

MASTER'S THESIS

# Inter-annual variation in the plant-pollinator network of a rupicolous plant community



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The MSc project was initiated in March 2017. I was provided with a three-year data set of pollinator-pollinator interactions.

My contribution to this manuscript has been:

- Literature search.
- Definition of the objectives and methodology (with help from supervisors).
- Preparation of the database.
- Data analysis.
- Interpretation of results (with help from supervisors).
- Writing and preparation of the manuscript (with help from supervisors).

The manuscript has been formatted attending to the guidelines of the journal *OIKOS*.



# Inter-annual variation in the plant-pollinator network of a rupicolous plant community

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## Abstract

Pollination networks are a representation of the interactions between the plant and pollinator communities in a particular location. Communities change in composition and structure from year to year, and therefore interactions are expected to change in accordance. These changes may affect not only the identity and strength (frequency) of the interactions, but also the structure of the interaction networks. In this study, we analyse the variation over three years of a plant community, its pollinators and the resulting interactions. Because the community is restricted to a very particular rupicolous habitat, we expect year-to-year variation to be less pronounced than in other plant-pollinator communities. We surveyed 14 plant species from April to June and recorded 76 pollinator species. The total number of plant-pollinator interactions recorded was 211. The flower composition of the plant community showed moderate levels of variation from year to year. Instead, variation in the composition of the pollinator community was higher, and pollinator species turnover was as high as 35-47%. Interaction composition identity and interaction strength was even more variable. Interaction turnover was close to 70%. Some metrics describing the structure of the network showed moderate levels of variability (connectance, interaction evenness). Generality and Vulnerability, on the other hand showed greater variation. The comparison of our results with those of similar studies suggests that, in agreement with our initial hypothesis, year-to-year variation is somewhat lower in our community.

## 1. Introduction.

The increase in studies analysing the importance of interaction between organisms is revealing that these relationships are largely supportive of the diversity of life on the planet (Naeem et al. 1999, Schemske et al. 2009). For instance, a large number of animal species depend closely on the resources that plants provide around their reproductive structures (Levey et al. 2002, Waser and Ollerton 2006). Among these interactions, there is one, the mutualism of pollination, which seems vitally important for the development and maintenance of life on earth. Not surprisingly, more than 85% of flowering plants require biotic vectors that transfer pollen between the reproductive structures of plants (Ollerton et al. 2011). For this reason, the interest in understanding the plant-pollinator mutual systems has become of vital importance both due to its importance in the development and maintenance of life on earth and for coping with the effects of global change (Potts et al. 2010).

In this sense, the development of complex network theory is facilitating the study of megadiverse ecological interactions (Jordano et al. 2009). Mutualistic webs define the nexus of ecosystems services such as pollination and seed dispersal, rather than population dynamics or energy fluxes per se (Ings et al. 2008). In fact, in the last years mutualistic interaction networks have been increasingly studied especially in pollination ecology.

Among other topics, interaction networks are helping to unravel the degree of fidelity between floral visitors and flowers. The discussion on whether pollination mutualisms are largely mediated by generalist or specialist interactions has sparked a huge debate in recent years (Waser et al. 1996, Gómez and Zamora 1999, Johnson and Steiner 2000, Waser and Ollerton 2006). Reviews of plant-pollinator mutualistic networks show that generalization is a common pattern in this type of interaction (Olesen and Jordano 2002) and the temporal fluctuation in the abundance and composition of the set of floral visitors is one of the most accepted causes of the existence of generalized pollination systems (Gómez 2002).

However, few studies have attempted to quantify spatial-temporal variation in species composition and network structure (Dupont et al. 2009); some (Olesen et al. 2008, Petanidou et al. 2008) reflect how the temporal dynamics are evident in the network topology, in addition to changes in interactions between plants and pollinators over time. Long-term studies have confirmed the opportunistic nature of plant-pollinator relationships, thus demonstrating the plasticity of interactions over time (Price et al. 2005).

In this study, we focus on the temporal dynamics of a community of plants growing in an environment of limestone outcrops. Most of these plant species are strictly rupicolous and grow exclusively in limestone crevices, overhangs and ledges. The rest of the species grow at the base of limestone outcrops. We argue that this dependence on a physiologically demanding and spatially limited environment such as limestone outcrops, should be accompanied by a certain stability in their sexual reproduction, and, therefore, on the dynamics of their biotic interactions such as pollination. However, research at the level of individual plant species has shown how the variation in pollination services can be huge, both spatial and temporally (Herrera 1988, Thompson 2001, Duan et al. 2007, Gómez et al. 2010, Castro et al. 2013). These temporal fluctuations have the potential to profoundly influence the ecological dynamics of plant populations and communities (Ashman et al. 2004). The characteristics of the plant community that we have studied, spatially restricted to a stressful environment, leads us to hypothesize that in this situation there should be a high fidelity between plants and pollinators, with low temporal variations. In this sense, our starting hypothesis is that the interactions of pollination in these plant species inhabiting a physiologically demanding environment, cannot vary too much in time, in order to ensure stable sexual reproduction over time. Therefore, we try to verify if the inter-annual variation of these plant-pollinator mutualistic networks is low, so that this ensures the persistence of the species.

The general objective of the study is to analyse temporal variation during 3 years in a pollination network. The specific objectives are to quantify: (I) changes in the composition and structure of the plant community; (II) changes in the composition and structure of the pollinator community; and (III) changes in the composition and structure of the plant-pollinator interaction networks.

## **2. Material and methods.**

### *2.1 Study area and species.*

The study was conducted in the El Bierzo region, in Northwestern Spain. The study area is characterized by an abrupt topography, dominated by limestone outcrops that give the landscape strong differences in altitude. This conditions a very rugged topography with deep gorges and

very marked reliefs in which the differential erosion has accentuated the fractured aspect of the landscape. The region has a Mediterranean climate, and the study community is located in limestone outcrops in a landscape composed of a mosaic of habitats with cultivated land and native vegetation, such as holm oak woodland (*Quercus ilex*, *Arbutus unedo* and *Quercus suber*), and different Mediterranean shrubland and pasture communities, many of them growing on former cultivated lands. Phytosociologically, the community of plants studied is integrated in the rupicolous associations *Petrocoptidetum grandiflorae* and *Petrocoptidetum viscosae* (Losa et al. 1975). Three of the populations studied are located in the Natural Park Serra da Enciña da Lastra (Fig 1): Vilardesilva (640m a.s.l.; 42°27'32''N, 6°49'34''W), Cobas, (477m a.s.l.; 42°28'15''N, 6°49'48''W) and Estrecho (438m a.s.l. 42°29'15''N, 6°49'58''W). A fourth population is located in La Chana (588m a.s.l. 42°28'31''N, 6°44'15''W).

