when small forest patches had limited capacity to supply pollination. However, no previous studies have explored the impact of fragmentation per se on key characteristics of plant–pollinator networks, such as nestedness, degree of specialization, and connectance. Consequently, it remains uncertain whether fragmented or aggregated landscape structures are better suited to accommodate networks with a higher degree of specialization or nestedness. Therefore, this study tries to address this important gap in plant–pollinator studies using simulated landscapes. The questions that this study answers are (1) what are the expected effects of landscape structure on the characteristics of plant–pollinator networks? (2) which pattern of patches probably provides specialized networks in an agricultural landscape?

Methods

Generating simulated landscapes

In this study, we focus more on landscapes, where several forest patches are present and, consequently, on plant pollination networks in which bees play a more important role. In these landscapes, each forest patch with flowers around it can form a matrix of interactions between bees and flowers (local network). If we calculate the interactions related to each patch in the landscape, then we will have a metanetwork for the entire landscape.

We used *nlm_randomcluster* function in the NLMR package (Sciaini et al. 2018) in Rv4.3 software to generate simulated agricultural landscapes covered by forest patches and farms or pastures including different

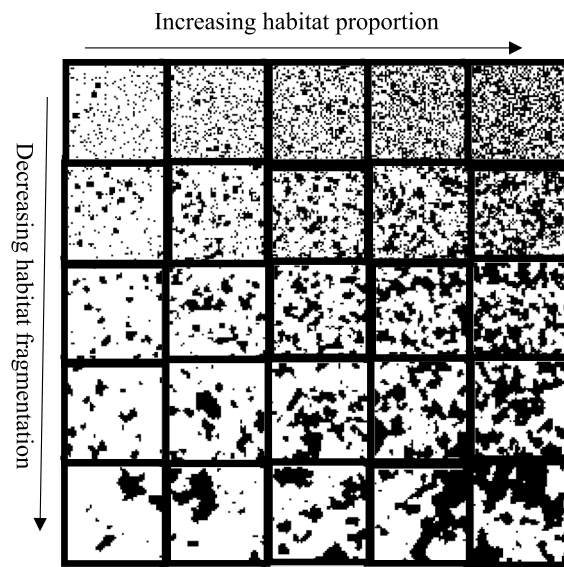


Fig. 1 Simulated landscapes in different forest proportions (black patches) and degrees of fragmentation

flowering plants. These maps were created with dimensions of 50 by 50 cells and have different percentages of forest amount and degree of fragmentation per se (Fig. 1). The proportion of forest patches was considered from 5% to 50% of each landscape. Therefore, we created 6 series of simulated landscapes based on the forest proportion (5, 10, 20, 30, 40, and 50 of the entire landscape). At each of these proportions, the degree of fragmentation per se changed from highest (0.01) to lowest (0.5) using parameter p (the proportion of elements randomly selected to form clusters) in the NLMR package. Therefore, landscapes with a degree fragmentation of 0.5 have the lowest fragmentation and as a result, forest patches have an aggregated pattern. Figure 1 shows several simulated landscapes in which the amount of forest patches is constant in each column but the degree of fragmentation changes vertically.

Extracting plant–pollinator networks from simulated landscapes

In this study, we considered two general assumptions for the interactions between pollinators and plants: (1) pollinators and plants are randomly distributed across the landscape, and (2) they interact randomly. In the introduction section, we mentioned that the interactions between plants and pollinators in many networks do not differ significantly from the patterns resulting from random interactions. The result is true for 70% of these networks (Krishna et al. 2008). Therefore, we assumed that pollinators are only present in forest patches and can randomly interact with flowers around

Table 1 Number of pollinators and flowers per each forest proportion scenario

Forest proportion (%)	No. pollinators	No. flowers
5	12	237
10	25	225
20	50	200
30	75	175
40	100	150
50	125	125

these patches up to 3 cells away from the patches. Therefore, we randomly assigned a number to each cell of forest patches and flowering habitat, which represents one species. Finally, a matrix of all the possible interactions between pollinators and flowers was obtained for each landscape.

Each landscape in the study consists of a total of 2,500 cells, and the proportion of cells covered by forest varies in each series of forest patch amounts. Consequently, the availability of pollinators is constrained by the extent of forest cover within each landscape. The maximum number of flower species and pollinators can be 250 for each group. To illustrate, in landscapes, where 10% of the cells are covered by forest, there are a total of 250 forest cells. Within these 250 cells, 25 distinct pollinator species were considered, while 225 flower species were assigned to non-forest cells (as shown in Table 1). The table provides details on the number of pollinators and flowers for each forest proportion. Notably, the table reveals that when 50% of a landscape is covered by forest, the number of flowers and bees is equal.

