

## Article

# Contrasting Response of Mountain Plant-Pollinator Network to Fragmented Semi-Natural Grasslands

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**Abstract:** The majority of the world's plants rely on animal pollinators for reproduction, making pollination a key ecosystem service for the maintenance of natural and cultivated plant communities. Mutual interactions between plants and pollinators, also called “plant-pollinator networks”, are becoming increasingly vulnerable due to the intensification of anthropogenic land use and climate change. Thus, due to the rapid decline of semi-natural grasslands in the Northern Apennines (Italy), we aimed at understanding how the fragmentation of these habitats, the spatial distribution, and the amount of semi- and natural areas surrounding them, could affect species diversity and plant-pollinator networks. Specifically, in the Northern Apennines, we monitored semi-natural grasslands belonging to the EU habitat type 6510 to evaluate the effect of fragmentation on plant and pollinator richness and on the plant-pollinator network. We carried out generalized linear models considering three taxonomical and six network descriptors as response variables and the combinations of grasslands size and isolation, as well as 10 other factors describing landscape composition as explanatory variables. We found a well-structured plant-pollinator network, characterized by a high diversity of both plants and pollinators, with mutual relations marginally specialized, highly affected by habitat fragmentation and the land use of surrounding grasslands. Moreover, large and neighboring patches increased pollinator richness and improved the overall network structure while the occurrence of meadows and shrubs around fragmented patches was important to ensure the continuity of floristic resources. Finally, extensive croplands and agricultural settlements significantly reduced plant and pollinator diversity, favoring generalist (probably invasive) species, which however increased the strength and stability of the network.

**Keywords:** landscape composition; landscape configuration; habitat fragmentation; mutualism; plant-pollinator networks; semi natural grasslands



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## 1. Introduction

Pollination is an ecological process occurring in all terrestrial ecosystems, which involves more than 90% of the angiosperms [1] and approximately one-third of the currently known animal species [2]. Thus, pollinators play an essential role in ecosystems as the sexual reproduction of most plant species depends on them [3]. Without plants producing pollen, nectar, and other resources, many pollinators would go extinct. This complex system of interaction between plants and pollinators, also called “plant-pollinator networks” is therefore a mutualistic process that provides for beneficial interdependence between the parties involved with the survival of one depending on that of the other. Moreover, the pollination process is an ecosystem service, i.e., a beneficial service provided to humans by ecosystems [4], and assumes a relevant economic value, as more than 35% of the world's supply of plant-based food comes from crops pollinated by insects [5].

However, if on the one hand, “plant-pollinator networks” are a strong demonstration of mutualism and coevolution, on the other, they constitute complex and fragile systems whose interrelation mechanisms are often difficult to understand [6]. Actually, in the case

of perturbation of natural functionality of the interaction network due to the decline of pollinators, it is hard to identify the ongoing causes of this decline, often not simply related to a decrease in flower availability [7].

Thus, the study of “plant-pollinator networks” is fundamental to fully understanding the interdependent relationships between animals and plants and to providing information on the stability of the network, as well as on the structuring elements of the community. Furthermore, in order to protect this complex mutualistic system, we urge a deep understanding of the environmental factors influencing the occurrence and abundance of pollinators, while investigating the dynamics underlying their relationships with vegetation types and land-use cover [6].

Among the many, habitat loss is a key factor in the decline of pollinators, for which restoration of semi- and natural ecosystems or the connectivity between them represents a potential solution [8]. Habitat restoration actions have to consider the distance between feeding sites, as well as the ability of pollinators to cross inhospitable matrices [8], as well as the ability of plants to settle and form stable communities attractive to pollinators [9].

Semi-natural grasslands are ecosystems with high plant richness due to long-time agro-pastoral activities, such as mowing and extensive grazing [10]. Plant richness, together with the high availability of suitable nesting sites, represents the ideal environment for pollinators [11,12]. However, they are gradually disappearing due to land abandonment or their conversion into arable lands or forests, and thus, to date, most semi-natural grasslands are protected at the European level (Annex I, Habitat Directive; sites of conservation importance, SCI). To counter the rapid decline of these habitats, a solution is certainly to restore the seedbed areas to the detriment of agricultural or forest environments [13]. Actually, in northern Europe, restoration actions on semi-natural grasslands proved the beneficial effects on biodiversity [14,15].

However, to date, these interventions are still extremely limited [16] and, in some countries, such as Italy, still completely lacking. Moreover, when habitat restoration interventions are planned to increase connectivity, rarely all the elements characterizing landscape structure are evaluated [17]. Specifically, the two main elements defining landscape structure are composition and configuration [18]. The former is the type and amount of habitat or cover types within a landscape, the latter reflects the spatial pattern or ‘fragmentation’ of landscape elements such as the degree to which patches within a landscape are connected or their size [19,20]. However, in most cases, management efforts to maintain biodiversity have focused on minimizing the effects of fragmentation [21,22], neglecting the influences of landscape composition, particularly habitat loss, on biodiversity [23–25]. Thus, unlike previous studies, in this research, we focus on the role of landscape composition in maintaining biodiversity against fragmentation processes.

Specifically, we aimed at understanding how the fragmentation of semi-natural grasslands in the Northern Apennines (the EU habitat type 6510 Lowland hay meadows), as well as the spatial distribution and amount of semi- and natural areas surrounding them, could affect species interactions and the structure of plant-pollinator networks.

