



# A demographic and ecological study of an Italian population of *Polyommatus ripartii*: the ESU *Polyommatus exuberans*

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## Abstract

*Polyommatus exuberans* is an evolutionarily significant unit (ESU) of the lycaenid butterfly *Polyommatus ripartii*. This ESU is known to survive at only two sites in the Susa Valley (NW Italy). Lack of correct management, reforestation and frequent wildfires severely threaten this ESU (listed as endangered species in the most recent IUCN Italian Red List). Although the taxonomic rank of this taxon is still debated, current threats could cause extinction of its two remaining populations before its taxonomic rank and its ecology are clarified. We collected data for the first time on this population at the small site of Mompantero (ab. 10 ha). We used butterfly GPS-positioning and the mark-release-recapture (MRR)-method to estimate its population size (269 individuals), sex-ratio (1.36 M/F), lifespan (4.76 days), density (47/ha) and mobility (median 153 and 33 m for males and females, respectively). Both sexes are equally catchable. Catchability increases around midday and decreases during overcast weather. While the size and density of this small population are comparable to those of other endemic *Polyommatus* species (such as *P. humedasa* and *P. gennargenti*), scarce mobility makes its populations isolated and even more seriously threatened.

**Implications for insect conservation** We suggest that implementing an active management plan, including mowing before July and/or in autumn, and supporting ant diversity, is of immediate importance. Management should be extended to road verges, where the larval host plant (*Onobrychis* sp.) is abundant, and would thus also serve as corridors to favour dispersion between sites. Our research is the first study to investigate this taxon, thus shedding some light on the ecological and biological aspects that are crucial for long-term survival.

**Keywords** Population size · MRR · Mobility · Extinction risk · Endangered species · Dispersion

## Introduction

Recent research has emphasized a global decline in insect populations during the last 30 years (Collen et al. 2012; Dirzo et al. 2014; Hallmann et al. 2017; Vogel 2017; Lister and Garcia 2018; Sánchez-Bayo and Wyckhuys 2019; Crossley et al. 2021). Butterflies are included in this phenomenon (Thomas et al. 2004; Forister et al. 2011; Habel et al. 2016; van Strien et al. 2019; Crossley et al. 2021). To

oppose this trend and to plan ad hoc conservation measures, it is crucial to understand the subtended mechanisms of interactions between species and their ecosystems. However, not all species are well studied, and there is a disjunction between scientific research and conservation needs (e.g. Di Marco et al. 2017). Indeed, research studies are not equally distributed among species; only a few species, such as the monarch butterfly *Danaus plexippus* (Linné 1758) (Wells and Wells 1992; Agrawal 2019), or, among lycaenid butterflies, the five European species of the genus *Maculinea* (Settele and Kühn 2009), have obtained much more attention than other very rare, scattered, fragmented and endemic species, such as *Erebia christi* Rätzer, 1890, *Polyommatus humedasa* (Toso and Balletto 1976) or *P. ripartii* (Freyer 1830) (Dincă et al. 2013; Bonelli et al. 2018). These butterflies are among the least studied butterflies in Europe; when a literature research on the ISI Web of Knowledge is performed, *Erebia christi* results in having three studies, of

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which one investigated the population size (Battisti et al. 2021); while for *P. humedasmae*, there was only one study. The ISI Web of Knowledge research shows 24 studies for *P. ripartii*, of which only three related to the ecology and biology of *P. ripartii* (Lafranchis and Lafranchis 2012; Przybyłowicz 2014, Pérez-Fernández et al. 2019). *P. ripartii* has scattered populations across southern Europe. These populations may show local adaptations such as having different host plants (*Onobrychis* spp.) or different ant species hosts. Thus, little is known about these butterfly species, even if the contribution of rare and endemic species to ecosystems is generally crucial due to their role in ecosystem functioning, which is usually different from common species (Kunin and Gaston 1993; Gaston 2012). Moreover, rare, scattered and endemic species are usually more prone to extinction due to characteristics such as lower overall reproduction and poorer dispersal abilities (Kunin and Gaston 1993; Işık 2011). There is, therefore, a high risk of losing these species without even noticing it (McGarrahan 1997; Bonelli et al. 2011; Theng et al. 2020). Conservation actions, such as habitat protection and restoration, are likely to be effective in opposing the decline of local insect populations (Samways 2007; Forister et al. 2019; Haddaway et al. 2020; Crossley et al. 2021). To be effective, policy and management must be supported by reliable knowledge accumulated from diverse sources of evaluated evidence on different aspects of species ecology and phenology.

*Polyommatus ripartii* presents a fragmented distribution, with scattered populations from Spain—in the west—to Mongolia—in the east—probably representing a relict distribution (Dincă et al. 2013). In Italy, *P. ripartii* is found in the Ligurian Alps at ten locations; in the Pollino and Orsorio Massifs formerly known as *P. galloi* (Balletto and Toso 1979) and in the Susa Valley at two locations (Bonelli et al. 2018). The population of the Susa Valley is known in Italy by the name of *Polyommatus exuberans* (see below for more information on its taxonomic status). According to Dincă et al. (2013), the highly fragmented populations of *P. ripartii* in the Susa Valley can be considered and studied as separate Evolutionarily Significant Units of Conservation (ESU; see Ryder 1986; Moritz 1994; Casacci et al. 2014). This approach has been adopted for other butterflies with similar distributional characteristics, such as *Lycaena dispar* (Haworth 1803) (Lai and Pullin 2004), and *Maculinea rebeli* (Hirschke 1905) (Casacci et al. 2014). Hereinafter, we consider *P. exuberans* as the Italian ESU of *P. ripartii* located in the Susa Valley (hereinafter *P. exuberans*). In the last IUCN Italian Red List (Bonelli et al. 2018), which follows Balletto et al. (2014), *P. exuberans* is considered as a separate species within a specific category: EN (Endangered). On the other hand, *P. ripartii* is classified as NT (Near Threatened) in Italy (Bonelli et al. 2018) and LC (Least Concern) at a European and Mediterranean level (van Swaay et al. 2014)

according to the IUCN Red List criteria. No information on the life cycle or the ethology of *P. exuberans* is currently available, and other information about this ESU is scarce. *P. exuberans* is—overall—in decline, following the extinction of six of its former populations, including at its type locality (“Oulx”), due to various reasons, corresponding to a loss of nearly 75% of its original distribution area (Bonelli et al. 2011). It currently survives at only two locations, where it is severely threatened mainly by the abandonment of traditional agro-pastoral activities and consequent reforestation, as well as by recurrent brush fires (the most recent took place at Mompantero during the last week of October 2017) and by over-collection (Sindaco et al. 2008; Bonelli et al. 2018). Its Extent Of Occurrence (EOO) is now much less than 5000 km<sup>2</sup>, while its Area Of Occupancy (AOO) is less than 500 km<sup>2</sup> (Bonelli et al. 2018). Munguira et al. (1993) previously evaluated this lycaenid as endangered, which was recently confirmed (EN), based on stricter IUCN criteria (Bonelli et al. 2018).

We decided to study *P. exuberans* as information about this ESU is fragmented and unclear, as its population is in decline and because, despite being inside the Natura 2000 network, the species is suffering from lack of management and uncontrolled fires. Specific management actions should be quickly adopted for conservation purposes. Collecting information about the ecology and biology of *P. exuberans* would corroborate the use of the ESU concept (Casacci et al. 2014), and should improve conservation management and policy (Haddaway et al. 2020). Here, we present the results of a pilot one-season investigation of the adult population located at Mompantero (NW Italy), which falls into two SAC (Special Areas of Conservation IT1110039 and IT1110030). The aims of our study, which represents a starting point for future investigations, were to (1) estimate the size of the adult population, its density, the sex ratio, and the mean lifespan; (2) analyse how catchability was influenced by the time of day; (3) evaluate adult mobility in relation to sex and weather conditions; (4) describe the use of nectar source by the two sexes.

### Taxonomic status of *P. exuberans*

*Polyommatus exuberans* (*Hirsutina admetus exuberans*) was originally described by Roger Verity in 1926. The name was chosen due to the exceptional wing size of the specimens of this butterfly collected by the author during the summer of 1925 in Oulx (Verity 1926). *Locust typicus*: “Cottian Alps, Oulx (July 25th–August 5th)”. While other authors classify *P. exuberans* as a member of the separate genus *Agrodiaetus* (Bertaccini 2003; Vila et al. 2010), in the present study we follow the most usual taxonomic approach (e.g. Wiemers et al. 2009; Przybyłowicz 2014; Lukhtanov et al. 2015 and many others), where *Agrodiaetus* is treated as a subgenus of

the broader genus *Polyommatus*. Species of *Agrodiaetus* are all of recent origin, since their most recent common ancestor dates back to ab. 0.87 Mya (Dincă et al. 2013). This makes these species poorly differentiated both at the morphological (they share identical genitalia) and the genetic level (Vila et al. 2010; Dincă et al. 2013; Lukhtanov et al. 2015).

Historically, the taxonomic position of *P. exuberans* changed from being considered a subspecies (e.g. Kudrna 1986) or even a synonym (Eckweiler and Häuser 1997) of *P. ripartii* (Freyer, [1831])—which is morphologically similar—to the rank of being a separate species (Toso and Balletto 1976; Balletto and Cassulo 1995; Hellmann and Bertaccini 2004; Balletto et al. 2014). In the last IUCN Italian Red List (Bonelli et al. 2018), which follows Balletto et al. (2014), *P. exuberans* is considered as a separate species.

Indeed, the enzyme electrophoretic study by Mensi et al. (1994) showed that *P. exuberans* and *P. ripartii* have allozyme profiles extremely similar to a Nei (1972) distance of only 0.074. Moreover, no diagnostic loci were found.

