



BEYOND GOOD AND EVIL: CONTEXT-DEPENDENT EFFECTS OF AGRICULTURE ON POLLINATORS' COMMUNITIES AND ITS INTERACTIONS

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Abstract: The role of agriculture as a menace or a contribution to the maintenance of the biodiversity and ecosystems function (such as pollination) in heterogeneous landscapes is critical to the balance in the tradeoff relationships between food production and biodiversity. Recent studies suggested that the role of agriculture to the maintenance of biodiversity can be context dependent. Therefore, this study aimed to evaluate the interplay between the proportion of agriculture and landscape heterogeneity on the maintenance of pollinators richness and abundance, and plant-pollinators interactions in agro-natural landscapes. Plant-pollinator surveys were conducted in seminatural areas near agricultural areas in 22 landscapes in the agricultural pole of Chapada Diamantina, Bahia, Brazil. By a combination of PCA and clustering analysis the landscapes were divided into two groups characterized by the inverse correlation of proportion of agriculture and heterogeneity. The first group had low proportion of agriculture and high landscape diversity and the second group had high proportion of agriculture and low landscape diversity. Using linear models, we investigated the differences in plant-pollinator networks structure between these two landscape groups and its relationship with the proportion of agriculture. Our results showed that there is a positive relationship between the plant-pollinator networks number of links, the pollinator species richness and native pollinators abundance with the proportion of agriculture in the landscapes. However, the most heterogeneous landscapes, with smaller proportions of agriculture have networks with more links, higher pollinator species richness and native pollinators abundance than more homogenous landscapes with greater proportions of agriculture. In this sense, even if agricultural areas can favor some pollinators, there are evident losses of pollinator diversity and plant-pollinator interactions associated with the landscape homogenization.

Keywords: Cerrado; landscape heterogeneity; networks; Savanna; structure.

INTRODUCTION

Habitat loss is an important threat to floral visitors, and the expansion of vast agricultural areas is recognized as one of the major worldwide drivers of pollination deficits (Winfree *et al.* 2009, Potts *et al.* 2010). Pollination by animals is an extremely important process for the maintenance of natural and agricultural ecosystems (Garibaldi *et al.* 2011, 2013). Its deficits can endanger world food production and food security. Pollination by animals is also fundamental for providing essential micronutrients to humans (Eilers *et al.* 2011, Chaplin-Kramer *et al.* 2014). Additionally, the cultivated area of pollinator-dependent crops is expanding faster than the area of crops that do not need pollinators (Garibaldi *et al.* 2011). However, the current mass-production agricultural model commonly used in most countries is mostly based on massive land clearing to increase crop areas, which can be detrimental to natural environments. The current conventional land management invariably leads to homogenized landscapes where most crops are placed far from the native vegetation where pollinators usually originate. This trend tends to generate negative feedback that can result in a progressive reduction in productivity for pollinator-dependent crops (Zhang *et al.* 2007). Such processes that arise from a tradeoff between crop production and ecosystem function may be especially important in the tropics, where there is the most diverse ecosystems and a higher proportion of pollinator-dependent crops (Ricketts *et al.* 2008, Power 2010, Garibaldi *et al.* 2011, Moreira *et al.* 2018). However, there is evidence that strategic landscape management which places smaller crop fields interspersed with natural ecosystems can enhance biodiversity and may support a variety of ecosystem services (*e.g.*, reduced erosion along hedgerows, filtration of runoff by buffer strips, pest control by natural predators or pollination by wild bees) (Foley *et al.* 2005; Fahrig *et al.* 2015). Additionally, agricultural practices that enhance surrounding habitats qualities (*e.g.*, hedgerows and flower strips) can also contribute to the heterogeneity of the local environmental, with plenty of floral and nesting resources for pollinators (Kennedy *et al.* 2013, Garibaldi *et al.* 2014).

Most pollination and landscape change studies however consider agricultural regions as non-habitat in a binary habitat/non-habitat system. This approach ignores the differential contributions of functionally distinct environments to species survival and ecosystem services stability. Fahrig *et al.* (2011) suggests that studies on the effect of landscape change over the organization of biological communities should explicitly address the functional heterogeneity of landscapes. Following this approach, in a previous work (Moreira *et al.* 2015), we found evidence that landscape heterogeneity positively influences the number of interactions and the nestedness of plant-pollinator networks in agro-natural savanna landscapes in Brazil. In this system, a higher proportion of agriculture at the landscape level can generate a dual non-linear effect on plant-pollinator networks. The environmental heterogeneity tended to be higher at low to medium (< 40%) than at high (> 40%) proportions of agriculture within a 250 m radius, providing a higher abundance and diversity of resources for insect pollinators. Moreover, landscapes with more than 40% of agricultural cover tended to environmental oversimplification, reducing resources and potentially jeopardizing plant-pollinator networks due to the lack of pollinating animals. Therefore, we would expect that in landscapes with less than 40% agriculture, plant-pollinator networks would be larger and better structured, whereas in landscapes with more agriculture than that, networks would become smaller and with fewer interactions. However, we did not find this relationship between agricultural land cover and network structure (Moreira *et al.* 2015).

For this reason, we inquired why the proportion of agriculture did not appear in our analysis as an important variable as the variables associated with landscape heterogeneity did. One possible explanation is that given the expected hump-shaped relationship between agricultural area and landscape heterogeneity the response of pollinators may change along the gradient accordingly (Stein *et al.* 2014, Moreira *et al.* 2015). Consequently, simply fitting a linear model to describe the relationship between the pollinator community and plant-pollinator networks to the amount of agricultural areas in the landscape may

not be the best approach to this problem. Therefore, the objective of this study is to evaluate if the pollinator community and plant-pollinators networks structure studied by Moreira *et al.* (2015) presents a context dependent response to the amount of agricultural areas in landscapes, considering the interplay between landscape heterogeneity and proportion of agriculture.

