SPATIO-TEMPORAL DIFFERENCES IN POLLINATOR SPECIES RICHNESS, ABUNDANCE AND CONSERVATION STATUS IN A MEDITERRANEAN ISLAND

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Abstract—Although the Mediterranean basin is a hotspot of pollinator diversity, little is still known about how such diversity is distributed in the region and about its conservation status. This study contributes to filling this information gap by studying pollinator diversity parameters in one of the main Mediterranean islands, Mallorca, and further evaluating their conservation category according to the IUCN criteria. We focus on three communities, two coastal and one mountain shrubland, which we have studied for several years. For each community, we obtained the following variables: (1) Shannon diversity (H'), (2) Pielou's index (J'), (3) Number of pollinators per plant (Lp), (4) Flower visitation rate (FVR), (5) Specialisation index (d') and (6) Normalised degree of pollinators, i.e. the number of plants visited per pollinator species relative to the total number of plant species in the community (ND). All pollinators were categorised into functional groups to test for differences in such variables among them. Differences across communities, years and functional groups were tested through GLMMs. The three communities showed differences in pollinator species composition, species richness and diversity. Pollinator diversity also varied with time, especially in the coastal community, which suffered a major disturbance during one of the study years. Regardless of the functional group, the pollinator specialisation degree seems context-dependent. Native and endemic species might disappear in the short term if appropriate management measures are not taken to narrow down the threats to pollinator populations. Further research is urgently needed to assess most insect pollinators’ conservation status in the Mediterranean before such rich diversity is lost forever.

Keywords—Diversity parameters, insect conservation, Mediterranean basin, plant-pollinator interactions, pollinator functional groups, temporal variability.

INTRODUCTION

The concern about the global “pollination crisis” has grown over the last two decades (Murray et al. 2009). Since Biesmeijer et al. (2006) published the first downward trends in bee-pollinated flowering plants and pollinators on a national scale, well-documented decreases in insect populations in several parts of the world have emerged (Sánchez-Bayo & Wyckhuys 2019). We know that one-third of the insect species worldwide are threatened with extinction, where Lepidoptera, Hymenoptera and Coleoptera are the most affected taxa (Sánchez-Bayo & Wyckhuys 2019). This critical insect decline brings worrisome consequences to global biodiversity (Biesmeijer et al. 2006; Burkle et al. 2013; Lundgren et al. 2016). About 60% of the bird species seem to depend on insects as a food resource (Morse 1971; Tallamy & Shriver 2021), whereas 94% of the wild plant species in tropical communities and 78% in temperate zones are estimated to rely on animals’ (mostly insects’) pollination services (Ollerton et al. 2011). The loss of insect pollinators also influences crop production; 75% of the 111 essential world crops rely on insects (Klein et al. 2007). In many studies, it has already been evidenced that domestic pollinators, like honeybees and bumblebees, are not sufficient to sustain many crops (Losey & Vaughan 2006; Aizen & Harder 2009; Garibaldi et al. 2013), and those wild pollinators contribute significantly to their...
fruit quality (Garibaldi et al. 2013; Garrat et al. 2014; Klatt et al. 2014). The main threats to pollinator populations are habitat loss and land-use change, pesticides and fertilisers, the introduction of alien invasive species, including pathogens, and climate change (Sánchez-Bayo & Wyckhuys 2019).

Despite knowing the critical situation of pollinators worldwide, there is still a huge gap of information on the conservation status of the large majority of species. The Global International Union for Conservation of Nature (IUCN) Red list evaluations for bees is available only for Europe (www.iucnredlist.org; Nieto 2014). The last evaluation showed that 9% (Nieto 2014) of the bees and 9% of the butterflies (Van Swaay et al. 2010) are threatened; however, the actual percentages are probably much higher (Van Swaay et al. 2010; Potts et al. 2016). Indeed, for some European countries, the National Red List of bees considers up to 50% of the species as threatened (Van Swaay et al. 2010; Nieto 2014; Potts et al. 2016). In particular, for the Mediterranean countries, about 50% of the Coleoptera and Lepidoptera show significant downward trends, and some regional bee extinctions are being detected (Sánchez-Bayo & Wyckhuys 2019). Compared to central and northern European countries, the Mediterranean basin has received less attention in pollination diversity studies (but see, for instance, Petanidou & Vokou 1990; 1993; Petanidou et al. 2008; Tur et al. 2013; Castro-Urgal & Traveset 2016; Beltran & Traveset 2018; Traveset et al. 2018; Azpiazu et al. 2020; Lázaro et al. 2020). Furthermore, the negative impacts of pollinators’ decline in the Mediterranean region at a community level have still been poorly described (Fontaine et al. 2006; Herrera 2020).