In accordance with Mensi et al. (1994), Vila et al. (2010) demonstrated that the two latter taxa share very similar mitochondrial and nuclear DNA (COI + COII + ITS-2) and did not support *P. exuberans* as a distinct species. Consequently, this taxon is excluded from the latest checklists of European butterflies, and it is likely considered as part of *P. ripartii* (Wiemers et al. 2018). Dincă et al. (2013) proposed considering the geographically highly fragmented genetic lineages of the *P. ripartii* group (including *P. exuberans* = *P. ripartii susae* Bertaccini, 2003) as separate Evolutionarily Significant Units of Conservation (ESU: see Ryder 1986; Moritz 1994; Casacci et al. 2014), while Lukhtanov et al. (2015), working on a set of two genetic markers (the mitochondrial COI barcode and the nuclear spacer ITS-2), demonstrated that the *P. ripartii* clade remains fundamentally unresolved. Therefore, protecting *P. exuberans* is greatly important for future studies of the phylogeny and zoogeographic history of *P. ripartii*'s clade and of taxonomically related species (Przybyłowicz 2014).

## Materials and methods

### Study species

The *P. ripartii* ESU is a highly localized butterfly of the Susa Valley in NW Italy (Hellmann and Bertaccini 2004). It is a monovoltine, heliophilous butterfly of the xerothermophilous grasslands, and is present at elevations between 500 and 1200 m (Hellmann and Parenzan 2010). The flying period of this butterfly lasts from mid-July to mid-August (Hellmann and Parenzan 2010). Males and females are similar in size, with a wingspan of 29–31 mm and 26–29 mm, respectively (Bertaccini 2003). Larvae of *P. exuberans* develop

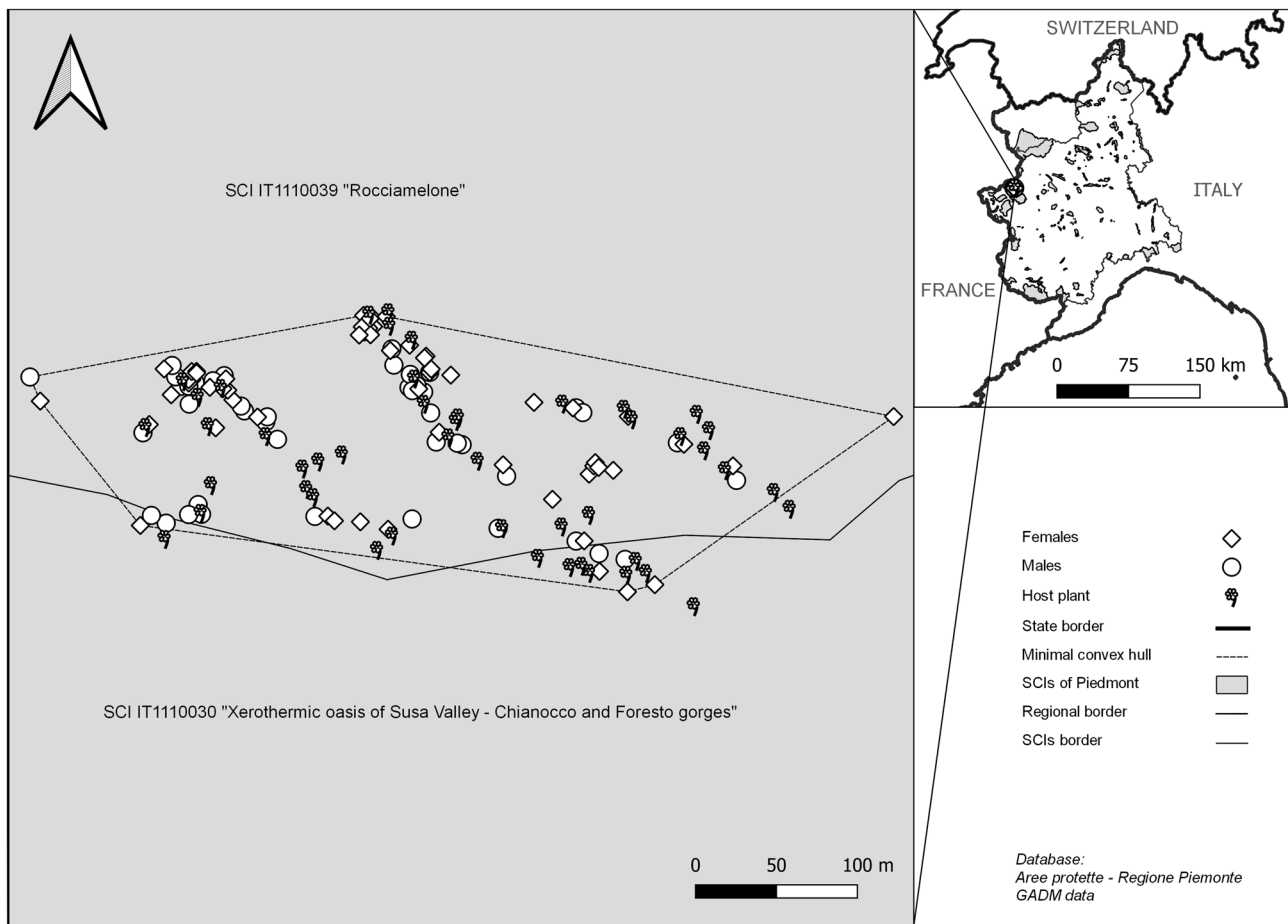
on sainfoin (complex of *Onobrychis viciifolia* Scop.). The females usually lay a single egg on the upper margin of a floral bract, and rarely on other parts of the host plant (Hellmann and Bertaccini 2004).

### Study area

The monitored area was in North-Western Italy (45° 09' N 7° 5' E, between 1060 and 1250 m a.s.l.), in the Susa Valley (Fig. 1), and is situated on the slopes of Mt Rocciamelone (3,538 m). The area extends for ca. 3.8 ha and is part of the SAC IT1110039 “Rocciamelone” and of the SAC IT1110030 “Xerothermic oasis of the Susa Valley—gorges of Chianocco and Foresto” within the Mompantero municipality. This area is occupied by spinneys with *Pinus sylvestris* and by xerophilous grassland with *Festuca vallesiaca*, and extends from west to east. The area is crossed by a dirt road leading to the Chiamberlando hamlet, and results in an ecotonal area. Host plants of *P. exuberans* (sainfoins) were abundant, especially on road verges, which are occasionally managed. Mowing of the road edges inside the monitored area took place during the last week of our monitoring, around mid-August.

### Mark-release-recapture (MRR)

Excursions were made periodically to verify the presence of the lycaenid in the monitored area. Capture events occurred every 2 days from 12th July to 17th August 2019. In the last two events (15th and 17th August) we did not find any individuals of *P. exuberans*. Two longer intervals between 5 to 8th August and from 10 to 13th August were due to unsuitable weather conditions. Altogether, the population was sampled 18 times. Each butterfly was netted and individually marked with a consecutive number on the underside of the right hindwing using a non-toxic violet fine-tip permanent marker, and immediately released at the same location. Recaptures of previously marked butterflies were recorded separately. Before releasing each specimen, we noted its individual number, sex, habitus, behaviour before netting, GPS position (Garmin® eTrex 20 with precision of ± 3 m) and time (date, hour) of the capture/recapture event. Behaviour was scored into six different categories: flying, basking, feeding, resting, copula and oviposition. When individuals were found nectaring, the plant species was also recorded and identified at the genus level. Weather conditions were recorded on a scale from 0 to 3 for both wind intensity (0 = absent, 1 = weak, 2 = medium, 3 = strong) and cloud cover (0 = no clouds, 1 = few clouds, 2 = many clouds, 3 completely overcast). To evaluate mobility and behaviour, we registered individuals that were captured more than once during the same day of activity.



**Fig. 1** Special areas of conservation of piedmont and a focus on the studied area with minimal convex hull, captures divided by sex and host plant locations. The precise location of the studied area is vague for reasons of conservation

## Demography

The data derived from the MRR method were analysed according to the Cormack–Jolly–Seber type constrained models (Schwarz and Seber 1999) with program MARK@ 2.1 (White and Burnham 1999). The best model was chosen on the basis of Akaike's information criterion (AIC). The model with the lowest AIC is taken as the best model for data fitting. Models with the AIC Delta < 2 and with the smallest number of parameters were considered as potential good model candidates (e.g. Burnham and Anderson 1998; Schtickzelle et al. 2002).

The program MARK estimates survival probability ( $\phi$ ; combining mortality and emigration) and capture probability ( $p$ ). These parameters may be constant ( $\cdot$ ), dependent on sex ( $g$ ) or on time ( $t$ ).

In MRR studies, the average life span of butterflies that emerge discontinuously from pupae is calculated as  $\hat{e} = \frac{1}{1-\phi} - 0.5$ , derived from Deevy's (1947) formula for

life expectancy of new-born individuals under the assumption of age-independent survival (Nowicki et al. 2005).

## Catchability

To define whether catchability varied during the day, we divided the time of capture (hour) data into three time slots: morning (8:30–11:30), midday (11:30–14:30) and afternoon (14:30–17:30).

We modelled the number of captured and recaptured individuals, subdivided by sex, in a generalized linear model (GLM, Poisson, maximum likelihood fit) where time slot and sex, as categorical variables, were used as additive explanatory variables. We tested the model for over/under-dispersion using the DHARMAs package in R (Obs/Sim = 0.91,  $p = 0.832$ ). Moreover, we evaluated if catchability changed according to weather conditions, specifically in relation to clouds and wind. We modelled the number of captures and recaptures, subdivided by sex, in a GLM (Poisson,

maximum likelihood fit), where cloudiness, as the ordinal variable (from 0 to 3), was added as an additive explanatory variable. We tested for over/under-dispersion of the model using DHARMAs package in R (Obs/Sim = 0.61,  $p = 0.176$ ). Similarly, we modelled the number of captures and recaptures in GLM (GLM, Negative Binomial, maximum likelihood fit) where wind, as the ordinal variable, was added as an additive explanatory variable. Considering that the model with the Poisson distribution family was over/under dispersed (dispersion test: Obs/Sim = 4.10,  $p < 0.001^{***}$ ), we used the Negative Binomial distribution family (according to Zuur et al. 2009).