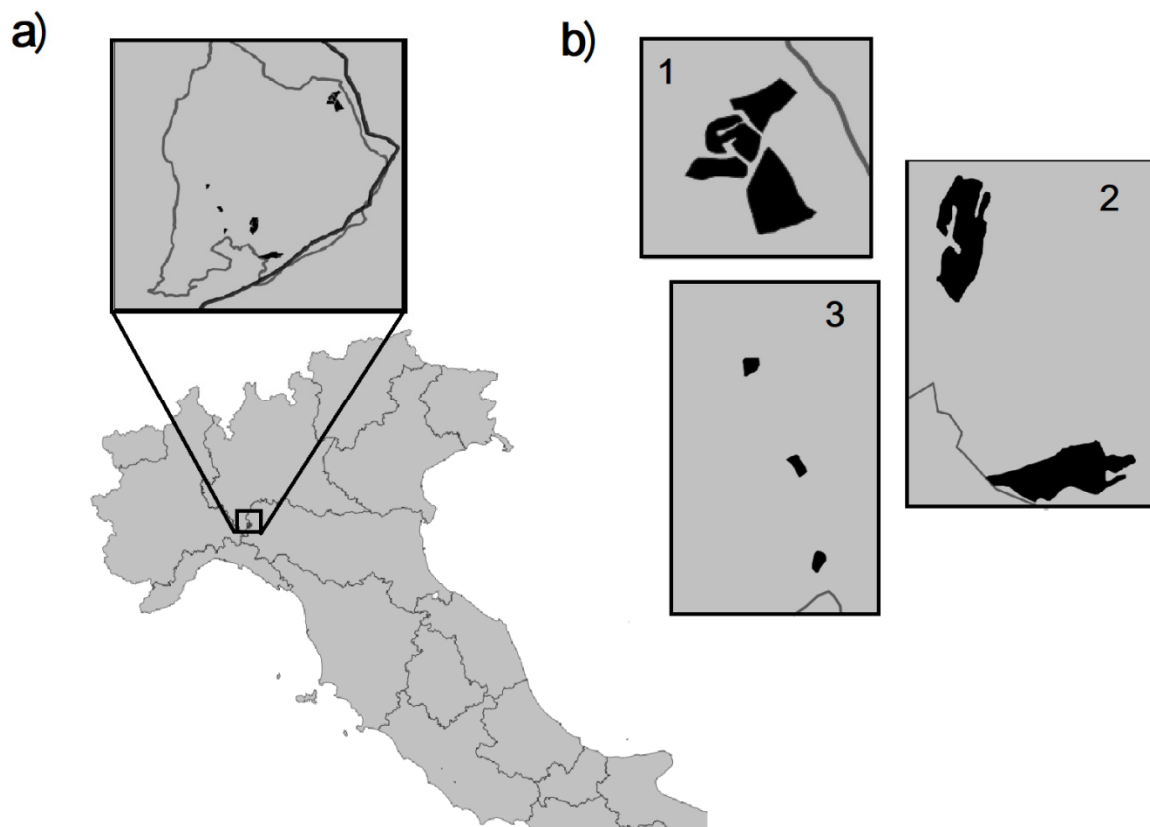
Thus, we addressed the following questions: (1) do size and distance (degree of habitat isolation and fragmentation) of mountain semi-natural grasslands have an effect on plant and pollinator richness and on plant-pollinator structure? (2) How does landscape composition, in terms of type and amount of habitat and land use, affect plant and pollinator richness and network structures?

## 2. Methods

### 2.1. Study Area

Our study was carried out in the Northern Apennines in the Lombardy region (Italy), within the SCI “Sassi Neri - Pietra Corva” (9.34° E, 44.82° N; Figure 1a), in a total of 667 hectares on the right orographic bank of the Tidone river, up to 1000 m a.s.l. The EU habitat type 6510 “Lowland hay meadows” extends for almost 25 hectares within the above-mentioned SCI and is covered by semi-natural grasslands rich in flowers corresponding to

hay meadows (therefore regularly cut) or rarely to pasture meadows [26]. They can host rare arboreal or shrubby species and are important for the fauna as well. In our study area, two stations of the EU habitat type 6130 (Calaminal grass formations of the *Violetalia calaminariae*; officially recognized by the Natura 2000 network) also occur (the only two in Lombardy). They are located on the ophiolitic massifs of the mountains and are characterized by the occurrence of several endemic species, herbaceous (annual and perennial) and shrubby (sporadic) that colonize cacuminal stations and rocky slopes [27]. Among the rarest plant species found in this habitat, there are: *Armeria arenaria* (Pers.) Schult., *Fritillaria montana* Hoppe ex W.D.J. Koch, *Linaria supina* (L.) Chaz., *Linum campanulatum* L., and the fern *Notholaena maranta* L.



**Figure 1.** Study area: (a) Geographical location of the SCI “Sassi Neri-Pietra Corva” in the Northern Apennines (Lombardy region); (b) shape and location of the nine semi-natural grasslands belonging to EU habitat type 6510 within the study area: (1) 9.53° E, 44.83° N; (2) 9.34° E, 44.81° N; (3) 9.33° E, 44.81° N.

Another EU habitat type occurring in our study area is the 6210 (semi-natural dry grasslands and scrubland facies on calcareous substrates—Festuco—Brometalia) composed of polyphytic grasslands dominated by perennial Hemicryptophytes, characterized by an edaphic condition, fluctuating between arid and semi-mesophilic [26]. This habitat type is part of a semi-natural agroecosystem, originated over the centuries, resulting in a high-altitude meadow-grazing system, fundamental for the local economy [28] and, presently supporting blooms of extraordinary beauty and abundance, where many species of orchids occur.

## 2.2. Sampling Design

Our sampling sites consisted of nine grassland patches belonging to the EU habitat type 6510 (Figure 1b) including three “contiguous” patches (distance < 50 m and surrounded by other patches of the same habitat) with a surface ranging between 1000 and 8000 m<sup>2</sup>

(medium size for this study), three “isolated” (distance from each other >100m) medium size patches, and three large patches (>1000 m<sup>2</sup>) isolated from each other. Within each patch, fixed square plots of 2.5 × 2.5 m were placed along linear transects, with a minimum distance of 20 m from each other. We investigated a total of 25 plots according to the criteria of [29]: two plots along a ≥60 m transect in patches between 1000 and 3000 m<sup>2</sup>, three plots along a ≥ 80 m transect for patches between 3000 and 8000 m<sup>2</sup>, and four plots along a ≥ 100 m transect for patches with a large extension.

Plant-pollinator interactions were quantified between May and July 2021, in standardized weather conditions (temperature ≥ 16 °C, maximum 50% cloud cover, absence of precipitation, and wind ≤ 4 m/s [8]) and in the hottest hours of the day (09:00–16:30), alternating in each sampling session the morning and the afternoon, in order to obtain data that covered the entire daily period. Our sampling sessions were carried out on alternative weeks. However, in cases of bad weather conditions or mowing interventions, we increased the frequency as necessary. Despite the increase in frequency, we monitored only 12 out of 40 plots in the entire study period.