Regarding wild pollinator species, the Iberian-Balearic region is one of the most diverse areas in Europe. It is especially rich in bees, with c. 1,100 species identified so far (Sánchez et al. 2018). Such high species richness is attributed to its Mediterranean condition (Nielsen et al. 2011; Lázaro et al. 2016), with high floral diversity and bare soil availability for nidification (Petanidou & Vokou 1990; Potts et al. 2003) enhanced by the traditional Mediterranean land management (Potts et al. 2006). Island ecosystems are more fragile than those from the continent due to the land limitation, lower number of species and less redundancy in ecological functions (Nilsson & Grelsson 1999; Whittaker & Fernández-Palacios 2007; Benítez et al. 2018); therefore, information on the pollinator diversity of such ecosystems is much needed.

Community-level studies, such as those encompassing plant-pollinator interaction networks, provide precious and updated information on the species composition and abundance of pollinators in specific areas. In the Balearic Islands, and specifically in Mallorca, studies with this network approach have been carried out at different locations, from sea level (Castro-Urgal et al. 2012; Castro-Urgal & Traveset 2014, 2016; Traveset et al. 2018; Lázaro et al. 2020) to the highest altitude of the island (Tur et al. 2013, 2016). However, no assessment of pollination diversity at the island level and the conservation status of the different taxa have been performed so far. Such information is required to develop effective conservation plans that ensure the ecosystem service they provide. In this study, we focused on three different plant communities from Mallorca and asked the following specific questions:

(1) How do the three communities differ in pollinator diversity? Since coastal communities usually show higher flower resources than inland ones (Scheper et al. 2015; Krimmer et al. 2019), we predicted a greater pollinator diversity in most functional groups in the former.

(2) Which are the most prevalent pollinator functional groups in each community? In mountain communities, higher flower visitation rates and species diversity have often been documented for coleopterans, dipterans and lepidopterans than for hymenopterans (Arroyo et al. 1982; Warren et al. 1988; Fontana et al. 2020); thus, we tested whether this pattern holds in our dataset.

(3) Which species and functional groups are the most specialised and generalised, and is this consistent across communities? We predict high spatial variation in the level of specialisation that could be driven by different factors related to plant community composition (Fründ et al. 2010; Gómez et al. 2010; Zografou et al. 2020).
(4) How large is the temporal variation in pollinator diversity, functional group prevalence, and degree of specialisation? Given the high temporal dynamics of insect populations and the different abundances of plant species across years (Olesen et al. 2008; Petanidou et al. 2008a; Dupont et al. 2009; Schwarz et al. 2020), we expect high temporal variation in these variables across the three communities.

(5) What fraction of the species in each functional group is under conservation concern, and are the endemic pollinator species threatened? Even though information on the conservation status exists for only a tiny fraction of the pollinator species in our dataset, we assessed the level of knowledge for each functional group. We unveiled which species are most at risk under a global change scenario and if measures to stop pollinators’ decline are not soon taken.

MATERIALS AND METHODS

STUDY SITES

Data were obtained from three different locations in Mallorca (Balearic Islands, Spain, Fig. 1): a coastal dune community -Son Bosc-, located at the north-eastern coast of the island (39°46’28.11’’N; 3°07’45.34’’E); a rocky coast at the eastern part of Mallorca, Cala Mesquida (39°44’37.63’’N; 3°26’02.12’’E) while the other is a high mountain shrub community at ca. 1100 m above sea level, in Puig Major (39°47’59.51’’N; 2°47’08.81’’ E). According to Bray-Curtis binary dissimilarity analysis, the three communities differ strongly in plant species composition, and flower abundances are much higher in the coastal than in the mountain community (Tur et al. 2013).