### Mobility

The distance between consecutive captures on different days (D) was calculated as a straight line connecting two consecutive points of butterfly capture (QGIS 10.0; ESRI, Redlands, CA, USA). According to Jugovic et al. (2017); we calculated the mean, median and maximum distances separately for males and females. Moreover, we modelled distances (D) in a linear model (LM, Gaussian, maximum likelihood fit), where sex was used as an explanatory variable. We tested the models for normality of the residuals (Shapiro–Wilk test:  $p = 0.07$ ).

The movements of adults were estimated separately for males and females, using distance between consecutive captures (D). To understand their dispersal abilities (Pennekamp et al. 2014), we estimated the probabilities of movements with respect to distance beyond those covered during the MRR study. Thus, we calculated the negative-exponential function (NEF) and the inverse-power function (IPF), according to Hill et al. (1996).

All distances were grouped into 50 m classes, separately for each sex. The probability (P) of an individual moving a certain distance (D), beyond that covered during the study, was calculated as:  $P_{NEF} = ae^{-kD}$ ,  $P_{IPF} = bD^{-n}$ . Parameters a, b, k and n are typical of the species, and k is a species-specific dispersal constant describing the shape of the exponential curve; k is equivalent to  $1/D'$ , see Harrison et al. (1988), where  $D'$  represents the average distance moved by individuals (Hill et al. 1996). Considering that log-transformed formulas can be expressed as linear relationships [i.e.  $\ln(P_{NEF}) = \ln(a) - kD$  and  $\ln(P_{IPF}) = \ln(b) - n \ln(D)$ ], and following Čelik (2012), the a, b, k and n parameters were estimated by LMs in R. The natural logarithms of the inverse cumulative proportions (ICP) of individuals moving certain distances ( $\ln P$ ) were regressed on distances (meters). Therefore, to estimate a, b, k and n parameters, we modelled natural logarithms of ICP into a LM (Gaussian, maximum likelihood fit) where sex (as a categorical variable), meters for NEF function, or natural logarithm of

meters for IPF function (as continuous variables), and their interaction (sex  $\times$  distance) were used as additive explanatory variables. We tested for the normality of the residuals for both models (Shapiro–Wilk test:  $p = 0.17$  and  $p = 0.11$  for NEF and IPF functions, respectively).

### Behaviour

According to Jugovic et al. (2017), we evaluated which behaviours were exhibited by individuals immediately before capture, as percentage values of the six observed behaviours (flying, basking, feeding, resting, oviposition and copula), separately for each sex. Within the feeding behaviour, nectar plant choices are also presented here as percentages, separately for each sex.

To assess if males and females exhibited different behaviours in relation to different weather conditions, we modelled behaviour frequencies in a LM (Gaussian, maximum likelihood fit), where sex and behaviours, as categorical variables, and weather conditions (separately: wind and clouds), as ordinal variables, were used as explanatory variables. We tested for normality of the residuals for both models (Shapiro–Wilk test:  $p = 0.412$  and  $p = 0.150$  for clouds and wind, respectively).

### Ant communities

Fiedler (1991) described *P. ripartii* as “steadily myrmecophilus”, with larvae presenting a complete set of organs for myrmecophily (a dorsal nectary organ and a pair of eversible tentacle organs), while there are no specific data for ESU *P. exuberans*. The ants which were observed to be associated with *P. ripartii* belong to genera *Camponotus*, *Plagiolepis*, *Crematogaster*, *Lasius*, *Lepisiota* and *Tapinoma* (Lafranchis et al. 2007).

As a pilot study, we evaluated the ant communities to see if the ant genera used by *P. ripartii* were present in the area. To explore the ant communities present in the study area, we prepared five  $5 \times 5$  m<sup>2</sup> plots, and we placed five pitfall traps within each plot. Traps were collected after 2 days of activation.

The collected ants were preserved in 70% alcohol inside a 2 ml microtube with a screw-cap. We identified ant samples at the genus level. To this end, we inspected the ants with a stereomicroscope Leica EZ4 D, and we followed the identification keys from “The ants (Hymenoptera, Formicidae) of Poland” (Czechowski et al. 2002), “Clé de reconnaissance des fourmis Françaises” (<http://cle.fourmis.free.fr/>) and “Ants of Britain and Europe. A Photographic Guide” (Lebas et al. 2019).

**Table 1** Summary of the MRR data used to determine the demography of ESU *P. exuberans* in NW Italy in 2019

	No. of marked individuals	No. (%) of recaptured individuals	No. of captures	No. (%) of recaptures
Males	25	12 (48)	44	19 (43)
Females	34	15 (44)	58	24 (41)
Total	59	27 (46)	102	43 (42)

## Results

### Demography

In total, 59 individuals (males:25, females:34) were marked, and 27 (46%) of them were recaptured (Table 1), of which 12 (44%) were recaptured more than once. Males were recaptured more often than females, respectively, 48% males (total number 12) and 44% of females (total number 14). In relation to this result, we calculated a sex ratio of 1.36, in favour of females.

The best model, evaluated by the Cormack Jolly-Seber (CJS) model (Online Appendix Table 2), indicates that survival probability ( $\phi$ ) and capture probability ( $p$ ) were not sex-specific and varied over time (Online Appendix Table 3).

Using Mark parameters, total population size ( $N$ ) was estimated as the sum of daily captured individuals (excluding recaptures), divided by  $p(t)$ . Daily population size ( $N_i$ ) was calculated as the number of captured and recaptured individuals, divided by  $p(t)$  along the flight period. For  $N_0$  (on 12/7/2019), we divided the number of captured individuals by  $p(1)$ . Standard errors were calculated as numbers of captured and recaptured males and females divided by  $p \pm p_{SE}$ .

According to Nowicki et al. (2005), daily recruitment ( $B_i$ ), i.e. the number of individuals entering the population between capturing sessions, was calculated separately for each sex as  $(1) N_{i+1} - N_i \times \phi^d$ , where  $d$  is the length of the interval between capturing occasions, measured in days. According to Jugovic et al. (2017), negative values were corrected to 0. Similarly to what was carried out for population size, standard errors of daily recruitment values were calculated by the same formula (1), using  $\phi \pm \phi_{SE}$  instead of  $\phi$ , and then subtracting the result from (1) (resulting in different amounts of positive and negative standard errors).

The estimated total population size was 269 individuals (ranging from 187 to 467 individuals), including 150 estimated females (ranging from 106 to 247) and 119 estimated males (ranging from 80 to 220). The minimal convex hull was 5.69 ha wide (Fig. 1), so that butterfly density was about 47 estimated individuals/ha, and 10 captured individuals /ha.

Daily recruitment was calculated along the flight period (Fig. 2a), and was in line with the trend of daily population size ( $N_i$ ), over time (Fig. 2b). Analysing the flight curve (Fig. 2b), flights of males reached a peak on July 20th. While males decreased after this peak, females continued to increase, reaching their first peak on July 28th, and a second peak on August 8th.

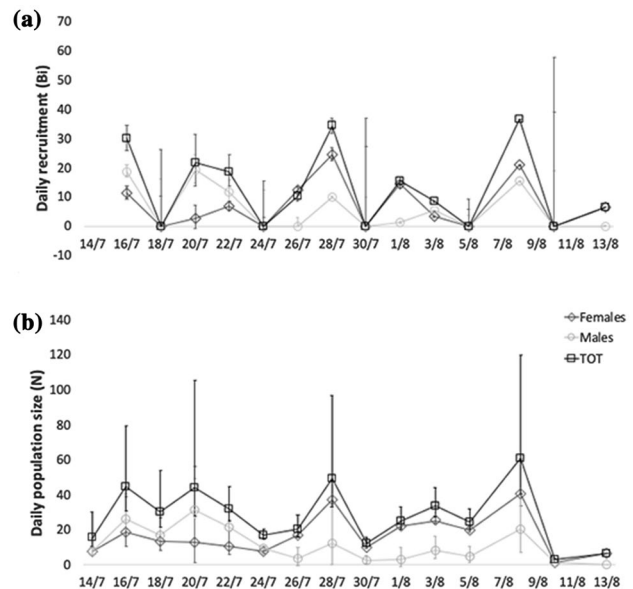
Using the average value of daily survival ( $\phi = 0.81 \pm 0.07$ ), we estimated an average lifespan of 4.76 days. The mean and maximum number of days between the first and the last captures of the same individual were: 6.89 and 19, respectively.

### Catchability

Catchability differed between time slots. During the midday slot we captured significantly more butterflies than in the morning slot ( $Z$  value = 3.38;  $p < 0.001^{***}$ ), while butterfly captures in the afternoon were not significantly different from in the morning ( $Z$  value = 0.85;  $p = 0.397$ ; Fig. 3a). We did not find any differences in catchability ( $Z$  value = -1.38;  $p = 0.167$ ) between sexes. In contrast, catchability decreased significantly with increasing cloud cover ( $Z$  value = -6.64;  $p < 0.001^{***}$ ; Fig. 3b), while it did not significantly change in relation to wind conditions ( $Z$  value = -1.17;  $p = 0.288$ ).

