Correlaciones ambientales del ciclo de vida de poblaciones de coleópteros de la superficie del suelo en dos estratos altitudinales al SE en Tenerife

Study of the life-cycle of populations of soil-surface beetles in two zones of an altitudinal gradient on the island of Tenerife in relation to the climate

Trabajo de Fin de Grado

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1. Abstract

Life cycles of some terrestrial soil-surface beetle species are analysed in relation to the seasonal climatic variations in two ecosystems located in the basal stratum and in the cloudy montane stratum in the southeast of Tenerife. The study period was from September 2018 to May 2019. Seven sampling plots were placed with pitfall traps and the catches were collected biweekly. A fraction of the sample was transported to the laboratory for ovarian maturation and weight analysis. Activity density, ovarian maturation, and dry weight models were correlated with seasonal climatic fluctuations. The comparisons made with the sampling periods of the 1980's and 2000's show climatic changes, disappearance of endemic species and the appearance of generalist species, as well as notable changes in population activity density models, more in ground-beetles than in darkling-beetles, due to its greater sensitivity to current hydric and thermal stress.

Keywords: coleoptera; life cycles; activity density; ovarian maturation; dry weight; environmental correlations.

Resumen

Se analizan los ciclos de vida de algunas especies de coleópteros terrestres de la superficie del suelo en relación con las variaciones climáticas estacionales en dos ecosistemas situados en el estrato basal y el montano húmedo del sureste de Tenerife. El periodo de estudio abarcó desde septiembre de 2018 hasta mayo de 2019. Se dispusieron siete cuadratines de muestreo con trampas de caída y las capturas se recogieron quincenalmente. Una fracción de la muestra se transportó al laboratorio para el análisis de la maduración ovárica y peso. Modelos de densidad-actividad, maduración ovárica, y peso seco se correlacionaron con las fluctuaciones climáticas estacionales. Las comparaciones realizadas con los periodos de muestreo de las décadas de los 80 y los 2000 manifiestan cambios climáticos, desaparición de especies endémicas y aparición de especies generalistas, así como notables cambios en los modelos de densidad-actividad de las poblaciones, más en carábidos que en tenebriónidos al ser más sensibles al estrés hídrico y térmico actual.

Palabras clave: coleópteros; ciclos de vida; densidad-actividad; maduración ovárica; peso seco; correlaciones ambientales

2. Introduction

2.1. Background

It is known that insects play important roles in ecosystems services, but most of their life-cycle processes are affected by climate (Patterson *et al.,* 1999). Therefore, important changes in their abundance and diversity will potentially alter the services they provide (Cornelissen, 2011). Thus, this group may be particularly suitable as environmental and ecological bioindicators, especially terrestrial soil-surface beetles, which have shown to be sensitive to human induced environmental changes (Gerlach *et al.,* 2013, Rainio & Niemelä, 2003). In the last years, some authors have use soil-surface beetles as environmental bioindicators for their researches (Wang *et al.,* 2014; Kaltsas *et al.*, 2012).

The characterization of the life cycles of the species is essential for studies of taxonomy, secondary production, conservation of habitats, as well as for the formulation of hypotheses related to the structure, stability, persistence, complexity and diversity of the community (Boesch et. al, 1976). Studies of soil-surface beetle life cycles have provided information of great importance for the elaboration of unifying concepts on the dynamics of insect populations (Mitchell, 1963; Thiele, 1977; Luff, 1979). Most of these works have been carried out in arctic, subarctic and continental climates, but few authors have addressed this problem in more southern areas (de los Santos *et al.,* 1985), where seasonal climatic fluctuations present very different nuances. In this context, Tenerife represent a suitable study area due to the remarkable climatic variation among its altitudinal strata. The incidence of climatic instability could be analysed in each elevation strata, where different life strategies (xerophilic vs. hydrophilic) could be affected in other ways. So, studying life-cycles will indicate adaptive responses as a result of environmental changes, especially climatic fluctuations.

2.2. Justification

Terrestrial soil-surface beetles, as good ecological indicators, were carried out to study the relationship between environmental changes, especially climatic, and their life-cycles (de los Santos *et al*., 2014). Climate related life-cycles variability could be studied within a framework of short-term fluctuations, seasonality and elevation gradients. One-year sampling in many ecosystems could be an exception, because of it is necessary to consider more sampling years in the study of climate change effects. The objective of this project is to complete a new sampling year and to compare it with the analyzed available data of the ecology area.

3. Objectives

It pretends to evaluate the relationships between climatic variability and soil-surface beetle populations life-cycles on two sampling strata at the southeast of Tenerife. The results obtained during this sampling period 2018/19 will be compare with the existing data of the years 1985/86 and 2001/02. The main questions we establish are: Have soil-surface beetle populations undergone alterations in their life-cycles? Are there even species that are no longer present? Do new species appear? Being all of this consequence of possible climate changes. Concretely, we could determine activity density, ovarian maturation and dry weight models related to climatic fluctuations and its variability.

Particularly, we can establish the following specific hypothesis:

1. In the data collection there are evidence of short-term thermal fluctuations.
2. Both basal stratum and cloudy montane stratum assemblages show different alternatives to environmental changes.
3. Activity periods of the species studied have varied in the last 34 years.
4. Asynchronies between activity density, ovarian maturation and average dry weight seasonal maxima for the same species among the sampling years.

4. Materials and methods

4.1. Study site

4.1.1. General description

Fieldwork was undertaken in two altitudinal strata, located on the S.E. (leeward) slope of the island of Tenerife, Valley of Güímar. This study was restricted to the basal stratum (38-43 m a.s.l. (metres above sea level)) and the cloudy montane stratum (570–680 m a.s.l.).

At the basal stratum, fieldwork was undertaken at the Special Natural Reserve of the Malpaís of Güímar, on volcanic laundries and sandy fringe. The climate of the study area is dry temperate, arid and warm. Mean annual temperature values shows only small annual fluctuations (16.5–21ºC), and the mean annual precipitation is about 300 mm (de los Santos, 2000). The dominant vegetation type in the volcanic laundries is xerophytic scrub, rich in succulents, especially cactiform or dendroid spurges (such as *Euphorbia canariensis* L., *E. balsamifera* Ait., *E. obtusifolia* Poir. and *Ceropegia fusca* Bolle). On the sandy fringe, it settles a pseudo-steppe gramineous formation of thatching-buffel grass, characterized by high cover of several hemicryptophytes: *Hyparrhenia hirta* (L.) Stapf in Oliver, *Cenchrus ciliaris* L., *Aristida adscensionis* L. and *Tetrapogon villosus* Desf. In their more typical aspect, they are accompanied by gorse (*Launaea arborescens* (Batt.) Murb.), bleats (*Plocama pendula* Ait.) and good firewood (*Neochamaelea pulverulenta* (Vent.) Erdtm.).

At the cloudy montane stratum (Ravine of Badajoz), two representative zones were chosen. One sampling plot at 500 m a.s.l., which was occupied in the past by crops, is currently in secondary succession, covered by midlands scrubs (such as *Artemisia thuscula* Cav., *Euphorbia lamarckii* Sweet, *Kleinia neriifolia* Haw. and *Lavandula canariensis* Mill.). A higher sampling plot at 700 m a.s.l., in the cloud zone due to trade wind inversion. The orographically induced uplift of the trade winds in this site results in high cloudiness below the temperature inversion, especially on the windward slope, decreasing radiation that contributes to a higher level of moisture. The mean annual temperature is quite constant, between 14.5ºC and 16.5ºC, although there are seasonal fluctuations, and the mean annual precipitation is 700 mm. The vegetation (xeric laurel forest) is mainly composed of *Ilex canariensis* Poir., *Arbutus canariensis* Veill. and *Erica arborea* L.