Figure 1. A) Study sites encompassing the three different communities on Mallorca Island. Son Bosc a coastal dune community, Cala Mesquida a rocky coastal community and Puig Major, a mountain community. B) Geographic position of Mallorca Island in the western Mediterranean Sea.
**Sampling Procedures**

The dataset used in our study was obtained by compiling previous data from other studies (Castro-Urgal et al. 2012; Tur et al. 2013; Castro-Urgal & Traveset 2014, 2016; Traveset et al. 2018). Direct censuses of pollinator visits to flowers were performed in 10-13 (50 x 2 m) belt transects in the coastal dune, in 30 random plots of 0.5 m² in the rocky coastal, and nine belt transects (three 20 m x 2 m, four 25 m x 2 m, one 30 m x 2 m and one 40 m x 2 m) in the mountain community. Each census lasted 10-15 minutes per plant individual. Flower density was calculated for each species as the number of open flowers divided by the total area surveyed. Each inflorescence was scored as an individual flower for species with tightly clustered inflorescences (e.g. the capitula of Asteraceae). In each census, the following variables were recorded: (1) the taxonomic identity of the plant species observed, (2) the taxonomic identity of the insect species visiting the flowers (unidentified species were captured and taken to the laboratory for later identification by expert taxonomists; only insects contacting the flowers and, thus, potentially pollinating them were recorded), and (3) number of visits of each pollinator species to the plant. All plant species in bloom were sampled weekly between 10:00 am and 5:00 pm on sunny and non-windy days between March and June (both included). Total time spent censusing plant-pollinator interactions was 16:05 h (2008), 42:18 h (2009), 49:39 h (2010) and 37:58 h (2011) in the coastal dune community; 22:50 h (2009) and 84:45 h (2010) in the rocky coastal community; and 13:20 h (2009) and 38:15 h (2010) in the mountain community.

Following Castro-Urgal & Traveset (2016), we classified the pollinators into eight functional groups, depending on insect size and foraging behaviour: coleopterans (CO), dipterans (DI), hoverflies (HO), large bees (> 1 cm) (LB), small bees (< 1 cm) (SB), wasps (WA), lepidopterans (LE), and a marginal group called "others" (OT) which includes ants, thysanopterans and hemipterans.

**Data Analyses**

We calculated a total of six parameters from each of the three communities:

**i)** Shannon index diversity (H’): is a widely used index to calculate alpha diversity that considers the number of species and the abundance of individuals in the community. It ranges from 0 (low diversity) to 4.5-5 (high diversity).

**ii)** Pielou’s index (J’): is a derivation of Shannon index diversity that measures the evenness in the abundance of species of a community, ranging from 0 (absolute homogeneity) to 1 (absolute heterogeneity).

**iii)** Number of pollinator species per plant (Lₜ): total number of pollinator species sharing the flowers of a plant species.

**iv)** Flower visitation rate (FVR): number of flowers contacted by each flower visitor species per unit time. As the sampling effort was not the same in each locality and year, the FVR was standardised following Castro-Urgal et al. (2012):

\[
FVR = \frac{N^v \text{visits/observation time (minutes)}}{N^m \text{censuses}}
\]

**v)** Complementary specialisation index (d’): it ranges from 0 (no specialisation, implying absolute opportunism, based on resource abundance) to 1 (perfect specialist, i.e. absolute selectiveness).

**vi)** Normalised degree (ND): number of links (degree) a species has to other species (partners) in the community, regardless of their abundance, standardised by the total number of possible partners. We calculate the number of plants each pollinator species visits divided by the total number of censused plant species in each community.

H’ and J’ were obtained using the ‘vegan’ package (v.2.5-6; Oksanen et al. 2013). The d’ and ND were obtained using the ‘bipartite’ package (v.2.3; Dormann et al. 2009) through R software v 3.3.3 (R Core Team 2019).