All the pollinator species sighted were identified at the species or genus level, except in some cases in which the morpho-species were assigned. Occasionally, individuals were collected in order to subsequently identify the species. At each sampling session, all plants were counted and identified within the plot. Both plants and pollinators were identified by the authors on the basis of their expertise on the entomofauna and flora of Northern Apennine [30] and by means of species identification keys [31–33].

The availability of floristic resources was also quantified by counting the number of flowering plants and the number of “pollination units” (single flowers or inflorescences occurring in each plant [30]). Specifically, a pollination unit was considered as the whole inflorescence if flowers were organized in a dense cluster with flowers opening sub-simultaneously (i.e., no need to fly for a medium-sized pollinator insect between flowers in the same unit), or a single flower if flowers were markedly separated within an inflorescence and had unsynchronized anthesis (i.e., flights strictly necessary between flowers) [30]. From these counts and for each plot, we derived the weekly floristic density (number of pollination units/m<sup>2</sup>) and the floral exposure (average number of the pollination units of all plants of each species in the period of maximum flowering).

Finally, within each plot, we quantified the number of plant and pollinator interactions that occurred during a time interval of 20 minutes. We defined the interactions between the single pollinator and the single plant as “contacts”. We defined “visits” as the number of pollination units that the pollinator visited for each contact (counting only the visits to different pollination units). As a measure of the interaction strength between plant and pollinator, we considered the frequency of contacts between plant species A and pollinator species B at each sampling session (“contact frequency”, hereinafter) as the number of contacts observed in that session between A and B divided by the number of pollination units of species A in that session [34].

### 2.3. Data Analysis

Due to the adverse weather conditions in May and the intense mowing activities in July that affected most of the patches investigated, we carried out statistical analyses on data collected in the month of June, when the most of plants occurring in our patches flowered. The period corresponding to the end of May and the whole of June is suggested to monitor habitat 6510 in the Apennine areas to assess its conservation status [35].

Since flower abundance varies over time, the interaction strength between plants and pollinators was weighed by the floristic density of the plants with which the pollinators interacted. Therefore, as a measure of the interaction strength between plant species A and pollinator species B in the period considered, we used the following formula [34]: sum of the “contact frequency” between A and B divided by the number of pollination units of species A multiplied by the floristic density of A per session. To graphically visualize the network based on the interaction strength between plants and pollinators we used

the “plotweb” function in the “bipartite” v.2.05 package [36] in the statistical environment R v.3.2.4 [37].

To characterize the role of each species within the network, we used three indices accounting for the interaction strength between plants and pollinators:

1. *Species strength*—which provides a quantitative measure of the importance of an insect species for its partners (host species) and *vice versa*. It is calculated as the sum of the dependencies of all partners on that species [38];
2. *Species interaction asymmetry*—a measure of the imbalance between the effect that a species has on its partners and the dependence of that species on its partners. We use the Push-pull index [39], which ranges from  $-1$  to  $1$ . Positive values indicate that a species affects its interaction partners more strongly than it is affected by them (“pusher” species). Negative values indicate that a species experiences strong effects from its interaction partners but does not exert a strong reciprocal effect on them (“puller” species), and  $0$  indicates total dependence symmetry;
3. *Generalization-specialization*—we use the  $d'$  index [40], which measures the level of specialization of a species accounting for the relative abundance of its partners, ranging from  $0$  (minimum specialization) to  $1$  (maximum specialization). This index is not affected by variations in the sampling effort and by the incomplete sampling of plant-pollinator interactions [41].

To characterize the plant-pollinator network based on the same measure of interaction strength used to calculate the reciprocal relationships between species, we calculated the following six indices:

1. *Nestedness*—a measure of the extent to which specialists interact with species that form a perfect subset of the species with which generalists interact. We use the weighted NODF index [42] as a measure of nestedness with  $100$  indicating perfect nestedness and  $0$  indicating randomly distributed interactions;
2. *Connectance (C)*—a measure of the relationship between the number of interactions actually carried out and those potentially achievable within the community [43]. This measure has values between  $0$  and  $100$  and, together with the Nestedness measure it is often used to indicate the level of complexity, robustness, and stability of a community against species extinction [44,45];
3. *Plant generality*—the weighted mean number of pollinator species visiting a plant species. Equivalent to vulnerability in food webs [46];
4. *Pollinator generality*—the weighted mean number of plant species visited by a pollinator species [46];
5. *Network specialization ( $H_2$ )*—for which we use the  $H_2'$  index [40], ranging from  $0$  (maximum generalization) to  $1$  (maximum specialization), a measure of the degree of exclusivity of the network. This index is not affected by variations in the sampling effort and by the incomplete sampling of plant-pollinator interactions [41];
6. *Interaction Evenness ( $E_2$ )*—a measure of the uniformity of interaction strengths in the network [47]. High  $E_2$  values indicate greater uniformity of interactions between species.

All the descriptors of the species and of the networks were calculated and graphically represented using the “bipartite” package [36] in R [37].

To test whether the network descriptors were significantly different from those expected by chance, weighted null models were generated for each patch using the “nullmodel” function with the method ‘r2dtable’ and  $10,000$  permutations in the “bipartite” package [36] in R [37]. Moreover, as network size and the number of links can affect all the above network descriptors (with the exception of  $H_2$ ), we standardized them relative to their null expectations [48,49]. Therefore, relative Nestedness was calculated for each network as  $(N - \mu N_s) / \sigma^2$ , where  $N$  is the observed value of Nestedness, and  $\mu N_s$  and  $\sigma^2$  are the mean and relative standard deviation, respectively, of the  $10,000$  simulated values of Nestedness.



Relative values of all the other networks (with the exception of  $H_2$ ) were calculated in the same way.