4.1.2. Climatic variables during the sampling period

Due to the lack of microclimatic information during the study period 2018/19, mesoclimatic data from weather stations located in the same elevational strata have been used to compare general temperature and precipitation trends between the three periods of years. In order to observe climatic fluctuations patterns, other scales have been used in the graphics in some cases. Because all the studied species present nocturnal activity, the minimum temperature defines its life cycle. Graphics of both strata (Figs. 1-2) show the same temperature variation trend for the three periods: the maximum peak of temperature is reached in mid-summer (August), then it decreases until mid-winter (January or February), when it is recorded the annual minimum temperature; later temperature increases again until August. However, the minimum temperature shows variations between the studied years: in the periods 1985/86 and 2001/02 the annual minimum temperature is recorded in February, while in 2018/19 there is a minimum peak of temperature in January. Comparing the graphics of each sampling period, it is noted an increase of minimum temperature. Although the climatic variables cannot be compared in the study sites, it is thought that if the comparisons were made, the results would also show an increase in the temperature in the Malpaís of Güímar and in the Ravine of Badajoz. This last winter of 2018 was one of the driest of the last 34 years, and it has been preceded by a spring in which, although it has rained, it has been an insufficient rainfall to conclude that the season has been humid.

4.1.2.1. Basal stratum

The graphs obtained from the climatic parameters of the sampling years 2018/19, 2002/01 and 1985/86 in the basal stratum are shown in Fig. 1. Graphics B with mesoclimatic data of this stratum, show an increase of the annual minimum temperature in 0,9ºC and of the annual maximum temperature in 0,6ºC. In the study period 2018/19 (B1), the annual minimum temperature has exceeded 15ºC and the maximum peak has exceeded 22ºC. Also, graphics show a decrease of the precipitation along the study periods. In 2018/19 (B1), precipitation has decreased 135,7 mm compared with 1985/86 (B3), and 270,75 mm compared with 2001/02 (B2). The period of 2018/19 has been very dry, with low precipitations, and warmer due to the increase of temperatures. This causes a situation of extreme climatic conditions, which reduces the resources in this basal stratum and affects the soil-surface populations.

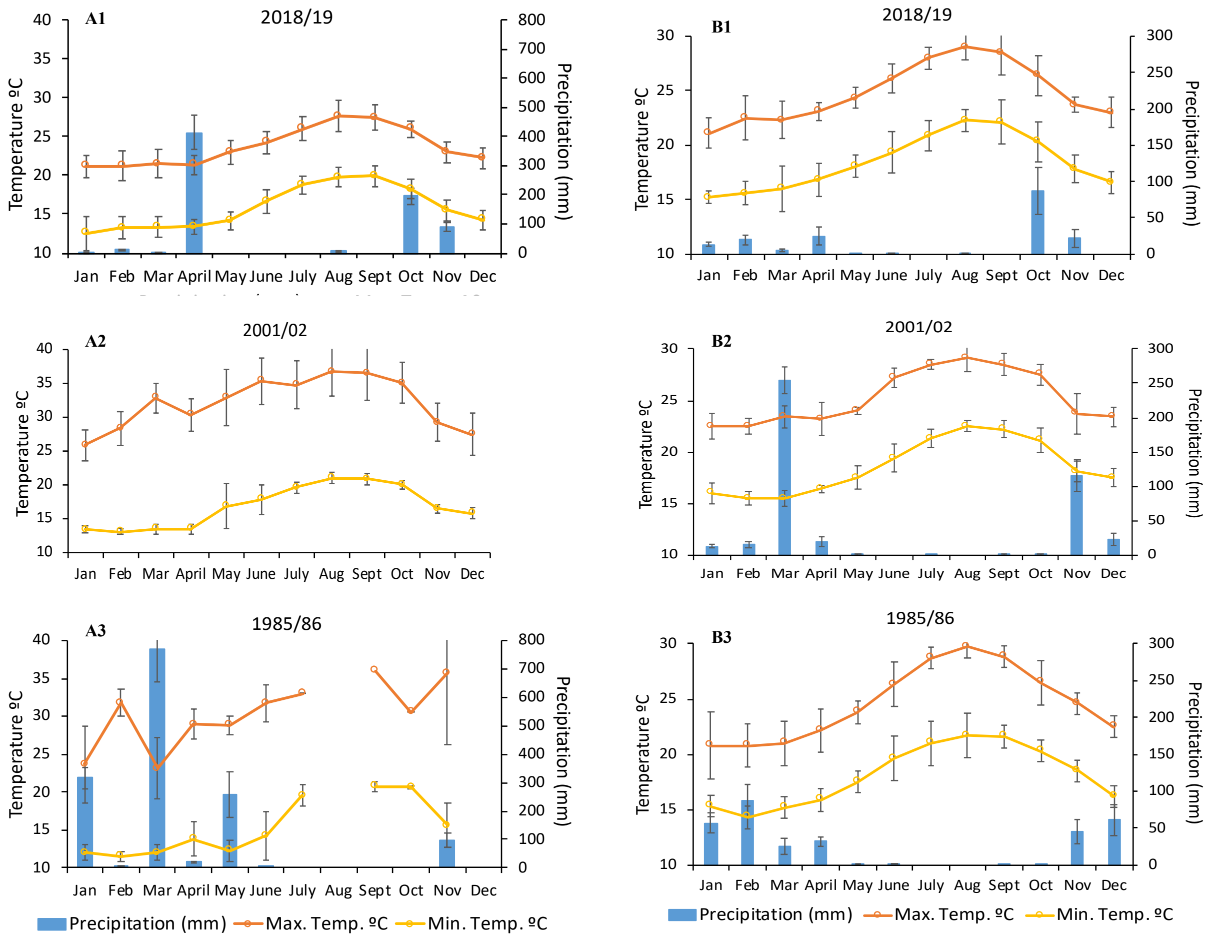

Fig. 1. Climatic parameters (maximum temperature, minimum temperature and precipitation) of the basal stratum in the sampling periods of 2018/19 (1), 2001/02 (2) and 1985/86 (3). Mesoclimatic data of Güímar weather station in A1 graphic and of Santa Cruz of Tenerife weather station in B graphics. Microclimatic data in A2 and A3 graphics. Mean number ±95% CI (vertical bars).

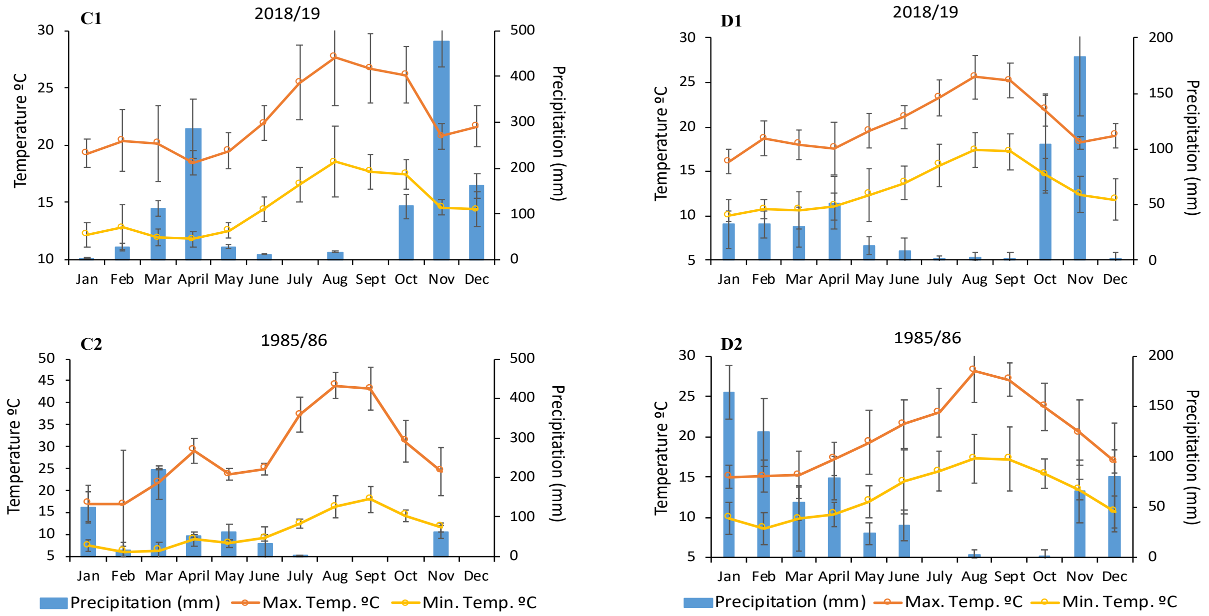

Fig. 2. Climatic parameters (maximum temperature, minimum temperature and precipitation) of the cloudy montane stratum in the sampling periods 2018/19 (1) and 1985/86 (2). Mesoclimatic data of the stations Lomo de Mena in C1 graphic and Tenerife North Ariport in D graphics. Microclimatic data in C2 graphic. Mean number ±95% CI (vertical bars).

