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Patterns of floral resources and pollination interactions along dry grassland succession

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Abstract

Succession following the abandonment of traditional management practices can pose severe consequences for the conservation of semi-natural dry grassland communities. In the present study, we investigated whether the quantity of floral resources changes during succession of semi-natural dry grasslands and how this is related to pollinator richness and the number of pollination interactions at the community level. We addressed this issue by quantifying floral resources (i.e., number of flowers, nectar volume and number of pollen grains) and monitoring pollination interactions in dry grassland communities at different stages of succession, defined as the total cover of plant species of forest edges. The relationship between the quantity of floral resources and cover of plant species of forest edges was significantly hump-shaped, i.e., regardless of the type of floral resource, all peaked at intermediate values of cover of plant species of forest edges. The richness of animal-pollinated plants in bloom also showed a hump-shaped relationship with the cover of plant species of forest edges, while the richness of pollinator species and the number of pollination contacts were indirectly related to the cover of plant species of forest edges, as they were significantly associated with the number of flowers and the richness of animal-pollinated plants in bloom. Results suggest that succession of dry grasslands after abandonment may affect a crucial function in terrestrial ecosystems, namely animal-mediated pollination. Nevertheless, the conditions of early succession, which could be achieved by the presence of scattered shrubs, could ultimately be favourable for the pollination function in dry grasslands.

Keywords

Abandonment, flowers, nectar, pollen, pollinators

Introduction

Human-induced environmental transformations are leading to biodiversity loss and ecosystem degradation (IPBES 2019).

In rural areas, two contrasting processes are affecting local biodiversity and ecosystem functioning, namely agricultural intensification and land abandonment, especially in remote, less productive areas (Cramer et al. 2008; Plieninger et al. 2014).

While the impacts of intensification have been extensively studied (see e.g., Tscharntke et al. 2005; Rakosy et al. 2022), comparatively little is known about land abandonment. The exclusion of human intervention can trigger 'passive rewilding' (Navarro and Pereira 2015), which facilitates the restoration of natural ecosystems and opens new opportunities for conservation. Rewilded areas can provide habitat for species (Boitani and Linnell 2015); forest regrowth can enhance carbon sequestration (Pugh et al. 2019), promote soil recovery (Pointereau et al. 2008) and help regulate the hydrological cycle (Stoate et al. 2009). However, while potentially beneficial, these processes often come at the expense of semi-natural open habitats, particularly pastures and grasslands, which are often of great conservation concern (Carboni et al. 2015).

This is especially true for semi-natural grasslands, which are secondary formations, created and maintained through centuries of traditional and low-intensity human practices (Valkó et al. 2018) and have become part of the traditional agricultural landscape. Among the semi-natural grassland types, dry grasslands are unique species-rich assemblages (e.g., Wilson et al. 2012) that harbour a high diversity of plant species and provide habitat for higher trophic level species, especially arthropods (Zulka et al. 2014; Labadessa et al. 2015). Not only do they have high conservation value, but they are also recognised for providing regulating, provisioning, and cultural ecosystem services (Tscharntke et al. 2005; Bengtsson et al. 2019).

Like all other semi-natural habitats, semi-natural dry grasslands are particularly vulnerable to abandonment (Schrautzer et al. 2009). After abandonment or under use, semi-natural grasslands undergo natural vegetation dynamics. Although successional patterns can be stochastic (Chesson 2012) and vary from site to site, they generally result in species turnover and/or changes in the three-dimensional architecture of the plant community (Pickett et al. 2003). In temperate Europe, the pattern of species turnover is associated with the loss of specialised grassland species (Gustavsson et al. 2007), the rapid establishment and spread of competitive graminoids (Carboni et al. 2015), and the increase of herbaceous and shrub species typical of forest edges, and tree seedlings (Schrautzer et al. 2009).

Several studies have investigated changes in plant species composition and structure during the succession process (e.g., Bonanomi and Allegrezza 2004; Habel et al. 2013), as well as the relationships between plant community composition and structure and higher trophic level species (e.g., Elliott et al. 2023), both from taxonomic (e.g., species richness) and functional perspectives (e.g., life history traits or ecological strategies; e.g., Kelemen et al. 2017). Overall, research has shown that abandoned grasslands have lower diversity than extensively managed semi-natural grasslands (Pykälä et al. 2005; Klimek et al. 2007). Conversely, species richness of higher trophic levels has been reported to increase, at least in the early stages of succession (Öckinger et al. 2006), as higher and structurally heterogeneous plant communities facilitate the occurrence of more diverse arthropod communities (Kruess and Tscharntke 2002), which respond strongly to habitat changes (Öckinger et al. 2006; Colom et al. 2021).

Although the relationship between grassland succession and plant and animal species richness and composition has been widely studied (e.g., Habel et al. 2013; Elliott et al 2023), little is known about how grassland succession affects interactions between species belonging to different trophic levels. Among the multiple biotic interactions, animal-mediated pollination has received considerable attention in semi-natural dry grasslands, as they provide resources (i.e., nectar and pollen), breeding, nesting and overwintering habitats for pollinators and effectively promote their conservation (Fantinato et al. 2021). Furthermore, plant-pollinator interactions have been shown to contribute to the assemblage and maintenance of grassland communities (Benadi and Pauw 2018; Fantinato et al. 2018, 2019a). Therefore, plant species turnover and changes in vegetation structure following grassland abandonment are likely to have noticeable effects on species dynamics, pollination interactions and pollination service (Fantinato et al. 2019b). Plant species turnover may lead to changes in floral resources availability on grasslands, e.g., by reducing the total number of entomophilous species by favouring competitive wind-pollinated grasses. Changes in plant species composition could thus have a major impact on pollination, as changes in the type or quantity of floral rewards pose a major threat to pollinators (Goulnik et al. 2021). Understanding the effects of grassland abandonment on floral resources and pollination interactions can therefore help inform management plans for semi-natural grasslands that ensure the maintenance of a diverse plant and pollinator community and the services they provide.

