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ORIGINAL ARTICLE

Distribution of butterflies (Lepidoptera) in a successional mosaic of Mediterranean mountain habitats

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Abstract. The distribution of butterflies was analysed in a mosaic of different types of habitats in a typical Ibero-Supramediterranean plant landscape. This mosaic landscape is composed of oak forests (*Quercus pyrenaica*) and their corresponding shrub and grassland successional communities. The observed patterns were based on butterfly-flower interactions in two consecutive years (2017–2018) recorded in different habitats. The results of the nestedness analysis indicated that the same butterfly community exploits all of the successional plant-communities, but some differences due to the availability of flowers. The foraging for nectar sources was mostly restricted to a few flowering plants: *Rubus ulmifolius*, *Carduus carpetanus*, *Thymus pulegioides* and *Dianthus deltoides*. Some butterflies changed their flower-visiting patterns over the two years studied. The distribution of butterflies was strongly linked to the distribution of their preferred nectar sources and changes in the use of these sources modified habitat use. The area of *Rubus* shrubland is a small but highly used habitat in this area, given the presence of *Rubus ulmifolius*, a plant species with high coverage and abundance of nectar, makes this area much better for foraging than other habitats. The *Cytisus* and *Rubus* shrublands were used more than grassland, indicating that seral habitats can be more valuable than traditional open grassland and forest habitats for butterflies.

INTRODUCTION

Butterfly imagoes use nectariferous flowers as food sources. The uses of nectar sources by butterflies in different habitats indicates they tend to prefer open habitats, such as grasslands, to closed ones, such as forests (Loertscher et al., 1995; Grill et al., 2005; Kitahara et al., 2008). Grasslands are perhaps the habitats where most butterfly distribution studies in relation to nectar sources are conducted (Jennersten, 1984; Severns et al., 2006; Ezzeddine & Matter, 2008). A direct relationship is recorded between the occurrence of nectariferous flowers and butterfly richness in grasslands (Pöyry et al., 2009; Krämer et al., 2012), although other evidence does not show such a clear relationship (Sharp et al., 1974). When grasslands are encroached by shrubs or trees, there are different, negative and positive, responses in terms of butterfly richness (Holl, 1995; Balmer & Erhardt, 2000; Söderström et al., 2001; Lien & Yuan, 2003; Öckinger et al., 2006). Specifically, a positive relationship between nectariferous flowers and butterflies at the edge of forests (van Halder et al., 2011). However, most of these studies are for temperate Europe and are scarce in the Mediterranean biodiversity hotspot region (but see Marini et al., 2009; Slancarova et al., 2016; Ubach et al., 2020; Colom et al., 2021).

The butterfly-plant species interactions are always focused on one or very few nearby habitats without assessing all the habitats comprising an ecological secondary succession. However, this kind of information would be very useful for conservation and other ecological studies, especially in the Mediterranean region, due to the diversity and patchiness of its habitats (Slancarova et al., 2016) and confirmed positive significant responses of biodiversity to fragmentation (Fahrig, 2017). Secondary succession, which is influenced by pre-existing communities, is characterized by a series of successional communities that follow each other until reaching a more developed seral stage (Rivas-Martínez et al., 2011). Although forest is generally considered the most developed seral stage, this depends on local conditions and in extreme regions it could be scrubland or grassland. This study focused on Sierra de Guadarrama (central Spain), where over 50% of the Iberian butterfly richness can be found (Gómez de Aizpúrua, 1987) and there is great diversity in other biological groups, such as fungi (Campoamor & Molina, 2001), vascular plants (Lobo, 2001), dung beetles (Martín-Piera et al., 1986) and vertebrates (Rey Benayas & de la Montaña, 2003). The most developed natural vegetation in this area corresponds to Pyrenaean oak (*Quercus pyrenaica* Willd.) Ibero-Supramediterranean forests at intermediate altitudes (900–1,400 m a.s.l.). These forests have traditionally been removed to encourage extensive pasture lands, but the abandonment of traditional uses and grazing by livestock has favoured the increase of shrubs and the growth of forest in recent years (Sánchez-Mata et al., 2017).

Our working hypothesis is that the habitat for nectariferous plants describes butterfly distribution at a local scale. In this research, for the first time, a comparative study of butterfly-flower interactions is carried out across an entire mosaic of habitats of an ecological successional series. As the habitats in the same ecological successional series intermingle at a local level, it is necessary to study the butterfly community as a whole in order to analyse if there is any type of pattern present in their distribution. Our specific objectives involved answering the following questions: (a) How is the community of Lepidoptera structured across the mosaic of seral vegetation throughout the secondary succession? (b) What are the main interactions between Lepidoptera and flowering plants? and (c) How does type of habitat influence butterfly distribution? We believe that studies like this can be valuable for butterfly conservation and faunistic studies of one of the most threatened groups of insects in Europe, especially in the Mediterranean area.