4.1.2.2. Cloudy montane stratum

The graphs with the climatic variables of the sampling years 2018/19, 2002/01 and 1985/86 in the cloudy montane stratum are shown in Fig. 2. Graphics D with mesoclimatic data of this stratum, show an increase of the annual minimum temperature in 1,4ºC. In the study period 2018/19 (D1), the annual minimum temperature has reached 10ºC. However, the maximum peak of the minimum temperature is similar in both periods. Respect to the precipitation, graphics shown a decrease along the study periods. In 2018/19 (D1), it has rain 166,85 mm less than in 1985/86 (D2). This situation of temperature increase and precipitation decrease, greatly affects all the populations of soil-surface beetles, which lives in the cloudy montane stratum and needs enough humidity to complete its life cycle.

4.2. Fieldwork

Along the altitudinal gradient of the Valley of Güímar, seven study plots were chosen, five plots in the basal stratum of the Island (Malpaís of Güímar) and two plots in the cloudy montane stratum (Ravine of Badajoz) (Table 1). Soil-surface beetle populations on each plot were sampled with a grid of 21 pitfall traps from September of 2018 to May of 2019. In each plot, a rectangular grid at 3x7 traps was established, with each row 5 m apart and the traps 10 m apart. Slopes, rocky surface and dense vegetation were avoided. A funnel trap was used (de los Santos *et al.*, 1982) in which neither baits nor killing–preserving agents were used; these traps were emptied biweekly. Soil-surface beetles were identified at species level, counted and after released within 2 m of each trap, except a fraction of the specimens captured biweekly, which was taken to the laboratory for further analysis, within a plastic container labelled according to date and plot.

Site	Zone	Landscape	Plot	Elevation (m a.s.l.)	Sampling periods
1	Malpaís of Güímar	Xerophytic scrub	1	41	11 Sept 18 - 12 May 19
1	Malpaís of Güímar	Thatching-buffel grass	2	40	13 Sept 18 - 12 May 19
1	Malpaís of Güímar	Thatching-buffel grass	3	38	13 Sept 18 - 12 May 19
1	Malpaís of Güímar	Xerophytic scrub	4	43	11 Sept 18 - 12 May 19
1	Malpaís of Güímar	Thatching-buffel grass	5	43	12 Sept 18 - 12 May 19
2	Ravine of Badajoz	Midland scrub	6	570	21 Sept 18 - 18 May 19
2	Ravine of Badajoz	Xeric laurel forest	7	680	19 Sept 18 - 18 May 19

Table 1. Sites studied (1 and 2) with indication of zone (Malpaís of Güímar and Ravine of Badajoz), landscape (xerophytic scrub, thatching-buffel grass, midland scrub, xeric laurel forest), plot (1-7), elevation (meters above sea level) and sampling period.

4.3. Laboratory work

The catch was transferred into 4% formaldehyde until further dissection to determine sex and ovarian maturation using established criteria (Gilbert, 1956; Barlow, 1973; Luff, 1975), as optimal storage method since it does not alter the estimate of body mass (Knapp, 2012). Testis maturation was not assessed. Reproductive condition was determined by dissecting females, examining the ovaries and counting the number of mature and immature eggs in the oviducts. Four reproductive categories were recognized: (1) immature females without eggs, (2) maturing females with small oocytes that have not yet developed the protective shell, (3) mature females with mature eggs in the oviducts and (4) spent females without eggs, but with corpus luteum. Subsequently, each individual was dried in an oven at 60ºC for 24 h, and afterwards cooling in a desiccator and then was weighed on an electronic balance to determine mean body weight to the nearest 0,01 mg (de los Santos, 2013).

4.4. Data processing

Population estimates for pitfall traps method were expressed in terms of activity density, which reflects the number of beetles that were more through the study area. Activity density pattern was calculated for every Tenebrionidae and Carabidae species. This parameter provides a good estimate of the role of a species in an ecosystem, not only depending on its frequency but also on its mobility (Thiele, 1977). It is calculated dividing the number of individuals caught by the product of multiplying the number of traps times the day that have passed. In this way fluctuations in the temporal dynamics can be established. The data obtained reflects the reproductive processes of adult coleoptera.

The monthly average variation of life histories features and seasonal patterns of activity density were compared over 34 years in relation to climatic variables by graphical and statistical analyses. Simple linear regression coefficients, Student's t-test and ANOVA F-test were performed using the Statistical Package for the Social Sciences version 25.0 for Windows (IBM SPSS Statistics, Inc., Chicago, IL, USA). The applied hypothesis test in this research for the difference between two regression coefficients is Student's t-test–Z values (Clogg *et al.*, 1995).

The most representative species of each elevation strata were chosen: *Hegeter amaroides* Solier, 1835 (Coleoptera: Tenebrionidae), *Hegeter tristis* (Fabricius, 1792) (Coleoptera: Tenebrionidae), *Arthrodeis obesus* (Brullé, 1838) (Coleoptera: Tenebrionidae), *Zophosis bicarinata* Solier, 1834 (Coleoptera: Tenebrionidae), *Pimelia canariensis* Brullé, 1838 (Coleoptera: Tenebrionidae) and *Carabus interruptus* Dejean, 1831 (Coleoptera: Carabidae).

4.5. Data sources

The accomplishment of part of the work has been thanks to the contribution of data from previous works carried out by Antonio de los Santos, who has given me the results to analyze and to compare it with those obtained during my sampling period.

Climatic variables were obtained from four weather stations of the AEMET (Agencia Estatal de Meteorología). From the basal stratum, were used Santa Cruz of Tenerife (C449C, 136 m a.s.l.) and Güímar (C439J, 115 m a.s.l.) weather stations. At the cloudy montane stratum, were selected Tenerife North Airport (C447A, 632 m a.s.l.) and Lomo de Mena (C437E, 500 m a.s.l) weather stations. Daily climatic data of maximum temperature, minimum temperature and precipitation, have been grouped by months and it has been calculated the monthly average of each parameters.

5. Results

5.1. Darkling-beetles (Col. Tenebrionidae)

5.1.1. Seasonal patterns of activity density

The activity density seasonal distribution of terrestrial darkling-beetle populations in the basal stratum is shown in Figs. 3-4. Species of Tenebrionidae, except *Pimelia canariensis,* present a surface activity period from the end of winter until the end of summer.

Hegeter amaroides (A) is the most abundant species of the Malpaís of Güímar. In summer, the population reached its monthly maximum of activity density when temperature increases. From November to April, when temperature decreases, the population reached its monthly minimum of activity surface. Graphics of *H. amaroides* show populations size fluctuations: in the period of 2001/02 (A2) this species presented a great activity density, but if we compare graphics of 1984 (A3) with 2018/19 (A1) its activity surface has not changed much.

Activity density of *Hegeter tristis* (B) is very low and irregular in every study period and presents great variations. Regularity is marked by the intensity of sampling and the sample size, when these are low the variations are greater. In graphic of 2001/02 (B2) it is detected an activity density seasonal model: during the winter this species presents its monthly minimum of activity density, which increases just like the temperature, reaching its monthly maximum of activity surface from July to October.