We conducted a generalised linear mixed model (GLMMs) with gamma distribution (link="log"), using the ‘glmmr’ function to assess differences in H’, J’, Lₜ and FVR among functional groups and communities. We considered data obtained in 2009 and 2010 with 335 pollinator species. Each parameter is the dependent variable, the year and the functional group are the fixed factors, and the community is the random factor. To test for differences in d’ and ND among communities, functional groups, and years, we
fitted a linear mixed-effect model (LMMs) with the function ‘lmer’ functional group and year as fixed factors, including the triple interaction among communities, functional group, and year. To evaluate the temporal variation in pollinator diversity, we used the dataset of the four years of censuses from 2008 to 2011, with 438 species gathered in the SB community, including the functional group as the predictor variable. We carried out Tukey’s post-hoc contrasts to unravel which pairs of communities, functional groups and years differed significantly.

All statistical analyses were performed with the R software using the ‘lme4’ package (v.3.1-1) to run these models (Bates et al. 2014).

The conservation status of each pollinator species was obtained by searching the following databases: the IUCN database, the European Red List of Bees (Nieto 2014) and the European Red List of Butterflies (Van Swaay et al. 2010). We sorted the species by their conservation status to evaluate the percentage of endangered species for each community considering the whole dataset (from 2008 to 2011) with 438 pollinator species.

RESULTS

DIFFERENCES IN POLLINATOR DIVERSITY ACROSS COMMUNITIES

The total number of pollinator species across the three communities, considering both 2009 and 2010, was 335 (Table S1), with the highest value in the coastal dune (N = 165), followed by the rocky coastal (N = 154) and the mountain community (N = 137). The coastal dune community showed a lower diversity of pollinators and a lower evenness than the two other communities ($X^2 = 11.390, P = 0.040$ and $X^2 = 17.780, P = 0.021$, respectively; Tab. 1), which did not differ between them. The standardised number of plants visited by each pollinator species (ND) was also lower in the coastal dune than in the other two communities ($X^2 = 37.913, P < 0.001$; Tab. 1). By contrast, FVR was c. 1.5x higher in the coastal dune than in the mountain community and c. 3.7x higher than in the rocky coastal community CM ($X^2 = 159.061, P < 0.001$; Tab. 1). Finally, the coastal dune community had a higher pollinator complementary specialisation index ($d'$) than the other two communities ($X^2 = 28.912, P < 0.001$) while no differences were found between these last two (Tab. 1).

DIFFERENCES IN POLLINATOR SPECIES RICHNESS ACROSS FUNCTIONAL GROUPS

The number of species varied strongly among pollinator functional groups ($X^2 = 76.313, P < 0.001$; Fig. 2), being dipterans the species richest group and lepidopterans the poorest. Dipterans, coleopterans, and large and small bees showed significantly higher species richness than hoverflies, butterflies and wasps (Fig. 3A). Coleopterans were more abundant (based on FVR) and species-rich in both coastal communities than in the mountain community, whilst hoverflies (HO) were mostly found in the mountain. Species in the different functional groups visited a similar proportion of plant species relative to those available in the community, i.e. showed no differences in ND ($X^2 = 10.504, P = 0.162$) and also showed similar FVR ($X^2 = 12.072, P = 0.098$; Fig. 3B).

Table 1. Mean and standard deviation of each community for the six response variables studied (Shannon diversity ($H'$); Pielou’s index ($J'$); Pollinator species richness per plant ($L_p$); Flower visitation rate (FVR); Complementary specialisation index ($d'$) and normalised pollination degree (ND) considering data recorded from two years (2009 and 2010) for each community studied: Son Bosc; coastal dune community, Cala Mesquida; rocky coastal community and Puig Major; mountain community. Communities showing significant differences ($P < 0.05$) are indicated by different letters.
Figure 2. The total number of pollinator species that belong to each functional group (in alphabetical order) in each study community: coastal dune community (DC), rocky coastal community (RC) and mountain community (MC). The functional groups are Coleopterans (CO), Dipterans (DI), Hoverflies (HO), Large bees (LB), Lepidoptera (LE), Small bees (SB), Others (OT), and Wasps (WA). Data from 2009 and 2010 were pooled.