To evaluate the effect of fragmentation on plant and pollinator richness and on the plant-pollinator network, we carried out Generalized Linear Models (GLMs) using as explanatory variables (Table 1) three parameters describing the landscape configuration (size and the level of isolation of the grasslands investigated and 10 parameters describing the landscape composition (nine land-use variables and their resulting Shannon habitat diversity index). Land-use variables were measured within a 1 km radius from each semi-natural grassland patch because previous studies showed that most pollinators have foraging ranges smaller than 1 km in radius [50,51]. Land-use variables were derived by the “Uso e copertura del suolo 2018–DUSAF 6.0” (available at <http://www.geoportale.regione.lombardia.it/download-ricerca>; accessed on 2 November 2022) and by the “Database Uso del Suolo–Geoportale Emilia Romagna” (available at <https://geoportale.regione.emilia-romagna.it/approfondimenti/database-uso-del-suolo>; accessed on 2 November 2022; Table 1). We resampled all these variables at a resolution of 10 m.

**Table 1.** Variables considered in the development of generalized linear models to estimate the effects of landscape composition and configuration on plant and pollinator richness and on seven network descriptors. Minimum; maximum; mean  $\pm$  standard deviation (SD) values are shown.

	Variables	Description	Unit	Min	Max	Mean	( $\pm$ ) SD	
Response variables	Inter_poll (N)	Number of Interacting pollinator species	n	3	18	10.33	5.29	
	Plants (N)	Total number of plants sampled	n	10	16	13.22	2.22	
	Inter_plants (%)	Percentage of interacting plants species over the total number of plant species	%	38.01	75.01	51.67	11.93	
	C	Connectance	Index	0.12	0.41	0.24	0.07	
	Nestedness	measured by the weighted (NODF) index	Index	0	26.92	11.21	8.41	
	$E_2$	Interaction evenness	Index	0.41	0.65	0.51	0.08	
	$H_2$	Network specialization	Index	0.63	1.00	0.82	0.12	
	HL	Plant generality	Index	1.24	2.05	1.67	0.22	
	LL	Pollinator generality (plant vulnerability)	Index	1.15	3.91	2.25	1.01	
<b>Landscape composition (%)</b>								
Explanatory variables	Shrublands	Shrublands	%	0	6.64	3.67	2.79	
	Woodlands	Woodlands	%	60.91	71.45	64.65	3.72	
	Wooded meadows	Grasslands with Trees	%	2.99	4.76	3.78	0.57	
	Open meadows	Grasslands without Trees	%	1.38	21.24	10.31	8.65	
	Croplands	Croplands	%	1.83	11.75	6.52	4.79	
	Arid croplands	Arid croplands	%	0	13.74	5.89	6.92	
	Rocks	Rocky areas	%	0	0.34	0.18	0.15	
	Agricultural and Livestock settlements	Agricultural and Livestock settlements	%	0.095	0.11	0.11	0.01	
	Human settlements	Human settlements	%	1.07	2.48	1.91	0.56	
	<b>Landscape composition (habitat diversity)</b>							
	Shannon diversity index of habitats	Shannon' habitat diversity index	Index	0.81	1.29	1.11	0.18	
<b>Landscape configuration</b>								
Near distance to not 6510 habitats	Distance to the nearest EU habitat type 6510	m	65	360	183.2	120.67		
Near distance to 6510 habitats	Distance to the nearest seminatural grasslands different from EU habitat type 6510	m	87	1077	614.2	322.47		
patch size	Patch size	m <sup>2</sup>	2178	17,637	7219	6094.5		

As response variables, we considered three taxonomical descriptors (Number of pollinator species observed interacting with plants, Total number of plants species sampled, and Number of plant species observed interacting with pollinators over the total plants species availability) and the six network descriptors mentioned above (Table 1).

To identify environmental variables related to species richness and network structure, we followed the Information-Theoretic Approach [52,53] with multi-model inference. This approach involves the development of as many GLMs as possible combinations of environmental variables considered (excluding only combinations including correlated variables,  $|r| > 0.7$  [54]). The models obtained were compared using the corrected (for small sample size) Akaike Information Criterion, AICc [55]. The model with the lowest AICc value was selected as the 'best' model and, to order the subsequent models, the difference ( $\Delta\text{AICc}$ ) between the AICc of the 'best' model and that of the other models was calculated. In addition to the best model ( $\Delta\text{AICc} = 0$ ), we considered all the models with  $\Delta\text{AICc} < 2$  [56]. We estimated standardized regression  $\beta$ -coefficients as well as significance and importance (calculated as the sum of the Akaike weights,  $W$ ) of all the predictor variables entered in the best model(s). For all these analyses, we used the R package 'MuMIn' (v. 1.0.0., [57]).