Both *Arthrodeis obesus* and *Zophosis bicarinata* are gregarious species and show a contagious spatial distribution, that explained the peaks which are observed in the graphics.

Graphics of *A. obesus* (C) show a mainly activity density during the spring and mid-summer, from July its surface activity decreases, reaching its monthly minimum of the activity surface along the winter. In September 2018 (C1) its activity density was greater than the past years, this can be a consequence of a summer with higher temperatures and low precipitation. However, in a global vision it seems that there is a certain reduction of its activity density throughout the years, but it is not conclusive.

Zophosis bicarinata (D) adults are active throughout the year, although its activity density is mainly from early spring to the end of summer. This species presents two peaks of maximum activity in the spring and in the fall. The seasonal patterns of activity density of this species have not present great variations throughout the years of study, and it remains constant for each period.

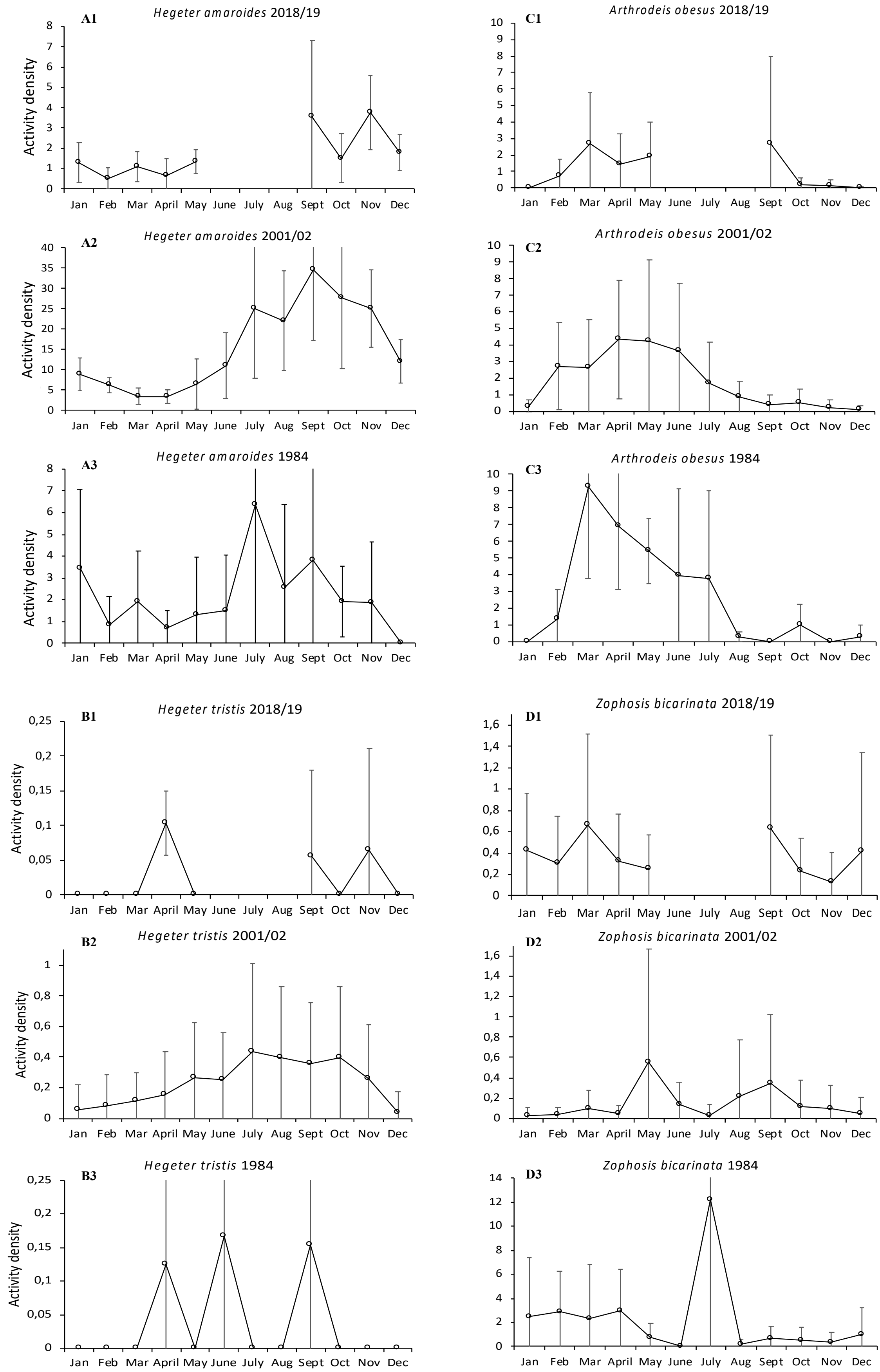

Fig. 3. Activity density patterns for predominant species of the Malpaís of Güímar: *Hegeter amaroides* (A)**,** *Hegeter tristis* (B), *Arthrodeis obesus* (C) and *Zophosis bicarinata* (D) in the basal stratum in the sampling years 2018/19 (1), 2001/02 (2) and 1984 (3). Mean number ±95% CI (vertical bars).

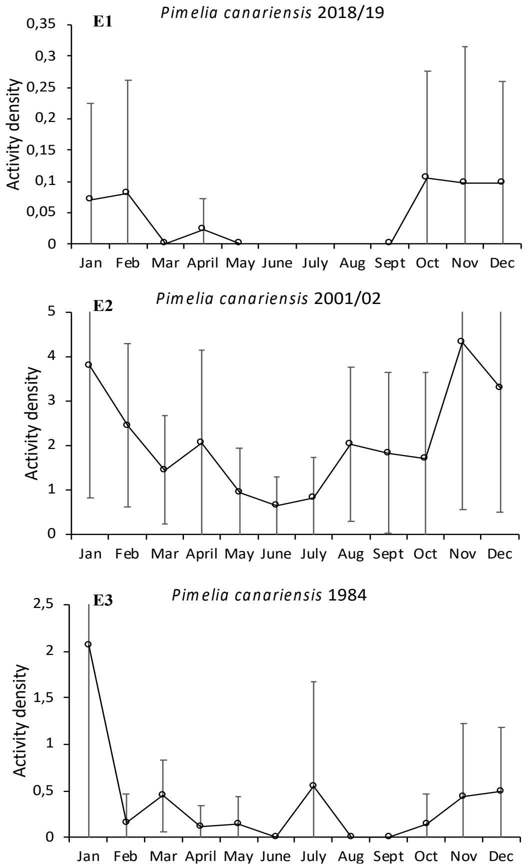

Fig. 4. Activity density patterns of *Pimelia canariensis* (E) in the basal stratum in the sampling years 2018/19 (1), 2001/02 (2) and 1984 (3). Mean number ±95% CI (vertical bars).

Pimelia canariensis (E) emerges on the soil surface toward the mid-summer when minimum average soil surface temperature is 21ºC (de los Santos *et al.*, 2006). In winter (January), the population reached its monthly maximum of the activity density when temperature decreased around its inferior limit of tolerance (12-14ºC). From February to July, when temperature increased, the population reaches its monthly minimum of the activity density.

P. canariensis adults are active throughout the year, although a preference exists for the wet season, and adults emerge over a relatively long period of time (May–October).

The activity density seasonal model remains constant along the study periods, although its activity surface has decreased throughout the years.

5.1.2. Life histories features

The temporal evolution of the sex ratio, the average number of eggs found in the ovaries of the females and the average dry weight during the study periods for the soil-surface darkling-beetle species are represented in Figs. 5-7.