In light of the above, this research aimed to answer the following questions: (i) How does the quantity of different types of floral resources (i.e., number of flowers, nectar volume, and number of pollen grains) change during succession of semi-natural dry grasslands? (ii) How does the species richness of plants and pollinators and their interactions change during the succession of semi-natural dry grasslands?

Materials and methods

Study area

Sampling took place in semi-natural dry grasslands of the Euganean Hills in northeastern Italy (45.265706 N, 11.698977 E; Fig. 1). The area is characterized by a warm, rainy climate with an average annual temperature of 13.0 °C, with a mean maximum temperature of 23.8 °C in July and a mean minimum temperature of 3.2 °C in January; the mean annual precipitation is 720 mm, with peaks in April and September (Fantinato et al. 2021). The long history of human influence on the area originated a complex rural landscape where arable fields, orchards, olive groves, vineyards, and semi-natural grasslands are intermingled with natural habitats, such as forests and rocky outcrops (Fantinato et al. 2019a).

The study focused on meso-xerophilous semi-natural grasslands that establish on shallow calcareous soils. Based on Terzi (2015), Euganean meso-xerophilous grasslands can be included in the *Festuco-Brometea* Br.-Bl. And Tx. Ex Klika and Hadač 1944 class and the SE-European-Illyrian order *Scorzoneretalia villosae* Kovačević 1959 (=*Scorzonero-Chrysopogonetalia*), and to the alliance *Saturejion subspicatae* Tomić-Stanković 1970 (Fantinato et al. 2016).

When subjected to proper management, the community is dominated by few, highly covering, anemophilous species (e.g., *Bromopsis erecta, Bothriochloa ischaemum, Carex halleriana, Koeleria pyramidata*) and several entomophilous species, including *Bupleurum baldense, Convolvulus cantabrica, Fumana procumbens, Globularia bisnagarica, Helianthemum nummularium* subsp. *obscurum*, and *Scabiosa triandra*. The proximity of roads and cultivated fields causes the entry of ruderal opportunistic species such as *Avena barbata, Euphorbia falcata, Melampyrum barbatum* subsp. *carstiense*, *Sonchus oleraceus* and *Trifolium angustifolium*.

Field sampling and data collection

The study was conducted on four grasslands with an average area of 6.89 ± 1.11 ha (M ± SD) and a minimum distance between grasslands of 1.2 km. While in the past, study grasslands were regularly (i.e., yearly) exploited for haymaking or cattle grazing, nowadays they are irregularly mown every three years (Slaviero et al. 2016). The inconsistency of management practices over time makes these grasslands crucial example of the first dynamic stages after abandonment, characterised by the spread of competitive graminoids (e.g., *Brachypodium rupestre*), and the increase in both herbaceous and shrub species typical of forest edges (e.g., *Cervaria rivini, Teucrium chamaedrys, Rosa canina, Spartium junceum*).

We placed 27 permanent plots of 2 m x 2 m in the four grasslands, in a number proportional to each grassland surface, using a stratified random sampling design (Random points inside polygons; Quantum Gis Development Team 2020). None of the 27 plots were closer than 25 m. Each plot was monitored every 15 days for a total of 12 surveys (from 1st April to 30th September of 2016). In each survey, we recorded the presence of entomophilous plants and the number of flowers per plant species. For plant species with flowers occurring together in a floral unit (e.g., *Thymus pulegioides*), we calculated the total number of flowers by multiplying the number of floral units by the average number of flowers per floral unit, based on counts of five specimens of each species. Flower heads of Asteraceae, Dipsacaceae and Plantaginaceae were treated as single flowers. We also recorded pollination interactions between plant and animal species during each survey. Animals were considered pollinators if they landed on the flowers, had direct contact with the reproductive organs of the flower and visited the flower for more than 1 second, so they were considered potential pollinators. Pollination interactions were recorded for 14 min in two 7-min sets per survey (between 10 a.m. and 1 p.m., and between 1 p.m. and 4 p.m.) to ensure observation of animals with different daily activity times (Lázaro et al. 2016). Overall, pollination interactions were observed for 3,276 min and 42 plant species and 76 species or morphospecies of pollinators were recorded.

At each survey, we also quantified for each plot the total volume of nectar (µl) and the number of pollen grains. The total volume of nectar and the number of pollen grains were determined by multiplying the number of flowers by the mean value of the nectar volume and the mean number of pollen grains for each species, respectively. The mean value of nectar and pollen grains was determined by averaging the quantity of nectar and pollen from 5-10 randomly selected flowers growing within a radius of 10 m from each plot (for details on floral resource quantification, see Fantinato et al. 2021).