Figure 3. Variation across pollinator functional groups (in alphabetical order) of the four response variables considered in this study. Boxplots indicating the median, the 25th and 75th percentiles and the data range (vertical bar): A) Pollinator species richness per plant species ($L_p$), B) Flower visitation rate (FVR), C) Complementary specialisation index ($d'$), and D) normalised pollinator degree. Functional groups are Coleopterans (CO), Dipterans (DI), Hoverflies (HO), Large bees (LB), Lepidoptera (LE), Others (OT), Small bees (SB) and Wasps (WA). Data from 2009 and 2010 were pooled. The bars that share letters are not significantly different from each other.
### Table 2. Complementary specialisation index ($d'$) of the five most generalised and specialised species in each year and community: Coastal dune community: Son Bosc. Rocky coastal community: Cala Mesquida and Mountain community: Puig Major. The IUCN status is given only for those taxa identified at the species level. The categories are DD (Data Deficient), EN (Endangered), LC (Least Concern), NE (Not Evaluated), and NT (Near Threatened). Species in bold are the endemic species to the Balearic Islands.

<table>
<thead>
<tr>
<th>Coastal dune</th>
<th>Rocky coastal</th>
<th>Mountain</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
<td><strong>Functional Groups</strong></td>
<td>$d'$</td>
</tr>
<tr>
<td><strong>2009 - Generalised</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Scolia hororum</em></td>
<td>WA</td>
<td>0,25</td>
</tr>
<tr>
<td><em>Andrena sp.</em></td>
<td>LB</td>
<td>0,28</td>
</tr>
<tr>
<td><em>Eristalis megecephalus</em></td>
<td>HO</td>
<td>0,31</td>
</tr>
<tr>
<td><em>Philanthus triangulum</em></td>
<td>WA</td>
<td>0,31</td>
</tr>
<tr>
<td><em>Prionyx kirbii</em></td>
<td>WA</td>
<td>0,31</td>
</tr>
<tr>
<td><strong>2009 - Specialised</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Curculionidae</em></td>
<td>CO</td>
<td>0,87</td>
</tr>
<tr>
<td><em>Sitona puncticollis</em></td>
<td>CO</td>
<td>0,88</td>
</tr>
<tr>
<td><em>Lasioglossum malachurum</em></td>
<td>SB</td>
<td>0,89</td>
</tr>
<tr>
<td><em>Thripidae</em></td>
<td>OT</td>
<td>0,92</td>
</tr>
<tr>
<td><em>Pontia daplidice</em></td>
<td>LE</td>
<td>1,00</td>
</tr>
<tr>
<td><strong>2010 - Generalised</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Oedemeridae flavipes</em></td>
<td>CO</td>
<td>0,22</td>
</tr>
<tr>
<td><em>Mordellistena sp.</em></td>
<td>CO</td>
<td>0,23</td>
</tr>
<tr>
<td><em>Stevenia deceptroria</em></td>
<td>CO</td>
<td>0,27</td>
</tr>
<tr>
<td><em>Nemotelus pantherinus</em></td>
<td>DI</td>
<td>0,32</td>
</tr>
<tr>
<td><em>Lasioglossum praasinum</em></td>
<td>SB</td>
<td>0,32</td>
</tr>
<tr>
<td><strong>2010 - Specialised</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ceyallicus variatus</em></td>
<td>SB</td>
<td>0,80</td>
</tr>
<tr>
<td><em>Andrena agilissima</em></td>
<td>LB</td>
<td>0,83</td>
</tr>
<tr>
<td><em>Osmia tricornis</em></td>
<td>LB</td>
<td>0,88</td>
</tr>
<tr>
<td><em>Smyconix sp.</em></td>
<td>CO</td>
<td>0,89</td>
</tr>
<tr>
<td><em>Anthophora plumipes</em></td>
<td>LB</td>
<td>0,93</td>
</tr>
</tbody>
</table>

**Differences in specialisation level across functional groups**

The $d'$ index was higher for small bees than for beetles, dipterans and wasps ($X^2 = 28.124, P < 0.001$; Fig. 3C), i.e. small bees were the most selective species considering the abundance of flower resources.