Hegeter amaroides (A) is a polyvoltine species, so it can have several generations per year. The dominance of females (A1 y A4) during the winter corresponded to the period of oviposition, while the dominance of males implied a period of copulation in the summer. Dry weight of males and females (A2 y A5) is very regular throughout the year, being it greater at the end of winter. The average number of immature and mature eggs (A3 y A6) found in females was greatest in fall and winter, with a maximum peak in mid-winter. Then, it decreases until the summer when it is shown a minimum average number of eggs. During the summer and the fall, the average number of immature eggs is greater, which decreases in winter what mean an increase of the average number of mature eggs. Population patterns seems to be similar in both periods of years.

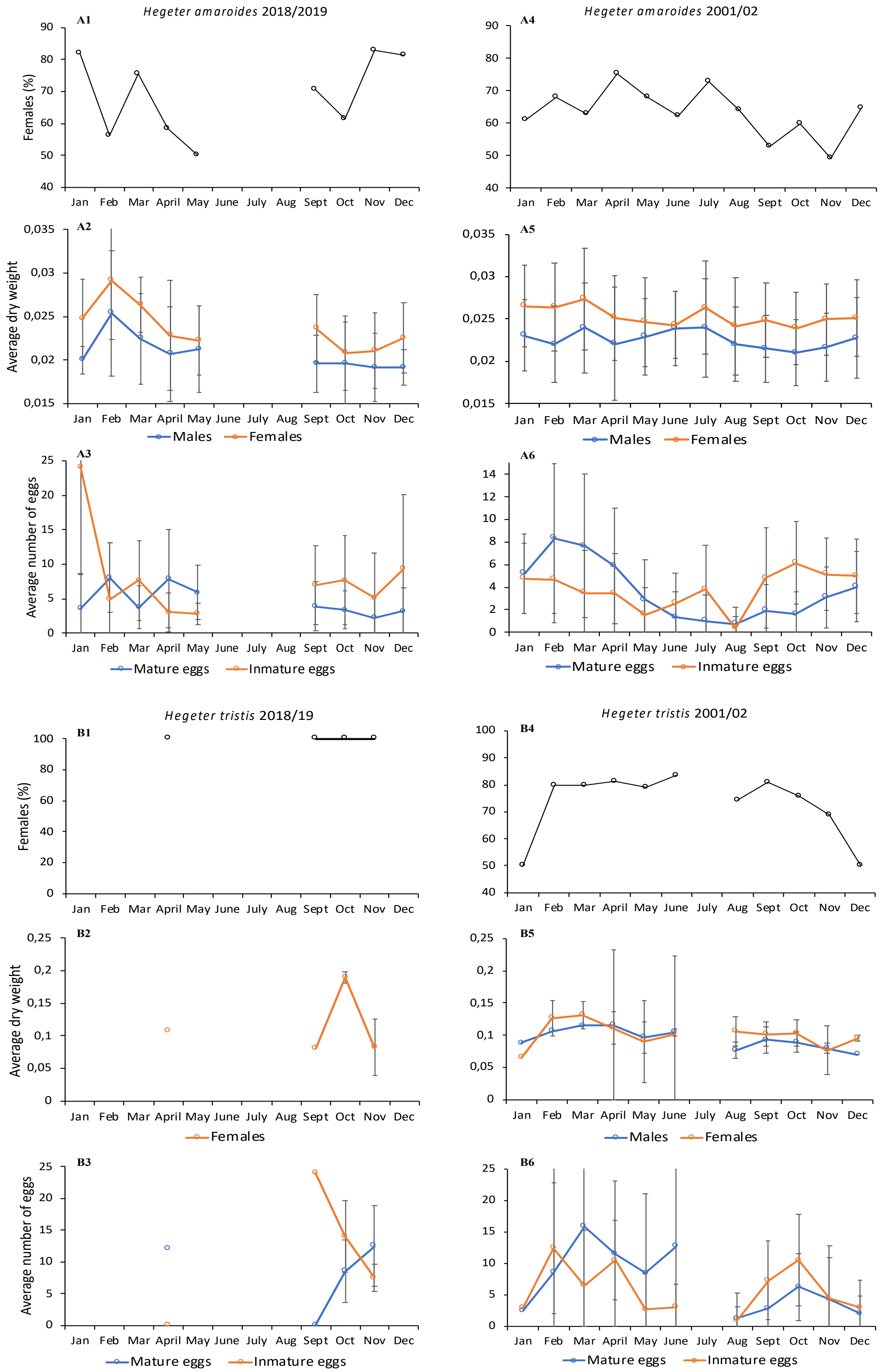

Fig. 5. Population parameters: sex ratio (1, 4), average dry weight (2, 5) and average number of mature and immature eggs in females (3, 6) of *H. amaroides* (A) and *H. tristis* (B) in the sampling periods 2018/19 (1, 2, 3) and 2001/02 (4, 5, 6). Mean number ±95% CI (vertical bars).

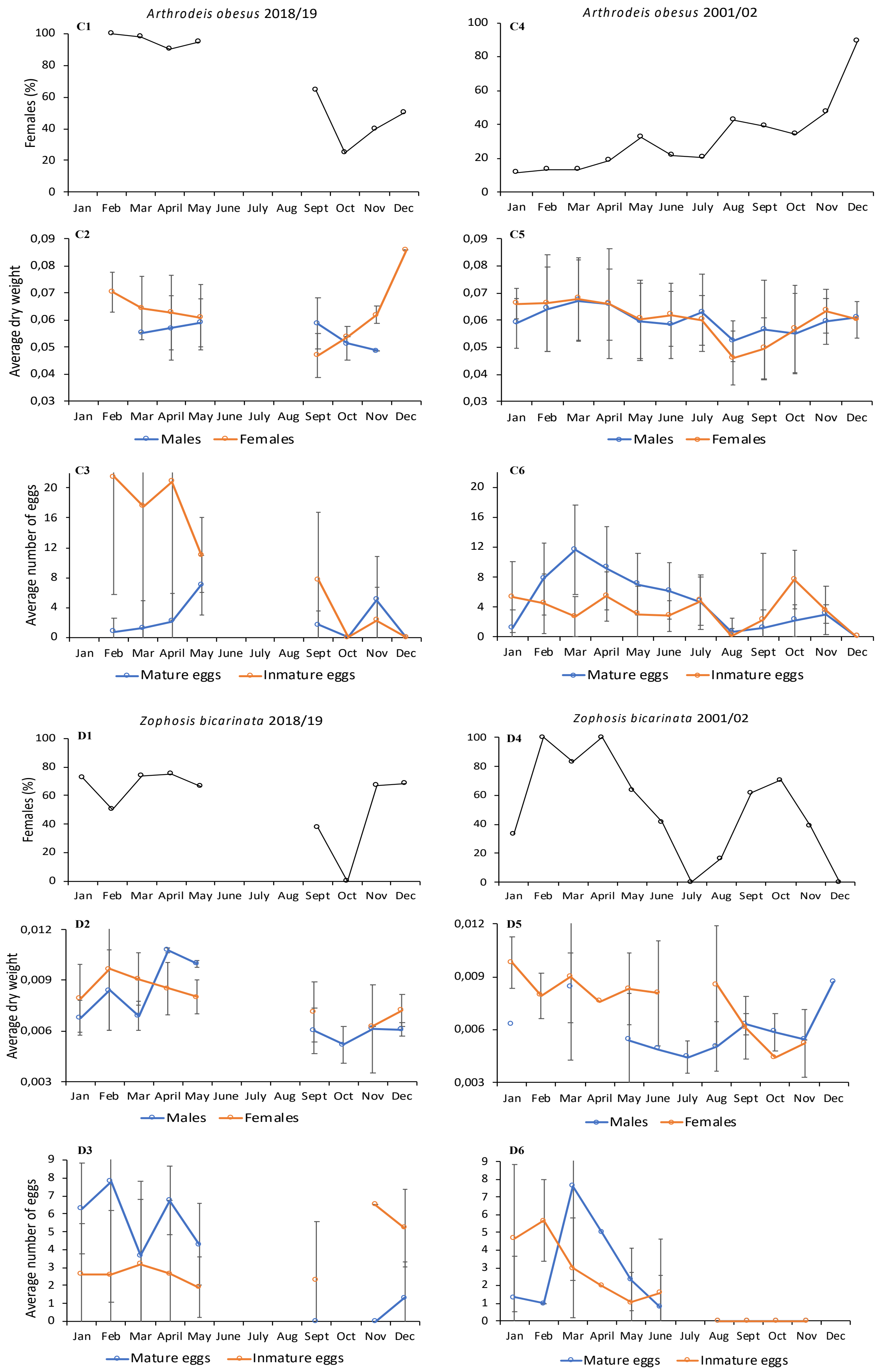

Fig. 6. Population parameters: sex ratio (1, 4), average dry weight (2, 5) and average number of mature and immature eggs in females (3, 6) of *A. obesus* (C) and *Z. bicarinata* (D) in the sampling periods 2018/19 (1, 2, 3) and 2001/02 (4, 5, 6). Mean number ±95% CI (vertical bars).