During the peak of the community's growing season (from mid-May to mid-June), all vascular plant species were recorded, and their percentage cover was visually estimated. Plant nomenclature was standardised following Bartolucci et al. (2018). In addition, for each plant species we retrieved ecological information on its habitat preferences (i.e., ruderal, grassland and forest edge species; Tab. I in Appendix) based on a) the definition in the BiolFlor database as "occurrence" within the "Grassland utilisation indicator values" (Klotz et al. 2002), b) Italian Vegetation Prodrome (Biondi et al. 2014; http://www.prodromo-vegetazione-italia.org/) and c) specific literature (Tasinazzo 2014).

Data analysis

We assumed the cover of plant species typical of forest edges as a proxy of the degree of succession. In this way, different successional stages were detectable based on the total cover of species typical of forest edges, whether herbaceous or woody. As a first step, we determined the degree of succession towards forest edges of each plot, by summing the cover of all plant species of forest edges and scaled the results to 100%. To explore the relationship between the

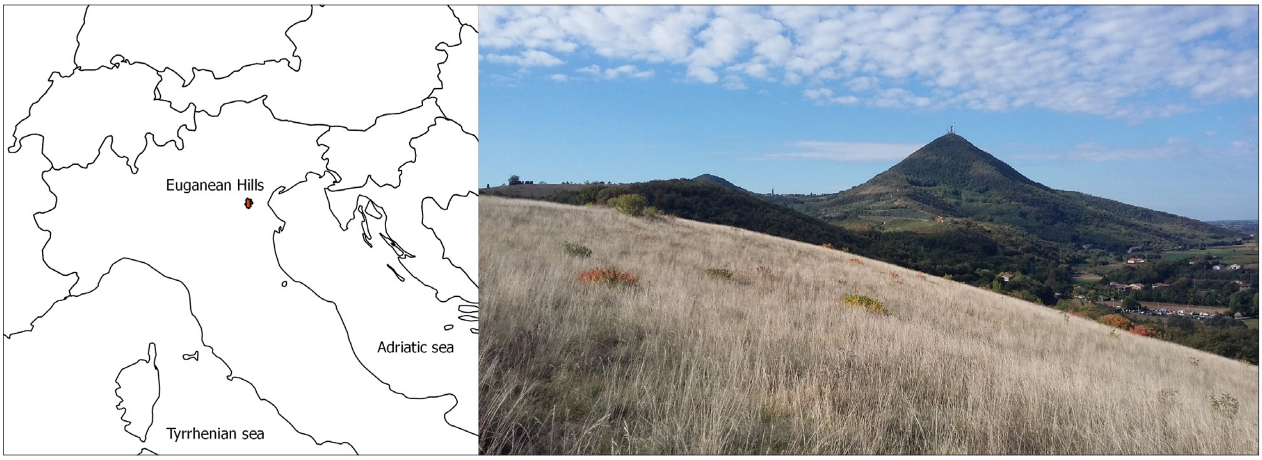

Figure 1. Map of the study area and picture of one of the studied grasslands.

cover of plant species of forest edges and the number of flowers, the volume of nectar, the number of pollen grains and the richness of animal-pollinated plants in bloom we used generalised linear mixed models (GLMMs, R version 3.4.3; package lme4). Specifically, each model included the cover of plant species of forest edges as independent variable, the number of flowers, the volume of nectar, the number of pollen grains and the richness of animal-pollinated plants in bloom as dependent variables and the plot identity as random factor. Moreover, we included the quadratic term of the cover of plant species of forest edges in the GLMMs to account for possible nonlinear relationships (without removing the linear term). We performed GLMMs using (a) Gamma error distribution and log link functions for the number of flowers, the volume of nectar and the number of pollen grains and (b) Poisson error distribution and log link function for the richness of animal-pollinated plants in bloom (after checking data overdispersion; dispersiontest function; package AER; Kleiber and Zeileis 2008). The significance of models was based on likelihood ratio tests (LRT; drop1 function; package stats) and the conditional and marginal coefficients of determination (R^2_c and R^2_m) for the GLMM models were calculated (r.squared function; package MuMIn; Barton 2015). R^2_c shows the model variance explained by both fixed and random factors, while R^2_m represents the variance explained by fixed factors alone.

Since the richness of pollinator species per plot showed an excess of zero counts, using a GLMM with Poisson marginal distribution would lead to a bias in the conclusions. Therefore, we opted for a zero-inflated model (Zuur et al. 2009; Buffa et al. 2021). Zero inflated Poisson model is the result of two distinct stochastic models. In the first model, a binomial family GLM is used to predict the probability of a non-zero count π (i.e., structural zeros); in the second model, a Poisson distribution is used to predict the richness of pollinator species recorded in a plot, with a probability $1-\pi$ and with mean λ. In the second model there is a non-zero probability to generate zeros. The resulting expected number of pollinator species is given by $(1-\pi)\lambda$. Higher values of π foster the absence of pollinator species, instead larger values of λ foster the richness of pollinator species. In our modelling framework, parameters π and λ are estimated jointly. We specified a zero-inflated model for the richness of pollinator species by including the (i) cover of plant species of forest edges, (ii) the number of flowers, (iii) the volume of nectar, (iv) the number of pollen grains and (v) the richness of animal-pollinated plants in bloom ad covariates. All covariates were ln-transformed before analysis. The same procedure was used to determine which covariates influence the number of pollination contacts.