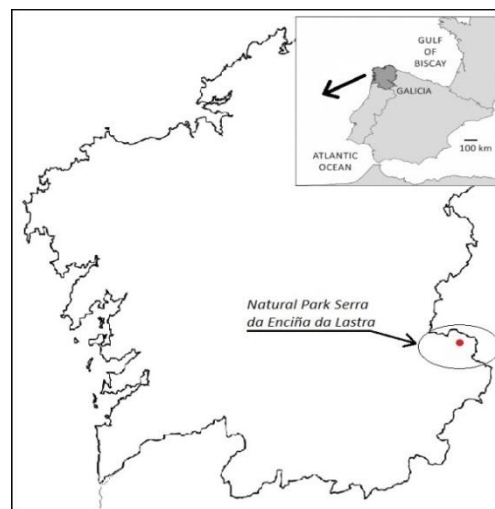


Figure 1. Location where the study was carried out. Three study sites (Vilardesilva, Cobas and Estrecho) are located in the Natural Park Serra da Enciña da Lastra and the fourth (La Chana) in the surroundings (42°28'40.2''N, 6°50'47.5''W) in Northwestern Spain.

## 2.2 Field observations and data collection

Data collection was conducted by Luis Navarro (University of Vigo) during the years 1992, 1993 and 1994. Sampling was carried out focusing on patches of rupicolous plant species in limestone walls of four localities.

In the limestone walls, plant-flower visitor interactions were sampled in sunny windless days during from April to June, covering the period of floral visitor daytime activity (08:00 – 21:00 GMT). Sampling consisted of both fixed and haphazard transects in which the sampling effort per plant species was proportional to flower abundance. We considered a visit only when the flower visitor clearly touched the anthers or stigma of the flower. The sampling dates varied between years owing to differences in weather conditions and trying to survey the flowering peaks of the species of plants studied. Thus, the beginning and ending of the surveys varied among years (1992: 9 April - 4 June; 1993: 11 April - 13 June; 1994: 7 April - 24 June).

Total sampling effort was 12,051 visits, recorded in 169.8 hours of sampling.

### 2.3 Data analysis.

With the data obtained in the surveys, a database was created containing all the observations of the 3 years of study. Each observation is classified with a rank (identification number), name of the observed plant and family to which it belongs, date and time of sampling, number of open flowers (abundance), location, survey duration (in minutes), pollinator species, and the number of visits recorded. The database contains information on 14 plant species, 76 pollinator species and 211 different interactions.

To describe plant community structure, we used the relative abundance (measured as the sum of open flowers over each study year) of each of the 14 plant species. Pollinator community structure was characterized by the number of individuals of each species recorded over each study year. To characterize plant-pollinator interaction strength (frequency), and since survey time differed across plant species, the number of visits recorded was divided by the number of open flowers surveyed and by the time (in minutes) spent in each survey.

We used the Bipartite package (Dormann et al. 2009) for R (R core team 2017) to build an “Interaction matrix” for each year, with plants in rows, pollinators in columns and interaction frequencies in the cells. We used the same package to build a plant-pollinator interaction graph for each year.

In order to measure inter-annual changes in the composition (relative flower abundance of each species) plant community, we used the Bray Curtis dissimilarity index  $\left(1 - \frac{\sum_{i=1}^n |Y_{ij} - Y_{ik}|}{\sum_{i=1}^n |Y_{ij} + Y_{ik}|}\right)$  (Bray and Curtis 1957). This index ranges between 0 and 1, where 0 indicates that the two years have the same flower composition and 1 that they differ completely. We used the same index to measure variation in pollinator composition (abundance of each recorded species). Specific plant-pollinator interaction can be treated in the same way as species, with interaction frequency being equivalent to species abundance. Therefore, we again used the index of Bray Curtis to compare differences in interaction composition between years.

To describe the structure of the plant-pollinator network we used “connectance” (realized proportion of possible links) (Dormann et al. 2009) and “interaction evenness” (Shannon’s diversity of interactions divided by  $\ln$  –plants species richness x pollinators species richness-) (Dormann et al. 2009), which indicates how equitable are the different interactions, where 1 is the maximum attainable. We also used the quantitative metrics “vulnerability” (weighted average number of pollinator species per plant) and “generality” (weighted average number of plant species per pollinator) (Bersier et al. 2002).

All metrics were calculated with Bipartite v.2.08 (Dormann et al. 2009).

## 3. Results

### 3.1 General description of the community

The 14 plant species studied bloomed each year (Table 1). Over the three years, 76 different pollinator species were recorded. The number of pollinator species showed little variation across years. The number of interactions recorded was highest in 1994. Importantly, the number of

interactions recorded did not increase with the number of pollinator species recorded. Interactions are presented in Fig. 2.

Table 1. Descriptors of the plant-pollinator community and interaction network metrics. *Connectance* is calculated as “number of interactions/(plant species X pollinator species)”. *Interaction evenness* indicates how equitable are the different interactions (maximum of 1); *Generality* is a quantitative measure of the degree of pollinators; *Vulnerability* is a quantitative measure of the degree of plants.

	1992	1993	1994	TOTAL
<b>Plant species</b>	14	14	14	14
<b>Pollinator species</b>	55	56	52	76
<b>Interaction number</b>	100	107	124	211
<b>Connectance</b>	12.98	13.65	17.03	-
<b>Interaction evenness</b>	0.578	0.546	0.536	-
<b>Generality</b>	2.168	2.619	2.985	-
<b>Vulnerability</b>	6.012	4.679	4.211	-

The interaction matrix (Fig. 2) presents a nested structure, with more interactions in the upper left corner. As expected, the most frequent interactions tend to occur in more than one year, as indicated by the accumulation of red and orange cells in the upper left corner of Fig. 2. It is important to note, however, that some rare interactions are also consistent in time and occur in more than one year. Based on the number and strength of interactions, *Petrocoptis grandiflora* and *Jasminum fruticosum* appear as to two main plant species organizing the structure of the interaction matrix.