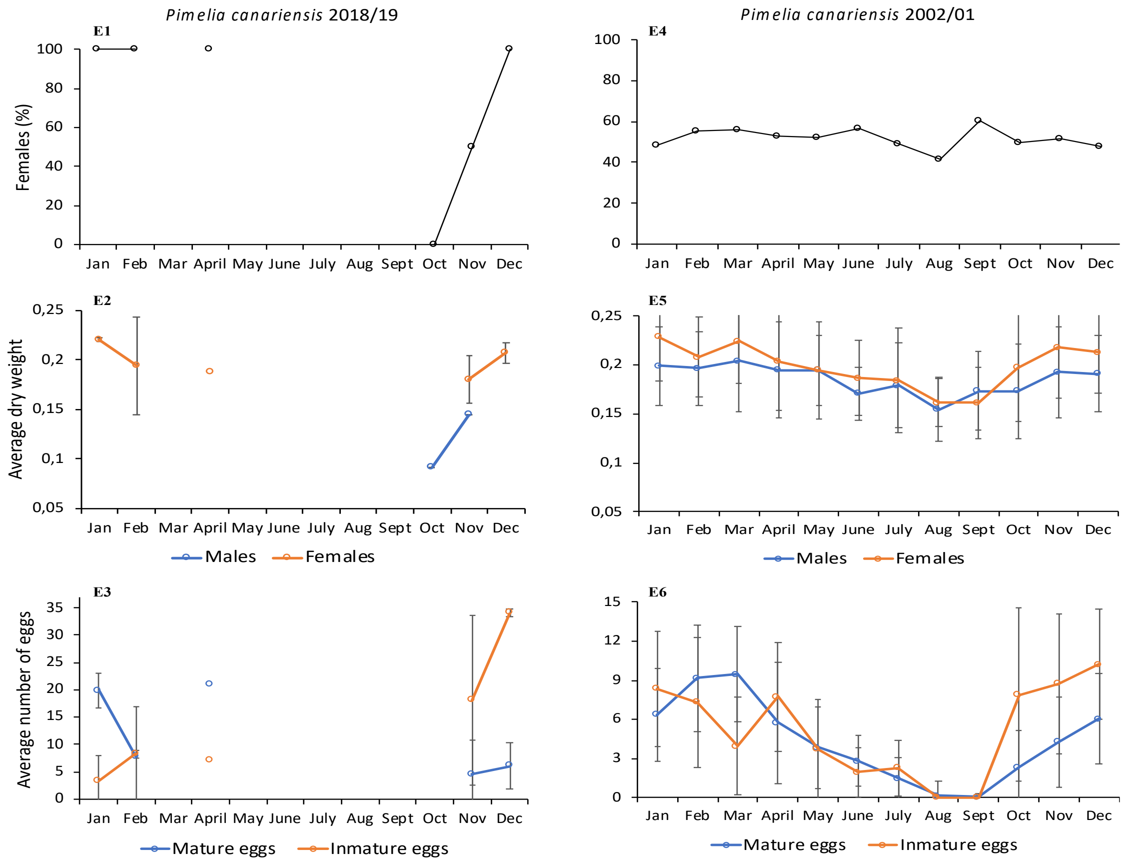

Fig. 7. Population parameters: sex ratio (1, 4), average dry weight (2, 5) and average number of mature and immature eggs in females (3, 6) of *P. canariensis* (E) in the sampling periods 2018/19 (1, 2, 3) and 2001/02 (4, 5, 6). Mean number ±95% CI (vertical bars).

Graphics of *Hegeter tristis* (B) show the period of oviposition (B1 y B4) during the spring. Average dry weight (B2 y B5) increases from mid-fall until the end of winter, when it presents its maximum peak. Average number of immature eggs (B3 y B6) increases from the end of summer until the winter when it shows a maximum. During the spring, average number of mature eggs is higher. In the summer, average number of eggs and average dry weight are minimum. In 2018/19 (B1-3) were captured a few individuals, so sample size is low.

The period of copulation of *Arthrodeis obesus* (C) is in summer, while the dominance of females (C1 y C4) in winter corresponded to the period of oviposition. The average dry weight (C2 y C5) is minimum at mid-summer, then it increases until the end of winter when it is maximum. Average number of mature eggs (C3 y C6) is greater from the end of the winter until early summer, and it presents a maximum peak at the end of winter. During the fall, average number of immature eggs is higher. Life histories features seems to be similar in both periods of years, although in 2018/19 there was a higher number of immature eggs during the end of winter.

Zophosis bicarinata (D) population presents an increment of the average dry weight (D2 y D5) of males from mid-summer to early winter, when it is maximum and there is a dominance of males (D1 y D4), what correspond to the period of copulation. From the end of winter until early spring the average dry weight of females increases. During the spring, average number of mature eggs (D3 y D6) is greater. There is a dominance of immature eggs in the end of winter, and a dominance of mature eggs in early spring. Seasonal distribution of populations parameters follows a similar model in both periods of years.

In *Pimelia canariensis* (E) emergence of new adults began in spring and peaked in October, both female and male dry weights (E2 y E5) during the months of summer were significantly smaller than those in autumn and winter. The average number of immature and mature eggs (E3 y E6) found in females was greatest in fall and winter, and mature eggs peaked at the end of winter. Mature egg production was high in winter when egg laying began. This species prolonged its oviposition period (E1 y E4) until end of spring and peaked in June. Due to the low species captured, there are great variations of the population parameters between each period; however, populations models remain constant.

5.1.3. Populations size fluctuations

Average annual number of darkling-beetles catches per sampling station in three elevational strata (basal stratum, low and high cloudy montane stratum) of the study periods 1985/86, 2001/02 and 2018/19 from September to May are shown in Table 2.

In the three altitudinal strata, it has been a great decrease of the number of darkling-beetle species captured along the periods of years. In the basal stratum, there is a great difference between the number of species captured throughout the years. Darkling-beetle species are characteristic of the basal stratum; however, its populations have been significantly reduced. In the period of 2001/02 a great number of darkling-beetle species were capture due to an intensive sampling. In 2018/19 the average number of species captured has decreased by 71,75% compared to 1985/86 and 87,9% respect to 2001/02. Highlight the great decreased of *Hegeter amaroides*, of which has been captured 78,75% less in this last period of 2018/19 in respect of 1985/86, and 91,41% less than in 2001/02.

In the low cloudy montane stratum, captures in both periods of years were low, but in 2018/19 different species have been captured. In the high cloudy montane stratum, only one species (*Crypticus navicularis*) has been captured in 2018/19, while four species were captured in 1985/86, of which *Hegeter proximus* was the most abundant in the past. This represents 97,97% less individuals captured in 2018/19 than in 1985/86 at high cloudy montane stratum.