MATERIALS AND METHODS

This study was carried out in the vicinity of the town of Miraflores de la Sierra (North of Madrid, Central Spain). The area studied was located 3 km to the NW of the town, in the west Guadalix valley of Sierra de Guadarrama (Fig. 1). There is a small altitudinal gradient in this area (1,319–1,550 m, with most of the plots between 1,400 and 1,500 m). The soils are characterized by being acidic, with siliceous materials, such as granite, gneiss, schists and quartzites. It is a typical Ibero-Mediterranean mountain landscape, which includes patches of remaining natural oak forests, together with extended meadows and grasslands that support an important livestock population, mainly cows, as well as pine plantations (Sánchez-Mata et al., 2017). According to biogeographic regionalization, the area studied belongs to the Mediterranean Region, West-Iberian-Mediterranean Province, Carpetanian-Leonese Province, Guadarramean Sector (Rivas-Martínez et al., 2014). The area is located within the Supra-Mediterranean altitudinal belt. Data was recorded within this altitudinal belt to minimize climatic variability, which can influence the occurrence and abundance of butterflies and plants (Pollard, 1988). The natural vegetation in the area corresponds to oak forest of *Quercus pyrenaica* with seral shrubland communities, including mesic shrublands characterized by Gentisates, especially *Cytisus oromediterraneus* Rivas Mart. et al. and hygrophilous thorny shrublands dominated by Rosaceae species, mainly *Rubus* sp. pl., such as *Rubus ulmifolius* Schott in Isis (Oken). Seral grasslands may also be classified as dry grasslands, characterized by *Poa bulbosa* L., and wet grasslands (meadows), characterized by *Nardus stricta* L. (Rivas-Martínez & Canto, 1987; Rivas-Martínez et al., 2011).

Field recording

A stratified recording method was used to obtain a proportionate sample of habitat diversity. Five types of vegetation were identified in the area studied: *Quercus pyrenaica* forest, *Cytisus oromediterraneus* shrubland, *Rubus ulmifolius* shrubland, *Poa bulbosa* grassland and *Nardus stricta* meadows. Identification of vegetation was based on floristic composition and physiognomy of the vegetation and phytosociological syntaxonomy (Molina Abril, 1994). A minimum of six plots was selected per habitat in the field and subsequently confirmed by aerial photography. The plots were located at least 100 m apart from each other to avoid overlaps. The number of plots was selected according to habitat type representativeness (frequency and extension) in the landscape up to a maximum of 11 plots per habitat. Thus, 11 plots of forests, 10 of *Cytisus oromediterraneus* shrublands, 6 of *Rubus ulmifolius* shrublands, 9 of *Poa bulbosa* grasslands and 8 of *Nardus stricta* meadows were studied. Plot size was 100 m^2 as this is the size commonly used (Chytrý & Otýpková, 2003) to reasonably represent the floristic variation in each habitat. Thus, the area studied constituted a total of 44 plots corresponding to 4,400 m^2. The surface of every habitat in the territory was calculated using the program QGIS 3.10 (QGIS Development Team, 2014).

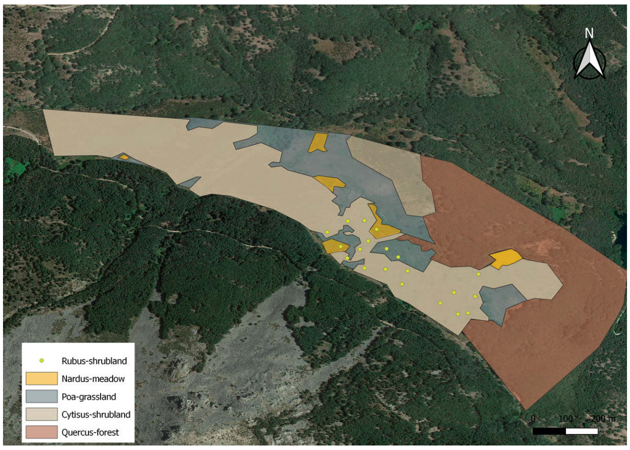

Fig. 1. Map of the area studied in the Guadalix valley (coordinates: 40°49´N, 3°48´W) showing the respective areas of the different habitats.

In each plot, the vegetation was recorded, visually estimating the percentage cover of each species of plant in each plot (100 m^2). Cover classes were not considered, but percentages were calculated as close as possible and based on several measurements. Subsequently, the observed coverages were corrected based on their representation in the area. Butterfly occurrence was recorded for 20 min per plot, during which the species that were found and moved within the plot were identified. The recorder moved within the limits of the plot trying to count all the butterflies without disturbing them. The number of feeding interactions between butterflies and plants was recorded as the total feeding times for each species of butterfly on the available flowers, along with sightings of butterflies simply passing by.

Recordings were carried out in the first fortnight of July in the years 2017 and 2018, on sunny days with no appreciable wind (Pollard, 1988). This period was selected to avoid significant variations in the phenology and abundance of butterflies and plants (Pollard & Yates, 1993). The order of observation (day and time) of each plot was previously randomised. Recordings started at 11:00 a.m. and finished at 4:00 p.m. as this time slot is considered the optimal time for butterfly activity (Pollard & Yates, 1993). Each plot was visited once a month each year. Climatic data were obtained from the closest Weather Stations [Rascafría, Puerto de Navacerrada, and Colmenar Viejo, Table S1; AEMET (State Meteorological Agency, Spain), 2017, 2018] to ensure that there would be no significant climatic variations during the recording period.

Statistical analyses

To determine whether the effort spent recording was sufficient and the number of species recorded approached the real number of species, a species accumulation curve was generated (Gotelli & Colwell, 2001). The curve was smoothed to avoid temporal or spatial biases and a non-parametric estimation of the potential richness based on Chao1 (Colwell, 2000) was calculated using the EstimateS program. The species accumulation curve was adjusted to the asymptotic curve of Clench using the CurveExpert 1.4 program (Hyams, 2010). Data were also analysed using nesting techniques to compare the plots on the basis of the number of species of butterflies recorded. These analyses were carried out using the Nestedness Temperature Calculator program (Atmar & Patterson, 1995, 2000). In addition, a cluster analysis based on the occurrences of butterfly species per plot was done in order to check for possible community structure. It was calculated using the Bray-Curtis similarity index and the group average amalgamation rule by means of the Primer-e program (Clarke & Gorley, 2006).

Another cluster analysis was carried out based on the cover of each species of plant present in each plot. The cover values were log-transformed and a resemblance matrix was obtained based on Euclidean distances. An amalgamation strategy based on the unweighted pair-group average rule was carried out to finally obtain a distance cluster for each period recorded.

