STRAWBERRY FIELDS FOREVER: THE EFFECT OF FARM-POLLINATOR INTERACTION NETWORK CENTRALITY ON STRAWBERRY PRODUCTION

Rafaela Jardim Bonet[1,2*] (ID), *Fernando Fortunato Jeronimo*[2,3] (ID)
& Isabela Galarda Varassin[2] (ID)

[1] Universidade Federal do Paraná, Setor de Ciências Biológicas, Programa de Pós Graduação em Ecologia e Conservação, Av. Cel. Francisco H. dos Santos nº100, Jardim das Américas, Curitiba, PR, CEP 81530-000, Brazil.

[2] Universidade Federal do Paraná, Setor de Ciências Biológicas, Departamento de Botânica, Laboratório de Interações e Biologia Reprodutiva, Av. Cel. Francisco H. dos Santos nº100, Jardim das Américas, Curitiba, PR, CEP 81530-000, Brazil.

[3] Universidade Federal do Paraná, Setor de Ciências Biológicas, Programa de Pós Graduação em Botânica, Av. Cel. Francisco H. dos Santos nº100, Jardim das Américas, Curitiba, PR, CEP 81530-000, Brazil.

E-mails: rafajardim27@gmail.com (*corresponding author); fernandofjeronimo@gmail.com; isagalarda@gmail.com

Abstract: Plant-pollinator networks are highly dynamic and may vary in their patterns and composition due to abiotic changes, anthropogenic influences, and landscape changes, leading to alterations in the pollinator communities and interactions between species. Biotic pollination plays a key role in strawberry fruit set and quality. Here, we explored how the topology of the farm-pollinator networks affects the qualitative and quantitative parameters of strawberry production (*Fragaria* spp.); the relative importance of a given node, be it a farm or a pollinator, is shown by centrality measures, revealing the distribution of interactions between all nodes. We expected that farms with higher centrality would positively influence strawberry production. We evaluated the quantitative (fruit mass and fruit set) and qualitative parameters (fruit shape, fruit quality, and stage of ripeness) of the strawberries produced. We sampled pollinators and conducted experiments on strawberry crops in five farms located in the basin of the Miringuava and Miringuava-Mirim rivers in São José dos Pinhais - PR. We show that biotic pollination positively contributes to strawberry production, directly affecting strawberries' shape, ripeness, and quality. We also found that more central farms, which means that farms with a higher degree centrality - with more pollinators - favor the pollination service, which contributes to strawberry production quality and quantity.

Keywords: agriculture; bees; crop production; ecosystem services; flies; *Fragaria*; pollination.

INTRODUCTION

Variations in interactions and structure in biological communities are due to various factors, such as environmental disturbances, habitat loss, and intrinsic variations in species habits and phenology (Mora *et al.* 2020). In pollinator communities, such changes can change the foraging pattern and resource availability for individuals and cause population divisions and randomization of demographic and genetic patterns of the groups involved. In addition, pollination contributes to

defining the composition and structure of plant communities, making its study relevant for influencing the functioning of ecosystems and agricultural maintenance (Fantinato *et al.* 2018).

Plant-pollinator interaction networks are intensely dynamic, and their patterns and composition may vary due to abiotic, ecological, biotic changes, and even anthropic influence, such as environmental disturbances and habitat destruction and fragmentation, leading to temporal fluctuations in the resilience of communities of pollinators and interactions between mutualistic species (Fantinato *et al.* 2018). Simple characteristics that describe interaction networks may be relevant for this analysis, such as centrality measures, which help direct efforts to conserve landscapes and species, outlining priority species and regions (Bodin 2009).

Several studies have looked at the effect of the structure of natural landscapes in agricultural areas on plant-pollinator interactions, and their consequences for food production. The anthropogenic impact translated into agricultural intensification has caused changes in the topology of plant-pollinator networks, decreasing the robustness of interactions (Morrison *et al.* 2019), also affecting the richness of pollinator species and the effectiveness of the ecosystem service they provide, consequently affecting food production (Connelly *et al.* 2015). The relationship between interaction networks and the structure of the landscape in which they are embedded is important for understanding what is needed to maintain the interactions embedded in dynamic landscapes (Fortin *et al.* 2021).

For the production of strawberries, even with moderate dependence on the pollination service, the frequency and consistency of pollinator visits result in a uniform and wide distribution of pollen, producing well-shaped fruits with greater weight (Malagodi-Braga 2018). The shelf life of strawberries also increases with this service, decreasing fruit loss by at least 11%, as well as their shelf life, compared to self-pollinated or wind-pollinated fruits (Klatt *et al.* 2014).

Thus, in the present study, we evaluated how the topology of farm-pollinator interaction networks composed of strawberry crops (*Fragaria* spp.) (Rosales, Rosaceae) in agricultural farms affects strawberry production. Based on network topology, through modularity, we evaluate the role of the pollinators in the network. Also, we evaluate the influence of farms' centrality on strawberry production.

We expected strawberry crops in farms with higher centrality (C_C - proximity centrality; C_B - betweenness; C_D - degree centrality) to positively influence strawberry production, increasing its qualitative (fruit shape, fruit quality, and stage of ripeness) and quantitative (fruit set and fruit mass) parameters. Regarding the role of the pollinators in the network, we expect to identify the key-pollinators to the network stability, by classifying them as peripherals, connectors, module hub or network hubs. We also expect pollinator-friendly landscapes to have a positive influence on centrality measures.

MATERIAL AND METHODS

Study area

We investigated five strawberry-producing farms (two with organic farm management and three with conventional farm management) in the region of the Miringuava and Miringuava-Mirim basins, sub-basins of the Iguaçu River located in São José dos Pinhais, Paraná, Brazil (Figure 1). The predominant vegetation cover is mixed rainforest belonging to the Atlantic Forest biome, with an average annual temperature of around 16 and 17ºC and average annual precipitation ranging from 1,400 to 1,600mm (Bossle 2010).