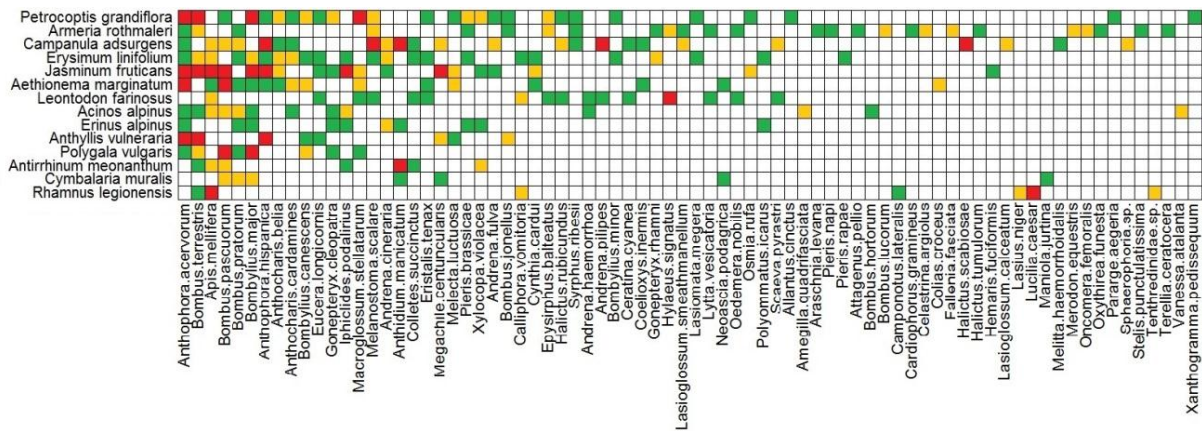


Figure 2. Interaction matrix of the 14 plants species and the 76 pollinators species recorded over the 3 years. Interactions occurring in three, two and one years are represented in red, orange and green, respectively. Plant (rows) and pollinator species (columns) are ordered left to right and top to bottom according to their number of interactions recorded (over the three years).

### 3.2 Plants community:

The timing of the maximum number of open flowers (flowering peak) occurred on 7 of May in 1992, on 30 of April in 1993, and on 8 of May in 1994. There are important changes year to year in the amount of flowers produced by the different plant species form year to year (Fig. 3). In 1992, the flower community is dominated by *Aethionema marginatum*, *Rhamnus legionensis* and *Petrocoptis grandiflora*; whereas in 1993 it is clearly dominated by *Anthyllis vulneraria*



and *Armeria rothmaleri*. In 1994, the distribution of flower abundances is much more equitable, without clearly dominant species.

The results of the Bray-Curtis dissimilarity index for the three pairs of years are: 1992-1993: 0.28; 1993-1994: 0.25; 1992-1994: 0.21. These results indicate that the variation between years in flower composition is quite high and similar across the years. That is, even if the identity of the flowering species does not vary (the 14 plant species bloom every year), the relative number of flowers produced by each species is highly variable. In other words, a plant species may bloom profusely in one year but very little in other years, and therefore the flower resources available to the pollinators are subject to strong fluctuations.

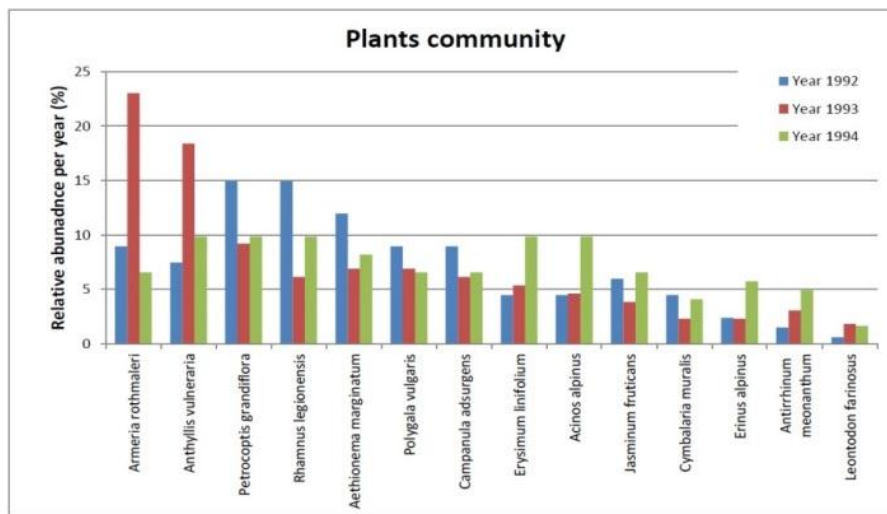


Figure 3. Relative abundance of flowers produced by each plant species in the three years of study. Relative abundance is the percentage obtained from the quotient of the maximum abundance of each species divided by the sum of the maximum abundances of all plants (separately for each year). Species ordered according to their total abundance (sum of the three years).

### 3.3 Pollinators community:

Over the 3 years of study 76 species of pollinator were recorded (Fig. 4). The distribution of abundance is characterized by a few very abundant species and a long tail of rare species. Many of these rare species were only recorded in one year. The number of pollinator species recorded each year is quite similar (Table 1), but the identity of the species varies a lot from year to year. Thus, the percentage of pollinator species turnover or replacement is 36.76% between 1992 and 1993, 45.71% between 1993 and 1994, and 47.14%, between 1992 and 1994.

Overall, the 4 most abundant pollinators are *Anthophora acervorum*, *Bombus terrestris*, *Bombus major* and *Macroglossum stellatarum*. These species are present every year, but their abundance varies considerably between years. Other species, such as *Eucera longicornis*, are very abundant one year (1994), but are absent or very rare the other years. As a result, the Bray-Curtis dissimilarity index are relatively high: 1992-1993: 0.52, 1993-1994: 0.54, 1992-1994: 0.61. It is important to note that these dissimilarities between years are higher than for plants, indicating that pollinators are more variable.

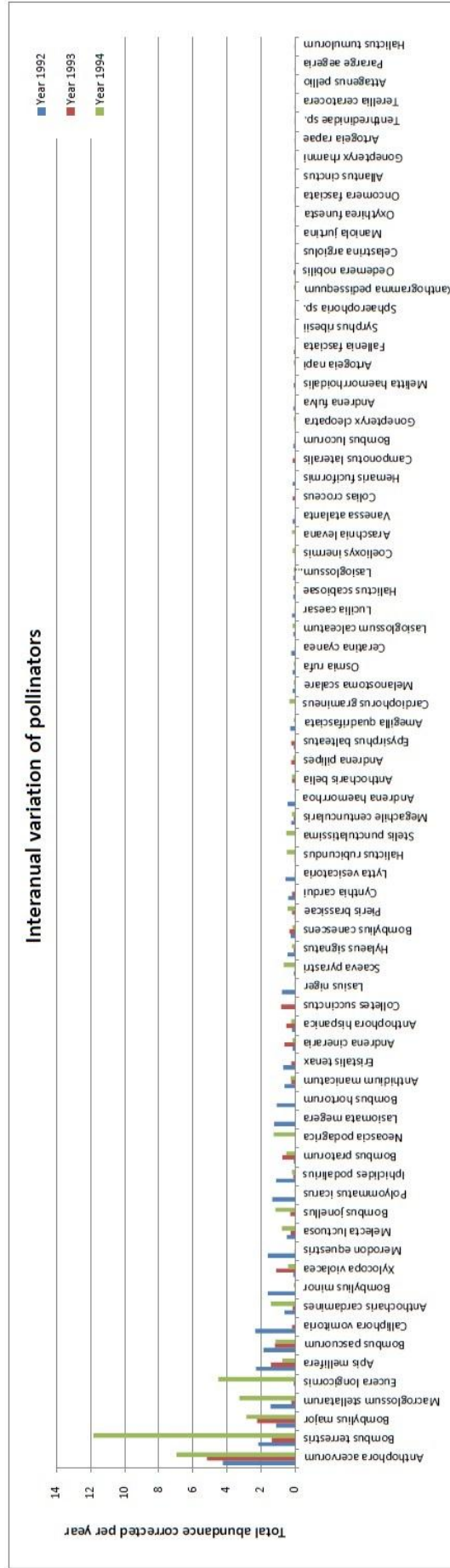


Figure 4. Rank-abundance distribution of pollinator species in the three years of study. The abundance of each pollinator is the total number of visits recorded corrected by the number of flowers sampled and the sampling time. Species ordered according to their total abundance (sum of the three years).