A Mann-Whitney U test was used to determine the differences between habitats in terms of the mean species richness of butterflies, in the two years considered. A Wilcoxon matched pairs test was also carried out to contrast differences between years within the same habitat. To verify whether there was a positive or negative relationship between butterfly-flowering plant species interactions, Generalized Linear Models were used. Only butterfly species for which at least 10 interactions with plants were recorded were considered (data could be considered anecdotal below 10). The number of interactions of each butterfly species per plot was considered to be the dependent variable, whereas the plant cover per plot of each species of flowering plant selected by the butterflies, temperature and humidity were considered to be independent variables. In order to explore the possible curvilinear relationship (Austin, 1980) between the dependent and independent variables, the statistical significance of the linear ($y = a + bx$), quadratic ($y = a + bx + cx^2$) and cubic functions ($y = a + bx + cx^2 + dx^3$) of the independent variables were determined. The goodness-of-fit of the models was evaluated by means of the deviance statistic, which was compared by means of F tests to determine whether the obtained functions represented a significant change in the deviation from a null or a complete model in which the number of parameters was equal to the total number of observations (McCullagh & Nelder, 1989; Dobson, 1999).

A non-parametric Kruskal-Wallis test was used to determine whether there were significant differences both in the total abundance of butterflies among the habitats and in the abundance of each butterfly species among the habitats. For this analysis, habitat type and total abundance of butterflies (encompassing both, interactions and simple sightings of individuals) were considered independent and dependent variables, respectively. All analyses were carried out using STATISTICA 10.0 program (StatSoft, 2011).

RESULTS

Recording effort and weather

The analysis of both recording effort curves for butterflies and plants indicate that the percentage of species recorded reached at least 70%, so the data is significantly accurate.

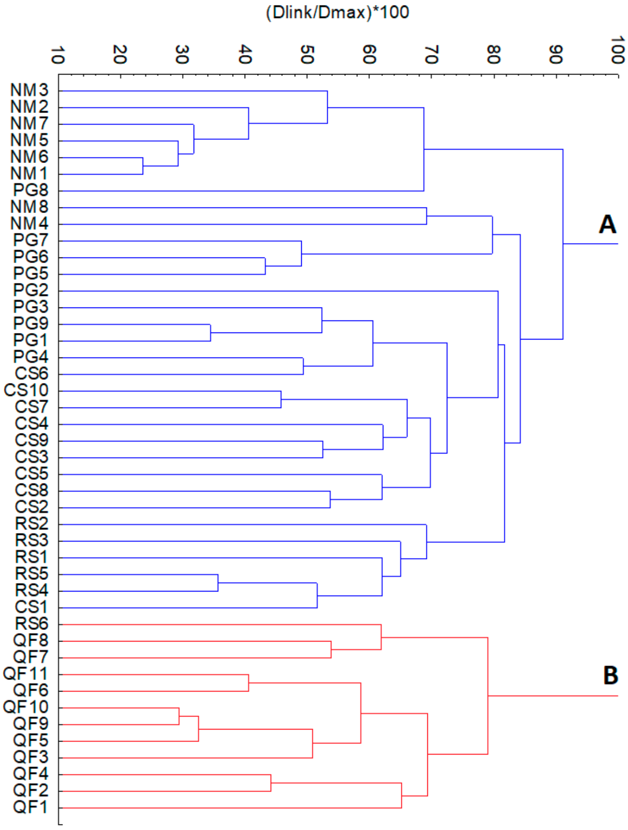

Fig. 2. Cluster analysis dendrogram of 44 plots of vegetation recorded in 2017, based on Euclidean distances and the unweighted pair-group average amalgamation rule. CS – *Cytisus* shrubland; NM – *Nardus* meadow; PG – *Poa* grassland; QF – *Quercus* forest; RS – *Rubus* shrubland. Numbers are those of the different plots. A and B indicate the results for the two floristic groups: plots of seral and open vegetation and *Q. pyrenaica* forest, respectively.

In addition, the statistical relationship between the number of butterfly interactions and climatic data indicates it is not significantly affected by either daily humidity or temperature, thus there are no climatic biases in the recording of data.

Structure of biological communities

The cluster analysis of vegetation revealed two main floristic groups (Fig. 2). Group A included the plots corresponding to the seral and open vegetation. Group B the rest of the plots, mostly corresponding to *Q. pyrenaica* forest. Within group A, some aggregation patterns were identified. Most of the plots with *Nardus* meadows, *Rubus* shrubland and *Cytisus* shrubland were close to each other.

The QGIS analysis revealed that *Cytisus* shrubland was the predominant habitat, occupying the highest percentage of the area studied (45.89%), followed by *Quercus* forest (40.13%), *Poa* grassland (12.43%), *Nardus* meadow (11.84%) and *Rubus* shrubland (0.0034%). During 2017 the number of flowering species of plants recorded was 31 (Table S2). The species with the highest cover was thistle *Carduus carpetanus* Boiss. & Reut. (4.1% on average, 13.8% of which were in *Poa bulbosa* grasslands),