Land cover in the basin was characterized by a longitudinal gradient, with a prevalence of anthropogenic areas to the west and natural areas to the east, but with a high permeation of areas intended for agriculture and livestock (MapBiomas 2021). Currently, the area is an essential agricultural hub in the Metropolitan Region of Curitiba, with 95% of crop production by family farming (Weins *et al.* 2021). To verify the influence of the pollinator interaction networks topology on strawberry production, we selected five farms spread across the landscape gradient (Figure 1) and sampled them from July to August 2021.

Pollinators sampling

We sampled the pollinators in the study areas during crop flowering period, for a total of five
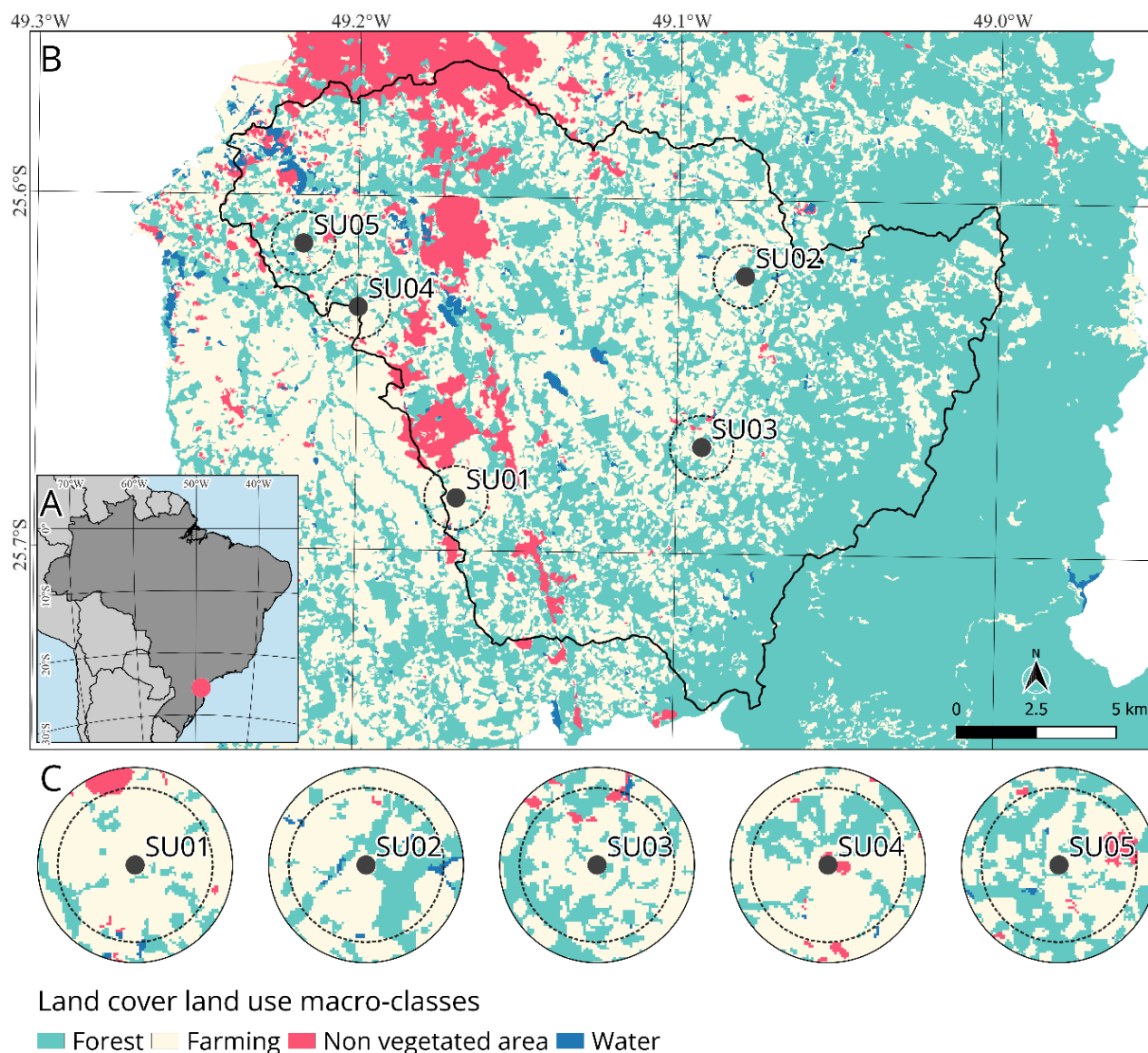
Figure 1. Map of the sampled area in Paraná State, Brazil (A), land use macro-classes in the Miringuava and Miringuava-Mirim river basins with the location of farms (B, black dots indicating sampling units -SU) and land use macro-classes in each farm (C). Green: forest formation; pink: non-vegetated area; beige: farming; blue: water.

days of sampling, one for each area. We collected the pollinators during rounds in plots of strawberry (*Fragaria* spp.) ground cultivation of the Albion and San Andreas varieties (Embrapa 2012). We performed 12 samples of 15 minutes, totaling four hours per site between 8:00 am and 1:00 pm. We randomized the sampling order and starting point to avoid temporal and spatial biases in sampling. The collected individuals were processed, assembled, labeled, and identified to the lowest possible level and deposited in the Entomological Collection Padre Jesus Santiago Moure (DZUP) from the Federal University of Paraná (UFPR).

Qualitative and quantitative fruit metrics

We evaluated the influence of biotic pollination on strawberry production through experiments. To this end, we carried out three treatments: pollinator exclusion treatment - pre-anthesis isolation of flowers (flower buds) to avoid the visit of potential pollinators, through voile fabric bags, control treatment, *i.e.*, open pollination - marking the flowers and keeping them exposed, without further manipulations and pollen supplementation treatment - complementing the pollen load with pollen from other flowers, located at least 20 meters

away from the sampled flowers. All harvested fruits were submitted to qualitative and quantitative measurements.