In both the GLMMs and zero-inflated models, the values of the response variables quantified for each survey were used as replicates.

Results

The sampled plots had different cover of plant species of forest edges, varying from 0.33% to 90.21% (mean ± SD; 29.26% ± 24.21%), indicating that the dry grassland communities recorded in the sampled plots were at different stages of succession. Plant species of forest edges that firstly occurred in the plots were *Brachypodium rupestre, Asparagus acutifolius, Teucrium chamaedrys, Geranium sanguineum* and *Cervaria rivini*. As soon as succession progressed (namely the cover of plant species of forest edges increased), seedlings of shrubs and trees also occurred, such as *Cornus sanguinea, Rosa canina, Spartium junceum, Fraxinus ornus*, and *Quercus pubescens*.

The quantity of floral resources varied greatly between the sampled plots. The number of flowers varied from 0.00 to 18,512.60 flowers per plot (mean ± SD; 465.38 ± 1570.45), the volume of nectar varied from 0.00 µl to 2,885.28 µl (mean ± SD; 75.44 µl ± 283.52 µl), while the number of pollen grains varied from 0.00 to 912,733,383.23 (mean ± SD; 2,148,660.32 ± 8,371,645.95).

The relationship between the number of flowers, the volume of nectar and the number of pollen grains with the cover of plant species of forest edges were all significantly hump-shaped, suggesting that regardless of the type of floral resource, all peaked at intermediate values of cover of plant species of forest edges (Table 1; Fig. 2).

Overall, 42 animal-pollinated plant species and 76 pollinator species were recorded in sampled plots. The richness of animal-pollinated plants in bloom per plot varied from 0.00 to 7.00 (mean ± SD; 1.51 ± 1.63); most frequent animal-pollinated plants in bloom were *Thymus pulegioides* (59% of sampled plots), *Helianthemum nummularium* subsp. *obscurum* (56%), *Globularia bisnagarica* (52%) and *Stachys recta* (48%). The richness of pollinator species varied from 0.00 to 8.00 (mean ± SD; 1.00 ± 1.50); the most frequent pollinator species were *Apis mellifera* (63% of sampled plots), *Bombus hortorum* (56%), *Epicometis hirta* (48%), *Episyrphus balteatus* (41%) and *Eristalis tenax*

Table 1. Statistics of the relationships between the number of flowers, the volume of nectar, the number of pollen grains and the richness of animal-pollinated plants in bloom and the cover of plant species of forest edges.

Dependent variable	Independent variable	t-value	p	χ^2	R^2_c	R^2_m
Number of flowers	Cover of plant species of forest edges^2	-2.154	0.048	3.884	0.033	0.432
Volume of nectar	Cover of plant species of forest edges^2	-4.697	<0.001	15.191	0.077	0.581
Number of pollen grains	Cover of plant species of forest edges^2	-2.159	0.038	4.288	0.030	0.597
Richness of animal-pollinated plants in bloom	Cover of plant species of forest edges^2	-2.209	0.044	4.047	0.059	0.321

(41%). The number of pollination contacts varied from 0.00 to 16.00 (mean ± SD; 1.73 ± 3.04). The most visited plant species per plot were *Globularia bisnagarica* (mean ± SD; 7.70 ± 8.36), *Potentilla pusilla* (mean ± SD; 4.66 ± 2.88), *Pilosella officinarum* (mean ± SD; 2.85 ± 3.07) and *Geranium sanguineum* (mean ± SD; 2.15 ± 2.65).

The relationship between the richness of animal-pollinated plants in bloom with the cover of plant species of forest edges was significantly hump-shaped (Table 1; Fig. 2), suggesting that the peak of richness of animal-pollinated plants in bloom was at low-intermediate values of cover of plant species of forest edges. Finally, the richness of pollinator species and the number of pollination contacts were significantly related to the same covariates, i.e. the probability of absence of pollinator species and of pollination contacts was negatively associated with the number of flowers (ln-transformed; Table 2; Fig. 3), with the probability of absence decreasing to zero once at least ten flowers were present, while the expected richness of pollinator species and the expected number of pollination contacts were positively related to the richness of animal-pollinated plants in bloom (ln-transformed; Table 2; Fig. 3). In other words, the probability of pollinator presence and pollination contacts depended on the number of flowers in the plot, while the expected richness of pollinators and the expected number of pollination contacts depended on the richness of animal-pollinated plants.

Discussion

The abandonment of traditional management practices has been shown to lead to significant changes in the environmental characteristics and structural attributes of dry grassland communities (Valkó et al. 2018).

In the present study, we have shown that succession of dry grasslands after abandonment affects structural properties of plant communities and has critical implication for a crucial function in terrestrial ecosystems, namely animal-mediated pollination, even in correspondence of the first dynamic stages.