### 3. Results

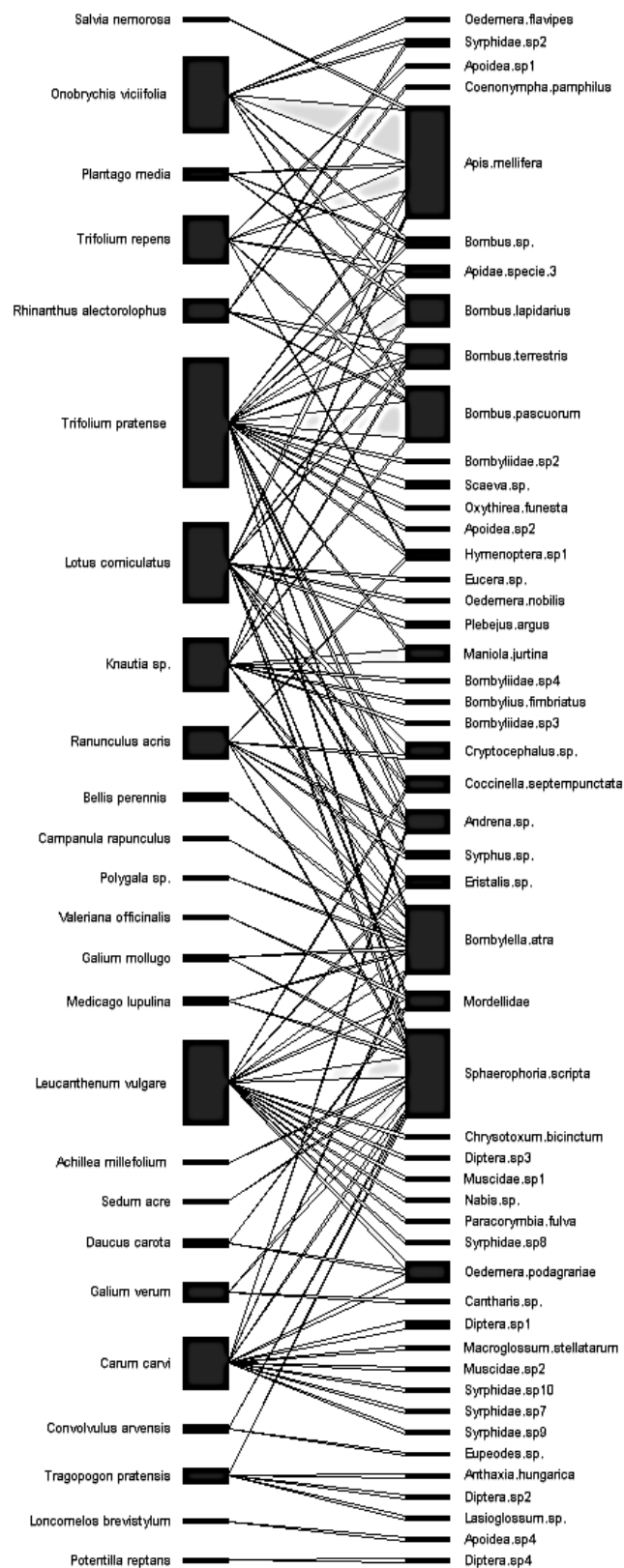
Within the nine semi-natural grasslands considered, we counted 10,633 plants and 14,964 "pollination units" belonging to 31 species (Table S1). Pollinators found interacting with plants belonged to 73 species: 15 Coleoptera, 28 Diptera, 1 Hemiptera, 18 Hymenoptera, and 11 Lepidoptera (Table S2). Pollinators interacted 879 times with 25 plant species (74% of the total number of plant species available).

We investigated grasslands characterized by a small number of strong interactions and many weak interactions (Figure 2). The plant species involved in the greatest number of interactions were *Onobrychis viciifolia* Scop. and *Trifolium pratense* L. The most active pollinator species were *Apis mellifera*, *Bombus pasquorum*, *Bombilida atra* and *Sphaerophoria scripta*. The strongest (i.e., with the greatest interaction strength) pollinator species were *Sphaerophoria scripta*, *Bomylidae atra* and *Apis mellifera*. These pollinators were also involved in the greatest number of interactions (Figures 2 and 3a). Among the plant species found in this habitat, *Trifolium pratense* L. and *Leucanthemum vulgare* Lam. were the most important for pollinators, showing high strength and high frequency of interaction, followed by *Carum carvi* L., *Lotus corniculatus* L. and *Knautia* sp. (Figures 2 and 3a).

The results show that the plants were about half "pusher" (i.e., they have positive values) and half "puller" (i.e., they have negative values). There were few plant species that establish a symmetrical interaction with their partners (Figure 3b). These include *Convolvulus arvensis* L., *Lancomelos brevistilus* (Wolfn.) Dostál. and *Potentilla reptans* L.

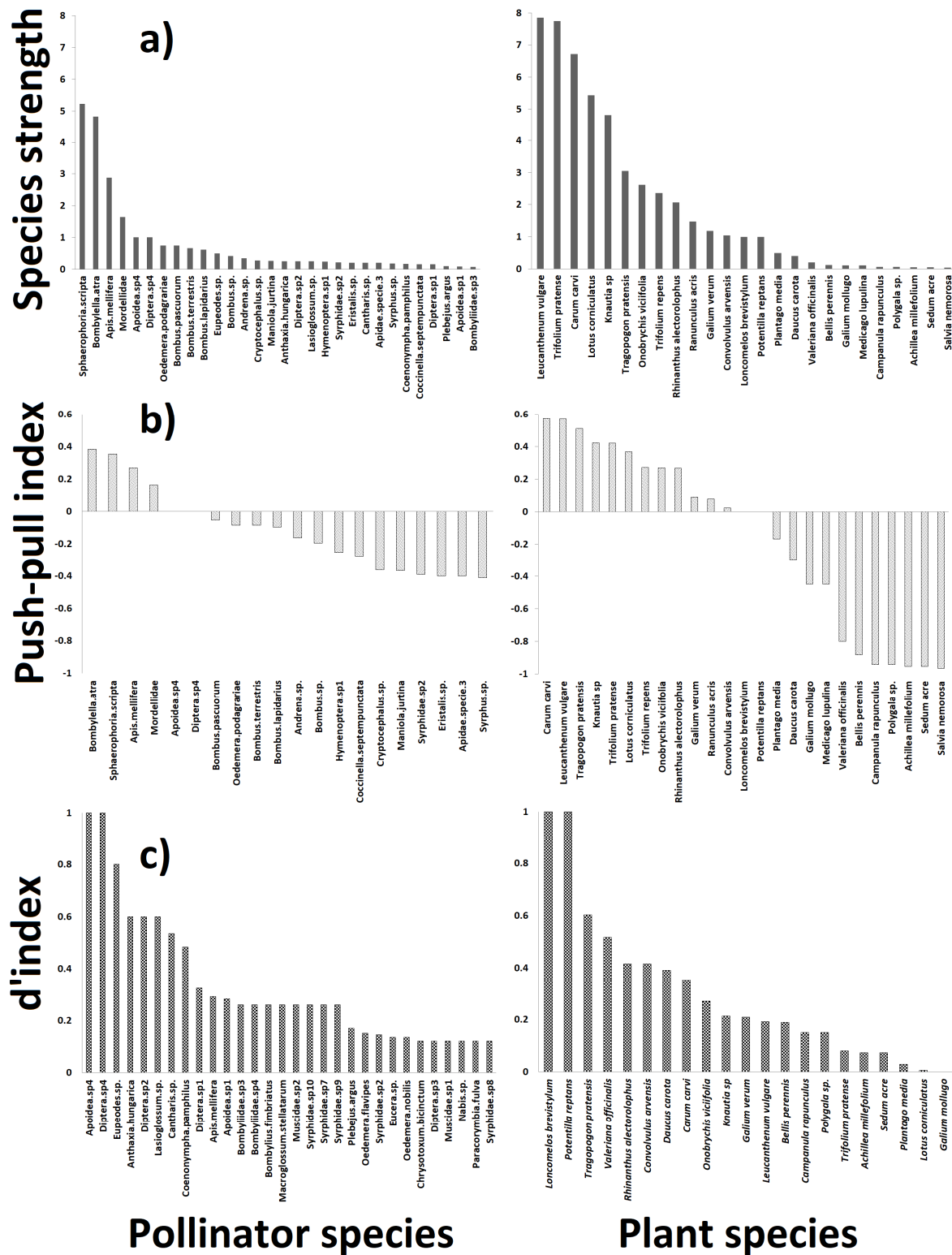
Pollinators, unlike plant species, are almost all "pullers" (Figure 3b). Pollinators acting as "pushers" were *Bombylella atra*, *Sphaerophoria scripta*, *Apis mellifera* and an undetermined species of mordellidae. In these rare cases, plants are heavily dependent on them for pollination.