Landscape metrics

To estimate the relationship between landscape structure and characteristics of plant–pollinator networks, we used landscape metrics available in Fragstats v4.2 software (McGarigal 1995). These metrics are commonly used for measuring landscape changes along with other alternative metrics (Rahimi et al. 2022b). Therefore, six commonly used metrics were calculated for all simulated landscapes at the class levels (Table 2). As the degree of fragmentation increases, the Largest Patch Index (LPI) decreases, because the mean area of patches (Area-MN) decreases. The edge density (ED) of patches also increases with increasing fragmentation and the number of patches (NP). In this situation, Euclidian distance between patches (ENN) decreases. Aggregation (AI) metric measures the degree of fragmentation and higher values of AI metrics show less habitat fragmentation.

Table 2 Descriptions of the selected landscape metrics

Category	Metric	Equation	Range
Area and Edge	LPI	a_{ij} / A	$0 < LPI \leq 100$
	Area-MN	$\frac{\sum_{j=1}^n x_{ij}}{n_i}$	Area-MN > 0
	ED	$\frac{\sum e_{ik}}{A} (10000)$	$0 \leq ED$, no limit
Aggregation	AI	$\left(\frac{g_{ii}}{\max g_{ij}} \right) (100)$	$0 \leq AI \leq 100$
	NP	n_i	$NP \geq 1$
	ENN	h_{ij}	$ENN > 0$

In this table, several metrics related to area and edge, shape, and aggregation categories have been presented and all of them measure landscape configuration aspects

a_{ij} = area (m²) of patch; A = total landscape area (m²); n_i = number of class i patches in the landscape; e_{ij} = total length (m) of edges of patch ij , including landscape boundary; $a_{ij}c$ = area (m²) within patch ij separated from its boundary by a user-specified buffer width (m); g_{ii} = the number of adjacencies (contiguity) between pixels of patch class i ; $\max g_{ij}$ = maximum possible number of adjacencies among pixels of patches of class i ; h_{ij} = distance (m) from patch ij to the nearest neighboring patch of the same type (class), based on patch edge-to-edge distance, computed from cell center to cell center (McGarigal et al. 2002)

Bipartite metrics

To measure the different characteristics of extracted networks, we used *networklevel* function in the bipartite package (Dormann et al. 2014, 2008) in R v4.3 software. We calculated 6 metrics for each network extracted from each landscape at network levels (Table 3). Networks metrics are calculated for the whole network but group-level metrics provide a value for higher and lower trophic levels. Details of each metric are presented in Table 3. To determine the effects of landscape structure on changes in plant–pollinator networks, the statistical relationship between landscape and bipartite metrics was calculated using Pearson’s correlation.

Results

Figure 2 illustrates the plant–pollinator networks in three simulated landscapes, each characterized by different forest percentages and degrees of fragmentation. Each landscape is represented by its corresponding plant–pollinator network plot. The top row of the plots represents 10 pollinators, while the bottom row represents 10 flowers, and their interactions occur randomly. In the first landscape (Fig. 2A), the forest habitat covers only 5% of the entire landscape and is fragmented to the maximum extent. In this scenario, each forest cell serves as a potential nesting habitat for a pollinator. The asymmetric abundance of pollinators influences their interactions with flowers based on their respective abundances. Moving to the second landscape (Fig. 2B), forest patches occupy 30% of the landscape, and the degree of fragmentation is considerably lower. As a result, the abundance of rare pollinators increases compared to the previous landscape, leading to an increased number of interactions

Table 3 Network-level bipartite metrics and their definition

Metric	Definition
Connectance	The realized proportion of possible links
Nestedness	Nestedness temperature of the matrix (0 means cold, i.e., high nestedness, 100 means hot, i.e., chaos)
Interaction strength asymmetry (ISA)	The asymmetry in the interaction strength of two interacting species. Negative values indicate that the plants exert a stronger effect on pollinators
Specialization asymmetry (SA)	Asymmetry (higher vs. lower trophic level) of specialization. Negative values show a higher specialization of the lower trophic level
Linkage density	Marginal totals-weighted diversity of interactions per species (quantitative)
H2	H2 is a measure of specialization. H2 is between 0 and 1, with 1 indicating maximum specialization

with flowers. In the third landscape (Fig. 2C), half of the landscape (50%) is covered by forest, and the degree of fragmentation of the patches is at a moderate level. This landscape exhibits a significant increase in the abundance of rare pollinators compared to the previous landscapes, resulting in a distinct plant–pollinator network topology. Overall, the example plots highlight how varying forest percentages and degree of fragmentation can influence the abundance of pollinators, and their interactions with flowers, and ultimately shape the structure of the plant–pollinator networks in the simulated landscapes.