The qualitative parameters selected for the fruits were: (1) fruit set (if formed or aborted), (2) stage of ripeness (whether ripe, intermediate or unripe); we considered as ripe the fruits with more than 2/3 of the fruit red (Figure 2A), intermediate when with up to ≅ 2/3 of the fruit red (Figure 2B), and green those with up to ≅ 1/3 of the fruit in the red staining (Figure 2C), (3) fruit shape (whether standard or deformed); we considered deformed fruits those with any shape deviation such as concavities, protuberances and constrictions, caused by a concentration of undeveloped and/or malformed achenes (Figure 2F; 2G; 2H), (4) fruit quality (whether intended for direct sale/by-product or disposal). Fruits intended for disposal were those without aesthetic conditions for direct sale and without biophysical conditions for using its pulp (*e.g.*, fruits that were completely green and malformed or in decomposition) (Figure 2G; 2H; 2I); we established these criteria based on the exchange of information with the producers. As a quantitative criterion, we measured fresh strawberry mass in the laboratory with a precision scale.

We analyzed pollination contribution (PC) and pollination deficit (PD). Pollination contribution refers to the difference in mass and number of fruits from the control treatment (C) and from the exclusion treatment (E) from the same individual (CP = C mass – E mass). This value represents the difference between the realized and minimum reproductive value, representing the reproductive value provided by the pollinators. Pollination deficit represents the difference in mass of a fruit from the control treatment (C) and a fruit from the supplementation treatment (S) from the same individual ($SD = C_{mass} – S_{mass}$). This value represents the difference between the realized and maximum reproductive value, and its result refers to the value provided by the treatment.

Statistical analysis for fruit metrics

To evaluate the effect of pollination on qualitative aspects of strawberry production in each farm, we performed a set of contingency tests using Pearson's chi-square, with the "chisq.test" function (package "stats" v3.6.2). The predictor variable in the four tests was the treatment applied to the flowers (control, pollinator exclusion, and pollen supplementation).
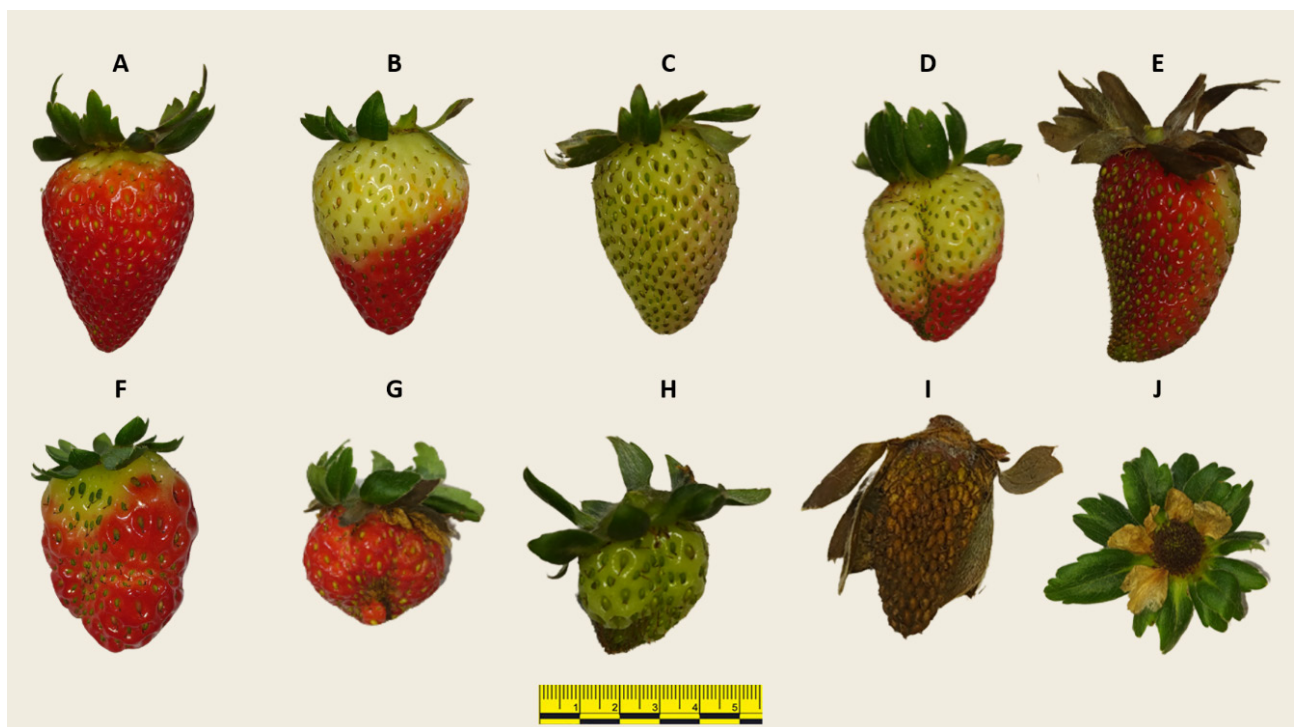

Figure 2. Standard fruits (A-C): A - ripe fruit, B - intermediate ripe fruit, C - unripe fruit; deformed fruits (D - H); E - F - fruits intended for by-products, H and I - discarded fruits; in I, fruit burned by frost. In J an aborted flower.

The response variables were fruit set, fruit shape, fruit quality, and stage of ripeness. We performed continuity correction using the Yates test for all these tests, and only results below the corrected alpha were considered significant. Finally, to analyze the magnitude of the pollination effect on fruit set, fruit shape, fruit quality, and stage of ripeness for the four models, we calculated the effect size by Cramér's V, using the "CramerV" function (package "rstatix" v.0.7.2).