### 3.4 Plant-pollinator interactions:

A total of 211 different interactions were recorded over the 3 years of study (Fig. S1). As with pollinators, the distribution of interaction strengths is characterized by a few very strong interactions and a very long tail of weak interactions. Many of these rare interactions only occur in one year. Even though the number of interactions recorded does not vary greatly from year to year (100 to 124), their turnover (replacement from year to year) is high: 1992-1993: 68.79%; 1993-1994: 74.32%, 1992-1994: 74.57%. Therefore, these turnovers are higher than those registered for pollinators.

To better visualize the inter-annual variation in interaction strength, only the 20 most important interactions for any of the three years (48 interactions) are represented in Fig. 5. A few interactions (e.g., *Petrocoptis grandiflora* × *Anthophora acervorum*, *Anthyllis vulneraria* × *Anthophora acervorum*) are strong in all three years. However, there are even more interactions (e.g., *Anthyllis vulneraria* × *Bombus terrestris*, *Petrocoptis grandiflora* × *Bombus terrestris*, *Leontodon farinosus* × *Eucera longicornis*) that are very strong in one year and very weak or even absent in the other years. As a result, the Bray Curtis index comparing dissimilarity of interactions between years is high: 1992-1993: 0.67; 1993-1994: 0.68; 1992-1994: 0.73. That is, the interaction dissimilarity between years is higher than for pollinators and much higher than for plants.

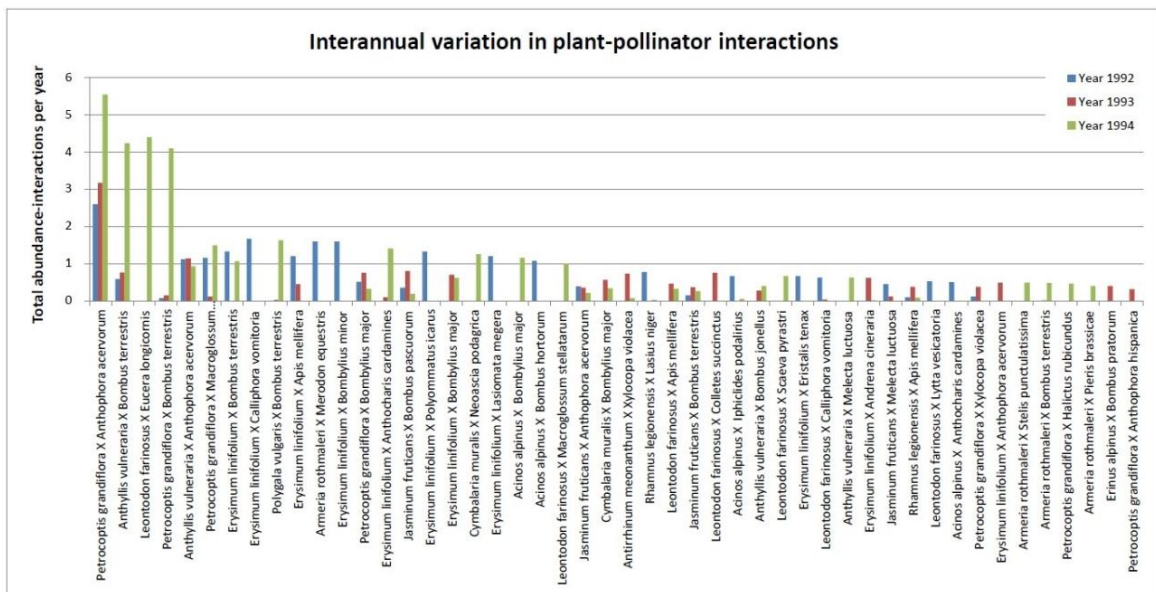


Figure 5. Rank-abundance distribution of the plant-pollinator interactions in each study year. Only the 20 most important interactions in any of the three years are represented (48 interactions). Interactions ordered according to their total strength (sum of the three years).

### 3.5 Networks structure:

Network metrics describe the structure of the network (Table 1). *Connectance* is similar in 1992 and 1993, and increases slightly in 1994 because the number of interactions is higher even though the number of pollinator species is lower. Variation in *interaction evenness* is also moderate, being slightly higher in 1992 than in the other years, when interactions are more similar in their strength (Fig. 6). Changes between years in *generality* are more important, increasing from 2 in 1992 to 3 in 1994 (Table 1). *Vulnerability* is also highly variable, and follows a trend opposite to generality, with highest values (6) in 1992 and lowest values (4) in 1994 (Table 1).

Fig. 6 provides a direct comparison of the structure of the interaction networks of the three years. They emphasize in colour the most important interactions according to their strength. In 1994, these 4 interactions have a similar strength. The only interaction that maintains a high level of strength in the other two years is *Petrocoptis grandiflora* × *Anthophora acervorum*. The other 3 marked interactions have a much smaller strength in 1992 and 1993 or even are completely absent *Leontodon farinosus* and *Bombus terrestris*.