The statistical relationship between landscape and bipartite metrics

Figure 3 shows the statistical relationship between landscape and bipartite metrics in different forest proportion scenarios. This figure shows that connectance has a positive correlation with metrics, such as the NP and ED. The positive correlation between connectance and landscape metrics is consistent in all scenarios of forest proportion. Similar to connectance, nestedness, and ISA metrics also show a similar relationship with landscape metrics in all forest proportion scenarios. However, as forest area increases, the correlation between link density and landscape metrics becomes more significant. Therefore, in a fragmented landscape, we expect more connectance, nestedness, and ISA, implying that less specialized networks can be found in landscapes with a high degree of forest fragmentation.

Unlike the previous metrics, the SA metric has a negative correlation with NP, and ED, metrics in all scenarios. However, in higher forest proportions, the correlation between SA and landscape metrics such as NP is significant. Similar to SA, linkage density also shows a similar relationship with landscape metrics. However, with the increase in the forest area, the correlation between linkage density and landscape metrics becomes more significant. This trend is also true to the H2 metric in such a way that only in forest proportions greater than 0.3 it shows a significant correlation with the landscape metrics. A

positive correlation between H2 and AI metric implies that fragmented landscapes have a lower degree of specialization. In other words, in landscapes the number of patches is low, and the mean area of patches is high, plants and pollinators constitute specialized networks.

Discussion

Our findings revealed that the relationship between the landscape structure and the topology of plant–pollinator networks is influenced by two key factors: the proportion of forest habitat in the landscape and the degree of fragmentation. In addition, fragmented landscapes tend to exhibit more general plant–pollinator networks, as indicated by metrics, such as nestedness and H2. While several landscape metrics are correlated and provide similar interpretations, we focused on the most significant and comprehensible ones in this study. Our analysis demonstrated that connectance and nestedness tend to increase with fragmentation. Connectance refers to the ratio of actual links to the total possible links in a network. Plant–pollinator networks are typically sparse, indicating that only a small fraction of potential interactions occur in nature, resulting in low connectance. Connectance decreases with higher species richness, suggesting that regions with high pollinator diversity, such as tropical areas, are likely to exhibit lower connectance (Vizentin-Bugoni et al. 2018). The low connectance in plant–pollinator networks contributes to the limited community-level generalization (Bosch et al. 2009). Nestedness, on the other hand, can either increase or decrease with changes in connection. We expect that the nestedness of rare species decreases as connectance increases. Nestedness tends to increase with higher connectance, as observed in previous studies (Vizentin-Bugoni et al. 2018). Furthermore, studies have shown that nestedness decreases with increasing patch connectivity (Santamaría et al. 2018). In fragmented landscapes with low connectivity, Ferreira et al. (2020) also found that nestedness increases.