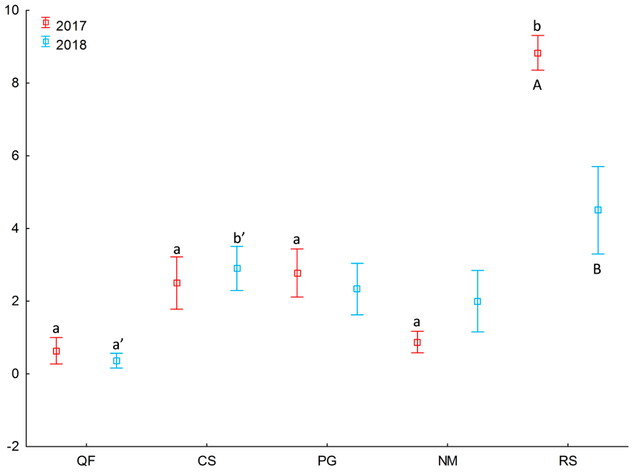

Fig. 3. Box plot of butterfly species richness in the different habitats. Data for 2017 are in red and that for 2018 in blue. The different letters above the graphs (2018 with apostrophes) refer to statistically significant differences, based on a Mann-Whitney U test, Bonferroni corrected. Different capital letters under the graphs refer to statistically significant differences, based on a Wilcoxon matched pairs test. CS – *Cytisus* shrubland; NM – *Nardus* meadow; PG – *Poa* grassland; QF – *Quercus* forest; RS – *Rubus* shrubland.

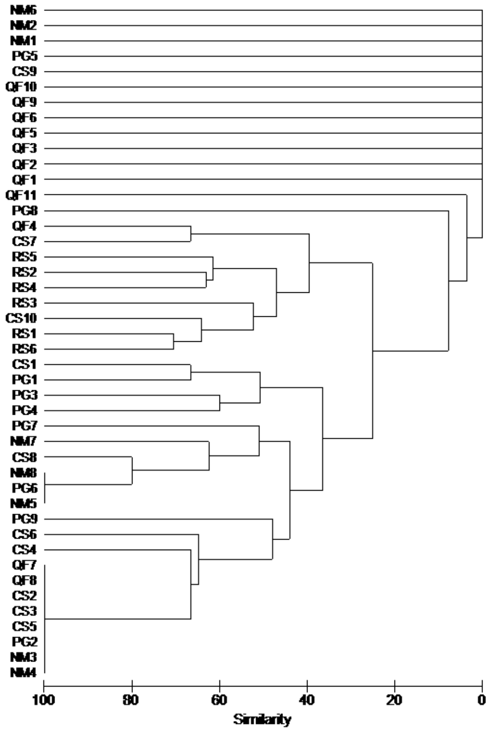

Fig. 4. Cluster analysis dendrogram of 44 plots based on the occurrences of butterfly species in 2017, the Bray-Curtis similarity index and the group average amalgamation rule. CS – *Cytisus* shrubland; NM – *Nardus* meadow; PG – *Poa* grassland; QF – *Quercus* forest; RS – *Rubus* shrubland. Numbers correspond to different plots.

followed by thorn blackberry, *Rubus ulmifolius* Schott (3.6%, with 54.5% in *Rubus* shrubland) and *Dianthus deltoides* L. (1.8%, with 5.8% in *Poa bulbosa* grassland). *Carduus carpetanus* and *D. deltoides* were found in most of the habitats, except oak forest. During 2018 the number of species was 39 (Table S3). The highest cover recorded was for *Cytisus scoparius* (L.) Link (5.37%, with 13.4% in *Quercus* forest), followed by *Galium verum* L. (3.8%, with 10.88% in *Nardus stricta* meadows) and *Ca. carpetanus* (3.3%, with 10.77% in *Poa bulbosa* grassland). The cover of *Carduus carpetanus* decreased in 2018 relative to that in 2017. *Rubus ulmifolius* was not fully in bloom, so its cover also decreased (1.1%) compared to the previous year, as did the cover of *D. deltoides* (1.6%).

The butterfly species richness (both in interactions and sightings) was 43, with 32 species identified per year and 21 (about 40%) species present both years (Table S4). The habitat with the lowest mean number of species in both years was *Quercus* forest (mean ± standard deviation: 0.50 ± 0.38; significant differences were observed in 2017 in the rest of the habitats; Fig. 3), followed by *Nardus* meadow (1.44 ± 1.10), *Poa* grassland (2.56 ± 0.10) and *Cytisus* shrubland (2.70 ± 0.26). *Rubus* shrubland had the highest mean butterfly species richness, but it differed significantly between the two years (8.83 ± 1.17 in 2017; 4.50 ± 2.95 in 2018).

The similarity analysis of plots based on butterfly species occurrences did not show any clustering in any year, except for the *Rubus* shrubland plots, which all appeared within the same clade (Fig. 4). However, the Nestedness Temperature Calculator analysis revealed that the plots were nested according to their butterfly composition in both 2017 ($P = 6.52*10^{-20}$) and 2018 ($P = 1.05*10^{-4}$). This nested structure of plots confirmed the existence of a single butterfly community. The most widely shared species among habitats were also those butterflies with the highest number of interactions, such as *Melanargia lachesis* Hübner, *Lycaena alciphron* (Rottemburg), *Issoria lathonia* (L.) and *Maniola jurtina* (L.). The rarest species in the whole area were *Hipparchia semele* L., *Satyrium ilicis* Esper and *Pyrgus malvoides* (Elwes & Edwards).

Butterfly-plant relationships

The number of butterfly-plant interactions in 2017 was 1183. The species with the highest number of interactions was *Me. lachesis* (589), followed by *Ly. alciphron* (120), *I. lathonia* (93) and *Ma. jurtina* (74). In 2018, the number of interactions was 773. The species with the highest number of interactions was *I. lathonia* (264), followed by *Argynnis pandora* Denis & Schiffermüller (130), *Aglais urticae* (L.) (86) and *Me. lachesis* (71). In addition, the number of butterflies that interacted with plants was similar: 27 and 25, in 2017 and 2018, respectively. Thus, the total number of interactions decreased by a third from 2017 to 2018, even though flowering plants increased (31 to 39). At the same time, sightings were reduced to an eighth.