Network-level metrics

We built the network with the strawberry crops in each farm as rows, pollinator species as columns, and cells filled by the number of visits of each pollinator registered in the strawberry crops for a given farm. Thus, node metrics were calculated for each farm and each pollinator species. Based on that, we evaluated how central a farm or a pollinator is in the interaction network, and the network modularity. Modularity (M), is a property related to the structuring of subgroups of pollinators and farms who interact more with each other than with other pollinators and farms in the same network (Mello *et al.* 2016).

To evaluate network's topology, we performed a set of tests based on functions of the "bipartite" package. We used the "plotweb" function to visualize the interaction network, and to calculate the network metrics, we used the "networklevel" function. To check the significance of the metrics that measure network structure, we compared them with values obtained from null models. We built the null models generating random networks, where the probability of interactions was proportional to the number of interactions. We kept the connectance of the random networks equal to that of observed networks, but without preserving the values of the total marginals. We generated the null models using the "suffle. web" method in a "bipartite" package (Dorman *et al.*, 2009) and calculated the Z-score for modularity.

Node-level network metrics

Centrality measures show the relative importance of a given node, a farm or a pollinator, in relation to all other nodes, giving the distribution of interactions between them (de Nooy *et al.* 2005). Degree centrality (C_D) represents the number of interactions a given node makes (Freeman 1979). According to this index, a farm is central when well connected to many floral visitors, representing how generalized the interactions are (Martín González *et al.* 2010). Likewise, a pollinator is central (C_D) when it connects with several farms. Closeness centrality (C_C) describes how much a given farm shares floral visitors with other farms, that is, a farm with a high CC shares many visitors with other farms. Likewise, a pollinator is central (C_C) when it shares several farms with other pollinators. Betweenness centrality (C_B) measures the minimum number of paths between two farms or pollinators, defining the central one with the lower number of paths (de Nooy *et al.* 2005). Thus, betweenness centrality describes the importance of farms or pollinators as connectors in a given network (Freeman 1979). A farm with high betweenness centrality indirectly connects subnetworks of the same assembly (*e.g.*, farms) through shared floral visitors. Likewise, a pollinator is central (C_B) when it indirectly connects subnetworks of farms. Thus, a farm can be central because it has many partners (high degree centrality), because it shares many flower visitors with other farms (high closeness centrality), and/or as a connector (high betweenness centrality), sharing partners with many farms who do not share common partners (Freeman 1979; Mello *et al.* 2015). Likewise, a pollinator can be central when it shares farms with other floral visitors (high degree centrality), when it connects farms indirectly (high betweenness centrality), or when it connects with several farms (high closeness centrality). We calculated all metrics with "bipartite" package in the R Studio v4.2.1 program.

We followed the methodology of Olesen *et al.* (2007) to classify the species of the network, based on a *cz* plot; *z* corresponds to the standardized within-module degree and c to among-module connectivity. Together, *c* and *z* define the roles of the species in the network, based on its position in comparison with other species in its module, and how well it connects with species in other modules in the network. The species are classified as: peripherals ($z \leq z_{critical}$; $c \leq c_{critical}$), which have few connections within their module and few connections with species from other modules, connector ($z \leq z_{critical}$; $c > c_{critical}$) stablishing connections with species from modules other than the one in which they are included, and are important for uniting different modules,

module hub ($z \geq z_{\text{critical}}$; $c \leq c_{\text{critical}}$), important for maintaining coherence within their own module or network hub ($z > z_{\text{critical}}$; $c > c_{\text{critical}}$), which are important for maintaining coherence within their module and between the other modules in the network. We calculated critical thresholds for c and z values established from the null models using 95% quantiles (Dormann & Strauss 2014) and cz values function in bipartite package.

Landscape metrics

We chose the following metrics to evaluate the landscape effect in farm-pollinator interaction networks structure and production in strawberry crops: (1) percentage of landscape (PLAND), which refers to the percentage of area covered by forest formations; (2) patch density (PD), which gives the number of forest patches per unit area (hectares) (Valenzuela *et al.* 2019); (3) edge density (ED), which corresponds to the ratio of the lengths of the edge segments present in the landscape and the total area studied (Oliveira *et al.* 2022); (4) cohesion, which characterizes the connectedness of forest patches and (5) landscape heterogeneity (LSI index), a measure of how different the parts of a landscape are in terms of their spatial configuration. We calculated all metrics with "landscapemetrics" package (Hesselbarth *et al.* 2019) in the R Studio v4.2.1 program, and based on land use mapping of the MapBiomas Brazil Project (2021), 7.0 collection for the city of São José dos Pinhais in 2021.

RESULTS

Effect of pollination on quantitative and qualitative aspects of strawberry production

Based on pollination experiments on 406 flowers, we harvested 310 fruits. We had 88% of fruit set on control treatments (n = 118 fruits), 88% supplementation treatment (n = 121 fruits) and 52% on exclusion treatment (n = 71 fruits) (Figure 3A). 96 fruits were aborted (control treatment: n = 16; supplementation treatment: n = 15; exclusion treatment: n = 65) and, therefore, were not harvested. The fruit set was dependent on the treatments applied ($X^2 = 65.744$; gl = 2, p < 0.001; v = 0.403 ; Figure 3A); the control and supplementation treatments resulted in lower aborted fruits unlike exclusion treatment, in which

the number of aborted fruits was higher. Fruits showed better shape in supplementation treatment and exclusion treatment fruits presented worse shape ($X^2 = 40.354$; gl = 2, p < 0.001; v = 0.361; Figure 3B). In control treatment there was no difference in fruit shape. Fruit quality presented dependence on the treatment applied ($X^2 = 7.496$; gl = 2, p = 0,024; v = 0.156; Figure 3C). Only exclusion treatment fruits had lower quality (destined for discard), with no difference in supplementation and control treatments. Finally, control treatment resulted in a higher number of ripe fruits and lower number of underripe fruits ($X^2 = 31.428$; gl = 1, p < 0.001 ; v = 0.005; Figure 3D). There was no difference for fruits at the intermediate stage of ripening. There was no difference in ripening in supplementation treatment, while exclusion treatment resulted in a higher number of underripe fruits.