Patterns of animal-mediated pollination interactions at community level are related to the type and quantity of floral resources (Fantinato et al. 2021). Our results have shown that the quantity of floral resources provided at the community level changed during dry grassland succession. In particular, the quantity of floral resources peaked at low-intermediate values of percentage cover of plant species of forest edges, regardless of the type of floral resource. Floral traits such as the number of flowers, the volume of nectar and the number of pollen grains produced have been shown to be genetically regulated (e.g., Tsuchimatsu et al. 2020), but they also respond to local environmental conditions. Roth et al. (2023), for example, have shown that plants produce fewer flowers per plant under drought conditions. Furthermore, the flowers tend

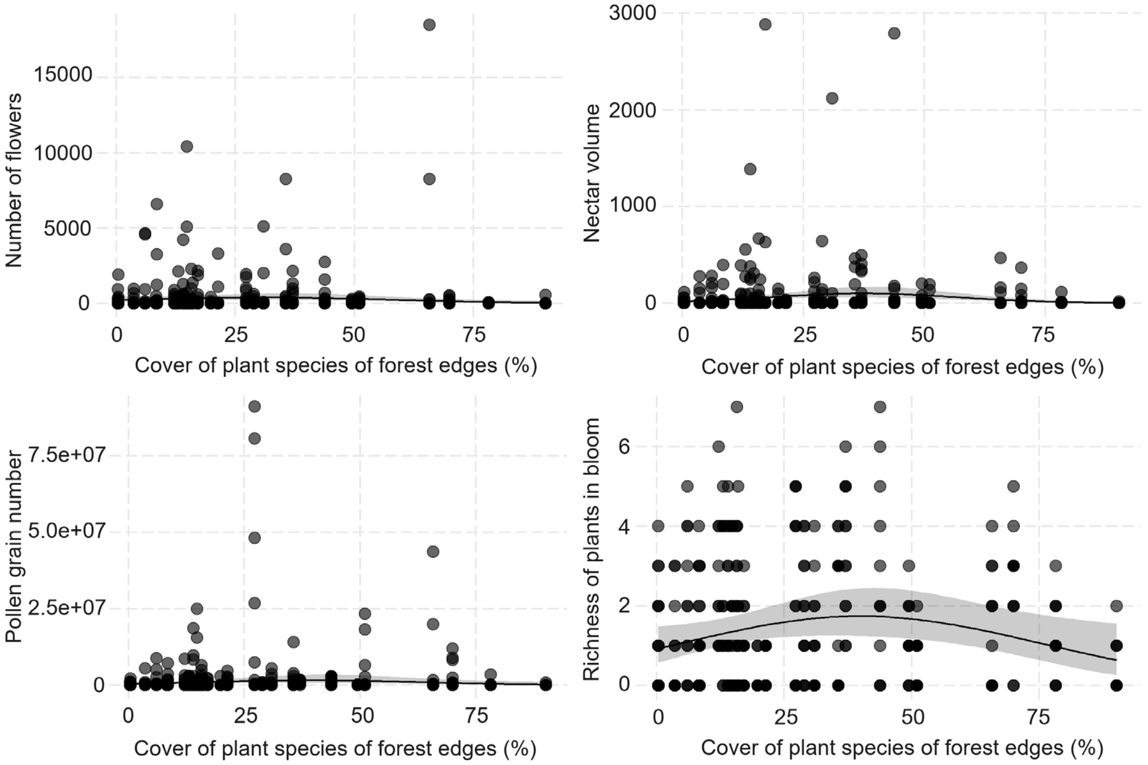

Figure 2. Relationship between the number of flowers, the volume of nectar (μl), the number of pollen grains and the richness of animal-pollinated plants in bloom and the cover of plant species of forest edges. The line represents the estimate of the Generalised Linear Mixed Model (GLMM). Fuzzy grey points are original data points (color intensity increases from light grey to black when points overlap), while the grey band represents 95% confidence interval around the regression line.

Table 2. Results of the zero-inflated Poisson model. Here π is the probability of not observing any individual pollinator or pollination contact in a plot, while λ is the expected richness of pollinators or the expected number of pollination contacts. Positive values of β^{π} indicate positive associations between covariates and the absence of pollinators or of pollination contact, while positive values of β^{λ} indicate positive associations between covariates and the expected richness of pollinators or the expected number of pollination contacts. Only coefficients of significant covariates were included.

Dependent variable	Covariate variable	Estimate $\beta\pi$	Standard Error $\beta\pi$	P-value $\beta\pi$	Estimate $\beta\lambda$	Standard Error $\beta\lambda$	P-value $\beta\lambda$
Richness of pollinator species	Number of flowers (ln-transformed)	-6.818	1.629	<0.001	.	.	.
	Richness of animal-pollinated plants in bloom (ln-transformed)	.	.	.	0.814	0.149	<0.001
Number of pollination contacts	Number of flowers (ln-transformed)	-1.199	0.189	<0.001	.	.	.
	Richness of animal-pollinated plants in bloom (ln-transformed)	.	.	.	0.643	0.131	<0.001

to become smaller (Kuppler and Kotowska 2021), bloom for a shorter time (Turner 1993) and produce less nectar (Phillips et al. 2018). In addition to soil moisture, soil nutrients have also been shown to influence floral traits and are positively correlated with flower size, nectar concentration and volume, and pollen grain number (Vaudo et al. 2022). In the early stages of grassland abandonment, the accumulation of litter leads to increased soil moisture and nutrient availability (e.g., Hassan et al. 2021), which can promote flower production as well as nectar volume and pollen grain number (e.g., Plos et al. 2023; Roth et al. 2023). However, as succession progresses, the spread of competing graminoids such as *Brachypodium rupestre* (Bonanomi and Allegrezza 2004) may ultimately lead to the exclusion of animal-pollinated plant species from the community, reducing the quantity of floral resources.