The butterflies that established significant relationships with flowering plants were 11 and 16 species, in 2017 and 2018, respectively, so butterfly-plant interactions changed from year to year. In 2017 the butterflies with the highest number of significant interactions according to GLMs was *Me. lachesis*, with a total of three interactions (average number of significant interactions in 2017: 1.36 ± 0.67 s.d.; Table 1), whereas for *Argynnis niobe* (L.), *Vanessa cardui*

Table 1. Summary of the significant relationships between butterflies and plants in 2017. For each relationship, the percentage of explained variation is shown and the number of asterisks indicates the P-value: < 0,05, < 0,01 and < 0,001 (! – marginal P-value < 0,1). The signs (+ or –) indicate a positive or negative relationship. ns – non-significant.

Species	*M.lachesis*	*A.pandora*	*I.alciphron*	*M.jurtina*	*G.cleopatra*	*C.croceus*	*A.paphia*	*I.latonia*	*A.niobe*	*A.aglaja*	*P.cecilia*
D. deltoides	7.56% !(+)				72.7% ***(+)						
R. ulmifolius	16.46% **(+)	76.02% ***(+)	38.08% ***(+)	23.77% *(+)			32.32% ***(+)	52.84% ***(–)	59.54% ***(–)	26.66% ***(+)	20.9% ***(+)
Ca. carpetanus	33.37% ***(+)	ns				6.35% !(+)					
T. pulegioides			ns	43.58% ***(–)				37.75% ***(+)			

(L.) and *Ag. urticae* there were up to two significant interactions in 2018 (average number of significant interactions in 2018: 1.25 ± 0.44 s.d.; Table 2).

Only four flowering plants were significantly visited by butterflies in 2017 (Table 1). *Rubus ulmifolius* was the the most visited by butterflies (9 species), followed by *Thymus pulegioides* L. (2), *Ca. carpetanus* (1) and *D. deltoides* (2). The interactions recorded in 2018 are shown in Table 2. *Rubus ulmifolius*, *T. pulegioides* and *Ca. carpetanus* were the most visited, whereas *D. deltoides*, *Lotus corniculatus* L., and *Jasione montana* L. only once.

Butterfly-habitat relationships

In 2017, *Rubus* shrubland was the habitat with the highest butterfly species richness (21), as well as interactions and sightings (567 and 471, respectively), while *Quercus* forest had the lowest richness scores (4), interactions and sightings (43 and 120, respectively; Table S4). In 2018, both *Cytisus* and *Rubus* shrublands were the habitats with the greatest butterfly species richness (14 and 12, respectively), interactions (296 and 249) and sightings (17 and 23). The *Quercus* forest was again the habitat with the lowest scores in butterfly species richness (3), interactions (8) and sightings (9). Inter-habitat Kruskal-Wallis tests revealed significant differences in butterfly habitat selection in both years ($P < 0.0001$). A more in-depth species-by-species Kruskal-Wallis analysis indicated that most butterflies showed significant habitat selection in 2017, but not in 2018 (Tables 1 and 2).

DISCUSSION

Cluster analysis of vegetation revealed a sharp differentiation between forest (closed habitat) and seral vegetation (open habitat), which is in accordance with the vegetation series described for the Guadarrama Mountains piedmont (Rivas-Martínez et al., 2011). The open (seral) plots with the same type of vegetation were mostly closely grouped by the cluster analysis, although some plots had intermediate floristic characteristics, which is common for a natural system with a mosaic of interspersed habitats.

In addition, based on our results, distributions of species of butterflies were nested at a local landscape scale. The same butterfly community exploited all habitats, but not equally, throughout the *Q. pyrenaica*-related vegetation series. Although nested distributional patterns of butterflies are usually documented at a regional scale (Fleishman & Murphy, 1999; Franzen & Ranius, 2004; Öckinger et al.,

Table 2. Summary of significant relationships between butterflies and plants in 2018. For each relationship, the percentage of explained variation is shown and the number of asterisks indicates the P-value: < 0,05, < 0,01 and < 0,001 (! – marginal P-value < 0,1). The signs (+ or –) indicate a positive or negative relationship. ns – non-significant.

	M.lachesis	*A.pandora*	*I.alciphron*	*M.jurtina*	*G.cleopatra*	*C.crocea*	*A.paphia*	*I.latonia*	*A.crataegi*	*V.cardui*	*A.urtica*	*P.icarus*	*I.io*
D. deltoides					9.34% * (+)								
R. ulmifolius	51.95% *** (–)							ns		22.17% *** (+)	63.97% *** (–)		41.16% *** (+)
Ca. carpetanus	ns	70.47% *** (+)				15.24% ** (+)	56.63% ***(+)		55.85% ***(+)				
T. pulegioides			76.47% *** (–)	53.72% *** (–)				92.89% *** (–)			17.03% **(–)		
Lo. corniculatus												86.96% ***(+)	
J. montana								ns					

2006), these results focused on a secondary vegetation succession at a reduced local scale. Thus, the same stationary butterfly community could inhabit the entire series and visit specific habitats according to the availability of resources over time at this local scale. This movement of butterflies between habitats in search of resources is previously reported for their movement between host plants (Dennis et al., 2003; Slancarova et al., 2015).