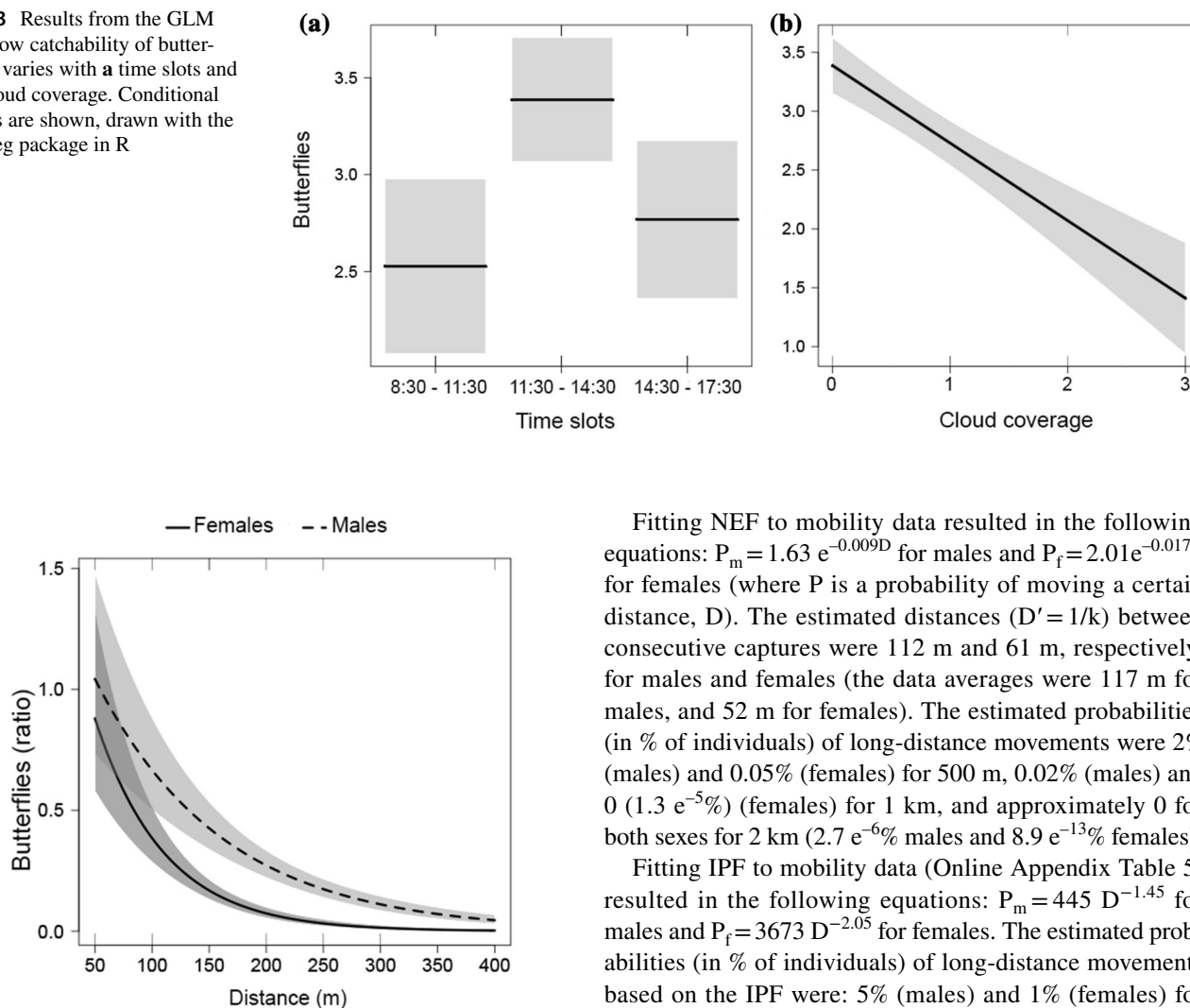
### Mobility

Median, mean and max distances recorded for males were 153 m, 180 m and 522 m, respectively. For females, these



**Fig. 2** Results from the best CJS model in the MARK program: **a** estimated daily recruitment ( $B_i$ ) and **b** estimated daily population size [ $N$ , evaluated as captures + recaptures divided by  $p(t)$ ]. The error lines represent the standard error

**Fig. 3** Results from the GLM on how catchability of butterflies varies with **a** time slots and **b** cloud coverage. Conditional plots are shown, drawn with the visreg package in R



**Fig. 4** Significant interactions between proportion of female (solid line) and male (dashed line) butterflies captured at distance  $D$ . Conditional plots are drawn with the visreg package in R

were 33 m, 77 m and 242 m, respectively. Mobility varied in relation to sex, where males tended to cover longer distances than females ( $t$  value = 2.28,  $p = 0.03^*$ ; Online Appendix Fig. 7). The natural logarithmic inverse cumulative proportion of moving butterflies decreased with increasing distances and was different for each sex, for NEF function (Sex  $\times$  Distance:  $t$  value = 4.52,  $p = 0.002^{**}$ ; Fig. 4; see Online Appendix Table 4), but not significantly different for IPF function (Sex  $\times$   $\ln(\text{Distance})$ :  $t$  value = 1.66,  $p = 0.13$ ; see Online Appendix Table 5). Moreover, the natural logarithm of inverse cumulative proportion decreased with the increase of distances covered for both functions: NEF (Distance:  $t$  value = -11.19,  $p < 0.001^{***}$ ; see Online Appendix Table 4) and IPF ( $\ln(\text{Distance})$ :  $t$  value = -7.04,  $p < 0.001^{***}$ ; see Online Appendix Table 5).

Fitting NEF to mobility data resulted in the following equations:  $P_m = 1.63 e^{-0.009D}$  for males and  $P_f = 2.01 e^{-0.017D}$  for females (where  $P$  is a probability of moving a certain distance,  $D$ ). The estimated distances ( $D' = 1/k$ ) between consecutive captures were 112 m and 61 m, respectively, for males and females (the data averages were 117 m for males, and 52 m for females). The estimated probabilities (in % of individuals) of long-distance movements were 2% (males) and 0.05% (females) for 500 m, 0.02% (males) and 0 (1.3  $e^{-5\%}$ ) (females) for 1 km, and approximately 0 for both sexes for 2 km (2.7  $e^{-6\%}$  males and 8.9  $e^{-13\%}$  females).

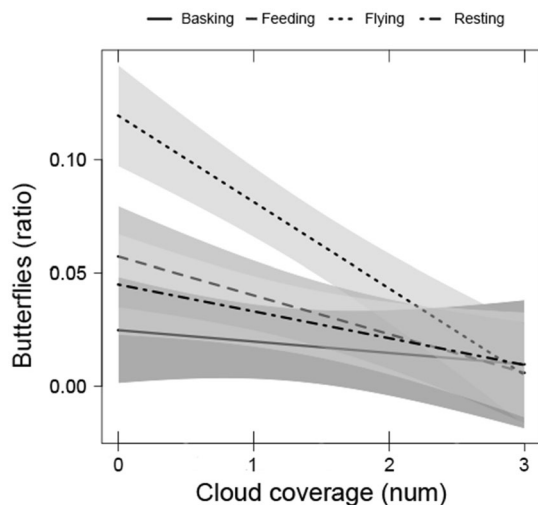
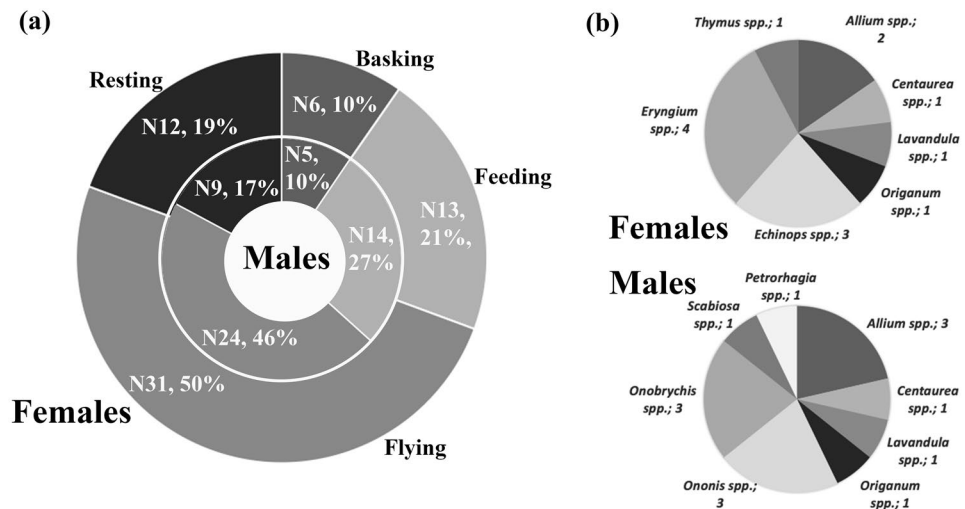
Fitting IPF to mobility data (Online Appendix Table 5) resulted in the following equations:  $P_m = 445 D^{-1.45}$  for males and  $P_f = 3673 D^{-2.05}$  for females. The estimated probabilities (in % of individuals) of long-distance movements based on the IPF were: 5% (males) and 1% (females) for 500 m, 2% (males) and 0.3% (females) for 1 km, and 0.7% (males) and 0.06% (females) for 2 km. The regression slope was steeper for females ( $t = 5.91$ ,  $df = 94$ ,  $p < 0.001$ ). IPF predicted a higher probability of movement for distances of over 300 m (males) and of over 200 m (females).

## Behaviour

Among recorded behaviours ( $N = 117$ ), flying was the most represented for both sexes: 50% ( $N = 31$ ) females and 46% ( $N = 24$ ) males; feeding (females,  $N = 13$ , 21%; males,  $N = 14$ , 27%); resting (females,  $N = 12$ , 19%; males,  $N = 9$ , 17%); and basking (females,  $N = 6$ , 10%; males,  $N = 5$ , 10%) (Fig. 5a). Since oviposition and copula were recorded only a few times, we omitted these behaviours from all evaluations.

During the feeding behaviour (nectaring), plants of 11 genera were recorded as nectar sources for *P. exuberans*. *Origanum* spp. was the most frequently visited nectar source for females ( $N = 4$ ), while males were found nectaring on *Onobrychis* spp., *Origanum* spp. and *Allium* spp. with the same frequency ( $N = 3$ ). The second most visited nectar

**Fig. 5** **a** Number and percentage of the different behaviours (flying, feeding, resting and basking) recorded for males (inner circle) and females (outer circle). **b** Within feeding behaviours ( $N=27$ ), number of visits on nectar plant genera by *P. exuberans* was recorded for both sexes



**Fig. 6** Results from the LM of butterflies in relation to cloud coverage (from 0 to 3) captured while exhibiting different behaviours. Conditional plots are shown, drawn with the visreg package in R

source by females was *Lavandula* spp. ( $N=3$ ), followed by *Allium* spp. ( $N=2$ ). *Centaurea* spp., *Echinops* spp., *Eryngium* spp., *Thymus* spp. were only used by females one time each. For males, only one observation was made of individuals nectaring on *Centaurea* spp., *Lavandula* spp., *Ononis* spp., *Scabiosa* spp. and *Petrorhagia* spp. (Fig. 5b).