Regarding mass, there was a significant difference between treatments (n = 310, p <0.001). In the exclusion treatment strawberries mass was lower (1.57 ± 0.02 g) than that of fruits from supplementation treatment (6.92 ± 1.16 g) and control treatment (6.97 ± 1.81 g), which didn't differ from one another (Figure 3E).

Interaction networks structure

During the sampling period, we collected 132 individuals belonging to 15 species and 5 different families: *Allograpta exotica*, *Allograpta falcata*, *Allograpta hastata*, *Allograpta neotropica*, *Eristalis* sp1, *Eristalis* sp2, *Syrphus phaeostigma*, *Syrphus shorae*, *Toxomerus watsoni* and *Xanthandrus palliatus* (Syrphidae, Diptera), *Apis mellifera* and *Trigona spinipes* (Apidae, Hymenoptera), *Eriopis connexa* (Coccinellidae, Coleoptera) and *Lagria villosa* (Tenebrionidae, Coleoptera) (Figure 4).

We found the pollinator-farm network to be more modular (*M* = 0.357, p>0.05, Figure 5) than expected by chance. Regarding the role of the species in the network (Figure 6), we found that *Eristalis* sp2, *Syrphus phaeostigma*, *Apis mellifera* and *Allograpta exotica* act as module hubs ($c \leq 0.72$; $z \geq 1.095$), while *Allograpta falcata*, *Allograpta hastata*, *Allograpta neotropica*, *Eristalis* sp1, *Syrphus shorae*, *Toxomerus watsoni*, *Xanthandrus palliatus*, *Trigona spinipes*, *Eriopis connexa* and *Lagria villosa* are peripherals ($c \leq 0.72$; $z \leq 1.095$).
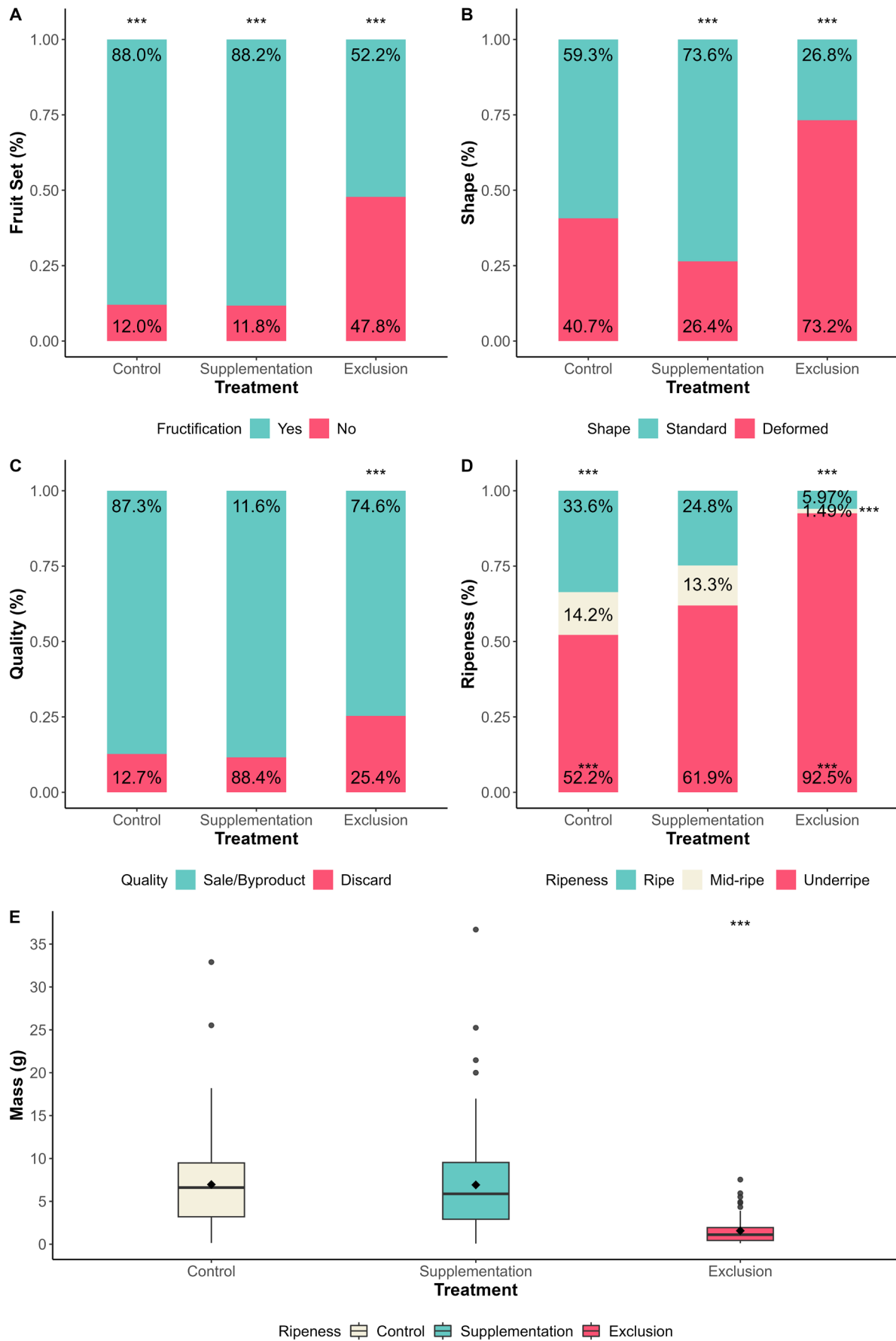
Figure 3. Variation of qualitative and quantitative parameters of strawberry production according to the treatment applied. A: fruit set; B: shape frequency; C: fruit quality; D: ripeness frequency; E: mass (g) ***: statistically significant results.
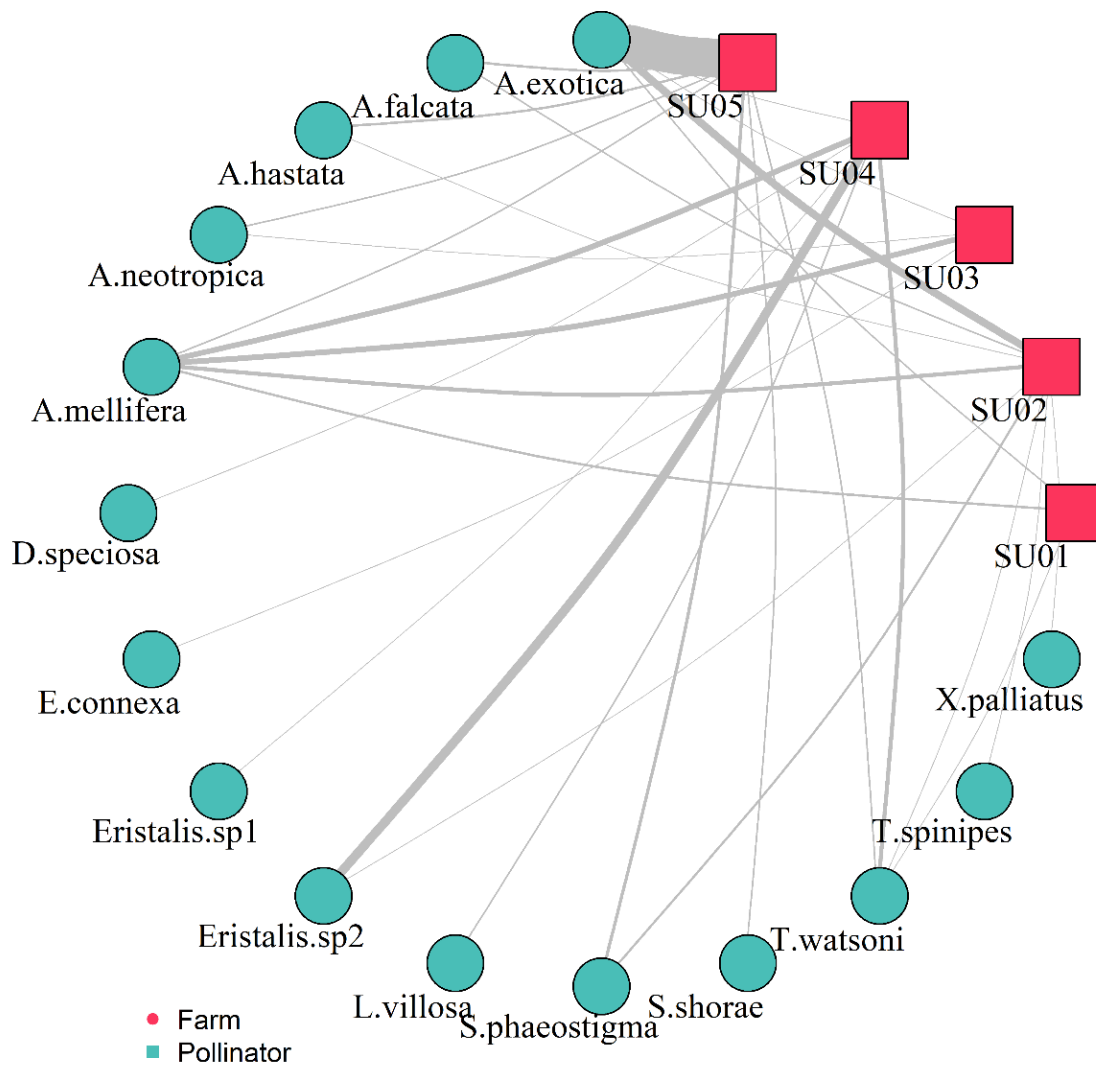