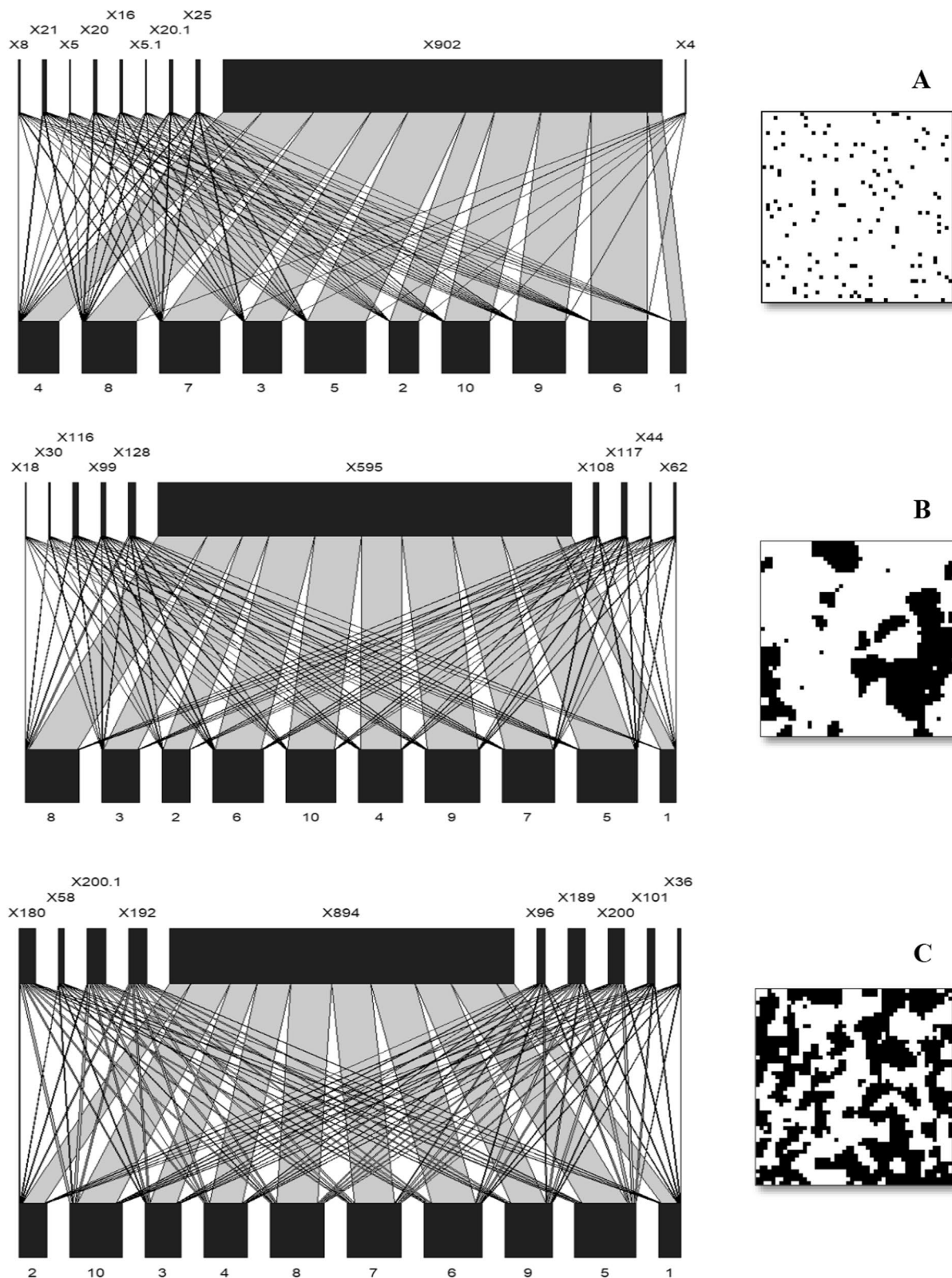


Fig. 2 Examples of simulated landscapes with corresponding plant–pollinator networks including 10 pollinators and 10 flowers. **A** Forest proportion = 5%, $p=0.01$, **B** forest proportion = 30%, $p=0.55$, **C** forest proportion = 50%, $p=0.3$