MATERIAL AND METHODS

Data sampling of the plant-pollinator interaction network was done in the agricultural pole of Chapada Diamantina, Bahia, Brazil (13°10'37" S, 41°29'5" W, Datum WGS84), which covers an area of approximately 197,931 ha, where there is a considerable variety of crops such as coffee, potato, apple, beans, vegetables, ornamental flowers, pumpkin, etc. Most of the territory delimited for this pole occupies the flattest area of Mucugê and Ibicoara municipalities, with altitude varying between 900 and 1400 meters. The climate in the region is tropical savannah (Aw), following the classification of Koppen-Geiger, characterized by average temperature of the coldest month of the year greater than 18°C, precipitation greater than the potential evapotranspiration and with two marked seasons, dry and humid, with the precipitation concentrated in the summer (Kottek *et al.* 2006, Peel *et al.* 2007). With an average annual precipitation of 1281 mm, this region presents a rainy period from November to April, with the mean cumulative rainfall for this period of 942 mm and 339 mm during the dry period, 153 mm monthly precipitation in the rainy season, 55 mm in the dry season, average temperature annual maximum 29°C and minimum 19.8°C, according to data from the Lençóis weather station, provided by the National Institute of Meteorology (INMET, data from 1961 to 2011). The predominant vegetation in the agricultural pole, aside the agriculture itself, is composed primarily of Brazilian savanna physiognomies (Cerrado), ranging from natural pastures such as grass-woody savanna to semideciduous seasonal forest, with a considerable floristic variation among these physiognomies, however the parkland savanna and woodland savanna are the preponderant physiognomies (Juncá *et al.* 2005, Moreira *et al.*

2015). The parkland savanna is characterized by a grassland formation interspersed with isolated nanocryptophytes, whereas the woodland savanna is characterized by nanocryptophytic physiognomy interspersed with graminoid hemicryptophytic vegetation (Veloso *et al.* 1991, IBGE 2012).

To study the plant-pollinator networks, we selected 22 landscapes considering a gradient of proportion of agriculture and landscape heterogeneity, as well as a minimal distance of 3 Km from the nearest-neighbor sampling unit. In the center of each landscape we established a hexagon with 25 m of side in an area covered by natural vegetation, separated from the nearest agricultural area by at least 50m. We sampled each landscape four times, in a period of one year, covering wet and dry seasons. In each sample collection, two collectors walked for ten hours through the sides, as well as towards the center of the hexagon in opposite directions, making ten-minute focal observations on the open flowers, collecting with entomological nets all the insects sighted making legitimate visits to the observed flowers. At the end of the sampling period, samples of the flowering plants were collected for identification. All the biological material is deposited in the entomological and botanical collections of the Museu de História Natural da Universidade Federal da Bahia.

To evaluate the landscape structure, we produced a land use map from the supervised classification of LANDSAT 5 images dated 14/sep/2011, with 13 classes, including, anthropic vegetation (abandoned areas recently occupied by ruderal vegetation), grass-woody savannah, parkland savannah, wooded savannah, woodland savannah, semideciduous forest, parkland savannah on rock surface (rupestrian), wooded savannah on rock surface (rupestrian), steppe savannah, anthropic use (mainly agriculture but also including roads, buildings and anthropogenic bare soil), water, clouds and shades (Moreira *et al.* 2015, Moreira *et al.* 2016). For this procedure, we used the software ArcGIS 9.3 ESRI 2008 and ENVI 4.7 ITT 2009. Based on this map, we calculated the landscape proportion of agricultural area (PA) and landscape Shannon's diversity index, adopted as descriptor of the landscape diversity (LD). We repeated these calculations for buffers varying from 250 to 12500 m. We performed these

calculations using Patch Analyst Queens Press, Ontario Ministry of Natural Resources, 2012 in ArcGIS 9.3 ESRI 2008. For more details on the data collection, landscape measurements and plant-pollinator network metrics see Moreira *et al.* (2015).

As an alternative approach to the applied by Moreira *et al.* (2015), we performed a principal component analysis (PCA) to better evaluate the relationship between proportion of agriculture and landscape Shannon diversity index in all scales of measurement (Quinn & Keough 2002). The two first components from the PCA (PC1 and PC2) represent 76.5% of the variation those variables and the analysis of the variances per components plot reviews that proportionally very little additional variance is explained by the successive increasing in number of components, what lead us to conclude that those two components were enough for our analysis (Figure 1a; Appendix 1). The analysis of the eigenvectors reveals that the first component (PC1, 62.1% of the variance) is clearly more associated the variation from landscapes with high proportion of agriculture and low landscape diversity in the negative extreme, to landscapes with low proportion of agriculture and high landscape diversity in the positive extreme whereas the second component (PC2, 14.4% of variance) is more associated with the variation among the scales of measurement of the landscape metrics (Figure 1a). In addition, the graphic shows that it is possible to draw a line through the zero value in the PC1 axes separating well the samples in two sets of landscapes, that would be the landscapes with high proportion of agriculture and low landscape diversity (LoDiv) on the left side, and landscapes with low proportion of agriculture and high landscape diversity (HiDiv) on the right side (Figure 1a).

We confirmed the existence of these two groups with two unsupervised clustering methods, the k-means and the Ward's hierarchical clustering using Euclidian distances for both procedures (Hothorn & Everitt 2014). First, we confirmed the number of clusters by the analysis of the within groups sum of residuals squares of the k-means in relation to the number of clusters calculated, where the abrupt deceleration of this relationship shows at least two cutting points. The first and

more important is on the iteration with two k-means, which explained 50.6% of the variation in contrast with the next iteration with three k-means that aggregate only 12.7% to the explained variance (Appendix 1). This classification with two k-means matches exactly with the separation of the studied landscapes into the LoDiv and HiDiv groups visualized in the PCA. The second cutting point is the iteration with four k-means and corresponds with the separation of positive and negative values in both PC1 and PC2 axes. Since we are only interested in the variation of landscapes in relation to the proportion of agriculture and landscape diversity, instead of the variation among scales, we decided by the first solution with two k-means. The Ward's hierarchical clustering produced similar results to the k-means with at least two levels of classification being the first and more important coincident with the distinction between LoDiv and HiDiv landscape groups and the second cut with the variation among landscape measurement scales (Appendix 1).

As a final step of the characterization of the landscape groups we compared the differences in the mean PA and LD across scales between these two groups through a one-way analysis of variance (ANOVA), adopting $\alpha = 0.05$ as the significance level. We found that these two groups exhibit statistically significant differences on the proportion of agriculture (PA) and the landscape Shannon diversity index (LD) across multiple scales, confirming the combination of low proportions of agriculture with high landscape diversity in the HiDiv and high proportion of agriculture with low landscape diversity in the LoDiv (Figure 1b and 1c; $p < 0.001$). It is possible that the differences between the two groups of landscapes made it impossible to Moreira *et al.* (2015) identify the correct scale of response for the proportion of agriculture in the previous analysis, when we adjusted a linear model to all sample unities together. Therefore, we use these landscape groups to further evaluate the relationship of pollinators community richness, abundance and the plant-pollinator networks characteristics with the landscapes' proportion of agricultural area and landscapes' diversity. We performed all the statistical analysis in the R environment, version 2.15.0, using the packages 'vegan' version 2.5-2 and 'ggbiplot' version 0.55.