c) 1994

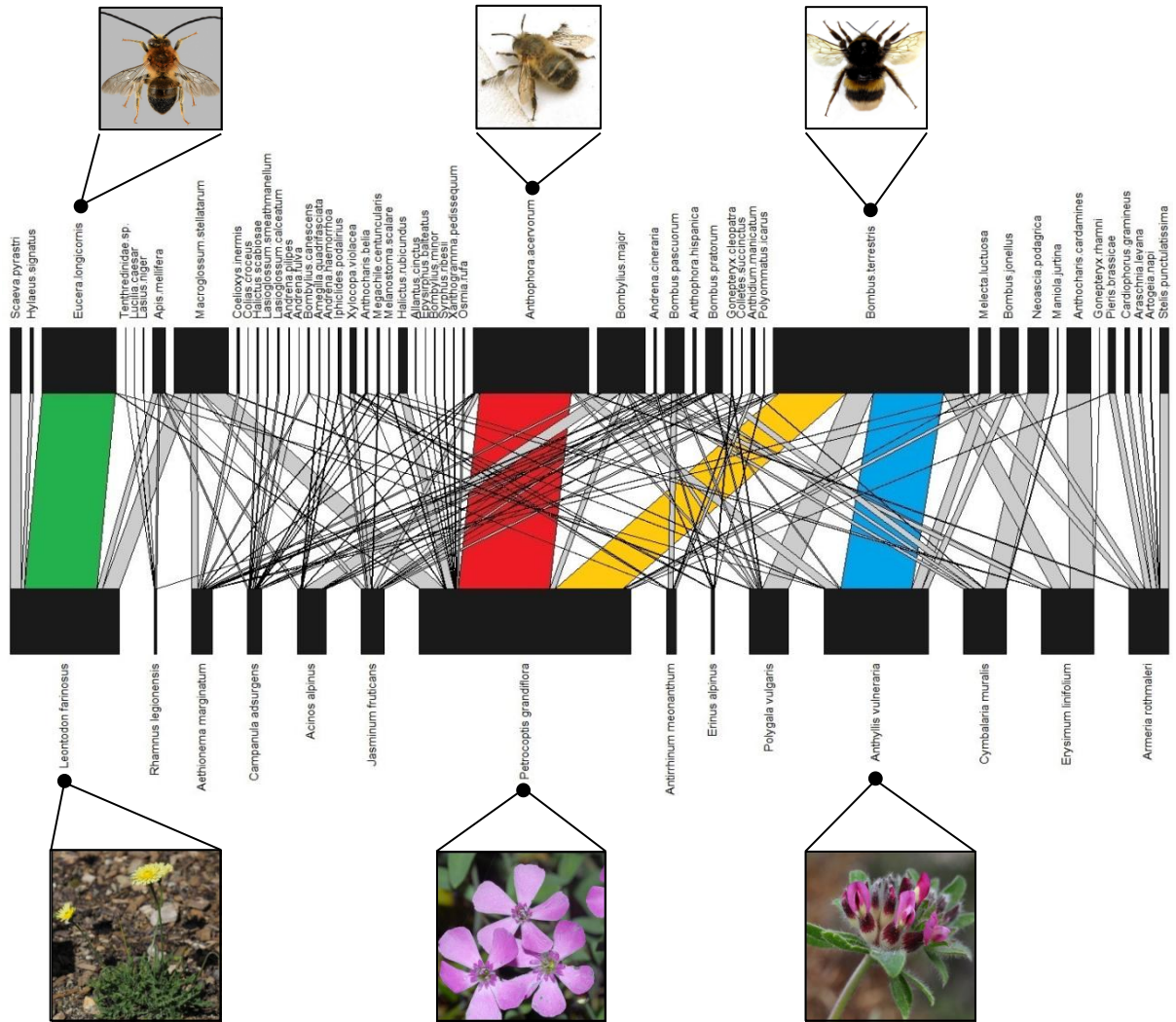


Figure 6. Plant-pollinator networks of the year 3 years of study. The width of the grey bands reflects interaction strength. The 4 most important interactions considering the three years are marked with different colours (1) *Petrocoptis grandiflora* x *Anthophora acervorum* (Red); (2) *Anthyllis vulneraria* x *Bombus terrestris* (Blue); (3) *Leontodon farinosus* x *Eucera longicornis* (Green); (4) *Petrocoptis grandiflora* x *Bombus terrestris* (Yellow).

#### 4. Discussion.

Our study analyses the inter-annual variation in the flower production of a plant community, as well as that of its pollinators and resulting plant-pollinator network. Our initial hypothesis is that, because this community is restricted to a very specific and localized kind of habitat, the level of variation of its interactions should be low.

The 14 plant species surveyed bloomed every year. This result may seem obvious, but years in which some species do not bloom are frequent in other drier habitats (Flo et al. 2017). The study of Flo et al. (2017) also shows that most of the variability between years is due to differences in flower production rather than in flowering phenology. Although all species of plants studied flower each year, their relative dominance varies between years, as reflected by the results of the Bray Curtis index. Importantly, this variability not only affects rare plants, but also some of the most abundant ones. This variation in flower abundance may have repercussions on the attractiveness of pollinators, as demonstrated by Heithaus et al. (1982) where pollinators are often attracted after the plant reaches a threshold density of flower availability. It is also important to keep in mind that the variation in flower abundance may be due both to abiotic factors – since precipitation is directly related to the production of flowers (Prieto et al. 2008) – and to biotic factors, such as seed production (mediated by pollination interactions) and flower or seed predators (Elzinga et al. 2007), which could influence bloom of the following year. Changes in flower density and composition have an effect on the community of pollinators, varying their choice of flowers and visitation rates, and therefore it has consequences on the reproductive success of plants (Lázaro et al. 2013).

Pollinators have a higher variation in abundance than plants, as indicated by the results obtained with the index of Bray Curtis. Pollinator species turnover from year to year was high (36-47%), but no as high as in other studies (Petanidou et al. 2008, Dupont et al. 2009, Olesen et al. 2011) in which turnover ranges from 44 to 73%. Among the group of more important species only 3 of them (*Anthophora acervorum*, *Bombus terrestris* and *Bombylius major*) maintain high abundance over the years of study. It is important to note that some species, such as *Eucera longicornis* indicating, like with plants, that the variation in abundance not only affects rare species, but also abundant ones. As found in other studies (Bosch et al. 2009, Potts et al. 2003), the pollinator community is characterized by a few very abundant species and a long tail of rare species. Even with their low interaction frequency, these rare species provide important support to the network when their interaction strength is considered collectively, and due to the high number of interactions in which they collectively participate. There are also some species, such as *Andrena fulva*, *Gonepteryx cleopatra* and *Syrphus ribesii* that in spite of their low interaction strength are present in the 3 years. This situation in which a small group of taxa has many interactions and many species have few interactions has already been documented in other networks (Dicks et al. 2002, Medan et al. 2002, Jordano et al. 2003).

The life history of pollinators may have effects on their abundance in the face of disturbances. Among the most important pollinator species, *Anthophora acervorum* is the one that remains more stable from one year to another, something also found in Navarro (2000). On the other hand, other abundant pollinators species, such as *Bombus terrestris*, show great variation. This variation of *Bombus terrestris* has already been noticed in other studies (Bosch et al. 2009, Navarro 2000). According to Owen et al. (2013), this variation could be attributed to climate change. These authors show that in years with warm autumns, *Bombus terrestris* queens do not enter winter diapause, and instead initiate colony development. However, workers of this

species are less capable to withstand freezing temperatures. As a result, these premature colonies may collapse if temperature fall below zero during the winter.

When important year-to-year changes occur in the communities of plants and pollinators, it is expected that their interactions will be even more dynamic. As a result, the interactions between both communities show a high turnover (68-74%). However, comparing our results with those of other studies, our community appears to be somewhat more stable. Dupont et al (2009) document interaction turnovers between 78-89%, and Petanidou et al (2008) conclude that interaction turnover can be as high as 95%.