The most specialized species (plants or pollinators) are those that interact exactly symmetrically with their partners (Figure 3b,c). All the others are placed in even less specialized positions as the value of the  $d'$  index decreases. For pollinators, the species that have been found to be more active or more important to plants are often in an intermediate position of specialization. For example, *Apis mellifera* and *Stenophora scripta*, characterized by having a strong interaction with their partners and a strong dependence on them, were not very specialized. Among plants, *Potentilla reptans* L. has been found to be highly specialized although it is a plant with little effect on its partners and has been involved in a few interactions. On the contrary, *Knautia* sp., a species involved in very frequent interactions, which establishes a strong dependence on its partners, has shown little specialization (Figure 3b,c).



**Figure 2.** Plant pollination network of Apennines semi-natural grasslands based on the interaction frequency between pollinators and plants weighted on the floristic density of the plants with which the pollinators interacted. Pollinator species are listed at the top. Plant species are listed at the bottom. The width of the black bar indicates the interaction frequency of each species; the width of the grey line indicates the strength of interaction. Plant species authority are shown in Table S1.





**Figure 3.** Species descriptors used to characterize the role of each species within the network; calculated taking into account the interaction strength between plants and pollinators: (a) *Species strength*: provides a quantitative measure of the importance of a species for its partners; (b) *Push-pull index* (Species interaction asymmetry): provides a measure of the imbalance between the effect that a species has on its partners and the dependence of that species on their partners; (c) *d' index* (Generalization-Specialization) provides a measure of the level of a species specialization taking into account the relative abundance of its partners. Plant species authority is shown in Table S1.

The best predictor models driving pollinators and plant species richness of the Apennines dry grasslands (EU habitat type 6510) under study always included the presence of croplands, shrublands, and wooded meadows in the surrounding landscape (Tables 2 and S3). However, while the presence of shrublands in the landscape favored plant and pollinator diversity, the presence of wooded meadows and croplands acted in the opposite direction.

**Table 2.** Results of multi-model inference carried out through generalized linear models to estimate the effects of landscape composition and configuration on plant and pollinators richness and on seven network descriptors. Average standardized coefficient ( $\beta$ ) of significant explanatory variables from models with  $\Delta AICc < 2$  are shown (see Table S3 for more details). Values in bold indicate the level of significance ( $p < 0.001$ ) while asterisks (\*) indicate the level of significance  $< 0.05$ . Explanatory variables are in columns; response variables are in rows.

	Inter_Poll (N)	Plants (N)	Inter_Plants (%)	C	Nestedness	E <sub>2</sub>	H <sub>2</sub>	HL	LL
<i>N Models</i>	1	1	1	9	<b>4</b>	7	8	2	2
(Intercept)	10.33	13.22	0.52	−3.67	<b>0.34</b>	−15.96	0.83	−10.27	−9.6
<i>Landscape composition (%)</i>									
Shrublands	<b>2.49</b>	<b>2.61</b>	<b>0.03</b>	-	-	-	-	-	-
Woodlands	<b>−10.6</b>	-	<b>−0.34</b>	-	-	-	-	-	-
Wooded meadows	<b>−10.31</b>	<b>−1.57</b>	<b>−0.27</b>	-	<b>8</b>	-	<b>0.07</b>	-	-
Open meadows	-	-	-	-	-	<b>11.06 *</b>	<b>0.07</b>	-	-
Croplands	<b>−17.21</b>	<b>−4.33</b>	<b>−0.4</b>	-	<b>6.98</b>	<b>−12.04</b>	-	-	-
Arid croplands	-	-	-	-	-	<b>−12.17</b>	<b>−0.06</b>	-	-
Rocks	-	-	-	<b>−3.01</b>	-	<b>−13.65</b>	-	-	-
Agricultural and Livestock settlements	-	<b>1.16</b>	<b>−0.13</b>	<b>8.96</b>	<b>4.86</b>	-	-	<b>27.53</b>	<b>29.18</b>
Human settlements	-	-	-	-	<b>−2.79</b>	-	-	-	-
<i>Landscape composition (habitat diversity)</i>									
Shannon diversity index of habitats	-	-	-	-	-	-	-	-	-
<i>Landscape configuration</i>									
Near distance to not 6510 habitats	<b>−3.33</b>	-	-	-	-	-	<b>0.07</b>	-	-
Near distance to 6510 habitats	-	-	-	-	<b>9.13</b>	-	-	<b>29.79</b>	<b>32.08</b>
Patches size	-	<b>0.8</b>	<b>−0.09</b>	<b>8.44</b>	<b>7.28</b>	-	-	<b>29.61</b>	<b>30.9</b>

Our results also showed that both the number of interacting pollinators and the proportion of interacting plants were negatively affected by forest cover in the surrounding ( $\beta = -10.6$  and  $\beta = -0.34$ , respectively;  $p < 0.001$ ). Moreover, the occurrence of agricultural and livestock settlements in a buffer of 1 km from our target semi-natural grasslands positively influenced plant diversity ( $\beta = 1.16$ ,  $p < 0.001$ ) but negatively affected the number of species with which pollinators interact ( $\beta = -0.4$ ,  $p < 0.001$ ).