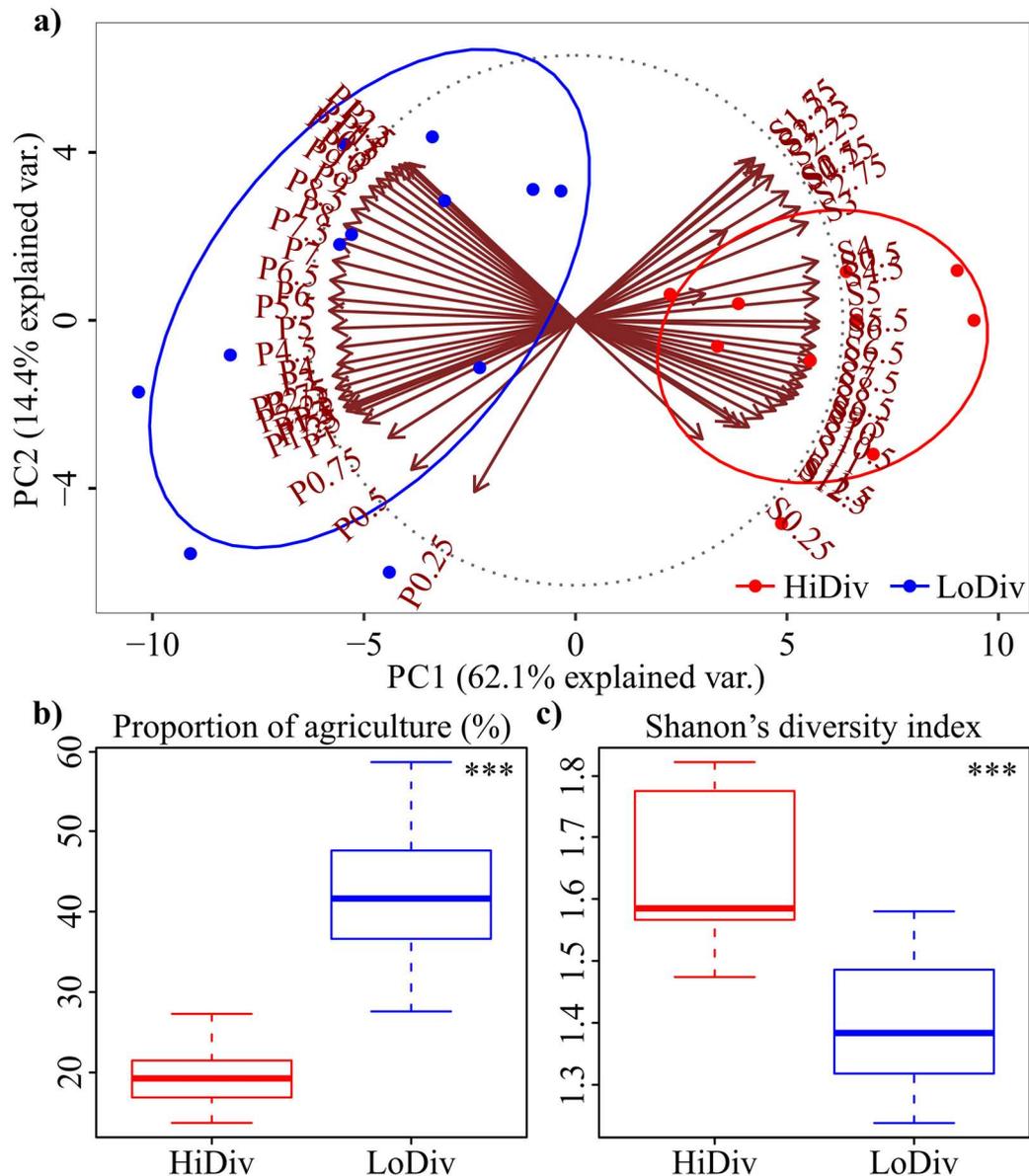


Figure 1. Biplot of the two first components of principal component analysis (PCA) of proportion of agriculture and landscape Shannon's diversity index in all scales of measurement (a), were the points represents the scores of the sampling unities, the two ellipses represent the normal contour line with probability 68% for each group groups HiDiv and LoDiv that are also indicated by the colors red and blue respectively, and the red arrows (eigenvector) indicate the direction of the correlation between proportion of agriculture (P) and landscape Shannon's diversity index (S) in each measurement scale varying from 0.25 to 12.5km and with the two first components from PCA (PC1 and PC2), the size of the arrows in relation to the grey dotted circle indicates the strength of these correlations where the circle is equivalent to a perfect correlation; In b and c there are the boxplot representing the differences between the proportion of agriculture (df = 20, $F = 62.55$, $R^2 = 0.76$, $p < 0.001$; b) and landscape Shannon's diversity index (df = 20, $F = 20.78$, $R^2 = 0.51$, $p < 0.001$; c) for two landscape groups, HiDiv (Red) and LoDiv (Blue), in b and c, the y-axis there are the mean values of the landscape proportion of agriculture and landscape Shannon's diversity index for each sampling unit considering buffers varying between 0.25 to 12.5 Km; the amplitude of proportion of agriculture varies among scales of measurement, however the lowest and highest values are 4 and 80% whereas for the mean proportion of agriculture across scales the minimum and maximum are 13 and 59%; the boxes represent the first and third quartiles, the bars inside the boxes represent the median, the bars outside the boxes represent the dispersion limits. Asterisks symbolize the p values as follows: * < 0.05 , ** < 0.01 , *** < 0.001 .