Butterflies were found to exhibit different behaviours in relation to cloud coverage, but not in relation to sex. In particular, increasing cloud presence decreased the percentage of butterflies in flight (behaviour  $\times$  cloud coverage:  $t$  value =  $-3.90$ ;  $p < 0.001$ \*\*\*; Fig. 6). We did not find any differences between the other behaviours (feeding and resting) in relation to cloud coverage (Online Appendix Table 6). In addition, we did not find any significant

differences between sexes and behaviours (basking was the reference category) in relation to wind (Online Appendix Table 7).

### Ant communities

We found 1479 ants belonging to 11 different genera: *Camponotus* ( $N=183$ ), *Formica* ( $N=175$ ), *Lasius* ( $N=842$ ), *Lapthorax* ( $N=1$ ), *Messor* ( $N=2$ ), *Monomorium* ( $N=1$ ), *Myrmica* ( $N=61$ ), *Plagiolepis* ( $N=5$ ), *Polyergus* ( $N=1$ ), *Solenopsis* ( $N=2$ ), *Tapinoma* ( $N=110$ ), *Temothorax* ( $N=24$ ) and *Tetramorium* ( $N=72$ ; Online Appendix Table 8). *Camponotus*, *Plagiolepis*, *Lasius*, *Lepisiota* and *Tapinoma* are used by *P. ripartii*. Therefore, these five genera of ants are candidates for use by *P. exuberans*.

### Discussion

The population of *P. exuberans* of the Mompantero site is small, restricted to a limited area (5.69 ha). We found that (1) the population size was estimated at about 269 individuals, i.e. 150 females and 119 males. Butterfly density was also low, about 47 individuals/ha, and comparable to those of other *Polyommatus* populations, equally confined to small sites, such as *P. humedasa* (Toso and Balletto 1976; Balletto 1993a). The sex ratio was slightly in favour of females (1.36). The estimated mean lifespan was 4.76 days. (2) As expected, catchability was significantly higher during midday hours, and significantly decreased under worsening weather conditions, specifically when cloud coverage increased. (3) Males covered longer distances than females, but both sexes only moved short distances (maximum 500 m). In both NEF and IPF estimations, approximately none of the individuals covered distances longer than 2 km.



(4) Butterflies decreased their flying behaviour when clouds increased. Both male and female butterflies preferably feed on *Origanum* sp., and *Allium* sp., but only males were found to feed on the host plant *Onobrychis* sp.; females, instead, prefer *Lavandula* sp.

## Demography

The presence of the first adults at the Mompantero site was observed on 12th July 2019, and continued throughout the whole flying season; no butterflies were detected after 13th August. Captures and recaptures were only 59 and 43 respectively, which are low numbers, but comparable with other studies on local rare lycaenidae populations (Marschalek and Deutschman 2008; Marschalek and Klein 2010). The probability of recapture (46%) was relatively high (Morton 1982; Polic et al. 2014), probably due to the small area where the population occurs, and to the low mobility of the butterflies. The number of marked males was lower than that of females, a rather atypical occurrence in MRR studies carried out on butterflies (Čelik 2012; Jugovic et al. 2017), resulting in an unusual female-biased sex ratio of 1.36. However, the high number of recaptures and the low individual mobility observed in this study show that individuals of either sex disperse rarely, and most of them occur together at the same site.

The longest recorded life span was 19 days, which is higher than that found for the lycaenid *Phengaris (Maculinea) arion* (Linné 1758), where it was shown to range from 7 to 17 days (Osváth-Ferencz et al. 2017). The mean lifespan value, calculated based on  $\phi$  (output of Software Mark), was about 4.76 days, which is slightly higher than that reported for *Pseudophilotes bavius hungarica* (Dioszegy 1913) (2.4–5.4 days; Crişan et al. 2014), and similar to that observed in *Zerynthia polyxena* ([Denis and Schiffermüller] 1775) (4.4 days; Čelik 2012). The lifespan was found to be lower, in contrast, compared to other univoltine, big-sized, butterflies, such as *Aporia crataegi* (Linné 1758) (about 7 days; Jugovic et al. 2017), which are known for having generally longer adult lives. Each individual specimen of *Parnassius apollo* was observed to survive for an average of about 2–4 weeks (Lafranchis et al. 2015).

Observed population density was generally low (47 estimated individuals/ha, versus 10 captured individuals/ha), especially considering that the species is strongly localized, but was similar to that recorded for other Italian endemic lycaenids, with dot-like distributions, such as *Polyommatus humedasa* (Toso and Balletto 1976) (about 11/ha; Balletto 1993a), *P. gennargentii* (Leigne 1987) (about 132/ha; Casula 2006), or *P. ripartii*'s ESU *Polyommatus galloi* (6–7/ha; Balletto 1993b).

The flight graph shows a non-parabolic trend in daily population sizes, which is atypical for univoltine butterfly

species (Jugovic et al. 2017). The presence of a peak (28/7), followed by a higher peak (08/8) during the flying period is generally not common for butterflies (Clarke and Dennis 2020), while protandry is instead a common characteristic (Baguette and Schtickzelle 2003; Fric et al. 2010; Čelik 2012; Jugovic et al. 2017). After the rainy day of 7th August, an increase in daily population size was detected. The subsequent decline in daily population size was shortly followed (2–3 days) by another rainy day on 12th August, and by the start of mowing activities. Both bad weather and mowing could have influenced the complete lack of recaptures after 10th August, and may have, therefore, accelerated the end of the flight period. Mowing in particular, may have forced the remaining adults to emigrate perhaps due to disturbance (Mouquet et al. 2005; Jugovic et al. 2017). However, although mowing only occurred on road verges, most nectar sources and still available host plants were concentrated at these sites.

## Catchability

Our results support the classification of *P. exuberans* as heliophilous (Hellmann and Parenzan 2010), thus it seems likely to find *P. exuberans* in xerothermic biotopes on the south-facing northern slope of the Susa Valley. Midday seems to be the optimal time to observe this butterfly. In addition, we did not detect any differences in catchability between sexes, which is a crucial factor for the reliability of results (Nowicki et al. 2008). Weather conditions have to be favourable too, with minimal cloud covering and light winds (Online Appendix Figs. 8 and 9).

## Mobility

The observed mobility parameters recorded for *P. exuberans* suggest that individuals from this population are particularly sedentary. The maximum distance recorded was higher for males (522 m) than for females (242 m). The opposite (298 m for males, 600 m for females) was reported for *Lycaena helle* ([Denis and Schiffermüller] 1775), another extremely sedentary lycaenid (Modin and Öckinger 2020). The maximum distance recorded for *P. exuberans* (522 m) is comparable to that observed by Kuussaari et al. (2014) for other *Polyommatus* species, namely 520 m for *P. amandus* (Schneider 1792), 510 m for *P. icarus* (Rottemburg 1775) and 520 m for *P. semiargus* (Rottemburg 1775). As a caveat, we recognize that, even though we examined the surrounding areas of the site, this dispersal analysis is influenced by the size of the site (Schneider 2003).

According to Čelik (2012), the longest movement observed for males was about equal to the distance between the maximum opposite angles of the minimal convex hull (530 m). Thus, males were able to cover the area on which

the population occurred but rarely covered longer distances. Indeed, based on NEF and IPF estimations, the percentage of males that covered longer distances, and migrated to other areas was estimated as being very low. According to Čelik (2012), the NEF predicted a lower probability of movement, indeed 0.2% of males dispersed 1 km. The IPF function predicted that 2% of males disperse 1 km. Movement was even scarcer in the case of females, with the maximum distance covered by females being 242 m, and the percentage of females dispersing up to 1 km was estimated to be almost 0, for both NEF and IPF functions. The scarce mobility observed for males and the really low mobility of females could be dangerous if unpredictable events were to destroy the site at the moment when adults begin to fly, such as wildfires, which frequently occur in the area. In most species of *Agrodiaetus*, pupation occurs in the litter.

According to the IUCN Italian Red List (Bonelli et al. 2018), *P. exuberans* only occurs in two localities that are several kilometres away from each other. Considering the population size and the area in which *P. exuberans* is present, it is unlikely that the Mompantero population would show a system of interconnected subpopulations, like that of *L. helle* (Fischer et al. 1999; Bauerfeind et al. 2009; Modin and Öckinger 2020), but only genetic analysis can confirm this hypothesis.

## Behaviour

Males and females showed similar behaviours, with flying being the most frequent activity. Behaviour of males could be explained as a way to patrol the area in order to search for females or resting places such as mud puddles. In fact, males drinking on the sides of water puddles along with other lycaenid species were observed on three occasions, but this behaviour was not included in the comparisons. Mud-puddling is common among adult male butterflies looking for water and minerals (Arms et al. 1974; Beck et al. 1999). For females, the observed flight activity that we recorded may be due to their higher density, which would result in more time spent looking for available host plants, likely using oviposition-detering pheromones to avoid deposition in spots already occupied (as already recorded for *Phengaris (Maculinea) teleius*: Sielezniew and Stankiewicz-Fiedurek 2013; and for *P. ripartii*: Przybyłowicz 2014).

The utilization of nectar from 11 plant genera suggests that, like most other butterflies, adults of *P. exuberans* are opportunistic feeders. For females, *Origanum* sp. was the most utilized nectar source. This was also the most abundant plant that was flowering during the flying period. For males, in addition to *Origanum* sp., *Onobrychis* sp. and *Allium* sp. were also equally visited. Since *Onobrychis* sp. is the host plant of preimaginal stages of *P. exuberans*, this may be connected to female research or male individuals recently

emerged from pupae. This high number of visits shown only by males suggests that the host plant may be used as a proxy of the presence of male adults during the flying period. *Origanum* sp. is reported as a favourite nectar source for *P. ripartii* in Greece (Lafranchis et al. 2007). The genus *Allium* sp. is known for including species appreciated by butterflies (Hantson and Baz 2013).