Species	Basal Stratum			Low Cloudy Montane Stratum		High Cloudy Montane Stratum	
	1985/86	2001/02	2018/19	1985/86	2018/19	1985/86	2018/19
Arthrodeis obesus, Brullé	112	116,667	45,8	0,00	0,00	0,00	0,00
Crypticus navicularis Brullé	0,00	0,00	0,00	0,00	0,00	0,00	1,00
Hegeter amaroides Solier	368,333	920,042	79	8,5	0,00	5,333	0,00
Hegeter brevicollis Brullé	0,00	0,00	0,00	0,00	3	0,00	0,00
Hegeter excisus Lindberg	0,00	0,00	0,00	4,5	0,00	1,333	0,00
Hegeter proximus Lindberg	0,00	0,00	0,00	0,00	0,00	41,333	0,00
Hegeter transversus Brullé	0,00	0,00	0,00	0,00	2	0,00	0,00
Hegeter tristis, Fabricius	8,333	12, 083	0,8	0,00	0,00	0,00	0,00
Nesotes altivagans, Wollaston	0,00	0,00	0,00	0,00	0,00	1,333	0,00
Nesotes fusculus, Wollaston	0,00	0,0833	0,00	0,00	0,00	0,00	0,00
Pimelia canariensis Brullé	3,2	152,167	3	0,00	0,00	0,00	0,00
Zophosis bicarinata Solier	27	10,083	18	0,00	0,00	0,00	0,00
TOTAL	518,866	1211,1253	146,6	13	5	49,332	1,00

Table 2. Average number of darkling-beetle species captured in each sampling plot in the study periods of 1985/86, 2001/02 and 2018/19 at three elevational strata (basal stratum, low cloudy montane stratum and high cloudy montane stratum).

5.2. Ground-beetles (Col. Carabidae)

5.2.1. Seasonal patterns of activity density

The activity density seasonal distribution of *Carabus interruptus* populations in the cloudy montane stratum is shown in Fig. 8. This species only presents activity surface (A) from the end of the fall and mid-spring. At the end of autumn in both periods, the first beetles were captured (average temperature 18.5ºC; range=15–22ºC). Within a few weeks, the population had reached a high activity density. The population present a peak of activity density in mid-winter, during the wettest month of the year (January): average temperature 15.5ºC, range=12–19ºC. In February the activity density decreased and then disappeared along the summer and early autumn.

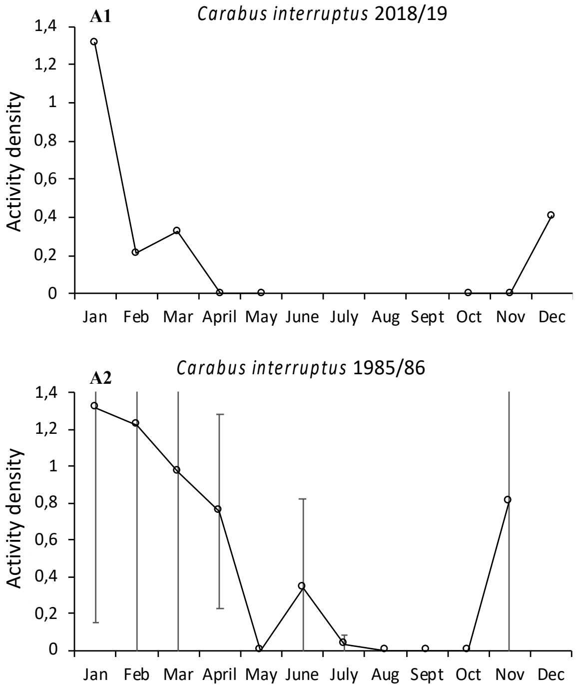

Fig. 8. Activity density patterns of *Carabus interruptus* (A) in the sampling years 2018/19 (1) and 1985/86 (2) at the cloudy montane stratum. Mean number ±95% CI (vertical bars).

Note that the seasonal-activity density pattern and seasonal-rainfall pattern were synchronous, and the maximum estimates recorded of activity density of *C. interruptus* and precipitation consistently occurred during the same seasons of its life cycle.

One main period of activity density was clear from the peak. The activity density was zero throughout the summer and increased after the November rain, which could have triggered renew activity. This species presents marked hydrophilic tendencies, depending on the climatic conditions between different years, its maximums may fluctuate, sensibly, throughout the period of activity. Even, the time in which it is active, can be shortened or lengthened (de los Santos, 2009). Due to the delay of the autumnal rains, in 2018/19 it begins its activity surface in December, reached its maximum activity density in January, and in February is decreased significantly; while in 2001/02 its activity surface remains high until mid-spring.

5.2.2. Life histories features

The temporal evolution of the sex ratio, the average number of eggs found in the ovaries of the females and the average dry weight during the study periods in the cloudy montane stratum for *Carabus interruptus* are represented in Fig. 9.

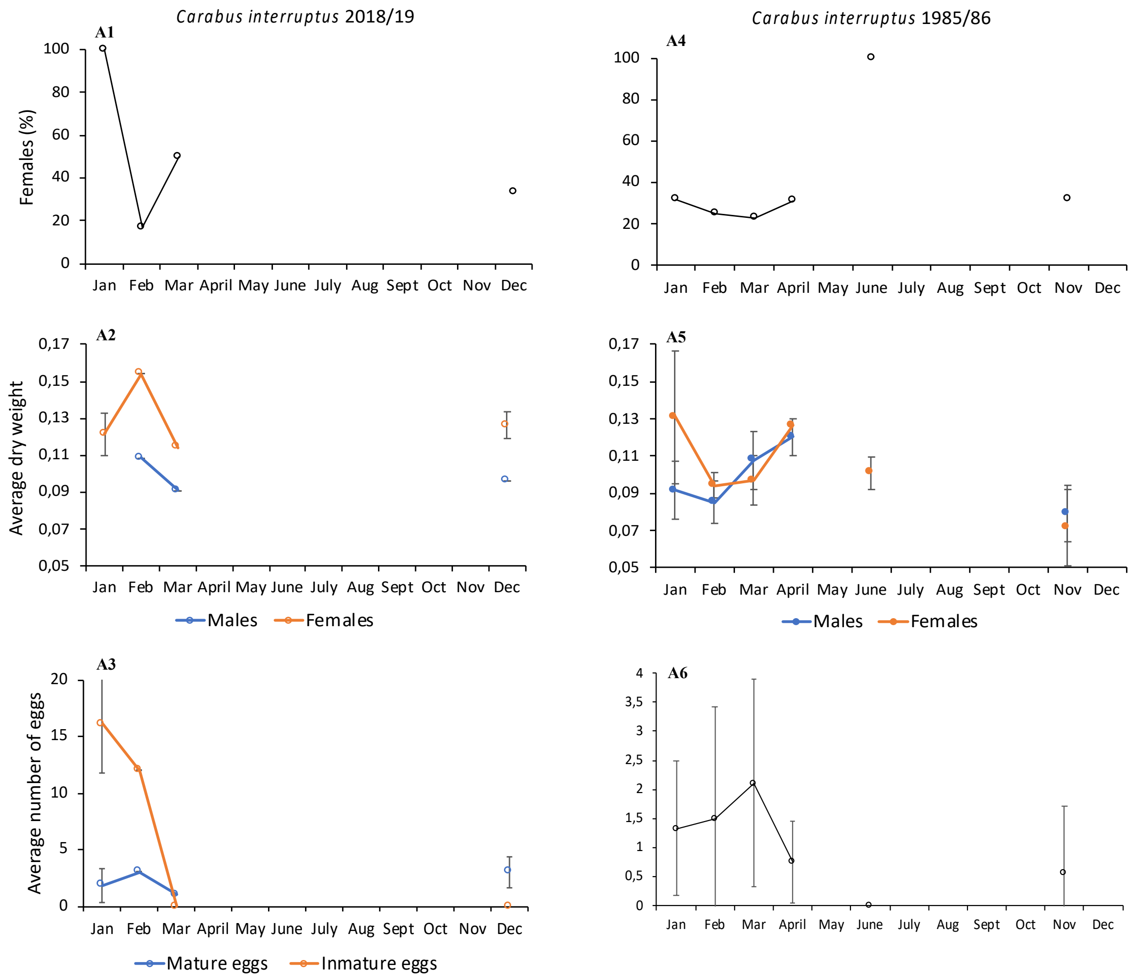

Fig. 9. Populations parameters: sex ratio (1, 4), average dry weight (2, 5) and average number of mature and immature eggs in females (3, 6) of *C. interruptus* (A) in the sampling periods 2018/19 (1, 2, 3) and 1985/86 (4, 5, 6). Mean number ±95% CI (vertical bars).