We investigated the differences between the two landscape groups (HiDiv and LoDiv) regarding the pollinator's community richness, abundance and plant-pollinator network characteristics, their response to the proportion of agriculture and possible interactions between these factors using Type II ANOVA with two factors to test the significance of the effects as well as multiple linear regressions with interactions to calculate the determination coefficients of each model. For this analysis, we adopted $\alpha = 0.05$ as the significance level. We characterize the plant-pollinator networks by the number of links, network interaction strength asymmetry, interaction specialization, weighted nestedness, pollinators' species richness and abundance (Bascompte *et al.* 2006, Dormann *et al.* 2008, Almeida-Neto *et al.* 2011). To estimate the interaction strength asymmetry, we used the index proposed by Bascompte *et al.* (2006). To estimate interaction specialization we used the H_2' (Blüthgen *et al.* 2006). And for network weighted nestedness, we used an index based on overlap and decreasing fill (Dormann *et al.* 2008; Almeida-Neto *et al.* 2011). We calculated these network indices with the R environment, version 2.15.0, using the package 'bipartite' version 1.17. To evaluate the behavior of the complete networks and of those with only native species, we examined the networks before and after the exclusion of the invasive exotic species *Apis mellifera* (Linnaeus, 1758), likewise Moreira *et al.* (2015).

RESULTS

We found that plant-pollinator networks have significantly more links in the HiDiv landscapes than in the landscapes from the LoDiv group, independent of the exclusion of *A. mellifera* (Table 1; Appendices 2a and 2b). Pollinator richness was also significantly higher in HiDiv than in LoDiv landscapes (Table 1; Appendix 2c). There was also a significant positive difference in pollinator abundance between HiDiv and LoDiv, but only after the exclusion of *A. mellifera* (Table 1; Appendix 2c). The proportion of agriculture had a significant positive effect in all response variables, with exception of pollinator abundance with *A.*

mellifera (Table 1; Figures 2a to 2e). Moreover, there is apparent difference between the models fit between the landscape groups, where the LoDiv landscapes appear to have a better fit with the response variables in general than the HiDiv landscapes.

Besides the non-significant results, it is worth noting the trends of interaction between the groups of landscape and the proportion of agriculture in the HiDiv group landscapes independently of the exclusion of *A. mellifera* records, specifically for the number of links and pollinator abundance (Table 1; Figures 2a to 2e). In addition, the pollinator abundance with *A. mellifera* also shows a clear trend with the proportion of agriculture. In both cases, the absence of significance is probably due to a combination of high variability and low degrees of freedom, which reduces the power of the statistical test. As regarding the others interaction network descriptors, weighted nestedness, interaction strength asymmetry and interaction specialization did not vary with the proportion of agriculture neither among the two landscape groups ($p > 0.05$).

DISCUSSION

These results presented here corroborate with the findings of Moreira *et al.* (2015), in which low landscape proportions of agriculture associated with high landscape heterogeneity may favor the maintenance of a greater diversity of pollinators in these landscapes. Because of its contribution to the landscape heterogeneity, agricultural areas can be positively associated with the maintenance of some pollinator species, although this may not necessarily be true for all pollinators (Westphal *et al.* 2003, Rundlöf *et al.* 2008, Diekötter *et al.* 2014, Fahrig *et al.* 2015, Rodriguez & Kouki 2017, Zou *et al.* 2017). This means that the agriculture is not inherently bad for diversity, it can be beneficial if it contributes to the landscape heterogeneity (Kennedy *et al.* 2013, Fründ *et al.* 2016, Zou *et al.* 2017). However, these results also show that the positive or negative effects of agriculture on pollinator communities can be context-dependent, where the positive effects of the proportion of agriculture tend to be less significant in heterogeneous landscapes in comparison to

Table 1. The effect of the proportion of agriculture and landscape group on number of interactions, pollinator species richness and abundance. Numb. Int. = number of interactions; Pol. Sp. Ric. = pollinator species richness; Abund. = pollinator abundance; Sum Sq = sum of squares; df = degrees of freedom; significance value at 0.05.

Response variable	Independent variable	Sum Sq	df	F statistic	p value
Numb. Int. CA	Proportion of agriculture	1212.00	1	11.64	< 0.01
	Landscape group	2104.20	1	20.22	< 0.01
	Interaction	261.00	1	2.51	0.13
	Residuals	1873.60	18		
Numb. Int. SA	Proportion of agriculture	1144.55	1	12.00	< 0.01
	Landscape group	2047.18	1	21.46	< 0.01
	Interaction	224.86	1	2.36	0.14
	Residuals	1717.10	18		
Pol. Sp. Ric.	Proportion of agriculture	693.84	1	9.06	< 0.01
	Landscape group	1018.39	1	13.29	< 0.01
	Interaction	1.65	1	0.02	0.88
	Residuals	1379.02	18		
Abund. CA	Proportion of agriculture	8559.00	1	2.51	0.13
	Landscape group	12853.00	1	3.76	0.07
	Interaction	6919.00	1	2.03	0.17
	Residuals	61462.00	18		
Abund SA	Proportion of agriculture	3821.80	1	5.99	0.02
	Landscape group	6754.10	1	10.58	< 0.01
	Interaction	2791.00	1	4.37	0.05
	Residuals	11492.70	18		

homogeneous landscapes. The difference in the response of plant-pollinator networks to the agricultural proportion between the HiDiv and LoDiv groups may illustrate this idea.

For pollinators and their interactions, the proportion of agriculture had a significant effect on both landscape groups. However, it is worth to note that the range of proportion of agriculture within the group of more heterogeneous landscapes varied from 0 to 30%. Therefore, future works extending that range to include landscapes with higher proportion of agriculture associated with high landscape heterogeneity would be interesting to better assess the effect of landscapes heterogeneity and proportion of agriculture. The positive effect of the proportion of agriculture was present in almost all cases analyzed, with only the exception of the abundance of the complete pollinator community. Equivalent results were previously reported in the literature, evidencing that landscape heterogeneity buffered the influence of agriculture over interaction network (Westphal *et al.* 2003, Rundlöf *et al.* 2008, Fahrig *et al.* 2015, Ferreira *et al.* 2015).

This effect may occur because the complementarity among different vegetation types that can enable the maintenance of a higher diversity of pollinators and buffer natural phenological variation (Fahrig *et al.* 2011). Consequently, in heterogeneous landscapes, pollinator maintenance may rely less on the floral resources available in agricultural fields (Rundlöf *et al.* 2008, Kennedy *et al.* 2013, Fründ *et al.* 2016, Zou *et al.* 2017). Nevertheless, in homogeneous landscapes, the resource input of massive flowering in agricultural areas can, at least through part of the year, counterbalance the phenological variation and scarcity of floral resources in the remaining natural areas and probably occupies a vital role in pollinator maintenance in such context (Westphal *et al.* 2003, Diekötter *et al.* 2014, Fründ *et al.* 2016, Zou *et al.* 2017).