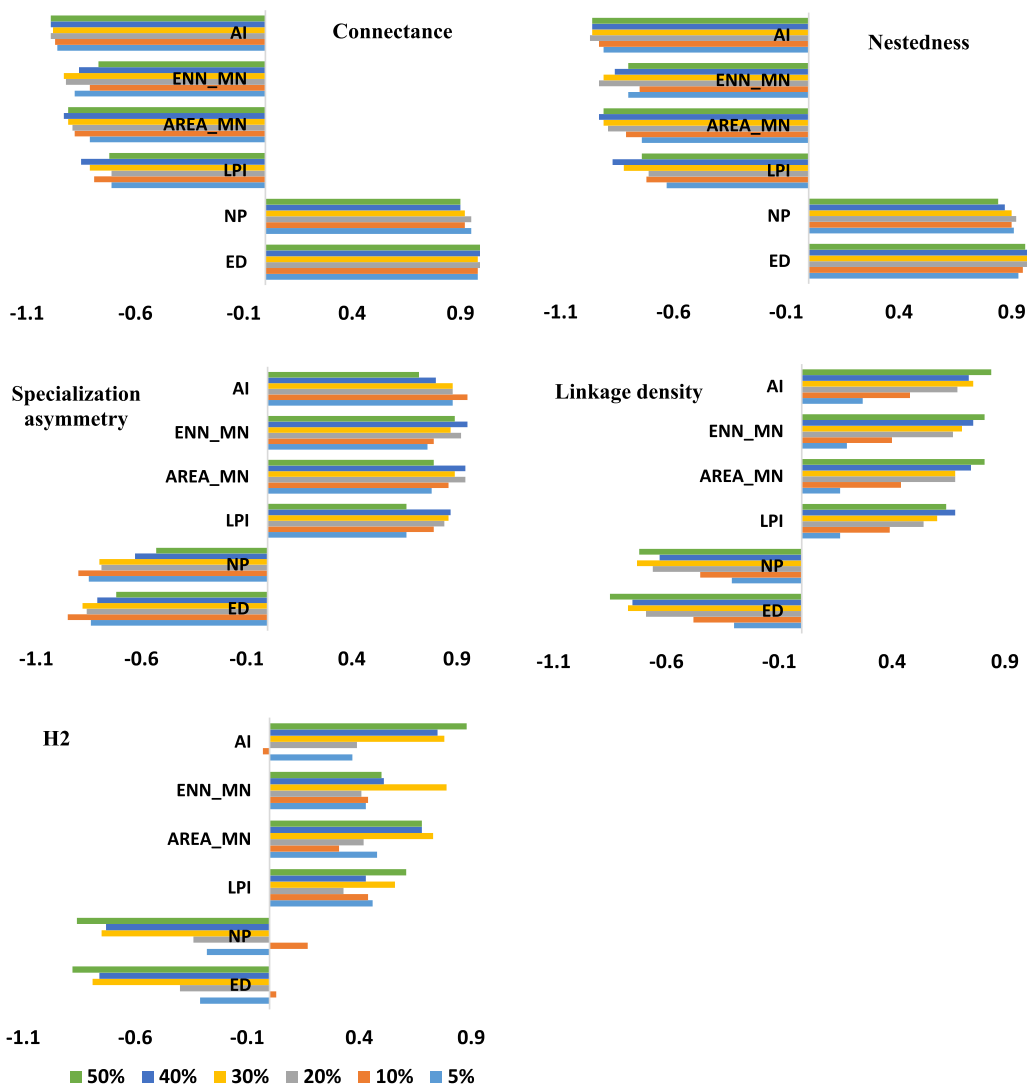


Fig. 3 Correlation values between landscape and bipartite metrics in different forest proportions

The observed positive relationship between connectance and fragmentation aligns with expectations. In fragmented landscapes, where forest patches are dispersed throughout the landscape, pollinators that rely on these patches have the opportunity to interact with a greater number of species. Consequently, flowers are distributed across the landscape, and only pollinators that exhibit a dispersed pattern of movement can access them all. Conversely, in aggregated landscapes, where pollinators are concentrated in large patches, certain pollinators may be located in central cells. As a result, considering their maximum foraging ranges, they may not have access to flowers that are situated far from their

location. The average maximum foraging distances for solitary bees, bumblebees, stingless bees, and honeybees have been estimated as 1220, 14,670, 1520, and 6313 m, respectively (Zurbuchen et al. 2010).

Our findings revealed that fragmented landscapes exhibit higher values of Interaction Strength Asymmetry (ISA), indicating that fragmentation amplifies the imbalance in interaction strength between species. Positive ISA values indicate a greater reliance on higher trophic level species on their interaction partners (Dormann et al. 2014). The concept of strength asymmetry describes situations, where a plant exhibits a high dependence on a particular pollinator, while that

pollinator has a low dependence on the plant. This weak asymmetry can be beneficial for the survival of mutualistic relationships, as the removal of one species would lead to the removal of the other. In reciprocal networks, which exhibit weak asymmetry, most species have a negative dependence on each other. The prevalence of asymmetric interactions reflects the limited potential for ecological and evolutionary pairing between plants and pollinators. In addition, it has been observed that rare species tend to have higher interaction strengths compared to abundant species (Bascompte and Scheffer 2023). It's important to note that species strength and interaction asymmetry are distinct measures. Interaction asymmetry quantifies the difference in dependence between two species, such as a plant's dependence on a pollinator vs. the pollinator's dependence on the plant. On the other hand, species strength examines the dependence that a plant has on each of its visitors, for instance (Soares et al. 2017).

The H2 metric, introduced by Blüthgen et al. (2006), offers a way to quantify the level of specialization in a network by accounting for abundance, richness, and sampling effects. It compares the actual network structure, based on factors, such as abundance or pollination syndrome, against random matrices to assess the fundamental level of specialization among species. When the recorded interactions involving a particular pollinator exceed what would be expected by chance, it indicates a strong preference for that pollinator for the host plant. Conversely, a low number of interactions suggests the presence of forbidden links, such as morphological mismatches (Blüthgen et al. 2008). In cases where interactions occur randomly, the H2 value is zero. Specialization can be measured qualitatively at both the species and network levels. The number of links determines the degree of specialization for individual species, while connectivity is used to assess specialization at the network level. As specialization increases, the H2 value decreases, ranging from 0 to 1, with 1 representing maximum specialization. A value of 0 indicates perfect nestedness within the network structure.