Dry grasslands are biodiversity hotspots harbouring a large diversity of animal-pollinated species (Fantinato et al. 2021). In our study, we have shown that succession following the abandonment of traditional management practices affects the richness of animal-pollinated species in bloom. Consistently with previous studies that found a hump-shaped relationship between vascular plant species richness and grassland succession (Kesting et al. 2015), we showed that the richness of animal-pollinated plants peaked at low-intermediate levels of cover of plant species of forest edges. In the early stages of grassland succession, the presence of plant species of forest edges in the community may initially increase overall plant richness. However, once dense stands of clonally growing graminoids dominate the community, the richness of plant species rapidly decreases. In addition, the accumulation of organic matter and increasing soil moisture promoted by grassland abandonment can alter soil fertility and nutrient cycling over time, further affecting the suitability of the habitat for grassland species (Deng et al. 2016). As the succession process progresses, increasing woody plant density and abundance reduces the overall grassland species diversity (Schrautzer et al. 2009).

Interestingly, the richness of pollinator species and the number of pollination contacts were not directly related to the percentage cover of plant species of forest edges, but rather indirectly, as they were significantly related to the number of flowers and the richness of animal-pollinated plants in bloom. Our results showed that the probability of absence of pollinators and of pollination contacts decreased to zero once at least ten flowers were present. In other words, the probability of pollinator presence and pollination contact was significantly related to the presence of flowers. Although the presence of floral resources such as nectar and pollen may ultimately lead pollinators to develop floral fidelity and therefore continue to visit flowers of the same species because they have learned that floral resources are present (Brosi 2016), it is attractive features of flowers (e.g., flower size, shape, colour, floral scent, etc.) that initially enable pollinators to locate floral resources (van der Kooi et al. 2023). This could explain why neither the volume of nectar nor the number of pollen grains influenced the probability of absence (or, conversely, presence) of pollinators and of pollination contacts.

The richness of plant species then significantly influenced the richness of pollinator species and the number of pollination contacts. These results can be explained by the fact that taxonomic richness usually positively correlates with functional richness (e.g., Dovrat et al. 2021), i.e., the richer the community of animal-pollinated plants, the higher the probability of plant species that differ in their floral traits and in the type and quantity of floral resources. This in turn would attract pollinators with different feeding preferences and flower handling abilities, ultimately increasing the richness of pollinator species and the chance of pollination contacts.

Conclusions

The abandonment of traditional management practices and the subsequent succession of dry grasslands towards forest edges has been shown to lead to biodiversity conservation issues and ecosystem changes, such as changes in soil properties and grassland productivity. In the present study, we have shown that the succession of dry grasslands also affects animal-mediated pollination, even in correspondence of early stages. Although animal-pollinated shrubs (e.g., *Cornus sanguinea, Rosa canina, Spartium junceum*) and trees (e.g., *Fraxinus ornus*) can provide floral resources, they only flower for a limited period of the year (usually in early spring) and rarely for more than a month. Beside showing restricted blooming periods, in some cases, shrubs and trees show high degrees of pollinator specialisation, namely, their floral morphology can be effectively handled only by a narrow group of pollinator species. This is the case, for example, of *S. junceum,* which shows mass blooming in late spring. However, the high degree of pollination specialisation of *S. junceum*, resulting from the complexity of its floral morphology and the thickness of its flowers, which allow only a few pollinators to forage, means that it occupies a peripheral position in the network of pollination interactions (i.e., it cannot sustain a broad community of pollinators on its own). Ultimately, this means that the contribution of dry grasslands to pollinator conservation cannot be replaced by shrub and forest communities.

Our results could provide useful insights for planning management practices that optimise the conservation of plants and pollinators in dry grasslands as well as pollination interactions.

The hump-shaped relationships that both the richness of animal-pollinated plants and the quantity of floral resources evidenced with the cover of plant species of forest edges suggest that the first dynamic stages ensure both an increase in plant species richness and in the quantity of floral resources supplied. Such a situation cannot be achieved through complete abandonment or even irregular management, that over time predictably lead to passive rewilding and grassland loss. Rather, improving grassland heterogeneity, leaving spatially scattered small areas where the frequency of mowing is temporarily slowed down to create conditions of early succession, can increase the number of niches for plant and animal species and improve the pollination function in dry grasslands.

This approach allows to create and maintain conditions of early succession, that contribute to increase the number of niches for plant and animal species and improve the pollination function in dry grasslands.