Regardless of any positive effects that agricultural areas may have on pollinators across scales, our results showed that more heterogeneous landscapes with less agriculture have plant-pollinator networks with more links and

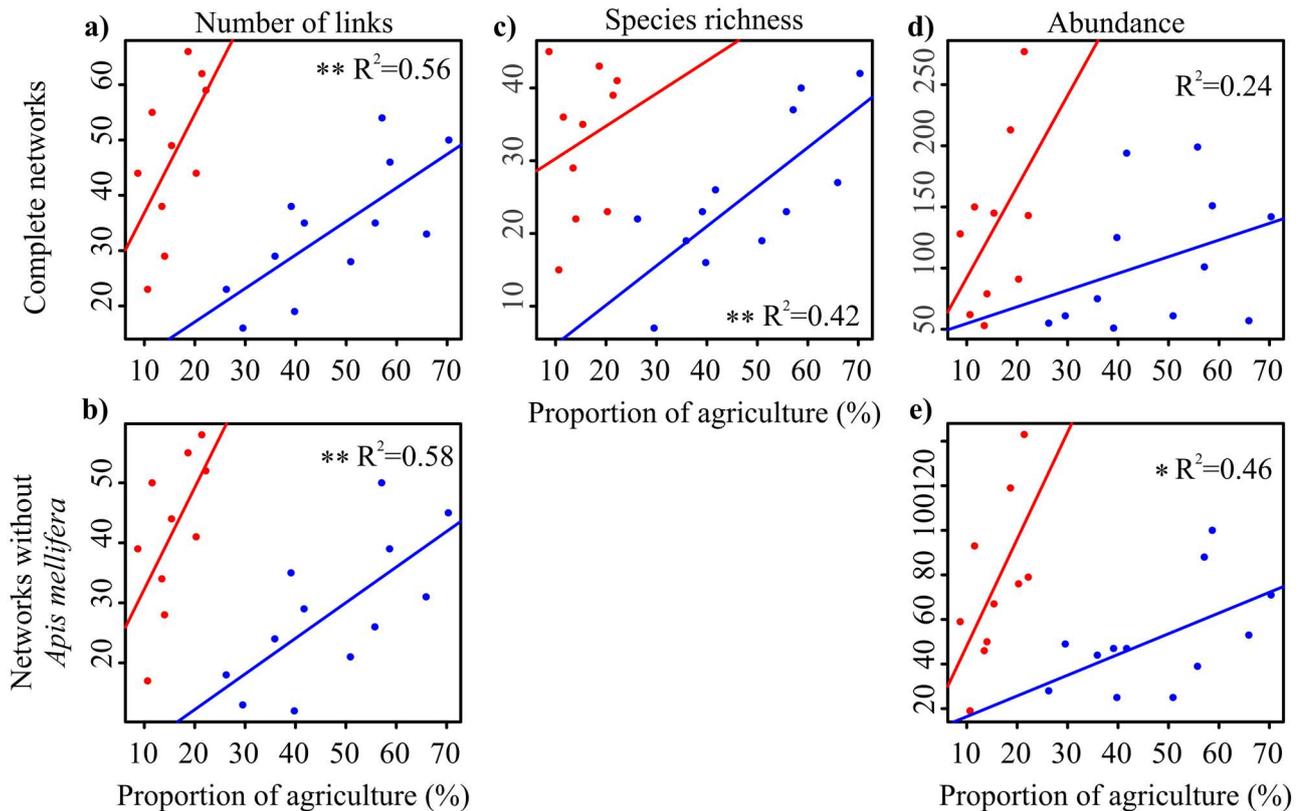


Figure 2. Relationship between the proportion of agriculture with the number of links observed in the complete networks (a) and networks without the invasive exotic species *A. mellifera* (b), pollinators' species richness (c), abundance of complete networks (d) and abundance without the invasive exotic species *A. mellifera* (e) for the HiDiv (red dots and lines) and LoDiv (blue dots and lines) groups of landscapes. Asterisks indicate the *P* values as follows: * < 0.05, ** < 0.01; *** < 0.001.

a tendency to more diverse pollinator communities than more homogeneous landscapes with more agriculture. Therefore, the homogenization of naturally heterogeneous landscapes due to the conversion of natural areas into agricultural fields can generate a loss of pollinator species at wider scales, despite any positive effect that agricultural areas may have for some pollinators on the crop fringes (Rundlöf *et al.* 2008, Fahrig *et al.* 2015, Zou *et al.* 2017). In consonance with that, a recent study realized in the same region found that coffee (*Coffea arabica* L.) fields close to natural areas and within landscapes with low proportion of agriculture have higher pollinator abundance and higher yield, indicating a synergistic relation between the pollinators maintenance in more heterogeneous landscapes and the agricultural production (Hipólito *et al.* 2018). They also show that low impact agriculture, such as that experienced in organic farms, usually

associated with small fields and higher within and among field heterogeneity, favors the maintenance of richer pollinator communities visiting coffee flowers, what may indicate that not only the quantity but also the quality of the agricultural management may promote lower or higher homogenization and therefore play an important role in the maintenance of biodiversity and the ecological services provided by it in agricultural landscapes (Garibaldi *et al.* 2016). As shown by Phalan *et al.* (2011), positive or negative effects of agricultural management strategies can also vary qualitatively among biological groups. Species with restricted distribution and with specific ecological requirements that could not benefit from agricultural areas may be benefited by the implementation of conservation areas that meet those requirements than by the mixing agricultural and natural areas. Therefore, caution is necessary to draw and apply the conclusions

from our results - one need to bear in mind the specific portion of the biodiversity to which they can be applied to.