Changes in the identity of the interactions do not necessarily imply changes in network structure. Not having performed statistical analyses of the metrics, we cannot state whether the observed variation in network metrics is significant or not. Nonetheless, our results suggest some trends. Connectance decreased with species number. In other words, large networks are less connected. This result is in agreement with other studies (Cohen, 1978, Dunne et al. 2002a, Jordano, 1987, Pimm, 2002), and it is explained by the fact that as the number of species in the community increases, the number of interaction also increases, but not as quickly as the number of potential interactions. Another suggestive trend in our network structure results is the negative trend between *generality* and *vulnerability* (understood as the generality of plants). When one diminishes the other increases. This result is contrary to expectations, since increases in *generality* are usually accompanied by increases in *vulnerability* (Dormann et al. 2009). In our case, vulnerability is highest in 1992, probably because interactions are more equitable (higher *interaction evenness*) in this year. That is, even though there are more pollinator species in 1992 (which would tend to increase vulnerability), the fact that these pollinators partition their interactions more equitably among the plants available makes vulnerability increase. In 1994 more interactions were recorded for the same number of plant species (14), but some of these interactions were strongly dominant (low interaction evenness), thus reducing vulnerability.

In conclusion, we find a certain level of variation in our plant-pollinator community and in the structure of the interaction network. However, and in agreement with our initial hypothesis, this variability seems to be somewhat lower than in other similarly studied plant-pollinator communities (Dupont et al. 2009, Olesen et al. 2011, Petanidou et al. 2008). These results show the important repercussion that the stability in the reproductive success of the plants, measured as variation on pollination interactions, of this peculiar rupicolous community has for its maintenance over long periods of time. However, our results should be interpreted with caution. We can ignore the fact that some Tertiary relictic plants, specialized to live in these limestone walls, are long-lived species (individuals of *Petrocoptis grandiflora* of more than 150 years have been described; L. Navarro unpublished data). These long-lived species can withstand periods of low reproductive success because longevity confers demographic stability regardless of small fluctuations that may occur in the communities of mutualists (García et al. 2012).



## 5. References.

- Ashman, T. L. et al. 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. - *Ecology*, 85: 2408-2421.
- Bersier, L.F. et al. 2002. Quantitative descriptors of food-web matrices. - *Ecology* 83: 2394-2407.
- Bosch, J. et al. 2009. Plant-pollinator networks: adding the pollinator's perspective. - *Ecology Letters*. 12: 409-419.
- Bray, J. R. and Curtis, J. T. 1957. An ordination of the upland forest communities in southern Wisconsin. – *Ecological Monographs* 27: 325-349.
- Castro, S. et al. 2013. So many visitors and so few pollinators: variation in insect frequency and effectiveness governs the reproductive success of an endemic milkwort. - *Plant Ecology* 214: 1233-1245.
- Cohen, J. E. 1978. Food webs and niche space. - Princeton Univ. Press.
- Dicks, L. V. et al 2002. Compartmentalization in plant-insect flower visitor webs. - *Journal of Animal Ecology* 71: 32-43.
- Dormann, C. F. et al 2009. Indices, graphs and null models: analyzing bipartite ecological networks. - *The Open Ecology Journal* 2:7-24.
- Duan, Y. W. et al. 2007. Interannual fluctuations in floral longevity, pollinator visitation and pollination limitation of an alpine plant (*Gentiana straminea* Maxim., Gentianaceae) at two altitudes in the Qinghai-Tibetan Plateau. - *Plant Systematics and Evolution* 26: 255-265.
- Dunne, J. A. et al. 2002a. Food web structure and network theory: the role of connectance and size. - *Proceedings of the National Academy of Sciences (USA)* 99: 12917-12922.
- Dupont, Y. L. et al. 2009. Spatio-temporal variation in the structure of pollination networks. - *Oikos* 118: 1261-1269.
- Elzinga, J. A. et al. 2007. Time after time: flowering phenology and biotic interactions. - *Trends in Ecology & Evolution* 22: 432-439.
- Flo, V. et al. (In review). Yearly fluctuations of floral landscape in a Mediterranean scrubland: consequences on floral resources availability. – *PlosOne* 00: 000-000.
- García, M. B. et al. 2012. Extreme reproduction and survival of a true cliffhanger: the endangered plant *Bordera chouardii* (Dioscoreaceae). – *PlosOne* 7(9): e44657.
- Gómez, J. M. 2002. Generalizations in the interactions between plants and pollinators. - *Revista Chilena de Historia Natural* 75: 105-116.
- Gómez, J. M. and Zamora, R. 1999. Generalization vs. specialization in the pollination system of *Hormathophylla spinosa* (Cruciferae). - *Ecology* 80: 796-805.
- Gomez, J. M. et al. 2010. Changes in pollinator fauna cause spatial variation in pollen limitation. - *Journal of Ecology* 98: 1243-1252.

- Heithaus, E. R. et al. 1982. Cumulative effects of plant-animal interactions on seed production by *Bauhinia unguolata*, a neotropical legume. - *Ecology* 63: 1294-1302.
- Herrera, C. M. 1988. Variation in mutualisms: the spatiotemporal mosaic of a pollinator assemblage. *Biological Journal of the Linnean Society* 35: 95-125.
- Ings, T.C. 2008. Ecological networks—beyond food webs. - *Journal of Animal Ecology* 78: 253-269.
- Johnson, S. D. and Steiner, K. E. 2000. Generalization versus specialization in plant pollination systems. - *Trends in Ecology & Evolution* 15: 140-143.
- Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence, asymmetries, and coevolution. - *The American Naturalist* 129: 657-677.
- Jordano, P. et al. 2003. Invariant properties in coevolutionary networks of plant-animal interactions. - *Ecology letters* 6: 69-81.
- Jordano, P. et al. 2009. Redes complejas de interacciones mutualistas planta-animal. *Ecología y evolución de las interacciones planta-animal: conceptos y aplicaciones*. - Editorial Universitaria, Santiago, Chile.
- Lázaro, A. et al. 2013. How do pollinator visitation rate and seed set relate to species' floral traits and community context?. - *Oecologia* 173: 881-893.
- Levey, D. J. et al. 2002. Seed dispersal and frugivory: ecology, evolution, and conservation. - CABI.
- Losa, J. M. et al. 1975. Comunidades rupícolas en el Bierzo. - *Anales del Instituto Botánico Cavanilles* 32: 215-234.
- Medan, D. et al. 2002. Plant-pollinator relationships at two altitudes in the Andes of Mendoza, Argentina. - *Arctic, Antarctic, and Alpine Research* 34: 233-241.
- Naeem, S. et al. 1999. Biodiversity and ecosystem functioning: maintaining natural life support processes. - *Issues in Ecology* 4(11).
- Navarro, L. 2000. Pollination ecology of *Anthyllis vulneraria* subsp. *vulgaris* (Fabaceae): nectar robbers as pollinators. - *American Journal of Botany* 87: 980-985.
- Olesen, J. M. and Jordano, P. 2002. Geographic patterns in plant-pollinator mutualistic networks. - *Ecology* 83: 2416-2424.
- Olesen, J. M. et al. 2008. Temporal dynamics in a pollination network. - *Ecology* 89: 1573-1582.
- Olesen, J. M. et al. 2011. Strong, long-term temporal dynamics of an ecological network. - *Plos One* 6(11): e26455.
- Ollerton, J. et al. 2011. How many flowering plants are pollinated by animals?. - *Oikos* 120: 321-326.