When selecting the five most generalised and the five most specialised species, we found no consistency in either space (across communities) or in time (between years) (Tab. 2). The species in each group were different and even belonged to different functional groups. Thus, for instance, three of the most generalised species in 2009 were wasps in the coastal dune and dipterans in the
rocky coastal community; in the mountain community, no functional group predominated among the most generalised species. The pattern was similar in 2010. Even within the same community, none of the species in any functional group was in either list of the most generalised or specialised consistently over the two years. However, large and small bees predominated as a specialised group in the dune system and the rocky coastal communities, respectively, while dipterans were dominant in the mountain community.

Interestingly, four out of five endemic species were generalised, with $d'$ values < 0.5. The exception was the small bee *Halictus microcardia*, which showed a high level of specialisation (Tab. 2).

**Temporal variation in pollinator diversity and specialisation**

The coastal dune community, for which we had four years of data, showed strong temporal variation in $L_p$, FVR, and $d'$ (Fig. 4). Specifically, $L_p$ was lower in 2011 than in 2008 and 2010 ($X^2 = 11.898, P = 0.008$; Fig. 4A) whereas FVR showed lower values in 2008 than in 2010 and 2011 ($X^2 = 63.464, P < 0.001$; Fig. 4B). Temporal variation was also confirmed for $d'$, being lower in 2009 and 2010 than in 2011 ($F = 36.884, P < 0.001$). By contrast, ND appeared to be fairly consistent across years ($X^2 = 2.775; P = 0.428$; Fig. 4). In the two other communities, $H'$ also showed temporal variation, higher in 2010 than in 2009 (Tab. 3). The mountain community showed the greatest temporal change in $J'$, with evenness values that doubled in 2010 compared to 2009. The rocky coastal community showed a similar evenness during the two study years.

**Pollinator conservation status**

Out of the 438 insect species (considering dataset from 2008 to 2011) in our dataset, only 295 (67.35%) could be identified at the species level. The IUCN conservation status (DD, LC, NT or EN) could only be obtained for 103 species, representing 23.52% of the entire dataset, with bees and lepidopterans being the nearly unique functional groups that could be assessed (Fig. 5).
Table 3. Shannon index diversity ($H'$) and Pielou's index ($J'$) in each year and community: coastal dune community, a rocky coastal community and a mountain community.

<table>
<thead>
<tr>
<th>Community</th>
<th>Year</th>
<th>$H'$</th>
<th>$J'$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal dune</td>
<td>2008</td>
<td>2.658</td>
<td>0.118</td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>3.087</td>
<td>0.199</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>2.815</td>
<td>0.135</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>2.909</td>
<td>0.215</td>
</tr>
<tr>
<td>Rocky coastal</td>
<td>2009</td>
<td>3.695</td>
<td>0.467</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>4.130</td>
<td>0.472</td>
</tr>
<tr>
<td>Mountain</td>
<td>2009</td>
<td>3.087</td>
<td>0.199</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>3.933</td>
<td>0.446</td>
</tr>
</tbody>
</table>

Figure 5: Number of pollinator species for each functional group that belong to the different IUCN categories, including the group of non-identified insects (NI) and those not yet evaluated (NE). The functional groups are Coleopterans (CO), Dipterans (DI), Hoverflies (HO), Large bees (LB), Lepidoptera (LE), Others (OT), Small bees (SB) and Wasps (WA). The IUCN conservation status is Data Deficient (DD), Endangered (EN), Least Concern (LC), and Near Threatened (NT). Data from 2008 to 2011 are pooled.

Specifically, 76% of the species of small bees (SB), 68% of lepidopterans (LE) and 62% of large bees (LB) could be assessed. In contrast, the percentages for the rest of the functional groups fell between 2 and 4.25%.

Nine species in the dataset were found within one of the threat IUCN categories. Three are categorised as endangered (EN); two are endemic to the Balearics - the ant Lasius balearicus and the small bee Halictus microcardia - and the third is a native small bee Lasioglossum soror. The other six species are in the nearly threatened (NT) category: five small bees, Lasioglossum punctatissimum, L. angusticeps, L. prasinum, L. littorale occitanicum, and Sphecodes rubicundus, and one large bee, Colletes abeillei. Moreover, three endemic species remain without evaluation but could also be threatened due to their limited distributional range; the small bees Lasioglossum nitidulum and Dufourea balearica, and the bombyliid Exoprosopa bowdeni.