The interpretation of our results regarding the plant-pollinator networks are not easy, mainly because there are only theoretical propositions concerning the influence of network topology on their robustness and resilience. Considering the number of links, there are many models suggesting that the number of links is positively related to mutualistic network robustness and resilience (Okuyama & Holland 2008, Fortuna *et al.* 2013). If this is the case, the number of interactions should improve pollination stability. However, this is not consensus and we need empirical studies to better evaluate the role of structural features in plant-pollinator robustness and resilience (Vieira & Almeida-Neto 2015, Soares *et al.* 2017). In addition, there is a controversy around the ecological meaning of the different network descriptors (Bascompte *et al.* 2006, Blüthgen *et al.* 2008, Tylianakis *et al.* 2010). Since number of links, nestedness and interaction strengths asymmetry are influenced by the network size and species frequency, the use of these indexes has been criticized in the specialized literature, that are usually interested in detecting pure network topology patterns hidden within the community structure (Blüthgen *et al.* 2008, Fründ *et al.* 2016). Therefore, they may not be good descriptors of the level of specialization of interaction networks and just act as a proxy of processes intensity and community structure (Blüthgen *et al.* 2008). In this context, indices such as H_2' were proposed, as well as the use of null models of interaction networks, to avoid such confusion between community structure and what could be considered meaningful network structure (Blüthgen *et al.* 2006, Blüthgen *et al.* 2007). However, this approach may not be the most adequate to empirical studies that aim to evaluate the impacts of human activity in biological communities and its functions, especially when among the major concerns are the consequences for conservation and sustainability. The major concern is that, as the H_2' index separates variation in the community structure from the variation in the degree of specialization in the network structure, it may alienate the most relevant variation associated with the major causal

mechanisms proposed to the relationship between landscape structure, pollinators and pollination (Moreira *et al.* 2018). It is possible that to detect any meaningful pattern associated with the effect of landscape structure over plant-pollinators specialization it would be necessary to design studies in other temporal scales, since the mechanisms necessary to explain the relationship between the level of specialization and landscape pattern, such as species sorting or environmental filtering, probably occur in a broader time window. This may be one of the reasons why the H_2' did not presented any significant results in our study. In addition, it is possible to have highly nested, specialized and asymmetric networks in low conservation value systems (Soares *et al.* 2017). Furthermore, few studies investigated the response of plant-pollinator networks to environmental gradients and to our knowledge there is no study that empirically investigated the effect of the plant-pollinator network structure over emergent properties with important consequences for conservation and sustainability such as resilience and robustness (Ferreira *et al.* 2013, Soares *et al.* 2017). Therefore, those indexes must be interpreted with caution, in association with other measures of network and community structure.

Putting aside the limitations and criticisms, the results for number of links can be informative, since it shows that the positive relationship between pollinator species richness and proportion of agriculture may not imply in a proportional increase in pollination service. Note that some sites with proportion of agriculture between 60-70% are among the highest values of pollinator richness. This is not true for the number of links in the plant-pollinator networks. The explanation for the difference between species richness and number of interactions patterns is twofold. First, a portion of this difference is due to the behavior of *A. mellifera*, which in the context of the more heterogeneous landscapes tends to increase its diet, contributing considerably to the increase in the number of connections in the networks of these landscapes (Moreira *et al.* 2015). This becomes clear when the results including and excluding *A. mellifera* interactions are compared. The second part of the explanation can be associated with the identity of the species that are

added as the proportion of agriculture increases in the less heterogeneous landscapes. Many of those are bees from the genus *Lasioglossum*, which are small solitary bees that build their nests in bare ground and are commonly associated with agricultural areas. The species of this genus are relatively weak contributors to the number of links since they usually present specialized feeding behavior, with diets containing only one or two plant species.

We can conclude that although there is, in a certain level, a positive relationship between the proportion of agriculture and pollinator abundance, species richness and number of links in plant-pollinator interaction networks. However, there is an important loss of biodiversity associated with the landscape homogenization created by large compact croplands. Accordingly, landscapes that are more heterogeneous across scales may favor the maintenance of richer pollinator communities, reducing effects on the negative tradeoffs of conventional agricultural management techniques. In addition, the increasing proportion of agriculture can induce a phase shift of pollinator communities. This may occur through landscape filtering processes across scales ranging from hundreds of meters to few kilometers, progressively allowing only the generalist species, which are able to rely on resources provided by agricultural areas. Future empirical studies should investigate this possibility in greater depth, especially the consequences of the topological changes of plant-pollinator networks described here.

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REFERENCES

- Almeida-Neto, M., & Ulrich, W. 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling & Software*, 26(2), 173–178. DOI: 10.1016/j.envsoft.2010.08.003
- Bascompte, J., Jordano, P., & Olesen, J. M. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, 312(5772), 431–3. DOI: 10.1126/science.1123412
- Blüthgen, N., Fründ, J., Vazquez, D. P., & Menzel, F. 2008. What do interaction network metrics tell us about specialization and biological traits? *Ecology*, 89(12), 3387–3399. DOI: 10.1890/07-2121.1
- Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B., & Blüthgen, N. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. *Current Biology*, 17(4), 341–6. DOI: 10.1016/j.cub.2006.12.039
- Blüthgen, N., Menzel, F., & Blüthgen, N. 2006. Measuring specialization in species interaction networks. *BMC Ecology*, 6(9), 1–12. DOI: 10.1186/1472-6785-6-9
- Chaplin-Kramer, R., Dombeck, E., Gerber, J., Knuth, K. A., Mueller, N. D., Mueller, M., & Klein, A. M. 2014. Global malnutrition overlaps with pollinator-dependent micronutrient production. *Proceedings Biological Sciences*, 281(1794), 1–2. DOI: 10.1098/rspb.2014.1799
- Diekötter, T., Peter, F., Jauker, B., Wolters, V., & Jauker, F. 2014. Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. *GCB Bioenergy*, 6(3), 219–226. DOI: 10.1111/gcbb.12080
- Dormann, C. F., Gruber, B., & Fründ, J. 2008. Introducing the bipartite Package: Analysing Ecological Networks, 8–11.
- Eilers, E. J., Kremen, C., Smith Greenleaf, S., Garber, A. K., & Klein, A. M. 2011. Contribution of pollinator-mediated crops to nutrients in the human food supply. *PloS One*, 6(6), e21363. DOI: 10.1371/journal.pone.0021363
- Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., & Mitchell, S. 2015. Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment*, 219–234. DOI: 10.1016/j.agee.20