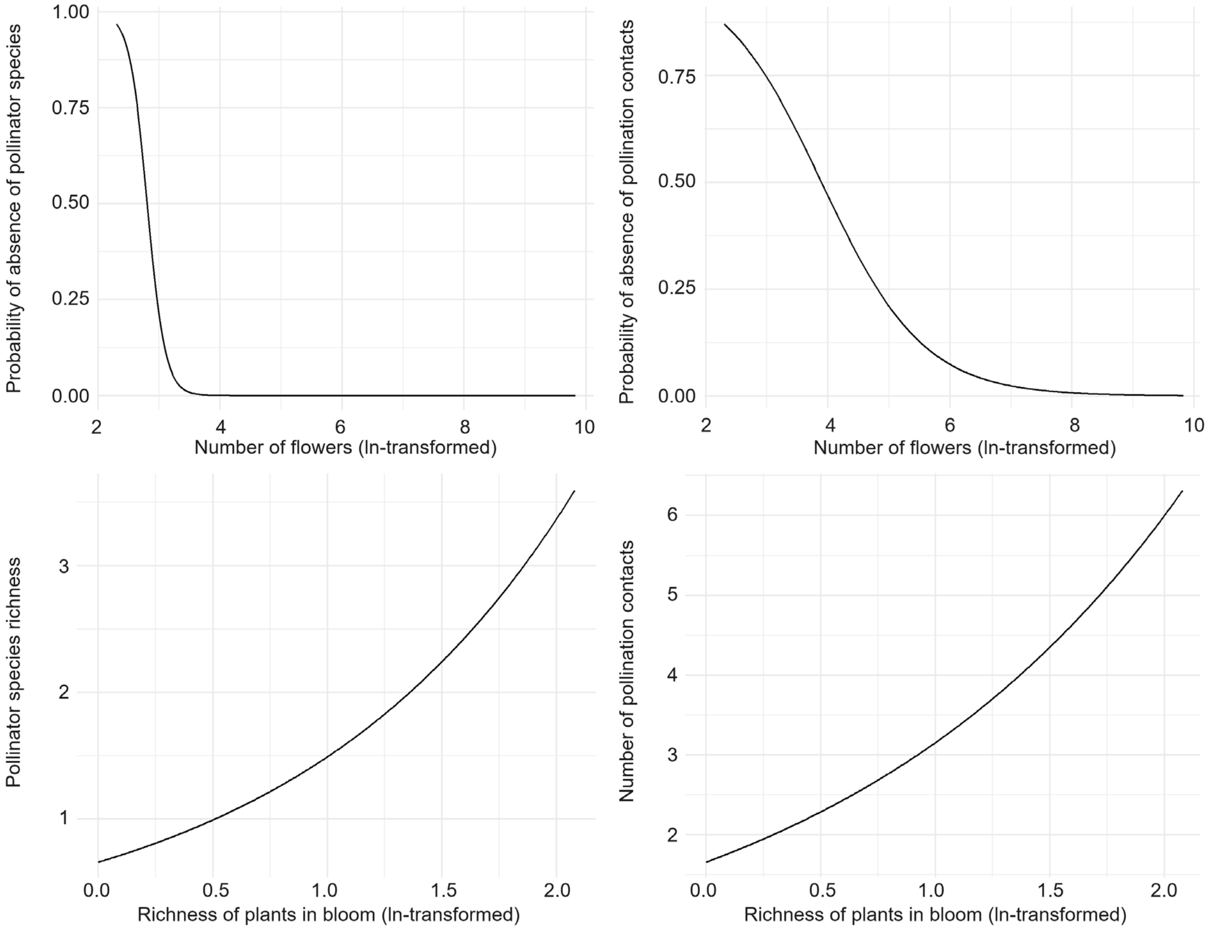

Figure 3. Association between the probability of absence of pollinator species and the number of flowers (ln-transformed), the probability of absence of pollination contacts and the number of flowers (ln-transformed), the richness of pollinator species and the richness of animal-pollinated plants in bloom (ln-transformed) and the number of pollination contacts and the richness of animal-pollinated plants in bloom (ln-transformed). For each covariate, the probability of absence was estimated as function of the selected covariate, setting the other covariates equal to their mean values.

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Appendix: List of plant species recorded on sampled plots.

Table AI. List of plant species recorded on sampled plots. For each species, the habitat preferences, the number of plot in which they were recorded and the mean percentage cover (± standard deviation) are provided. Species nomenclature follows Bartolucci et al. (2018).