## Ant communities

The ants seen in association with *P. ripartii* belong to the genera *Camponotus*, *Plagiolepis*, *Crematogaster*, *Lasius*, *Lepisiota* and *Tapinoma* (Lafranchis et al. 2007). Three of these genera in the studied area (*Camponotus*, *Lasius* and *Tapinoma*) were found in all the investigated plots, while the genus *Plagiolepis* was present in only two plots (Online Appendix Table 8). Considering most of the Italian *Polyommatus* are myrmecophilous, including *P. ripartii*, *P. exuberans* would likely present ant-associations. Thus, it is important to confirm this hypothesis on its myrmecophily and to study the ant genera involved (e.g. Tartally et al. 2019). Local adaptations to different ant species or genera could reinforce the differences with other populations of *P. ripartii*, as seen for myrmecophilous hoverflies (Schönrogge et al. 2002). Moreover, the use of different ant species would corroborate *P. exuberans* as a separate ESU of *P. ripartii* (Casacci et al. 2014). Different ant species required different microhabitats, determined by temperature and humidity at the soil level, soil texture and composition (Boulton et al. 2005; Casacci et al. 2011).

## Conclusions

This is a pilot investigation that studied a small localized rare butterfly population in Mompantero. We demonstrated that the population is small in a restricted area, but with parameters comparable to other butterflies with similar characteristics. Considering that the species being studied is in decline, a general management of the area may help to reverse this trend. As a caveat, we recognize that other research has to be carried out to clarify the taxonomic status of *P. exuberans*, to identify the local host plant, to understand the possible myrmecophily and to study the connections between Susa Valley populations through genetic analysis (the latter has been carried out by Przybyłowicz et al. (2014) for *P. ripartii* in Poland). Specifically on the unresolved taxonomy status, and given the results obtained from mitochondrial markers and enzyme electrophoresis studies, it is crucial that molecular analysis is broadened to include a set of nuclear markers (see Hinojosa et al. 2019).

*Polyommatus exuberans* is an oligophagous species whose larvae feed on a single plant genus (*Onobrychis*

sp.). This may be an important factor determining the butterfly species' spatial distribution. It is crucial to verify the host plant of *P. exuberans* at the species level [either *O. vicifolia* Scop. and/or *O. arenaria* (Kit.) DC.].

Five out of the eleven genera of ants found within the study area have been reported to be used by the *P. ripartii* larvae. If myrmecophily is also confirmed for *P. exuberans*, the Susa population may be supported by the same taxa or different ones. The latter scenario may support *P. exuberans* as an ecologically distinct ESU of *P. ripartii*.

Considering that the populations are rare and far from each other, a metapopulation dynamic is difficult to expect. Information on the biology of this species is scarce, while its distribution is poorly understood. Genetic distances among populations could be important to study in order to understand connections and dynamics among populations.

The biggest threats to *P. exuberans* are over-collecting and reforestation (Sindaco et al. 2008; Bonelli et al. 2018). While the former seems mostly under control, the latter remains a problem, due to the abandonment of traditional agro-pastoral activities. One of the main forces opposing this phenomenon is wildfires, of which the last one occurred in October 2017. The critical situation in which the *P. exuberans* ESU is found necessitates a proper management of the area. Plants used by *P. exuberans* as nectar sources suggest that traditional management may be sufficient to maintain a suitable habitat for this species, in a landscape where host plants are mainly distributed along dirt road verges. *Onobrychis* sp. represents a feeding source both for the larval and the adult stages of *P. exuberans*. Thus, it is suggested to take into account both the butterfly phenology, the presence of *Onobrychis* sp. and the ant diversity when planning ordinary maintenance work of the road verges in the area. To ensure minimal anthropic disturbance, it is preferable to cut the grass on road verges and on the bordering grassland—where *Onobrychis* sp. is found—shortly before the flight period starts (early July). Grass cutting in the autumn appears more problematic, since the overwintering of taxa of the *P. ripartii* group remains under-investigated. In this way, road verges could be good habitats (Phillips et al. 2020) for both oviposition and feeding and, at the same time, they might favour dispersion as possible corridors (Modin and Öckinger 2020). Grass cutting causes temporary habitat deterioration (Bauerfeind et al. 2009; Halbritter et al. 2015), while heavy grazing limits the growth and expansion of *Onobrychis*, (Lafranchis et al. 2007). A combination of mowing and grazing is still to be encouraged, since these practices, while keeping reforestation at low levels, are known to contribute to support healthy lepidopteran communities (Mouquet et al. 2005; Bauerfeind et al. 2009; Skórka et al. 2013), including *P. ripartii* (Lafranchis et al. 2007).

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**Data availability** All data are available at the Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Turin, Italy.

**Code availability** Not applicable.

## Declarations

**Conflict of interest** The authors have no conflicts of interest to declare that are relevant to the content of this article.

**Ethical approval** No butterflies were harmed during this research. The authors took extreme care to keep the specimens for marking for the shortest time possible, and always in the shade to reduce stress. All ant samples collected during this research are conserved at the Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Turin, Italy.

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## References

- Agrawal AA (2019) Advances in understanding the long-term population decline of monarch butterflies. *Proc Natl Acad Sci* 116(17):8093–8095. <https://doi.org/10.1073/pnas.1903409116>
- Arms K, Feeny P, Lederhouse RC (1974) Sodium: stimulus for puddling behaviour by tiger swallowtail butterflies, *Papilio Glaucus*. *Science* 185(4148):372–374. <https://doi.org/10.1126/science.185.4148.372>