- 14.11.018
- Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., & Martin, J. L. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, 14(2), 101–112. DOI: 10.1111/j.1461-0248.2010.01559.x
- Ferreira, P. A., Boscolo, D., Carvalheiro, L. G., Biesmeijer, J. C., Rocha, P. L. B., & Viana, B. F. 2015. Responses of bees to habitat loss in fragmented landscapes of Brazilian Atlantic Rainforest. *Landscape Ecology*, 30(10), 2067–2078. DOI: 10.1007/s10980-015-0231-3
- Ferreira, P. A., Boscolo, D., & Viana, B. F. 2013. What do we know about the effects of landscape changes on plant-pollinator interaction networks? *Ecological Indicators*, 31, 35–40. DOI: 10.1016/j.ecolind.2012.07.025
- Foley, J. A., DeFries, R., Asnes, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., & Snyder, P. K. 2005. Global consequences of land use. *Science*, 309, 570–574. DOI: 10.1126/science.1111772
- Fortuna, M. A., Krishna, A., & Bascompte, J. 2013. Habitat loss and the disassembly of mutualistic networks. *Oikos*, 122, 938–942. DOI: 10.1111/j.1600-0706.2012.00042.x
- Fründ, J., McCann, K. S., & Williams N, M. 2016. Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model. *Oikos*, 125, 502–513. DOI: 10.1111/oik.02256
- Garibaldi, L. A., Carvalheiro, L. G., Vaissière, B. E., Gemmill-Herren, B., Hipólito, J., Freitas, B. M., & Zhang, H. 2016. Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*, 351(6271), 388–391. DOI: 10.1126/science.aac7287
- Garibaldi, L. A., Carvalheiro, L. G., Leonhardt, S. D., Aizen, M. A., Blaauw, B. R., Isaacs, R., & Winfree, R. 2014. From research to action: Enhancing crop yield through wild pollinators. *Frontiers in Ecology and the Environment*, 12(8), 439–447. DOI: 10.1890/130330
- Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., & Klein, A. M. 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. *Science*, 339(6127), 1608–1611. DOI: 10.1126/science.1230200
- Garibaldi, L. A., Aizen, M. A., Klein, A. M., Cunningham, S. A., & Harder, L. D. 2011. Global growth and stability of agricultural yield decrease with pollinator dependence. *Proceedings of the National Academy of Sciences of the United States of America*, 108(14), 5909–14. DOI: 10.1073/pnas.1012431108
- Hipólito, J., Boscolo, D., & Viana, B. F. 2018. Landscape and crop management strategies to conserve pollination services and increase yields in tropical coffee farms. *Agriculture, Ecosystems & Environment*, 256, 218–225. DOI: 10.1016/j.agee.2017.09.038
- Hothorn, T., & Everitt, B. S. 2014. A handbook of statistical analyses using R. 3rd ed. Chapman & Hall/CRC: p. 456.
- IBGE. 2012 Manual técnico da vegetação brasileira. 2nd ed, Manuais Técnicos em Geociências, Rio de Janeiro. p. 271
- Juncá, F.A., Funch, L., & Rocha, W. 2005. Biodiversidade e conservação da Chapada Diamantina. Ministério do Meio Ambiente, Brasília: p. 411.
- Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., & Kremen, C. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, 16(5), 584–599. DOI: 10.1111/ele.12082
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. 2006. World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, 15(3), 259–263. DOI: 10.1127/0941-2948/2006/0130
- Moreira, E. F., Ferreira, P. A., Lopes, L. E., Soares, R. G. S., & Boscolo, D. 2018. Ecological Networks in Changing Tropics. In: W. Dáttilo, & V. Rico-Gray (Eds.), *Ecological Networks in the Tropics*. pp. 155–169. Springer, Cham. DOI: 10.1007/978-3-319-68228-0_11
- Moreira, E. F., Lorena, R., De, W., Sant, J., Boscolo, D., & Pigozzo, C. M. 2016. Comparison and performance of parametric algorithms in supervised classification of naturally heterogeneous and dynamic area. *Revista Brasileira de Cartografia*, 68(3), 581–594.
- Moreira, E. F., Boscolo, D., & Viana, B. F. 2015.

- Spatial heterogeneity regulates plant-pollinator networks across multiple landscape scales. *PLoS ONE*, 10(4), 1–19. DOI: 10.1371/journal.pone.0123628
- Okuyama, T., & Holland, J. N. 2008. Network structural properties mediate the stability of mutualistic communities. *Ecology Letters*, 11(3), 208–216. DOI: 10.1111/j.1461-0248.2007.01137.x
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11, 1633–1644. DOI: 10.5194/hess-11-1633-2007
- Phalan, B., Onial, M., Balmford, A., & Green, R. E. 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science*, 333(6047), 1289–1291. DOI: 10.1126/science.1208742
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25(6), 345–53. DOI: 10.1016/j.tree.2010.01.007
- Power, A. G. 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1554), 2959–71. DOI: 10.1098/rstb.2010.0143
- Quinn, G. P., & M. J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press: p. 553.
- Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng, A., & Viana, B. F. 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, 11, 499–515. DOI: 10.1111/j.1461-0248.2008.01157.x
- Rodríguez, A., & Kouki, J. 2017. Disturbance-mediated heterogeneity drives pollinator diversity in boreal managed forest ecosystems. *Ecological Applications*, 27(2), 589–602. DOI: 10.1002/eap.1468
- Rundlöf, M., Nilsson, H., & Smith, H. G. 2008. Interacting effects of farming practice and landscape context on bumble bees. *Biological Conservation*, 141(2), 417–426. DOI: 10.1016/j.biocon.2007.10.011
- Soares, R. G. S., Ferreira, P. A., & Lopes, L. E. 2017. Can plant-pollinator network metrics indicate environmental quality? *Ecological Indicators*, 78(July), 361–370. DOI: 10.1016/j.ecolind.2017.03.037
- Stein, A., Gerstner, K., & Kreft, H. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17, 866–880. DOI: 10.1111/ele.12277
- Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. 2010. Conservation of species interaction networks. *Biological Conservation*, 143, 2270–2279. DOI: 10.1016/j.biocon.2009.12.004
- Veloso, P. H., Filho, R. R. L. A., & Lima, A. C. J. 1991. *Classificação da vegetação brasileira, adaptada a um sistema universal*. Fundação Instituto Brasileiro de Geografia e Estatística. IBGE: p. 117.
- Vieira, M. C., & Almeida-Neto, M. 2015. A simple stochastic model for complex coextinctions in mutualistic networks: robustness decreases with connectance. *Ecology Letters*, 18(2), 144–152. DOI: 10.1111/ele.12394
- Westphal, C., Steffan-Dewenter, I., & Tschardt, T. 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, 6, 961–965. DOI: 10.1046/j.1461-0248.2003.00523.x
- Winfree, R., Aguilar, R., Vazquez, D. P., LeBuhn, G., & Aizen, M. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, 90, 2068–2076. DOI: 10.1890/08-1245.1
- Zhang, W., Ricketts, T. H., Kremen, C., Carney, K., & Swinton, S. M. 2007. Ecosystem services and dis-services to agriculture, 1–8. DOI: 10.1016/j.ecolecon.2007.02.024
- Zou, Y., Bianchi, F. J. J. A., Jauker, F., Xiao, H., Chen, J., Cresswell, J., & van der Werf, W. 2017. Landscape effects on pollinator communities and pollination services in small-holder agroecosystems. *Agriculture, Ecosystems and Environment*, 246, 109–116. DOI: 10.1016/j.agee.2017.05.035