Our findings revealed a positive correlation between the H2 metric and fragmentation metrics, such as AI, indicating that fragmented landscapes tend to exhibit less specialization in plant–pollinator networks. In fragmented patterns, pollinators have a wider range of options and interact with various flowers. In our study, we assumed a random distribution of pollinators and flowers, which implies that rare pollinators in large patches (in less fragmented patterns) may not

have access to all the flowers scattered across the landscape. Several studies have also reported less specialized networks in fragmented landscapes. For instance, Jauker et al. (2019) examined the impact of calcareous grasslands on plant–pollinator network structure in the Leine–Bergland region of Lower Saxony, Germany, which encompasses approximately 35% forest cover. Their results indicated a decrease in the number of links within the network as habitat loss increased. Furthermore, H2 decreased as patch size decreased. Similarly, Ferreira et al. (2020) investigated seven landscapes in the Brazilian Atlantic Forest and found that reduced forest cover and isolated forest patches resulted in less specialized networks. Conversely, aggregated landscapes with greater forest cover and connectivity exhibited more specialized networks, as indicated by higher H2 values. The size of the network and the number of interactions were positively influenced by forest cover, with both metrics increasing alongside patch area.

Conclusion

We showed how landscape structure can change the topology of plant–pollinator networks through changes in species abundance and limiting their interactions. Experimental studies have shown that landscape structure plays an important role in shaping the topology of plant–pollinator networks. The increase in the area of the patches also caused an increase in the number of visits and, as a result, an increase in the symmetry of the network. Even the fragmentation effects of landscape structure on biodiversity are significant only below a critical proportion of habitat, pollination also follows the idea concerning fragmentation effects when the area of the habitat like a forest is less than 10% of the total landscape. We also found that in landscapes covered by a low amount of forest (5%), some bipartite metrics were not correlated with landscape structure. However, as the forest proportion increased, all bipartite metrics showed a significant relationship with landscape metrics. As we found that the topology of plant–pollinator networks was influenced by forest amount and degree of forest fragmentation in the landscape, the degree of forest fragmentation was the most important factor that affected the topology of plant–pollinator networks, because in each forest proportion scenario, fragmented landscapes accommodated less specialized networks.

Appendix

R code for creating simulated landscapes

```
install.packages("NLMR")
```

```
library(NLMR)
```

Usage: `nlm_randomcluster(ncol, nrow, resolution=1, p, ai=c(0.5, 0.5), neighborhood=4, rescale=TRUE).`

Our code: `for (i in 1:100){filename=paste('mypic_',i,'.tif').`

```
random_cluster<-nlm_randomcluster(50, 50, 1, 0.1, ai=c(0.25, 0.25, 0.5)).
```

```
writeRaster(random_cluster,filename=fle.Path("my folder"),overwrite=TRUE)}.
```

R code for calculating bipartite metrics

```
install.packages("bipartite")
```

```
library(bipartite)
```

Usage: `networklevel(web, index="ALLBUTDD", level="both", weighted=TRUE,`

`ISAmethod="Bluethgen", SAMethod = "Bluethgen", extinctmethod = "r", nrep = 100, CCfun=median,`

`dist="horn", normalise=TRUE, empty.web=TRUE, logbase="e", intereven="prod", H2_integer=TRUE,`

`fcweighted=TRUE, fcdist="euclidean", legacy=FALSE)`

Our code: `data<- read.csv(my data)`

```
networklevel(data)
```

Abbreviations

NP	Number of patches
LPI	Large Patch Index
ENN-MN	Mean Euclidean nearest-neighbor distance
Area_MN	Mean patch area
ED	Edge density
AI	Aggregation Index
ISA	Interaction strength asymmetry
SA	Specialization asymmetry

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Author contributions

ER has written the paper and have done the modeling part of the analysis. CJ has reviewed the paper, interpreted the results and final edition.

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Availability of data and materials

Python code for assigning pollinators and plants to landscape cells is available on request from the authors only based on logical requests.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

The authors confirm that they have no conflicts of interest to disclose concerning this publication.

Competing interests

The authors declare that they have no competing interests.

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