- Baguette M, Schtickzelle N (2003) Local population dynamics are important to the conservation of metapopulations in highly fragmented landscapes. *J Appl Ecol* 40(2):404–412
- Balletto E, Toso GG (1979) On a new species of *Agrodiaetus* (Lycaenidae) from southern Italy. *Nota Lepidopterol* 2:13–22
- Balletto E (1993a) *Polyommatus humedasa* (Toso & Balletto, pp 88–89). In: New TR (ed) Conservation biology of *Lycaenidae* (butterflies). Occasional paper of the IUCN species survival commission no. 8, IUCN, Gland, p 174
- Balletto E (1993b) *Polyommatus galloi* (Toso & Balletto, pp 90–91). In: New TR (ed) Conservation biology of *Lycaenidae* (butterflies). Occasional paper of the IUCN species survival commission no. 8, IUCN, Gland, p 174
- Balletto E, Cassulo LA (1995) Lepidoptera hesperioidea, papilionoidea. In: Minelli A, Ruffo S, La Posta S (eds) Checklist delle specie della fauna italiana. Calderini, Bologna, p 89
- Balletto E, Cassulo LA, Bonelli S (2014) An annotated checklist of the Italian butterflies and skippers (Papilionoidea, Hesperioidea). *Zootaxa*. <https://doi.org/10.11646/zootaxa.3853.1.1>
- Battisti A, Gabaglio M, Ruggetti M, Bionda R, Amstutz R, Dusej G, Vodá R (2021) Use of the single rope access technique reveals habitat use patterns for the elusive *Erebia christi* (Lepidoptera:Nymphalidae). *J Insect Conserv* 25(1):77–87. <https://doi.org/10.1007/s10841-020-00284-6>
- Bauerfeind SS, Theisen A, Fischer K (2009) Patch occupancy in the endangered butterfly *Lycaena helle* in a fragmented landscape: effects of habitat quality, patch size and isolation. *J Insect Conserv* 13(3):271–277. <https://doi.org/10.1007/s10841-008-9166-1>
- Beck J, MuÈhlenberg E, Fiedler K (1999) Mud-puddling behaviour in tropical butterflies: in search of proteins or minerals? *Oecologia* 119(1):140–148. <https://doi.org/10.1007/s004420050770>
- Bertaccini E (2003) Prima segnalazione in Piemonte di *Agrodiaetus ripartii* (Freyer, 1831) e descrizione di *A. ripartii susae* ssp. nova (Insecta Lepidoptera Lycaenidae). *Quaderno Di Studi e Notizie Di Storia Naturale Della Romagna* 17:127–138
- Bonelli S, Cerrato C, Loglisci N, Balletto E (2011) Population extinctions in the Italian diurnal Lepidoptera: an analysis of possible causes. *J Insect Conserv* 15(6):879–890. <https://doi.org/10.1007/s10841-011-9387-6>
- Bonelli S, Casacci LP, Barbero F, Cerrato C, Dapporto L, Sbordoni V, Scalercio S, Zilli A, Battistoni A, Teofili C, Rondinini C, Balletto E (2018) The first red list of Italian butterflies. *Insect Conserv Divers* 11(5):506–521. <https://doi.org/10.1111/icad.12293>
- Boulton AM, Davies KF, Ward PS (2005) Species richness, abundance, and composition of ground-dwelling ants in northern California grasslands: role of plants, soil, and grazing. *Environ Entomol* 34(1):96–104
- Burnham KP, Anderson DR (1998) Practical use of the information-theoretic approach. Model selection and inference. Springer, New York, pp 75–117
- Casacci LP, Witek M, Barbero F, Patricelli D, Solazzo G, Balletto E, Bonelli S (2011) Habitat preferences of *Maculinea arion* and its *Myrmica* host ants: implications for habitat management in Italian Alps. *J Insect Conserv* 15(1–2):103–110. <https://doi.org/10.1007/s10841-010-9327-x>
- Casacci LP, Barbero F, Balletto E (2014) The “evolutionarily significant unit” concept and its applicability in biological conservation. *Ital J Zool* 81(2):182–193. <https://doi.org/10.1080/1125003.2013.870240>
- Casula P (2006) Evaluating hypotheses about dispersal in a vulnerable butterfly. *Ecol Res* 21(2):263–270. <https://doi.org/10.1007/s11284-005-0130-1>
- Čelik T (2012) Adult demography, spatial distribution and movements of *Zerynthia polyxena* (Lepidoptera:Papilionidae) in a dense network of permanent habitats. *Eur J Entomol*. <https://doi.org/10.14411/eje.2012.028>
- Clarke HE, Dennis EB (2020) A new method for calculating butterfly abundance trends for small regional areas. *J Insect Conserv*. <https://doi.org/10.1007/s10841-020-00251-1>
- Collen B, Böhm M, Kemp R, Baillie JEM (2012) Spineless: status and trends of the world’s invertebrates. Zoological Society of London, London
- Crişan A, Sitar C, Craioveanu MC, Vizauer TC, Rakosy L (2014) Multi-annual population size estimates and mobility of the endemic *Pseudophilotes bavius hungarica* (Lepidoptera:Lycaenidae) from Transylvania (Romania). *North-West J Zool* 10:S115–S124
- Crossley MS, Smith OM, Berry LL, Phillips-Cosio R, Glassberg J, Holman KM, Holmquest JG, Meier AR, Varriano SA, McClung MR, Moran MD, Snyder WE (2021) Recent climate change is creating hotspots of butterfly increase and decline across North America. *Glob Change Biol*. <https://doi.org/10.1111/gcb.15582>
- Czechowski W, Radchenko A, Czechowska W (2002) The ants (Hymenoptera, Formicidae) of Poland. Museum and Institute of Zoology, Warszawa, p 200
- Deevey ES Jr (1947) Life tables for natural populations of animals. *Q Rev Biol* 22(4):283–314
- Di Marco M, Chapman S, Althor G, Kearney S, Besancon C, Butt N, Maina JM, Possingham HP, von Bieberstein KR, Venter O, Watson JE (2017) Changing trends and persisting biases in three decades of conservation science. *Glob Ecol Conserv* 10:32–42
- Dincă V, Runquist M, Nilsson M, Vila R (2013) Dispersal, fragmentation, and isolation shape the phylogeography of the European lineages of *Polyommatus (Agrodiaetus) ripartii* (Lepidoptera:Lycaenidae). *Biol J Lin Soc* 109(4):817–829
- Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJ, Collen B (2014) Defaunation in the anthropocene. *Science* 345(6195):401–406. <https://doi.org/10.1126/science.1251817>
- Eckweiler W, Häuser CL (1997) An illustrated checklist of *Agrodiaetus* Hübner, 1822, a subgenus of *Polyommatus* Latreille, 1804 (Lepidoptera:Lycaenidae). *Nachr Ent Ver Apollo* 16:113–166
- Fiedler K (1991) European and North West African Lycaenidae (Lepidoptera) and their associations with ants. *J Res Lepid* 28(4):239–257
- Fischer K, Beinlich B, Plachter H (1999) Population structure, mobility and habitat preferences of the violet copper *Lycaena helle* (Lepidoptera: Lycaenidae) in Western Germany: implications for conservation. *J Insect Conserv* 3(1):43–52
- Forister ML, Jahner JP, Casner KL, Wilson JS, Shapiro AM (2011) The race is not to the swift: long-term data reveal pervasive declines in California’s low-elevation butterfly fauna. *Ecology* 92(12):2222–2235. <https://doi.org/10.1890/11-0382.1>
- Forister ML, Pelton EM, Black SH (2019) Declines in insect abundance and diversity: we know enough to act now. *Conserv Sci Pract* 1(8):e80. <https://doi.org/10.1111/csp2.80>
- Fric Z, Hula V, Klimova M, Zimmermann K, Konvicka M (2010) Dispersal of four fritillary butterflies within identical landscape. *Ecol Res* 25(3):543–552. <https://doi.org/10.1007/s11284-009-0684-4>
- Gaston KJ (2012) The importance of being rare. *Nature* 487(7405):46–47. <https://doi.org/10.1038/487046a>
- Habel JC, Segerer A, Ulrich W, Torchyk O, Weisser WW, Schmitt T (2016) Butterfly community shifts over two centuries. *Conserv Biol* 30(4):754–762. <https://doi.org/10.1111/cobi.12656>
- Haddaway NR, Grames EM, Boyes DH, Saunders ME, Taylor NG (2020) What evidence exists on conservation actions to conserve insects? A protocol for a systematic map of literature reviews. *Environ Evid* 9(1):1–8. <https://doi.org/10.1186/s13750-020-00214-8>
- Halbritter DA, Daniels JC, Whitaker DC, Huang L (2015) Reducing mowing frequency increases floral resource and butterfly (Lepidoptera:Hesperioidea and Papilionoidea) abundance in managed roadside margins. *Fla Entomol* 98:1081–1092

- Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörrén T, Goulson D, de Kroon H (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* 12(10):0185809. <https://doi.org/10.1371/journal.pone.0185809>
- Hantson S, Baz A (2013) Seasonal change in nectar preference for a Mediterranean butterfly community. *J Lepid Soc* 67(2):134–142. <https://doi.org/10.18473/lepi.v67i2.a5>
- Harrison S, Murphy DD, Ehrlich PR (1988) Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *Am Nat* 132(3):360–382
- Hellmann F, Bertaccini E (2004) I Macrolepidotteri della Valle di Susa. Museo regionale di scienze naturali, Turin
- Hellmann F, Parenzan P (2010) I macrolepidotteri del Piemonte. Museo regionale di scienze naturali, Turin
- Hill JK, Thomas CD, Lewis OT (1996) Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *J Anim Ecol* 65:725–735
- Hinojosa JC, Koubínová D, Szenteczki MA, Pitteloud C, Dincă V, Alvarez N, Vila R (2019) A mirage of cryptic species: genomics uncover striking mitochondrial discordance in the butterfly *Thymelicus sylvestris*. *Mol Ecol* 28(17):3857–3868
- Işik K (2011) Rare and endemic species: why are they prone to extinction? *Turk J Bot* 35(4):411–417. <https://doi.org/10.3906/bot-1012-90>
- Jugovic J, Črne M, Lužnik M (2017) Movement, demography and behaviour of a highly mobile species: a case study of the black-veined white, *Aporia crataegi* (Lepidoptera: Pieridae). *Eur J Entomol*. <https://doi.org/10.14411/eje.2017.016>
- Kudrna O (1986) Butterflies of Europe. 8. Aspects of the conservation of butterflies in Europe. Aula Verlag, Wiesbaden
- Kunin WE, Gaston KJ (1993) The biology of rarity: patterns, causes and consequences. *Trends Ecol Evol* 8(8):298–301. [https://doi.org/10.1016/0169-5347\(93\)90259-R](https://doi.org/10.1016/0169-5347(93)90259-R)
- Kuussaari M, Saarinen M, Korpela EL, Pöyry J, Hyvönen T (2014) Higher mobility of butterflies than moths connected to habitat suitability and body size in a release experiment. *Ecol Evol* 4(19):3800–3811. <https://doi.org/10.1002/ece3.1187>
- Lafranchis T, Lafranchis A (2012) Five blues on a flower: Interactions between polyommata butterflies (Lepidoptera, Lycaenidae), ants and parasitoids in the northern Peloponnese (Greece). *Nachr Entomol Ver Apollo* 33:23–29
- Lafranchis T, Gil TF, Lafranchis A (2007) New data on the ecology of 8 taxa of *Agrodiaetus* Hübner, 1822 from Greece and Spain: host-plants, associated ants and parasitoids (Lepidoptera: Lycaenidae, Hymenoptera, Diptera). *Atalanta* 38(12):189–197
- Lafranchis T, Jutzeler D, Guillosson JY, Kan B, Kan P (2015) La vie des Papillons de France: écologie, biologie et comportement des Rhopalocères de France. 750 pp, 1 CD rom. Diathéo, Montpellier
- Lai BCG, Pullin AS (2004) Phylogeography, genetic diversity and conservation of the large copper butterfly *Lycaena dispar* in Europe. *J Insect Conserv* 8:27–36. <https://doi.org/10.1023/B:JICO.0000027478.35309.46>
- Lebas C, Galkowski C, Blatrix R, Wegnez P (2019) Ants of Britain and Europe. A photographic guide. Bloomsbury Wildlife, London
- Lister BC, Garcia A (2018) Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc Natl Acad Sci* 115(44):E10397–E10406. <https://doi.org/10.1073/pnas.1722477115>
- Lukhtanov VA, Dantchenko AV, Vishnevskaya MS, Saifitdinova AF (2015) Detecting cryptic species in sympatry and allopatry: analysis of hidden diversity in *Polyommatus (Agrodiaetus)* butterflies (Lepidoptera: Lycaenidae). *Biol J Lin Soc* 116(2):468–485
- Marschalek DA, Deutschman DH (2008) Hermes copper (*Lycaena [Hermelycaena] hermes*: Lycaenidae): life history and population estimation of a rare butterfly. *J Insect Conserv* 12(2):97–105. <https://doi.org/10.1007/s10841-006-9064-3>
- Marschalek DA, Klein MW (2010) Distribution, ecology, and conservation of Hermes copper (Lycaenidae: *Lycaena [Hermelycaena] hermes*). *J Insect Conserv* 14(6):721–730. <https://doi.org/10.1007/s10841-010-9302-6>
- McGarrahan E (1997) Much-studied butterfly winks out on Stanford preserve. *Science* 275(5299):479–480. <https://doi.org/10.1126/science.275.5299.479>
- Mensi P, Lattes A, Cassulo L, Balletto E (1994) Biochemical taxonomy and evolutionary relationships in *Polyommatus* (subgenus *Agrodiaetus*) (Lepidoptera, Lycaenidae). *Nota Lepidopeterologica* 5:105–114
- Modin H, Öckinger E (2020) Mobility, habitat selection and population connectivity of the butterfly *Lycaena helle* in central Sweden. *J Insect Conserv* 24(5):821–831. <https://doi.org/10.1007/s10841-020-00254-y>
- Moritz C (1994) Defining ‘evolutionary significant units’ for conservation. *Trends Ecol Evol* 9:373–375
- Morton AC (1982) The effects of marking and capture on recapture frequencies of butterflies. *Oecologia* 53(1):105–110
- Mouquet N, Belrose V, Thomas JA, Elmes GW, Clarke RT, Hochberg ME (2005) Conserving community modules: a case study of the endangered lycaenid butterfly *Maculinea alcon*. *Ecology* 86(12):3160–3173
- Munguira M, Martin J, Balletto E (1993) Conservation biology of Lycaenidae: a European overview, pp. 23–34. In: New TR (ed) Conservation biology of Lycaenidae (butterflies). Occasional paper of the IUCN species survival commission no. 8, IUCN, Gland, p 174
- Nei M (1972) Genetic distance between populations. *Am Nat* 106(949):283–292
- Nowicki P, Richter A, Glinka U, Holzschuh A, Toelke U, Henle K, Woyciechowski M, Settele J (2005) Less input same output: simplified approach for population size assessment in lepidoptera. *Popul Ecol* 47(3):203–212. <https://doi.org/10.1007/s10144-005-0223-2>
- Nowicki P, Settele J, Henry PY, Woyciechowski M (2008) Butterfly monitoring methods: the ideal and the real world. *Isr J Ecol Evol* 54(1):69–88
- Osváth-Ferencz M, Bonelli S, Nowicki P, Peregovits L, Rákossy L, Sielezniew M, Kostro-Ambroziak A, Dziekańska I, Kőrösi Á (2017) Population demography of the endangered large blue butterfly *Maculinea arion* in Europe. *J Insect Conserv* 21(3):411–422. <https://doi.org/10.1007/s10841-016-9944-0>
- Pennekamp F, Garcia-Pereira P, Schmitt T (2014) Habitat requirements and dispersal ability of the Spanish fritillary (*Euphydryas desfontainii*) in southern Portugal: evidence-based conservation suggestions for an endangered taxon. *J Insect Conserv* 18(3):497–508. <https://doi.org/10.1007/s10841-014-9655-3>
- Pérez-Fernández R, Rodríguez N, Postigo M (2019) *Polyommatus (Agrodiaetus) fabressei* (Oberthür, 1910) and *P.(A.) ripartii* (Freyer, 1830) in the center of the Iberian Peninsula, Guadalajara (Spain). Geographical distribution and aspects of their morphology, ecology and biology (Lepidoptera: Lycaenidae). *SHILAP Revista De Lepidopterología* 47(187):449–474
- Phillips BB, Wallace C, Roberts BR, Whitehouse AT, Gaston KJ, Bullcock JM, Dicks LV, Osborne JL (2020) Enhancing road verges to aid pollinator conservation: a review. *Biol Conserv*. <https://doi.org/10.1016/j.biocon.2020.108687>
- Polic D, Fiedler K, Nell C, Grill A (2014) Mobility of ringlet butterflies in high-elevation alpine grassland: effects of habitat barriers, resources and age. *J Insect Conserv* 18(6):1153–1161. <https://doi.org/10.1007/s10841-014-9726-5>