**DISCUSSION**

DIFFERENCES IN POLLINATOR DIVERSITY ACROSS COMMUNITIES

Although coastal communities tend to present higher flower resources than inland communities (Tur et al. 2013; Scheper et al. 2015; Krimmer et al.
We did not find support for our prediction of a greater pollination diversity in the former. In fact, despite the coastal dune showed the highest plant richness, the number of pollinator species was not higher than in the other two communities. Pollinator diversity and evenness were even lower in the dune community. The number of plant species that each pollinator visited, relative to all plants available, was smaller in the dune, probably because it holds a greater number of plant species than the other communities. Based on the frequency of flower visitation, it also seems that the dune has the highest abundance of pollinators, especially compared to the rocky coastal community, which showed an FVR four times lower. The rocky coastal community holds the lowest plant richness (N = 48 species), and periodical measurements of flower abundance showed lower values than the dune community (unpublished data). Flower abundance has been repeatedly associated with pollinator richness and abundance (Fontaine et al. 2006; Lázaro et al. 2016; Lowe et al. 2021). It is also widely known that both pollinator richness and abundance decrease with altitude, often due to physiological constraints to withstand low temperatures (Lara-Romero et al. 2019; Chesshire et al. 2021). Thus, it is not surprising that the mountain community, at an altitude of c. 1,100 m, showed a frequency of flower visitation c. 1.5 lower than the dune community. Regarding the degree of specialisation, pollinators in the dune community are more selective when visiting flowers than pollinators in the other two communities, i.e. they visit plant species that are rare or little abundant in the community.

Differences in Pollinator Species Richness Across Functional Groups

The most species-rich functional groups were flies (other than hoverflies), beetles and bees. Nevertheless, such species richness varied across communities (Fig. 2). Interestingly, the two coastal communities hold more bees (large and small), coleopterans, dipterans, and wasps than the mountain community. We attribute this to their greater plant species richness and flower abundance. These variables are known to directly influence flower visitation rates by pollinators (Venjakob et al. 2016), especially in coastal communities (e.g. Vázquez & Aizen 2004; Scheper et al. 2015; Krimmer et al. 2019). By contrast, flower abundance is often lower in mountain communities (Hegland & Boeke 2006; Hegland et al. 2009), where hoverflies (Totland 1993) and lepidopterans (Ezzeddine & Matter 2008) appear to be common, as we could confirm in this mountain community in Mallorca (Puig Major). Hoverflies prefer white and yellow petals (Sajjad et al. 2010; Klecka et al. 2018), such as the endemic Hypericum balearicum, and the native Cistus monspeliensis, both very abundant in our mountain community. Lepidopterans are particularly prevalent in the mountain community, attributed to the high quantity of nectar usually present in mountain flowers and attractive to these pollinators (Ezzeddine & Matter 2008). Furthermore, mobility skills for flying long distances may benefit butterflies and hoverflies in the mountain community where more extended spaces separate flowers than in coastal communities (Torné-Noguera et al. 2014; Doyle et al. 2020). The fact that there were larger bees than small bees in the mountain community could indeed be because they can fly longer distances (Gill et al. 2016).

Pollinator Specialisation Level Across Communities

The variation in insect density in a community partly depends on their specialisation level and mobility skills (Hambäck et al. 2010). Generalised and migratory butterfly species, for instance, have shown a constant negative density–area relationship, while specialised species are more variable in the density–area relationship as they rely on their mobility (Hambäck et al. 2010; Hegland et al. 2009). In our study, small bees showed to be the most specialised overall (with higher d’ values), visiting some plant species despite being less abundant than others. The identity of the most generalised and specialised pollinator species varies among communities and times. Thus, the specialisation level probably varies depending not only on the pollinator-specific requirements but also on the availability of floral resources at a given site and time, i.e., it is mainly context-dependent. The only two species that showed to be consistently generalised were the hawkmoth Macroglossum stellatarum and the hoverfly Chrysotoxum intermedium, both from the mountain community. Interestingly, the endemic small bee Halictus microcardia, categorised as endangered, appeared in the rocky coastal community among the five most specialised...
species in the two consecutive years, relying only on the plants *Atractylis cancellata*, *Eryngium maritimum* and *Santolina chamaecyparissus*.