- Owen, E. L. et al. 2013. Can winter-active bumblebees survive the cold? Assessing the cold tolerance of *Bombus terrestris audax* and the effects of pollen feeding. - PLoS ONE 8(11): e80061.
- Petanidou, T. et al. 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. - Ecology Letters 11: 564-575.
- Pimm, S.L. 2002. Food webs, Second edition. – University of Chicago Press, Chicago.
- Potts, S. G. 2003. Linking bees and flowers: how do floral communities structure pollinator communities?. – Ecology 84: 2628-2642.
- Potts, S. G. 2010. Global pollinator declines: trends, impacts and drivers. - Trends in Ecology & Evolution 25: 345-353.
- Price, M.V. et al. 2005. Temporal and spatial variation in pollination of a montane herb: a seven-year study. - Ecology 86: 2106-2116.
- Prieto, P. et al. 2008. Precipitation-dependent flowering of *Globularia alypum* and *Erica multiflora* in Mediterranean shrubland under experimental drought and warming, and its inter-annual variability. - Annals of Botany 102: 275-285.
- R Core Team 2017. R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Schemske, D. W. et al. 2009. Is there a latitudinal gradient in the importance of biotic interactions. – Annual Review of Ecology and Systematics 40: 245-269.
- Thompson, J.D. 2001. How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system?. - Oecologia 126: 386-394.
- Waser, N. M. and Ollerton, J. (Eds.). 2006. Plant-pollinator interactions: from specialization to generalization. Univ. of Chicago Press.
- Waser, N. M. et al. 1996. Generalization in pollination systems, and why it matters. - Ecology 77: 1043-1060.

## 6. Appendix.

**Table S1.** Plant species used in the study.

<b>Specie</b>	<b>Family</b>
<i>Acinos alpinus</i> (L.) Moench	Lamiaceae
<i>Aethionema marginatum</i> (Lapeyr.) Montemurro	Brassicaceae
<i>Anthyllis vulneraria</i> L.	Fabaceae
<i>Antirrhinum meoanthum</i> Hoffm. & Link.	Plantaginaceae
<i>Armeria rothmaleri</i> G. Nieto Feliner.	Plumbaginaceae
<i>Campanula adsurgens</i> Leresche & Levier.	Campanulaceae
<i>Cymbalaria muralis</i> P. Gaertner, B. Meyer & Scherb.	Plantaginaceae
<i>Erinus alpinus</i> L.	Plantaginaceae
<i>Erysimum linifolium</i> (Pers.) J. Gay.	Brassicaceae
<i>Jasminum fruticans</i> L.	Oleaceae
<i>Leontodon farinosus</i> Merino & Pau.	Asteraceae
<i>Petrocoptis grandiflora</i> Rothm.	Caryophyllaceae
<i>Polygala vulgaris</i> Asso.	Polygalaceae
<i>Rhamnus legionensis</i> Rothm.	Rhamnaceae

**Table S2.** Pollinator species identified in the study.

<b>Specie</b>	<b>Family</b>
<i>Allantus cinctus</i> (Linnaeus, 1758)	Tenthredinidae
<i>Amegilla quadrifasciata</i> (de Villers, 1789)	Apidae
<i>Andrena cineraria</i> (Linnaeus, 1758)	Andrenidae
<i>Andrena fulva</i> (Müller, 1766)	Andrenidae
<i>Andrena haemorrhoa</i> (Fabricius, 1781)	Andrenidae
<i>Andrena pilipes</i> (Fabricius, 1781)	Andrenidae
<i>Anthidium manicatum</i> (Linnaeus, 1758)	Megachilidae
<i>Anthocharis belia</i> (Linnaeus, 1767)	Pieridae
<i>Anthocharis cardamines</i> (Linnaeus, 1758)	Pieridae
<i>Anthophora acervorum</i> (Latreille, 1803)	Apidae
<i>Anthophora hispanica</i> (Fabricius, 1787)	Apidae
<i>Apis mellifera</i> (Linnaeus, 1758)	Apidae
<i>Araschnia levana</i> (Linnaeus, 1758)	Nymphalidae
<i>Attagenus pellio</i> (Linnaeus, 1758)	Dermestidae
<i>Bombus hortorum</i> (Linnaeus, 1761)	Apidae
<i>Bombus jonellus</i> (Kirby, 1802)	Apidae
<i>Bombus lucorum</i> (Linnaeus, 1761)	Apidae
<i>Bombus pascuorum</i> (Scopoli, 1763)	Apidae
<i>Bombus pratorum</i> (Linnaeus, 1761)	Apidae
<i>Bombus terrestris</i> (Linnaeus, 1758)	Apidae
<i>Bombylius canescens</i> (Mikan, 1796)	Tabanidae
<i>Bombylius major</i> (Linnaeus, 1758)	Tabanidae
<i>Bombylius minor</i> (Linnaeus, 1758)	Tabanidae
<i>Calliphora vomitoria</i> (Linnaeus, 1758)	Calliphoridae
<i>Camponotus lateralis</i> (Olivier, 1792)	Formicidae
<i>Cardiophorus gramineus</i> (Scopoli, 1763)	Elateridae
<i>Celastrina argiolus</i> (Linnaeus, 1758)	Lycanidae
<i>Ceratina cyanea</i> (Kirby, 1802)	Apidae
<i>Coelioxys inermis</i> (Kirby, 1802)	Megachilidae
<i>Colias croceus</i> (Geoffroy, 1785)	Pieridae