Figure 4. Interaction network between the five strawberry farms (pink squares) visited by the 15 species identified (blue circles). The figure illustrates the interactions between pollinators and farms using the lines (links), each link is an established interaction and its width indicates the intensity of the interactions.

We found the farms 2 ($C_D = 0.63$) and 5 ($C_D = 0.56$) to be the most central in degree centrality. Farm closeness and betweenness centrality presented no variation $C_C = 0.2$; $C_B = 0$. The species *Allograpta exotica*, *Apis mellifera*, and *Toxomerus watsoni* presented the highest centrality for the three metrics (C_D, C_C, C_B) with variation in degree and closeness centralities, with *Eristalis* sp1 showing high degree centrality and *Eristalis* sp2 high closeness centrality (Table 1).

The role of the centrality of farms on strawberry producing landscapes

Farm centrality had a positive influence on strawberry production (Table 3). Hence, farms with a higher centrality had a greater contribution from pollination. Regarding the landscape aspects of the farms, the two central farms (farms 2 and 5) presented high edge density, patch density and landscape heterogeneity values. However, they did not have the highest values for all the landscape metrics compared to the other farms (Table 2).

DISCUSSION

We found a significant effect of biotic pollination in strawberry fields. Biotic pollination increased the fruit set, producing better quality, better shaped, more ripe and bigger fruits. Besides that, we detected that this increase in strawberry production occurred in more central farms in pollinator-farm networks. Those farms occurred in landscapes with higher forest cover and patch density and were from organic producers.