**Temporal variation in pollinator diversity and specialisation.**

The four years of data from the coastal dune community revealed that despite the slightly higher number of pollinator species present in this community, compared to the other two communities, their Shannon index diversity and the evenness in their abundances were consistently lower in time. Several studies have already reported high temporal variation in pollinator diversity (e.g., Petanidou et al. 2008; Dupont et al. 2009; Souza et al. 2018), and it mirrors the usual high fluctuations in insect diversity found in many different habitats worldwide (Simmons et al. 2019; Van der Sluijs 2020). Moreover, a large disturbance that caused a drop of c. 50% of the vegetation cover in the dune community translated into a lower number of pollinators per plant species (Traveset et al. 2018). However, the flower visitation rate to the remaining plant species did not notably change the year following the perturbation.

The degree of specialisation $d'$ did increase in 2011, indicating that, after the disturbance, pollinators were more selective on the remaining flowering species, visiting those that were rare (or had few flowers). A decline in pollinator species richness and abundance has previously been associated with more specialised interactions (Tur et al. 2013; Traveset et al. 2018; Mathiasson & Řehounková 2020), thus increasing their vulnerability to future disturbances (Valdovinos 2019; Morales-Linares et al. 2021).

**Pollinator conservation status**

Only a small fraction (< 25%) of all pollinator species found in the three communities have been assessed for their conservation status. Even so, such an assessment is more biased towards bees and butterflies. Thus, for all the large species richness in the other functional groups (dipterans, beetles, etc.), we have no information from the IUCN database. Hence, there is no possibility of knowing how endangered our local pollinator communities are if the functional groups with higher species richness do not have any conservation status assigned (Fig. 5). Our study has revealed that the Mallorcan endemic ant *Lasius balearicus* in the mountain and the Balearic endemic small bee *Halictus microcardia* in the rocky coastal community is endangered. Another Balearic endemic small bee, *Lasioglossum littorale occitanicum*, also found in this coastal community, is nearly threatened. Thus, these three species should receive urgent attention if we are to preserve them. Moreover, three more endemic species, two small bees and one bombyliid fly remain to be assessed. However, given the increasing disturbances in the areas where they have been found, they should probably be considered endangered (Drivdal & Van der Sluijs 2021).

**Conclusions**

The three different types of Mallorcan communities showed differences in pollinator community composition, species richness and diversity, which likely respond to floral resource differences, pollinator mobility skills or even thermal constraints. The degree of specialisation of a given pollinator species, regardless of the functional group to which it belongs, appears to be context-dependent. Thus, it can vary in space and time, probably depending on the floral resources available at a particular site and moment. As previously reported in other studies, species richness, pollinator diversity, and specialisation levels vary strongly with time and after disturbances, like the one that occurred in 2010 in the coastal dune community. The perturbation led to increased vulnerability in the face of a future disturbance or response to a decrease in flower resources, for instance, droughts, which are becoming more common under a climate change scenario such as the current one. The more specialised pollinator species will likely be detrimentally influenced (Maes et al. 2006; Řehounková et al. 2016; Dudley et al. 2019). More information is urgently needed on the conservation status of many pollinator species. Native and endemic species might disappear in the short term if decision-makers do not take urgent measures to narrow down the threats to pollinator populations (Herrera 2020) and decrease the impact of anthropogenic activities on them. Our study identified some endemic species that are catalogued with some threat level and, thus, conservation strategies should be planned to avoid their extinction. Other threatened species should
also be considered to study, especially their role in the community, to assess the consequences that their extinction can trigger.

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We dedicate this work to the memory of David Baldock for his immense and valuable work to know the Balearic bees and wasps.

**APPENDICES**

Additional supporting information may be found in the online version of this article:

Table S1. Pollinator species list registered in the censuses from 2008 to 2011 in Mallorca.

**REFERENCES**


Spatio-temporal variation in pollinator communities


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