	HABITAT PREFERENCES	PLOT PRESENCE	MEAN COVER (%) ± SD
Bromopsis erecta	Grassland	27	50.56 ± 24.63
Poterium sanguisorba	Grassland	25	1.42 ± 1.30
Artemisia alba	Grassland	22	14.55 ± 13.91
Dactylis glomerata	Grassland	20	4.48 ± 5.35
Thymus pulegioides	Grassland	16	1.94 ± 1.38
Helianthemum nummularium subsp. *obscurum*	Grassland	15	3.50 ± 4.02
Globularia bisnagarica	Grassland	14	2.07 ± 1.48
Silene vulgaris subsp. *tenoreana*	Grassland	14	0.75 ± 0.43
Stachys recta	Grassland	13	3.00 ± 2.84
Koeleria pyramidata	Grassland	11	2.91 ± 3.74
Galium verum	Grassland	11	3.82 ± 6.10
Eryngium amethystinum	Grassland	10	2.35 ± 1.70
Euphorbia cyparissias	Grassland	10	1.10 ± 0.91
Linum tenuifolium	Grassland	10	1.35 ± 1.42
Scabiosa triandra	Grassland	10	1.25 ± 1.40
Bupleurum baldense	Grassland	9	3.28 ± 3.08
Medicago falcata	Grassland	8	2.38 ± 1.98
Bothriochloa ischaemum	Grassland	7	24.36 ± 21.20
Plantago lanceolata	Grassland	7	0.57 ± 0.19
Convolvulus cantabrica	Grassland	7	6.86 ± 4.10
Fumana procumbens	Grassland	7	5.64 ± 5.45
Lotus corniculatus	Grassland	7	0.57 ± 0.19
Odontites luteus	Grassland	7	0.71 ± 0.57
Ononis reclinata	Grassland	7	3.00 ± 2.63
Salvia pratensis	Grassland	7	3.00 ± 2.06
Cleistogenes serotina	Grassland	6	6.50 ± 6.66
Lotus dorycnium subsp. *herbaceus*	Grassland	6	3.67 ± 3.44
Thliphthisa purpurea	Grassland	5	2.20 ± 1.89
Medicago minima	Grassland	5	0.70 ± 0.27
Potentilla pusilla	Grassland	5	1.40 ± 1.08
Carex halleriana	Grassland	4	2.25 ± 0.50
Anacamptis pyramidalis	Grassland	4	0.88 ± 0.25
Galatella linosyris	Grassland	4	1.00 ± 0.00
Hippocrepis comosa	Grassland	4	1.75 ± 2.18
Onobrychis arenaria	Grassland	4	8.25 ± 5.38
Ononis natrix	Grassland	4	9.50 ± 7.59
Thymus oenipontanus	Grassland	4	1.13 ± 0.63
Trifolium campestre	Grassland	4	4.75 ± 4.50
Carex flacca	Grassland	3	3.67 ± 2.31
Allium sphaerocephalon	Grassland	3	0.50 ± 0.00
Colchicum autumnale	Grassland	3	0.67 ± 0.29
Galium lucidum	Grassland	3	2.67 ± 2.08
Pilosella officinarum	Grassland	3	4.00 ± 1.73
Catapodium rigidum	Grassland	2	1.25 ± 1.06
Centaurea scabiosa	Grassland	2	1.75 ± 1.77
Crupina vulgaris	Grassland	2	0.50 ± 0.00
Dianthus sylvestris	Grassland	2	0.50 ± 0.00
Leontodon hispidus	Grassland	2	0.75 ± 0.35
Filago pyramidata	Grassland	1	1.00
Achillea roseoalba	Grassland	1	1.00
Cynanchica pyrenaica	Grassland	1	5.00
Centaurea deusta	Grassland	1	5.00
Crepis taraxacifolia	Grassland	1	0.50
Pilosella piloselloides	Grassland	1	0.50
Teucrium montanum	Grassland	1	1.00
Tragopogon pratensis	Grassland	1	0.50
Trifolium scabrum	Grassland	1	1.00
Euphorbia falcata	Ruderal	6	1.33 ± 1.81
Erigeron annuus	Ruderal	3	0.50 ± 0.00
Triticum vagans	Ruderal	3	3.00 ± 1.73
Melampyrum barbatum subsp. *carstiense*	Ruderal	2	3.00 ± 0.00
Sonchus oleraceus	Ruderal	2	0.50 ± 0.00
Centaurium erythraea	Ruderal	2	0.50 ± 0.00
Arabis hirsuta	Ruderal	1	0.50
Myosotis arvensis	Ruderal	1	0.50
Allium vineale	Ruderal	1	0.50

TableA I. Continuation.

	HABITAT PREFERENCES	PLOT PRESENCE	MEAN COVER (%) ± SD
Avena barbata	Ruderal	1	0.50
Campanula rapunculus	Ruderal	1	0.50
Cota tinctoria	Ruderal	1	0.50
Erigeron canadensis	Ruderal	1	0.50
Muscari neglectum	Ruderal	1	0.50
Trifolium angustifolium	Ruderal	1	1.00
Brachypodium rupestre	Forest edge	22	36.57 ± 34.8
Teucrium chamaedrys	Forest edge	14	8.00 ± 13.52
Asparagus acutifolius	Forest edge	10	3.10 ± 1.96
Geranium sanguineum	Forest edge	8	8.56 ± 12.43
Cervaria rivini	Forest edge	8	1.19 ± 0.70
Fraxinus ornus	Forest edge	5	1.10 ± 0.55
Rubus caesius	Forest edge	5	2.10 ± 1.88
Vitis vinifera	Forest edge	4	4.00 ± 4.08
Hypericum perforatum	Forest edge	4	0.63 ± 0.25
Cornus sanguinea	Forest edge	3	2.00 ± 2.60
Lathyrus latifolius	Forest edge	3	1.50 ± 0.87
Rosa canina	Forest edge	3	2.83 ± 2.25
Spartium junceum	Forest edge	3	0.50 ± 0.00
Ligustrum vulgare	Forest edge	2	1.50 ± 0.71
Quercus pubescens	Forest edge	2	1.25 ± 1.06
Trifolium rubens	Forest edge	2	1.50 ± 0.71
Agrimonia eupatoria	Forest edge	2	1.50 ± 0.71
Berberis vulgaris	Forest edge	2	0.75 ± 0.35
Buphthalmum salicifolium	Forest edge	2	0.50 ± 0.00
Crataegus monogyna	Forest edge	2	1.50 ± 0.71
Cytisus hirsutus	Forest edge	2	6.50 ± 4.95
Pentanema spiraeifolium	Forest edge	2	1.00 ± 0.00
Orchis purpurea	Forest edge	2	0.75 ± 0.35
Viburnum lantana	Forest edge	2	0.50 ± 0.00
Cotinus coggygria	Forest edge	1	3.00
Ostrya carpinifolia	Forest edge	1	1.00
Clematis vitalba	Forest edge	1	2.00
Genista tinctoria	Forest edge	1	0.50
Himantoglossum adriaticum	Forest edge	1	0.50
Muscari comosum	Forest edge	1	0.50
Robinia pseudoacacia	Forest edge	1	0.50