<i>Colletes succinctus</i> (Linnaeus, 1758)	Colletidae
<i>Cynthia cardui</i> (Linnaeus, 1758)	Nymphalidae
<i>Episyrphus balteatus</i> (De Geer, 1776)	Syrphidae
<i>Eristalis tenax</i> (Linnaeus, 1758)	Syrphidae
<i>Eucera longicornis</i> (Linnaeus, 1758)	Apidae
<i>Fallenia fasciata</i> (Fabricius, 1805)	Nemestrinidae
<i>Gonepteryx cleopatra</i> (Linnaeus, 1767)	Pieridae
<i>Gonepteryx rhamni</i> (Linnaeus, 1758)	Pieridae
<i>Halictus rubicundus</i> (Christ, 1791)	Halictidae
<i>Halictus scabiosae</i> (Rossi, 1790)	Halictidae
<i>Halictus tumulorum</i> (Linnaeus, 1758)	Halictidae
<i>Hemaris fuciformis</i> (Graeser, 1888)	Sphingidae
<i>Hylaeus signatus</i> (Panzer, 1798)	Colletidae
<i>Iphiclides podalirius</i> (Linnaeus, 1758)	Papilionidae
<i>Lasioglossum calceatum</i> (Scopoli, 1763)	Halictidae
<i>Lasioglossum smeathmanellum</i> (Kirby, 1802)	Halictidae
<i>Lasiommata megera</i> (Linnaeus, 1767)	Nymphalidae
<i>Lasius niger</i> (Linnaeus, 1758)	Formicidae
<i>Lucilia caesar</i> (Linnaeus, 1758)	Calliphoridae
<i>Lytta vesicatoria</i> (Linnaeus, 1758)	Meloidae
<i>Macroglossum stellatarum</i> (Fabricius, 1781)	Sphingidae
<i>Maniola jurtina</i> (Linnaeus, 1758)	Nymphalidae
<i>Megachile centuncularis</i> (Linnaeus, 1758)	Megachilidae
<i>Melanostoma scalare</i> (Fabricius, 1794)	Syrphidae
<i>Melecta luctuosa</i> (Scopoli, 1770)	Apidae
<i>Melitta haemorrhoidalis</i> (Fabricius, 1775)	Melittidae
<i>Merodon equestris</i> (Fabricius, 1794)	Syrphidae
<i>Neoscia podagrica</i> (Fabricius, 1775)	Syrphidae
<i>Oedemera nobilis</i> (Scopoli, 1763)	Oedemeridae
<i>Oncomera femoralis</i> (Olivier, 1803)	Oedemeridae
<i>Osmia rufa</i> (Linnaeus, 1758)	Megachilidae
<i>Oxythyrea funesta</i> (Poda, 1761)	Cetoniidae
<i>Pararge aegeria</i> (Linnaeus, 1758)	Nymphalidae
<i>Pieris brassicae</i> (Linnaeus, 1758)	Pieridae
<i>Pieris napi</i> (Linnaeus 1758)	Pieridae
<i>Pieris rapae</i> (Linnaeus 1758)	Pieridae
<i>Polyommatus icarus</i> (Rottemburg, 1775)	Lycaenidae
<i>Scaeva pyrastris</i> (Linnaeus, 1758)	Syrphidae
<i>Sphaerophoria</i> sp.	Syrphidae
<i>Stelis punctulatissima</i> (Kirby, 1802)	Megachilidae
<i>Syrphus ribesii</i> (Linnaeus, 1758)	Syrphidae
<i>Tenthredinidae</i> sp.	Tenthredinidae
<i>Terellia ceratocera</i> (Hendel, 1913)	Tephritidae
<i>Vanessa atalanta</i> (Cramer, 1779)	Nymphalidae
<i>Xanthogramma pedissequum</i> (Harris, 1776)	Syrphidae
<i>Xylocopa violacea</i> (Linnaeus, 1758)	Apidae

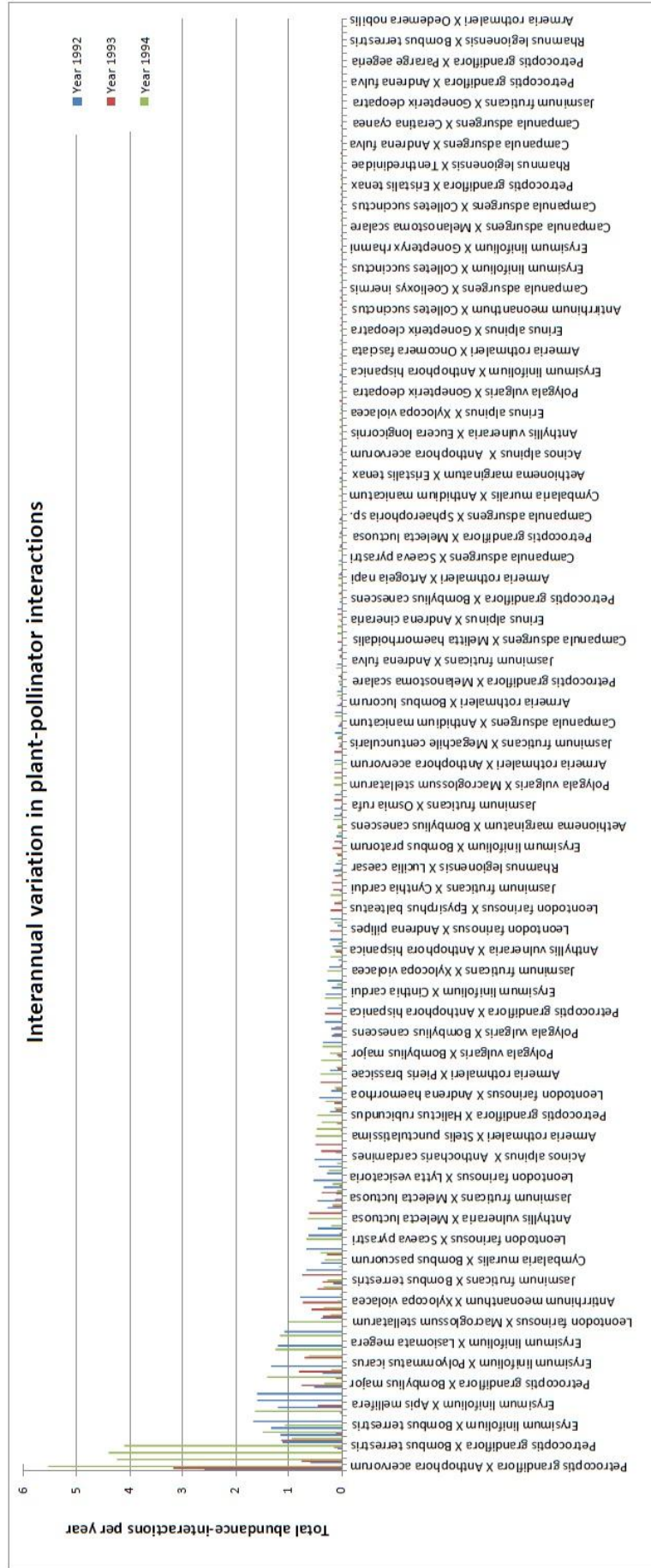


Figure S1. Abundance of plant-pollinator interactions compared for the three years of study, presented according to their abundance for each year. Ordered by the abundance of each interaction, corrected for the number of contacts by the sampling time and abundance of open flowers for each year.