Semi-natural grasslands configuration in the landscape showed contrasting effects on plant and pollinator species diversity. Our results showed that the degree of connection between patches had no effect on species diversity, while patch size did, even if only on plants. Specifically, we found that large patches positively influenced plant diversity ( $\beta = 0.8$ ,  $p < 0.001$ ) and negatively influenced the number of species with which pollinators interact ( $\beta = -0.09$ ,  $p < 0.001$ ). In contrast to plant species, pollinators were not affected by the configuration of the habitat under study. However, they were more abundant in patches close to other types of semi-natural grasslands ( $\beta = -3.33$ ,  $p < 0.001$ ), where available (Tables 2 and S3).

The average *Connectance* over all the sites was 0.1, which indicates that approximately 10% of all possible feeding links are actually realized in food webs compiled “within” habitats where species are likely to be relatively well mixed (Table 1). The highest *Connectance*

network (0.4) among those investigated is a small web dominated by *A. mellifera*. We found an increase in *Connectance*, *Nestedness*, *Plant*, and *Pollinator Generality* in relation to the increase of patches size and distance to patches of the same habitat ( $\beta = 8.44$ ,  $\beta = 7.28$ ,  $\beta = 29.61$ ,  $\beta = 30.9$ , respectively,  $p < 0.001$ ).

Landscape composition affected plant and pollinator richness and network structure (Tables 2 and S3). Among the natural habitats surrounding the semi-natural grasslands investigated, only shrublands seem to favor greater plant and pollinator richness ( $\beta = 2.49$ ,  $\beta = 2.61$ , respectively,  $p > 0.001$ ) while closed habitat, such as woodlands or wooded meadows, induced not only a decrease in species richness ( $\beta = -10.31$  for pollinators and  $\beta = -1.57$  for plants,  $p < 0.001$ ) but also an increase in *Nestedness* and *Specialization* ( $\beta = 8$  and  $\beta = 0.07$ , respectively,  $p < 0.001$ , Tables 2 and S3).

Croplands affected negatively pollinator and plant species richness as well as the network *Evenness* ( $\beta = -17.21$ ,  $\beta = -4.33$ ,  $\beta = -12.04$ , respectively,  $p < 0.001$ ). However, a large extension of croplands induced an increase in *Network Nestedness* in the fragmented semi-natural grasslands ( $\beta = 6.98$ ,  $p < 0.001$ ). Moreover, the presence of meadows in the areas surrounding the investigated patches leads to an increase in the specialization of the plant-pollinator networks ( $0.07$ ,  $p = 0.04$ , Tables 2 and S3).

The presence of agricultural and livestock settlements in a buffer of 1 km from the investigated studied patches induced an increase in *Connectance*, *Nestedness*, *Plant*, and *Pollinator generality* ( $\beta = 8.96$ ,  $\beta = 4.86$ ,  $\beta = 27.53$ ,  $\beta = 29.18$ , respectively,  $p < 0.001$ ).

#### 4. Discussion

We investigated grasslands hosting a well-structured plant-pollinator network characterized by a high diversity of plants and pollinators whose mutual relations were generally little specialized. Most of the plant species occurring in our study area were pollinated by more than one pollinator species as well as most of the pollinator species observed in our study area interacted with more than one plant species. Few generalist pollinators, such as *Sphaerophoria scripta*, *Bomylella atra*, and *Apis mellifera*, were found to be more important than others for the reproduction of most of the plant species present in this habitat. *A. mellifera* is a bee able to establish links with many plant species and exert a particularly strong influence on network architecture [58,59]. Since the territory investigated is characterized by a high environmental diversity and a moderate agricultural component, it is very probable that a part of the individuals observed in the study sites belongs to managed *A. mellifera*. Despite the abundance of generalist species in some of the sites investigated, they turned out not to be the most important pollinators placing third after *Sphaerophoria scripta*, and *Bomylella atra*. *S. scripta* is a generalist syrphid, typical of open and anthropophilic habitats able to pollinate plants belonging to several families such as Apiaceae, Asteraceae, Campanulaceae, Euphorbiaceae, Lamiaceae, Papaveraceae, Ranunculaceae, and Rosaceae [60,61]. The important role of syrphids as pollinators, especially under the current general decline in social bee populations, is well documented [62]. However, the role of *S. scripta* is not limited to the pollination process. A recent study carried out in Portugal highlighted the importance of *S. scripta* also as pest control [63]. Therefore, the distribution and abundance of *S. scripta* are encouraging, especially in light of sustainable management of the agroecosystem [63]. In this sense, the persistence of semi-natural grasslands in an agriculturally dominated landscape may promote syrphids mediated-ecosystem services such as pest control and pollination in crops.

Several plant species among those collected in the study sites were used by pollinators and almost half of them are fundamental for pollination. Among these, we found *Trifolium pratense* L. and *Leucanthemum vulgare* Lam., *Carum carvi* L., *Lotus corniculatus* L., and *Knautia* sp. They represent key species for the pollination service provided by habitat 6510. They are common species that can be easily propagated in specialized nurseries and their use, both as seeds and individuals, is therefore strongly suggested in restoration projects of habitat 6510.

The network investigated is characterized by highly asymmetric interactions among plants and pollinators meaning that if a plant is highly important for a pollinator (a high percentage of the pollinator's visits occur to this particular plant), this pollinator's importance for the plant is low (a low percentage of the visits received by the plant comes from this pollinator). This asymmetric nature of the interactions within a network may enhance long-term coexistence and facilitate biodiversity maintenance within ecosystems [64,65]. Moreover, the observed weak dependence (high degree of species generality) between plants and pollinators and the uniform distribution of the interactions between them in the habitat investigated gives the network strong stability favoring a greater ability of individuals to adapt to eventual variations in the specific composition [66]. The presence of many species able to use the same resource in the same way, allows the entire system to quickly respond to external perturbations [66]. Therefore, if even one or more of the pollinator species in this network became extinct, there would be others able to compensate for its absence by providing the same ecosystem services as the disappeared species [45].