Table 1. Degree, closeness, and betweenness centrality values for each pollinator species recorded.

Pollinators	Degree Centrality (C_D)	Closeness Centrality (C_C)	Betweenness Centrality (C_B)
Allograpta exotica	**1.0**	**0.08**	**0.3**
Allograpta falcata	0.4	0.07	0.03
Allograpta hastata	0.4	0.07	0.03
Allograpta neotropica	0.4	0.06	0.04
Apis mellifera	**1.0**	**0.08**	**0.3**
Diabrotica speciosa	0.2	0.06	0
Eriopis connexa	0.2	0.05	0
Eristalis sp1	0.2	0.06	0
Eristalis sp2	0.4	0.07	0.098
Lagria villosa	0.2	0.06	0
Syrphus phaeostigma	0.4	0.07	**0.03**
Syrphus shorae	0.2	0.06	0
Toxomerus watsoni	**0.8**	**0.08**	0.18
Trigona spinipes	0.2	0.06	0
Xanthandrus palliatus	0.2	0.06	0

Table 2. Landscape metrics calculated for each of the five farms: farming management was included to help characterize the farms. Mean values for pollination contribution and pollination deficit were included to contextualize the pollination influence on strawberry production in each farm. Higher values for landscape metrics in bold.

Farm	Farming management	Pollination contribution	Pollination deficit	Percentage of landscape covered by forests	Cohesion	Edge density	Forest patch density	Landscape heterogeneity
SU01	Convencional	6.72	-1.57	17.456	97.499	49.015	3.742	**0.209**
SU02	Organic	6.33	1.20	34.105	96.964	74.109	4.060	0.161
SU03	Convencional	0.59	-0.73	34.506	97.066	**88.266**	**4.539**	0.188
SU04	Convencional	2.54	1.50	33.278	**98.009**	67.793	2.626	0.146
SU05	Organic	7.95	-0.28	**37.048**	97.309	80.992	3.743	0.164

Table 3. Results for farms' degree centrality (C_D) influence on strawberry production.

Variable	Estimate	Std. Error	z-value	p-value
(Intercept)	2.464	1.455	1.693	0.0904
Centrality Degree	6.619	3.526	1.962	0.0497