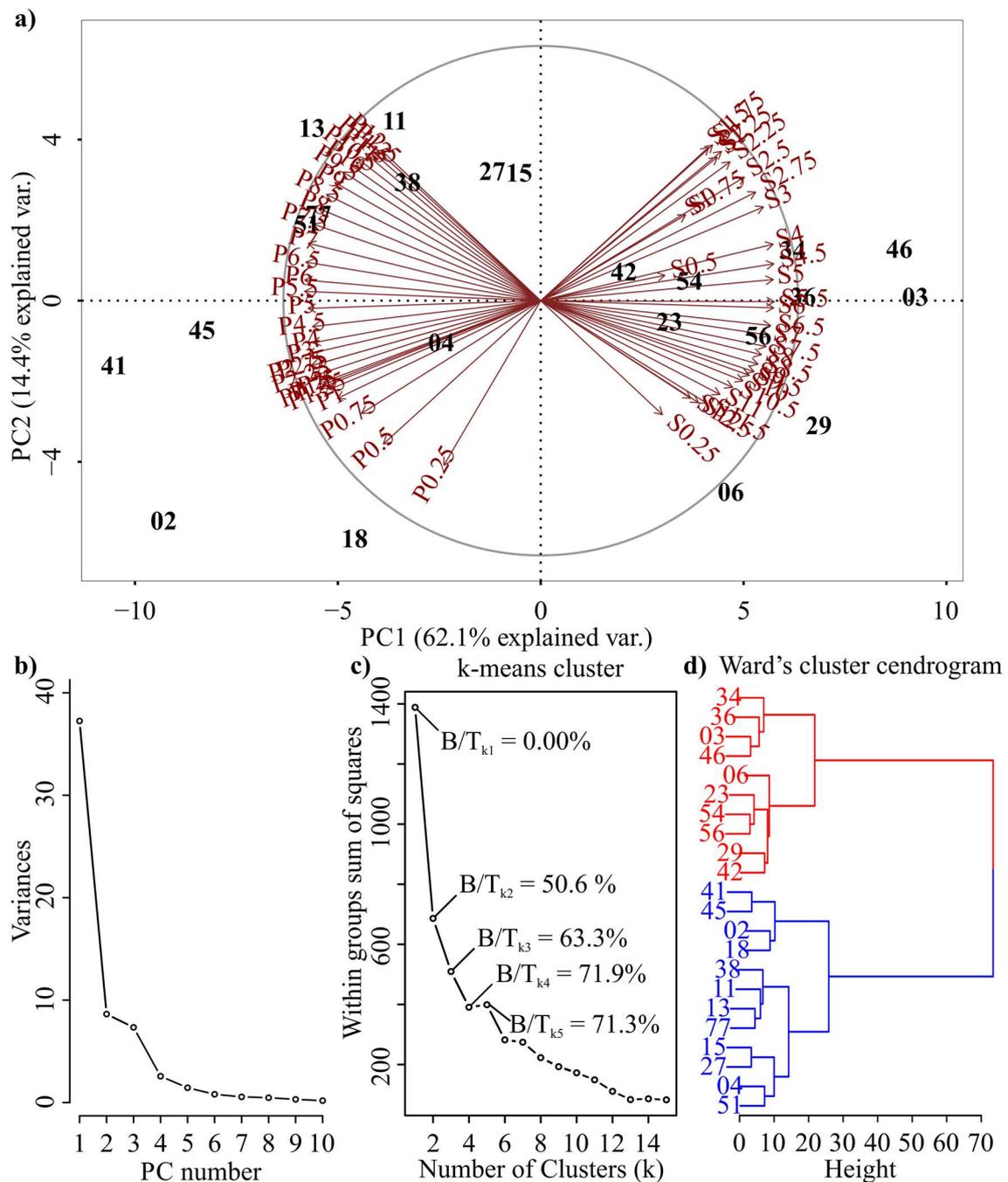
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Appendix 1. Biplot of the two first components of principal component analysis (PCA) of proportion of agriculture and landscape Shannon's diversity index in all scales of measurement (a), where the numbers represents the sampling units ID positioned at their scores in PC1 and PC2 axes, the red arrows (eigenvector) indicate the direction of the correlation between proportion of agriculture (P) and landscape Shannon's diversity index (S) in each measurement scale varying from 0.25 to 12.5 Km and with the two first components from PCA (PC1 and PC2), the size of the arrows in relation to the grey circle indicates the strength of these correlations were the circle is equivalent to a perfect correlation; (b) plot of the variance associated with each principal component (PC) from the PCA analysis described in a; (c) plot of the within groups sum of squares of each iteration of k-means clustering applied on the same dataset used for the PCA with number of clusters (k value) varying from 1 to 14, the ratio of between sum of squares (B) and total sum of squares (T) are indicated in perceptual for the four k values 1 to 4; (d) Cluster resulted from the Ward's hierarchical clustering method applied on the same dataset used for the PCA, the distances between landscapes is represented by the size of the bars in the vertical axe (Height), the numbers represent the sampling units ID and the red and blue colors represents the HiDiv and LoDiv landscape groups respectively, this landscape group color code is used through all paper.



Appendix 2. Differences between the two landscape groups regarding the number of links of complete networks (a) and networks without the invasive exotic species *Apis mellifera* (b), pollinator species' richness (c), pollinators abundance of complete networks (d) and pollinators abundance without the invasive exotic species *A. mellifera* (e). The boxes represent the first and third quartiles, the bars inside the boxes represent the median and bars outside the boxes represent the dispersion limits where the dots represent outliers. Asterisks indicate the p values as follows: * < 0.05, ** < 0.01; *** < 0.001.