Although data were recorded at the same period of the year, there was only an overlap of 40% in the species of butterfly recorded in the two years of this study. Just as the coverage of plants (and, therefore, of nectariferous flowers) is not the same from one year to the next, even in the same period of the year, the presence of one or another species of the butterfly community is not the same. There are species whose presence is more stable, since they are more generalists, have a greater dispersal capacity or are more widely distributed throughout all habitats and throughout the year. However, there are other species that are only present when habitat conditions are particularly suitable, as they are more sensitive to various environmental factors, such as weather (Montagud & García Alama, 2010). In 2017, *D. deltoides, T. pulegioides* and *Ca. carpetanus* were only visited by two or three species of butterfly compared to the nine species attracted to *R. ulmifolius*. However, in 2018, the butterfly species attracted by these flowering plants was more equitable (four species for *T. pulegioides*, *Ca. carpetanus* and *R. ulmifolius*, only one for *D. deltoides*). Our results, however, underline the low number of species of flowering plants exploited by butterflies in the area studied, which is in line with the findings of other similar studies (Jennersten, 1984; Loertscher et al., 1995; Severns et al., 2006; Ezzeddine & Matter, 2008).

The specificity of butterflies with respect to different nectariferous plants has been differently explained, by variations in nectar availability or optimization of feeding (Corbet, 2000); for example, the genus *Rubus* in another study is reported as a source of an abundance of nectar compared to other species (Holl, 1995). Our study revealed that when *R. ulmifolius* is scarce, butterflies used other plants as an alternative. This indicates that there is a trophic preference gradient, along which butterflies optimize foraging by looking for the most optimal cost-benefit plant. A trophic preference of butterflies is reported for a small number of flowering species, which depends on their availability (Goulson et al., 1997; Lebeau et al., 2017; Szigeti et al., 2018).

In Europe, the great richness of butterflies in mountain grasslands is well known (van Swaay, 2002; Krämer et al., 2012) and species replacement is reported in butterfly communities in seral succession habitats associated with grasslands (Steffan-Dewenter & Tscharntke, 1997; Stefanescu et al., 2009). Nevertheless, there are reports of different trends in butterfly richness and composition associated with encroachment of grassland (Balmer & Erhardt, 2000; Söderström et al., 2001; Fartmann et al., 2013; Bubová et al., 2015; Stefanescu et al., 2011).

As nectar resources are dispersed throughout an area and concentrated in certain habitats, butterflies are not distributed homogeneously in all habitats. This study revealed that open seral habitats, specifically woody shrublands, were the areas most widely used by butterflies. In those habitats where there was a concentration of resources, butterflies also temporarily concentrated. Thus, even though the density of vegetation may be an obstacle to counting butterflies it increases the ease of encountering them and their visibility (Nwokwu & Sanderson, 2009).

Rubus shrubland only occupies a tiny area in the area studied, yet its use was disproportionate (Fig. 1). This preference is due to the optimal foraging for *R. ulmifolius* nectar in a small habitat. When the flowering of *R. ulmifolius* ceases, butterflies compensate by visiting *Cytisus* shrublands and *Poa* grasslands, which contain the other plants they visited. Thus, the distribution of nectariferous plants determines that of butterflies at a local scale (Loertscher et al., 1995; Pöyry et al., 2009; van Halder et al., 2011; Fartmann et al., 2013). In some studies, no relationship is reported between plants in flower and the distribution of butterflies in habitats (Sharp et al., 1974; Holl, 1995). Thus, it is difficult to generalize about the diversity of butterflies in mosaic habitats based on a short study. However, we believe that butterflies gradually change their use of habitats based on the availability of certain flowering plants.

Cytisus scoparius, which is most characteristic of *Q. pyrenaica* forest-edges (Rivas-Martínez et al., 2011; Sánchez-Mata et al., 2017), was the most abundant plant in flower in 2018, although no significant interaction with butterflies was observed. Flowers of *Cy. scoparius* are not visited by butterflies, as they are neither attractive nor accessible since the flowers do not produce nectar and some force is required to open them (Parker, 1997; Parker et al., 2002).

Mature successional stages (forests and shrublands) are often considered to be poor habitats for butterflies (Grill et al., 2005; van Swaay et al., 2006; Kitahara et al., 2007; Colom et al., 2021) and based on the present results the lowest butterfly richness was recorded in oak forest. Nevertheless, this habitat includes specialized species, such as species of *Hipparchia* and *Pararge* (Schmitt, 2003; Bobo et al., 2006). In contrast, *Rubus* shrubland includes a flowering plant with the highest number of trophic relationships with butterflies in early summer, which makes these areas the most interesting habitats within the Guadarramean Mountains in terms of conservation. In addition, as the butterfly species community was nested across habitats, it can be inferred that protecting *Rubus* shrubland would be a priority for safeguarding the highest diversity of butterfly species in the area, followed by *Cytisus* shrubland and to a lesser extent other grasslands. Thus, apart from oak forest, the woody habitats of seral vegetation has a strong positive effect on butterfly species richness (Dennis, 2004; Marini et al., 2009).

This study, however, was carried out in a specific season and although it was the month when most species and individuals were known to be present, it is necessary to carry out studies in more locations and other seasons to determine the importance of habitats in landscapes. Furthermore, our results indicate that butterflies change habitat depending on the resources available in each habitat, and when one habitat is poor in nectar they feed in another. This indicates that habitat patches throughout an area act as complementary resources (Dennis et al., 2003; Oliver et al., 2010) and are a useful buffer against changes in the phenology of nectar resources. Habitats in European mountains are changing due to the loss of traditional practices of fire, logging and grazing livestock, which results in the homogenization of the landscape in mature forests and the disappearance or reduction of the seral stages of grasslands and thickets (Slancarova et al., 2016; Ubach et al., 2020). This work highlights the importance of heterogeneity and the advantage of a succession of different stages for butterflies (Slancarova et al., 2014).

CONCLUSION

For the first time this study compared the butterfly-flower interactions in a mosaic of related habitats in an ecological succession. The same butterfly community was recorded in all the habitats, but the phenology of the butterfly-plant interactions changed as the different species of butterflies selected habitats based on the availability of nectar from certain plants.