Biotic pollination had a more significant influence on the quality parameter in the fruits from the exclusion treatment, generating fruits that did not develop to their full potential and were considered by-products or destined for disposal as Klatt *et al.* (2014) found for strawberry crops. Biotic pollination in strawberry fields thus results in fruits with higher commercial value according to their appearance. The absence of biotic pollination also directly affected the ripeness of the fruit once those developed with the presence of the ecosystem service were predominantly ripe or medium ripe at the harvest moment. The difference between fruits from the pollen supplementation and control treatments may be associated with the greater allelic diversity of the pollen in the control treatment, which may favor fruit ripening. This factor may also be related to the diversity of pollinators (Holzschuh *et*
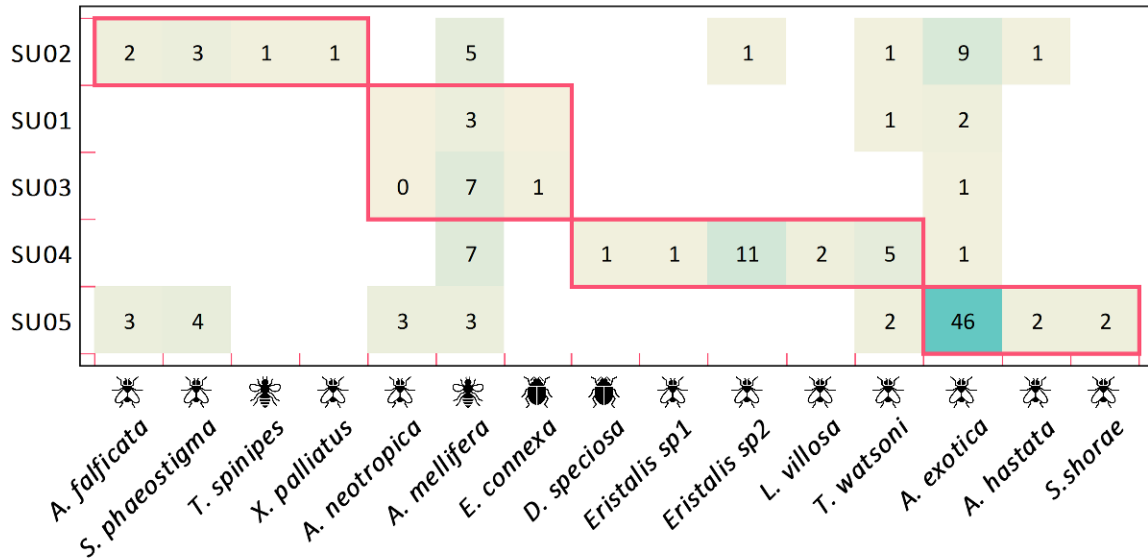
Figure 5. Representation of the modules formed from the interactions between pollinators and farms. There are four modules formed: between farm two and *Allograpta falcata, Syrphus phaeostigma, Trigona spinipes* and *Xanthandrus palliatus*, between farms one and three and *Allograpta neotropica, Apis mellifera* and *Eriopis connexa*, between farm four and *Diabrotica speciosa, Eristalis* sp1, *Eristalis* sp2, *Lagria villosa* and *Toxomerus watsoni* and a module formed between farm five and *Allograpta exotica, Allograpta hastata* and *Syrphus shorae*. The intensity of the colors indicates the frequency of the interactions: the darker, the more frequent.
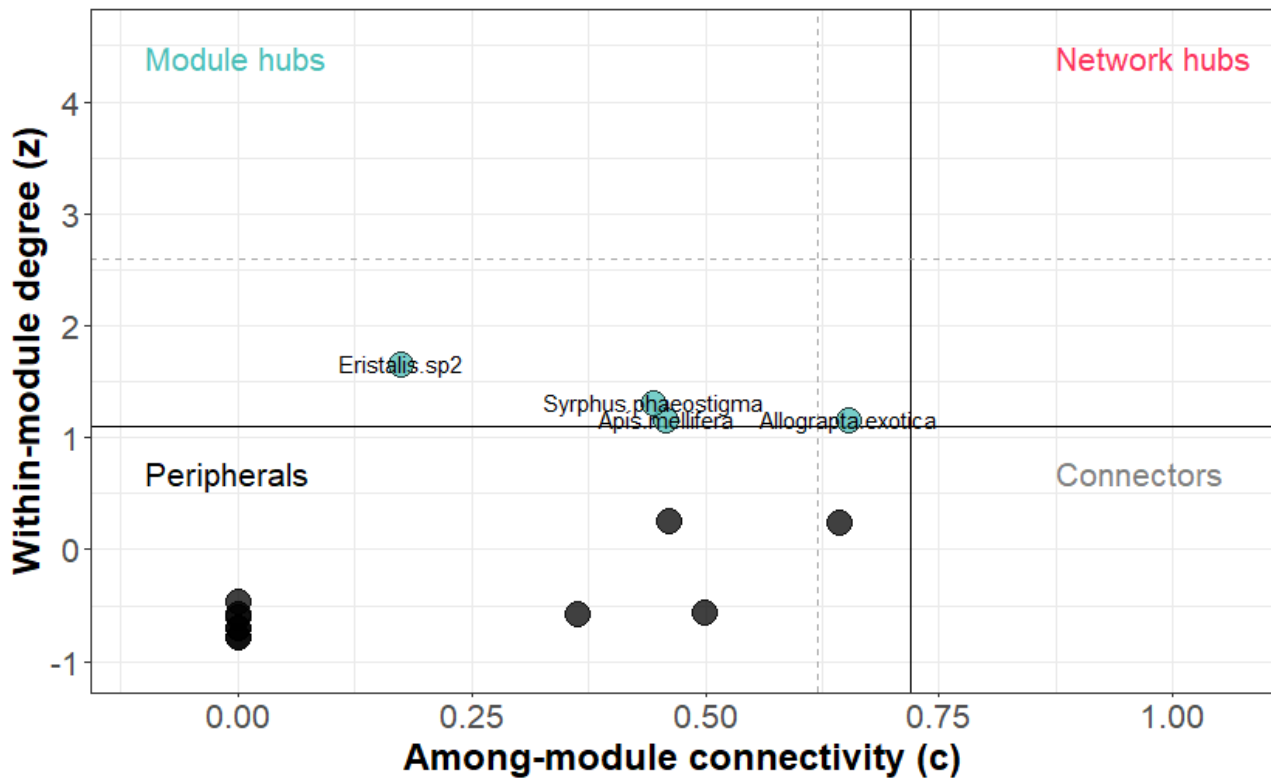
Figure 6. Distribution of pollinator species according to their network role on a *cz* plot; *c* represents the values of among-module connectivity and *z* represents standardized within-module degree. Based on *c* and *z* values, four of the fifteen species (*Allograpta exotica, Eristalis* sp2, *Syrphus phaeostigma* and *Apis mellifera*) were classified as module hubs ($c = 0.72$; $z = 1.095$) and the other eleven species (*Allograpta falcata, Allograpta hastata, Allograpta neotropica, Eristalis* sp1, *Syrphus shorae, Toxomerus watsoni, Xanthandrus palliatus, Trigona spinipes, Eriopis connexa* and *Lagria villosa* are peripherals) were classified as peripherals ($c < 0.72$; $z > 1.095$).

al. 2012), which can bring a more diverse pollen load to strawberry flowers during service provision. The observation that more central farms produce more and better fruits also supports the positive effect of pollinator richness in strawberry production.

We found a modular network with no network hubs or connectors but module hubs and peripherals species, indicating that interactions are organized in local modules. This supports the idea the interaction modules result from habitat imposed subsystems (Pimm & Lawton, 1980) that might be related to landscape effects on local composition of pollinators (Morrisson *et al.* 2020, Winsa *et al.* 2017). In this system, the module hub species *Eristalis* sp2, *Syrphus phaeostigma*, *Apis mellifera* and *Allograpta exotica* assume an important role at local level, maintaining the interactions within the modules formed with the farms. Thus, integrating the role of the species in the network help us to identify the outcomes of the interaction established, such as the provision of the ecosystem service of pollination (Ulrich & Peters, 2023).

Farms 2 and 5 were the most central in the degree centrality metric (C_D), a result that indicates that these are farms with a particular role in the connection with the other ones evaluated, sharing floral visitors with the different areas and also connecting them through shared floral visitors (Freeman 1979). Although the reproductive success of crops is generally associated with the richness of pollinators, our results indicate that there is relevance of the farms' centrality in the contribution of the ecosystem service of pollination to agricultural production, as shown in Ricketts *et al.* (2004) study in which biotic pollination had a positive influence on coffee production on more central farms and near those located in a pollinator-friendly landscape. Few studies have evaluated this relationship, but our significant result corroborates those found by Allasino *et al.* (2023), which indicate a relationship between the centrality of farms and the increase in their productive yield. In this way, understanding the structure of interaction networks can be an important tool for the spatial planning of agricultural areas and practices. Also, understanding the structure of interaction networks and their changes is important for understanding the impact these changes have on farm-pollinator interactions (Morrinson *et al.* 2019).

Even though pollinator-friendly indices characterized the most central farms, of all farms had quite similar landscape metrics. However, what the two central farms have in common is their organic management; thus, our results suggest that there may be a relationship between the centrality of the farms and the management of the crops, and consequently in the production of strawberries, a matter that could benefit from further studies.

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