- Przybyłowicz Ł (2014) *Polyommatus ripartii*: the biological basis for the conservation and the morphology of the developmental stages of a critically endangered, relict population in Central Europe. *J Insect Sci* 52(1):44–51. <https://doi.org/10.1093/jisesa/ieu109>
- Przybyłowicz Ł, Lukhtanov V, Lachowska-Cierlik D (2014) Towards the understanding of the origin of the Polish remote population of *Polyommatus* (*Agrodiaetus*) *ripartii* (Lepidoptera:Lycaenidae) based on karyology and molecular phylogeny. *J Zool Syst Evol Res* 52(1):44–51. <https://doi.org/10.1111/jzs.12040>
- Ryder OA (1986) Species conservation and systematics: the dilemma of subspecies. *Trends Ecol Evol* 1:9–10
- Samways MJ (2007) Insect conservation: a synthetic management approach. *Annu Rev Entomol* 52:465–487. <https://doi.org/10.1146/annurev.ento.52.110405.091317>
- Sánchez-Bayo F, Wyckhuys KA (2019) Worldwide decline of the entomofauna: a review of its drivers. *Biol Conserv* 232:8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>
- Schneider C (2003) The influence of spatial scale on quantifying insect dispersal: an analysis of butterfly data. *Ecol Entomol* 28(2):252–256
- Schönrogge K, Barr B, Wardlaw JC, Napper E, Gardner MG, Breen J, Elmes GW, Thomas JA (2002) When rare species become endangered: cryptic speciation in myrmecophilous hoverflies. *Biol J Lin Soc* 75(3):291–300
- Schtickzelle N, Le Boulengé E, Baguette M (2002) Metapopulation dynamics of the bog fritillary butterfly: demographic processes in a patchy population. *Oikos* 97(3):349–360
- Schwarz CJ, Seber GA (1999) Estimating animal abundance: review III. *Stat Sci* 14:427–456
- Settele J, Kühn E (2009) Insect conservation. *Science* 325(5936):41–42. <https://doi.org/10.1126/science.1176892>
- Sielezniew M, Stankiewicz-Fiedurek AM (2013) Behavioural evidence for a putative oviposition-deterrence pheromone in the butterfly, *Phengaris* (*Maculinea*) *teleius* (Lepidoptera:Lycaenidae). *Eur J Entomol* 110(1):71–80
- Sindaco R, Selvaggi A, Savoldelli P (2008) La Rete Natura 2000 in Piemonte—I Siti di Importanza Comunitaria. Regione Piemonte, 122–127
- Skórka P, Lenda M, Moroi D, Kalarus K, Tryjanowski P (2013) Factors affecting road mortality and the suitability of road verges for butterflies. *Biol Conserv* 159:148–157. <https://doi.org/10.1016/j.biocon.2012.12.028>
- Tartally A, Thomas JA, Anton C, Balletto E, Barbero F, Bonelli S, Bräu M, Casacci LP, Csósz S, Czekes Z, Dolek M, Dziekańska I, Elmes G, Fürst MA, Glinka U, Hochberg ME, Höttinger H, Hula V, Maes D, Munguira ML, Musche M, Nielsen PS, Nowicki P, Oliveira PS, Peregovits L, Ritter S, Schlick-Steiner BC, Settele J, Sielezniew M, Simcox DJ, Stankiewicz AM, Steiner FM, Švitra G, Ugelvig LV, Van Dyck H, Varga Z, Witek M, Woyciechowski M, Wynhoff I, Nash DR (2019) Patterns of host use by brood-parasitic *Maculinea* butterflies across Europe. *Philos Trans R Soc B* 374(1769):20180202. <https://doi.org/10.1098/rstb.2018.0202>
- Theng M, Jusoh WFA, Jain A, Huertas B, Tan DJX, Tan HZ, Kristensen NP, Meier R, Chisholm RA (2020) A comprehensive assessment of diversity loss in a well-documented tropical insect fauna: almost half of Singapore's butterfly species extirpated in 160 years. *Biol Conserv* 242:108401. <https://doi.org/10.1016/j.biocon.2019.108401>
- Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT, Lawton JH (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303(5665):1879–1881. <https://doi.org/10.1126/science.1095046>
- Toso GG, Balletto E (1976) Una nuova specie del *Agrodiaetus* Hübn. (Lepidoptera:Lycaenidae). *Annali Del Museo Civico Di Storia Naturale Giacomo Doria* 81:124–130
- van Strien AJ, van Swaay CA, van Strien-van Liempt WT, Poot MJ, WallisDeVries MF (2019) Over a century of data reveal more than 80% decline in butterflies in the Netherlands. *Biol Conserv* 234:116–122. <https://doi.org/10.1016/j.biocon.2019.03.023>
- van Swaay C, Wynhoff I, Wiemers M, Katbeh-Bader A, Power A, Benyamini D, Tzirkalli E, Balletto E, Monteiro E, Karaçetin E, Franeta F, Pe'er G, Welch H, Thompson K, Pamperis L, Dapporto L, Šašić M, López Munguira M, Micevski N, Dupont P, Garcia-Pereira P, Moulai R, Caruana R, Verovnik R, Bonelli S, Beshkov S (2014) *Polyommatus ripartii*. The IUCN Red List of Threatened Species 2014 e.T174232A53713577. IUCN SSC Butterfly Specialist Group
- Verity R (1926) *Zygaena*, *Grypocera* and *Rhopalocera* of the Cottian Alps compared with other races. *Entomol Rec J Var* 38:120–126
- Vila R, Lukhtanov VA, Talavera G, Gil-t F, Pierce NE (2010) How common are dot-like distributions? Taxonomical oversplitting in western European *Agrodiaetus* (Lepidoptera:Lycaenidae) revealed by chromosomal and molecular markers. *Biol J Lin Soc* 101(1):130–154
- Vogel G (2017) Where have all the insects gone? *Science* 356(6338):576–579. <https://doi.org/10.1126/science.356.6338.576>
- Wells H, Wells PH (1992) The monarch butterfly: a review. *Bull South Calif Acad Sci* 91(1):1–25
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(sup1):S120–S139. <https://doi.org/10.1080/00063659909477239>
- Wiemers M, Keller A, Wolf M (2009) ITS2 secondary structure improves phylogeny estimation in a radiation of blue butterflies of the subgenus *Agrodiaetus* (Lepidoptera:Lycaenidae:*Polyommatus*). *BMC Evol Biol* 9(1):300. <https://doi.org/10.1186/1471-2148-9-300>
- Wiemers M, Balletto E, Dincă V, Fric ZF, Lamas G, Lukhtanov V, Munguira ML, van Swaay CAM, Vila R, Vliegenthart A, Wahlberg N, Verovnik R (2018) An updated checklist of the European butterflies (Lepidoptera, Papilionoidea). *ZooKeys* 811:9. <https://doi.org/10.3897/zookeys.811.28712>
- Zuur A, Ieno EN, Meesters E (2009) A beginner's guide to R. Springer, New York

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