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Table S1. Average and standard deviation of the temperature (T, in °C) and humidity (H, in %) recorded by the AEMET (State Meteorological Agency, Spain) stations in Colmenar Viejo, Rascafría, P. de Navacerrada on the days in July 2017 and 2018 when the records were collected. The global average and standard deviation (SD) are also shown.

2017	Colmenar Viejo		Rascafría		P. de Navacerrada		Average global	
	T	H	T	H	T	H	T	H
Average	26.5	33.3	25.5	33.0	21.1	41.4	24.3	35.9
SD	3.5	5.0	2.7	4.4	2.7	3.6	2.9	2.5
2018	T	H	T	H	T	H	T	H
Average	23.61	39.87	24.77	38.39	18.77	44.70	22.38	40.99
SD	1.85	1.16	1.25	3.09	1.83	4.78	1.59	2.55

Table S2. Average cover (in %) of the flowering plants grouped by habitat in 2017. The average total was corrected based on the area of the habitat in the area studied using QGIS.

Year 2017	*Quercus*-forest	*Cytisus*-shrubland	*Poa*-grassland	*Nardus*-meadow	*Rubus*-shrubland	Average total
Adenocarpus complicatus L.	2.73	0	0	0	1.67	0.88
Campanula rapunculus L.	0.09	0	0	0	0	0.02
Carduus carpetanus Boiss. & Reut.	0	4.9	13.89	5	5.83	5.92
Carum verticillatum (L.) W.D.J. Koch	0	0	0	0.63	0	0.13
Clinopodium vulgare L.	1	0	0.22	0	0	0.24
Cruciata laevipes L.	0	0	0.33	0	0	0.07
Dianthus deltoides L.	0.45	2	5.89	1.25	0.83	2.09
Dianthus lusitanica L.	0.45	0	0	0	0	0.09
Eryngium campestre L.	0	0	1	0	0	0.2
Galium aparinella L.	0.09	0	0	0	0	0.02
Galium verum L.	0	0.8	2.56	2.25	0.17	1.15
Geranium robertianum L.	0	0.1	0.33	0	0	0.09
Hieracium pilosela L.	0.73	1.2	0.44	1	1.33	0.94
Jasione montana L.	0.27	1	0.67	0	0	0.39
Lactuca virosa L.	0	0	0	0	0.83	0.17
Lavandula stoechas L.	0.91	0	0	0	0	0.18
Linaria elegans Cav.	0	1.5	1.89	0.63	0.33	0.87
Linaria nivea Boiss. & Reut.	0	0.5	0	0	0	0.1
Lotus corniculatus L.	0	0.4	1.33	0	0	0.35
Lotus pedunculatus Cav.	0	0	0	0	0.83	0.17
Potentilla sp. L.	0	0	0	1.38	0.17	0.31
Prunella vulgaris L.	0	0	0	0.38	0.33	0.14
Ranunculus ophioglossifolius Vill.	0	0	0	0.38	0	0.08
Rubus ulmifolius L.	6.27	2	0	0	54.5	12.55
Santolina rosmarinifolia L.	0	0	0.56	0	0	0.11
Sedum forsterianum L.	0	0	0.33	0	0	0.07
Senecio jacobaea L.	0	0.6	2.22	1.25	0.83	0.98
Thymus pulegioides L.	0	3.7	0	0	0	0.74
Trifolium pratense L.	0	0	0	0.75	0	0.15
Trifolium repens L.	0	0	0	0.25	0	0.05
Wahlenbergia hederacea (L.) Rchb	0	0	0	1.13	0.83	0.39

Table S3. Average cover (in %) of the flowering plants grouped by habitat in 2018. The average total was corrected based on the area of the habitat in the area studied using QGIS.

Year 2018	*Quercus*-forest	*Cytisus*-shrubland	*Poa*-grassland	*Nardus*-meadow	*Rubus*-shrubland	Average total
Adenocarpus complicatus L.	1.54	0	0	0.625	1.66	0.76
Andryala integrifolia L.	0.45	0.3	0	0	0	0.15
Allium sp. L.	0	0	0.33	0	0	0.06
Campanula rapunculus L.	0.18	0	0	0	0	0.03
Carduus carpetanus Boiss. & Reut.	0	4.2	10.77	2.125	2.5	3.91
Carum verticillatum (L.) W.D.J. Koch	0.36	0	0.55	5	0.83	1.3
Cerastium glomeratum Thuill.	0	0	1.11	0	0	0.222
Conopodium pyrenaeum (Loisel.) Miégev.	0	0.4	2.33	0	0.83	0.71
Clinopodium vulgare L.	1.27	0	0.55	0	0	0.34
Cytisus scoparius (L.) Link	13.4	0	0	0	0	2.68
Digitalis purpurea L.	0	0.5	0	0	0	0.1
Dianthus deltoides L.	0	2.9	2.22	0.375	0	1.09
Galium aparinella L.	0.81	0	0	0	0	0.16
Galium rivulare Boiss. & Reut.	0.18	0	0	0	0	0.03
Galium robertianum L.	0.36	0	0	0	0	0.07
Galium verum L.	4.27	1.7	10.88	3.625	2.5	4.59
Geranium sylvaticum L.	0.27	0	0	0	0	0.05
Hieracium pilosela L.	0	1.4	0.55	0.75	2.5	1.04
Hypochaeris radicata L.	0.45	0	0	0.625	0	0.21
Hypericum perforatum L.	0	0	0.55	0	0	0.11
Jasione montana L.	1.18	1.6	0	0.625	1	0.88
Lamium hybridum Vill.	0.45	0	0	0	0	0.09
Lavandula stoechas Lam.	0	0	0	0.625	0	0.1
Leucanthemopsis pallida (Mill.) Heywood	0	0.2	0	0.25	0	0.09
Linaria elegans Cav.	0	0.2	0.77	0.125	0	0.219
Linaria nivea Boiss. & Reut.	0	1.9	0	0	1.66	0.71
Lotus corniculatus L.	0	0.2	0.77	0.5	0	0.29
Lotus pedunculatus Cav.	0	0	0	3.25	1	0.85
Pedicularis schizocalyx (Lange.) Steininger	0	0	0	0.125	0	0.02
Potentilla sp. L.	0	0	0	0.375	0	0.07
Prunella vulgaris L.	0	0	0	1.375	0.16	0.30
Rosa canina L.	0.9	1.5	0	0	5	1.48
Rubus ulmifolius L.	1.18	1	0	0	53.4	11.11
Sedum amplexicaule DC.	0.45	0	0.55	0	0	0.2
Thymus pulegioides L.	0.54	3.5	0	2.875	0	1.38
Trifolium pratense L.	0	0	0	0.375	0	0.07
Trifolium repens L.	0	0	0	3	0	0.6
Veronica sp. L.	0	0	0.33	0	0	0.06
Wahlenbergia heredacea (L.) Rchb	0	0	0	0.5	0	0.1