Despite the general robustness of the networks investigated, the structure of the web was highly affected by the degree of habitat fragmentation as well as the land use of the surrounding grasslands. The communities of plants and pollinators of EU habitat type 6510 investigated are mutually and strictly dependent on each other. These mutual relationships varied significantly along a connectivity gradient reflecting the robustness and resilience of the entire network. Previous studies showed that the decline of pollinators is closely linked to the disappearance of their most important host plants [67]. Conversely, the composition of plant communities may be relatively robust against the loss of particular pollinators, at least in the short term [68], but becomes inexorable in the long term. Therefore, the fragmentation process described in this work, although acting on two different levels, produces significant alterations in the entire network. In general, we found that neighboring patches of similar habitats affect positively the richness of plants and pollinators and reduced the network *Nestedness*, a characteristic attributable, according to some authors, to less geographic isolation and/or higher dispersal ability [69]. Moreover, the presence of other EU semi-natural open habitats in the vicinity increases pollinator richness and reduces the specialization of the networks, favoring the entry into the community of generalist plants and pollinators and reducing the risk of local extinctions [70,71]. Greater stability of the network is also ensured by the increase in *Connectance* found in larger patches. However, the size of semi-natural grasslands seemed to have less effect on network structure and acted mainly on the plant community. Plants are more likely to be constrained by habitat size probably because they cannot disperse actively in a short time [72]. Conversely, pollinators have high mobility and also high potential for adaptively switching interaction partners [73]. This pollinator's ability also explains why the number of plant species with which pollinators interacted did not decrease despite the evident decrease of available plant species in smaller patches. The increase of generalist plants and pollinators in the larger areas of habitat 6510 could be due to the increase in available resources (richness of plant species), which is reflected in a greater number of species visited by insects [74]. Asymmetric interactions in networks favor the establishment of more stable associations between mutualistic communities [38,75] because it is more advantageous for a specialized species to rely on a generalist species (asymmetry) rather than on another specialist (symmetry), in case the other specialist becomes less reliable and both specialist partners are therefore vulnerable to co-extinction [76]. Therefore, networks in larger patches may be more stable than those in smaller patches.

However, while patch size significantly affects almost all the descriptors considered, the degree of isolation does not show an equally evident effect. Undoubtedly, the composition of the environmental matrix in which this habitat is immersed played a decisive role in the structure of the hosted plant-pollinator network. The environmental matrix certainly influences ecological dynamics as demonstrated by a meta-analysis conducted by [77] in which the importance of some characteristics of the matrix such as the abundance and distribution of wildflowers and cow dung on the improvement of the network structure

in isolated patches is reported. Other studies argue that the matrix can also influence resource availability [78], animal dispersal [79], habitat occupancy (fragment; [80,81]), and population distribution and dynamics within a fragment [77,82]. The similarity between matrices and fragments is also an important feature that facilitates gene flow and animal dispersal [82]. In our study, we found contrasting effects of landscape composition on plants and pollinator communities of the semi-natural grasslands. Natural elements surrounding the patches under study had an overall positive effect on network structure with shrublands and meadows favoring an increase in species richness and network specialization, respectively. The importance of shrublands for pollinators is probably to the abundance of nesting materials and nest sites [83] and the availability of floral resources such as Rosaceae (*Crataegus* spp., *Prunus* spp., *Pyrus communis* L., *Rosa* spp., *Rubus* spp.), Leguminosae (*Cytisophyllum sessilifolium* L. O. Lang, *Colutea arborescens* L., *Genista tinctoria* L.), *Rhamnus cathartica* L., and *Ligustrum vulgare* L. [84,85], which are insect pollinated.

The occurrence of open meadows provides additional floral resources and could thus mitigate the effect of habitat fragmentation by preventing specialist extirpation [86]. Several studies have shown that pollinators tend to be more generalized as habitat fragmentation increases due to changes in flora composition and scatter in floral resources, so any remaining pollinators may need to behave as generalists in order to survive [87,88]. However, a more specialized network is expected to reduce the opportunity for species to facilitate one another by sharing mutualistic partners and thus have a destabilizing effect [49].

Among the anthropogenic elements, the most important on the structure of the network were the extension of croplands and the occurrence and extension of agricultural and livestock settlements in the surroundings. Fragmented semi-natural grasslands in a matrix mainly constituted by these kinds of environments undergo shifts in network indices such as *Connectance*, *Nestedness*, and *Evenness* and an increase in network size due to the entrance of generalist plant and pollinator species [89].

## 5. Conclusions

This study shows a clear instability of the structure of plant pollination networks due to the fragmentation process. The smaller and more isolated areas are overall more specialized and therefore more susceptible to elements of external perturbation. Land-cover changes, implying the loss and fragmentation of habitat 6510, caused by the abandonment and consequent increase in the forest areas and/or by cultivated crops, lead to a reduction in native vegetation and a relative alteration of the abundance and richness of pollinators. However, the landscape matrix plays a substantial role in positively supporting even smaller fragments, ensuring continuity of floristic resources essential for pollination and offering nesting sites for pollinators. Therefore, creating and maintaining locally diverse natural elements and well-connected habitat structures across the landscape will favor the stability and diversity of wild pollinator populations.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/land12020356/s1>, Table S1: List of plant species found in the Apennines dry grasslands (EU habitat type 6510) of the study area. Number of plants (N) and number of “pollination units” (PU) per species is reported. Table S2: List of the Apennines dry grasslands (EU habitat type 6510) pollinator species and morpho-species found interacting with plants during the sampling season. The number of plant species contacted by each pollinator is also reported. Table S3: Results of multi-model inference based on corrected Akaike Information Criterion (AICc), carried out through generalized linear models to detect the effects of landscape composition and configuration on plant and pollinators richness and on seven network descriptors. Average standardized coefficient ( $\beta$ ),  $\pm$ standard error, of predictors from models with  $\Delta$ AICc < 2 and relative importance from Akaike weights (W) are shown.

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