Table S4. Number of interactions and sightings of butterfly species per habitat and total area sampled in the years 2017 and 2018. Zeros indicate the absence of a species in that year.

	Quercus-forest		*Cytisus*-shrubland		*Rubus*-shrubland		*Poa*-Grassland		*Nardus*-meadow		Total area		Sightings	
Butterfly species	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
Aglais urticae (L.)	0	0	0	0	9	74	0	0	0	12	9	86	0	0
Aporia crataegi (L.)	0	0	0	3	0	1	0	14	0	0	0	18	0	0
Argynnis adippe (Denis & Schiff.)	0	0	0	0	8	0	2	0	0	0	10	0	1	0
Argynnis aglaja (L.)	0	0	0	4	32	8	8	1	0	0	40	13	0	0
Argynnis niobe (L.)	0	0	0	2	13	8	2	13	0	8	15	31	0	0
Argynnis pandora (Denis & Schiff.)	0	0	1	44	19	23	10	62	0	1	30	130	1	0
Argynnis paphia (L.)	0	0	0	4	18	5	1	7	0	2	19	18	3	0
Aricia cramera (Eschscholtz)	0	0	0	0	0	0	3	0	0	0	3	0	0	0
Boloria dia (L.)	0	0	0	0	3	0	0	0	0	0	3	0	0	0
Brintesia circe (Fabricius)	0	0	0	0	2	0	2	0	0	0	4	0	175	3
Celastrina argiolus (L.)	0	0	0	0	2	0	0	0	0	0	2	0	0	0
Coenonympha arcania (L.)	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Coenonympha pamphilus (L.)	0	0	0	0	0	0	0	0	0	0	0	0	8	0
Colias alfacariensis Ribbe.	0	0	0	8	0	0	0	0	0	0	0	8	0	0
Colias croceus (Geoffroy)	0	0	1	4	5	0	4	6	5	0	15	9	7	1
Gonepteryx cleopatra (L.)	0	0	10	6	0	0	61	0	0	4	71	10	8	0
Gonepteryx rhamni (L.)	5	0	11	0	0	0	0	0	0	0	16	0	0	0
Hipparchia alcyone (Denis & Schiff.)	0	0	0	0	0	0	0	0	0	0	0	0	5	0
Hipparchia semele (L.)	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Hyponephele lupinus (O.Costa)	0	0	0	0	3	0	0	0	0	0	3	0	4	0
Hyponephele lycaon (Rottemburg)	0	0	0	0	3	0	0	0	0	0	3	0	6	0
Inachis io (L.)	0	0	0	0	6	18	0	0	0	0	6	18	2	0
Iphiclides feisthamelii (Duponchel)	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Issoria lathonia (L.)	0	1	37	176	56	53	0	0	0	34	93	264	4	0
Lampides boeticus (L.)	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lasiommata megera (L.)	1	0	2	0	0	2	0	0	0	0	3	2	0	0
Lycaena alciphron (Rottemburg)	0	0	25	13	94	2	1	0	0	0	120	15	16	0
Lycaena phlaeas (L.)	0	0	0	5	8	0	0	0	0	1	8	6	0	0
Maniola jurtina (L.)	2	0	25	13	47	7	0	0	0	3	74	23	29	1
Melanargia lachesis (Hubner)	35	6	68	8	204	34	194	5	88	18	589	71	166	37
Melanargia russiae (Esper)	0	0	0	0	0	0	2	0	0	0	2	0	0	0
Melitaea deione (Geyer)	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Melitaea didyma (Esper)	0	1	3	0	0	0	0	0	0	0	3	1	0	0
Melitaea parthenoides Keferstein	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pieris rapae (L.)	0	0	0	0	0	0	0	0	0	2	0	2	0	0
Poliommatus icarus (Rottemburg)	0	0	1	0	2	0	0	10	0	1	3	11	1	2
Poligonia c-album (L.)	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pyrgus malvoides (Elwes & Edwards)	0	0	0	0	0	0	0	0	0	2	0	2	1	0
Pyronia cecilia (Vallantin)	0	0	0	0	32	0	0	0	0	0	32	0	0	0
Satyrium ilicis (Espe)	0	0	0	0	0	0	0	0	0	1	0	1	1	1
Thymelicus sylvestris (Poda)	0	0	0	6	1	0	6	3	0	3	7	12	0	1
Vanessa cardui L.	0	0	0	0	0	14	0	0	0	6	0	20	0	0
Zerynthia rumina L.	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Richness of butterfly species	4	3	11	14	21	13	13	9	2	16	27	24	19	14