The emergence of new adults of *C. interruptus* (A) occurred only in spring and the body dry weight peaked in February of 2018/19 (A2) and in April of 2001/02 (A5), from that months the weight decreased in most females and males to early summer. Both female and male dry weights were significantly small during the months of summer signalizing the outset of the diapause period. At the end of autumn, the weight recovered to the initial values of the cycle, increased and peaked in January. Monthly variation in the dry weight of males and females was relatively high throughout the study period of 2001/02. At the end of autumn females were considered mostly immature individuals and in state of maturity (A3 y A6). The maturation was almost completed during the months of November and December, and most of females dissected in January were mature. This species prolonged its oviposition period (A1 y A4) from mid-autumn to early spring. The average number of eggs found in females was maximum in winter, and mature eggs peaked for January - March trimester when egg laying probably began. The period of oviposition ranges from December to March.

5.2.3. Populations size fluctuations

Average annual number of ground-beetles catches per sampling station in three elevational strata (basal stratum, midland scrub and xeric laurel forest) of the study periods 1985/86 and 2018/19 from September to May are shown in Table 3.

Species	Basal Stratum			Low Cloudy Montane Stratum		High Cloudy Montane Stratum	
	1985/86	2001/02	2018/19	1985/86	2018/19	1985/86	2018/19
Calathus ascendens Wollaston	0,00	0,00	0,00	0,00	0,00	5,67	0,00
Calathus depressus Brullé	0,00	0,00	0,00	0,00	0,00	270,67	0,00
Calathus freyi Colas	0,00	0,00	0,00	0,50	0,00	69,00	0,00
Calathus rectus Wollaston	0,00	0,00	0,00	2,75	0,00	22,33	0,00
Carabus interruptus Dej.	0,00	0,00	0,00	0,00	0,00	42,33	14,00
Harpalus schaumi Wollaston	0,00	0,00	0,00	0,00	3,00	0,00	0,00
Nesarpalus cynopus sanctae-crucis Woll.	1,00	0,00	0,00	0,00	0,00	3,67	0,00
Orthomus berytensis, Reiche&Saulcy	0,00	0,00	0,20	0,00	137,00	0,00	26,00
Platyderus languidus alticola Wollaston	1,60	0,167	0,00	14,00	0,00	4,33	0,00
Scarites buparius, Förster	2,20	0,083	0,00	0,00	0,00	0,00	0,00
Trechus flavocintus flavocintus Jeann.	0,00	0,00	0,00	0,50	0,00	1,33	0,00
Zabrus laevigatus Zimmermann	0,80	0,00	0,00	6,75	0,00	4,33	0,00
TOTAL	5,6	0,25	0,2	24,5	140	423,66	40

Table 3. Average number of ground-beetle species captured in each sampling plot in the study periods of 1985/86, 2001/02 and 2018/19 at three elevational strata (basal stratum, low cloudy montane stratum and high cloudy montane stratum).

It is shown the disappearance in the three elevational strata of most ground-beetle species captured in the 1985/86 sampling period, which were very abundant especially at the high cloudy montane stratum. *Calathus depressus* which was a very frequent and abundant species in the past, it has not been captured throughout the period of 2018/19. Nowadays, *Carabus interruptus* is the only darkling-beetle species that remains at the Ravine of Badajoz, although the average number of captured specimens in 2018/19 has decreased by 66,93% in respect to 1985/86.

However, it has appeared a new generalist species, *Orthomus berytensis*, which is colonizing all the ecological niches that the rest of species have left empty in the three elevational strata. This new ground-beetle species presents a high average number of captured specimens, especially at the low cloudy montane stratum, which represents 97,85% of individuals captured at this stratum.

5.3. Changes of population parameters

The results of the one-way ANOVA analysis are presented in Table 4. It is performed to test whether population parameters (activity density, average dry weight and average number of eggs) varied among the years of study during the last 34 years. For this analysis, *Hegeter tristis*, *Hegeter amaroides*, *Arthrodeis obesus*, *Zophosis bicarinata*, *Pimelia canariensis* and *Carabus interruptus* were chosen.

At a 95% level of confidence, there's statistical significance of changes in the activity-density in the last 34 years in *Hegeter amaroides* ($p = 0{,}001 < 0{,}05$), *Hegeter tristis* ($p = 0{,}004 < 0{,}05$), *Zophosis bicarinata* ($p = 0{,}000 < 0{,}05$) and *Pimelia canariensis* ($p = 0{,}000 < 0{,}05$). Also, there's statistical significance of changes in the average number of eggs in females in *Pimelia canariensis* ($p = 0{,}012 < 0{,}05$).

STRATA	SPECIES	Dependent Variable	Source	df	Mean Square	F	Sig.
BASAL	*Hegeter amaroides*	Activity density	Year	2	479,925	9,499	**0,001**
		Average dry weight	Year	1	0,000	2,891	0,111
		Average number of eggs	Year	1	54,595	2,615	0,128
	Hegeter tristis	Activity density	Year	2	0,060	7,303	**0,004**
		Average dry weight	Year	1	0,001	0,497	0,507
		Average number of eggs	Year	1	55,233	1,656	0,246
	Arthrodeis obesus	Activity density	Year	2	3,942	0,694	0,511
		Average dry weight	Year	1	0,000	0,169	0,689
		Average number of eggs	Year	1	27,225	0,421	0,529

	Zophosis bicarinata	Activity density	Year	2	5,434	12,646	**0,000**
		Average dry weight	Year	1	0,000	0,000	0,989
		Average number of eggs	Year	1	14,299	0,856	0,373
	Pimelia canariensis	Activity density	Year	2	14,951	28,398	**0,000**
		Average dry weight	Year	1	0,002	1,566	0,239
		Average number of eggs	Year	1	384,635	9,938	**0,012**
CLOUDY MONTANE	*Carabus interruptus*	Activity density	Year	1	0,862	3,570	0,088
		Average dry weight	Year	1	0,000	2,749	0,173
		Average number of eggs	Year	1	139,937	3,415	0,138

Table 4. Tests of Between-Subjetcs Effects. It is tested the variation of population parameters among the years of study during the last 34 years. (Abbreviations: df – degrees of freedom; F – ANOVA F-test; Sig – probability; bold values indicate statistical significance at the 95% level or higher).

5.4. Climatic correlation with population parameters

The relationship between population parameters ("Activity density", "Average dry weight" and "Average number of eggs") and climatic variables ("Min. T" - minimum temperature; "Max. T"- maximum temperature; "Precip." - precipitation) is assessed through a simple linear regression and it is shown in Table 5.

At a 95% level of confidence, there's positive correlation between average dry weight and all climatic variables for *Pimelia canariensis*. Also, there is positive correlation for *Zophosis bicarinata* between average dry weight and maximum temperature, and between average number of eggs and maximum and minimum temperature.

STRATA	SPECIES	Dependent Variable	Variable Entered	R	R Square	Adjusted R Square	F	Sig.	Beta
BASAL	*Hegeter amaroides*	Activity density	Min. T	0,658	0,433	0,339	4,582	0,076	-2,830
			Max. T	0,629	0,395	0,295	3,924	0,095	-5,694
			Precip.	0,157	0,025	-0,138	0,152	0,710	1,669
		Average dry weight	Min. T	0,476	0,227	0,098	1,761	0,233	0,029
			Max. T	0,476	0,226	0,097	1,755	0,233	0,033
			Precip.	0,526	0,276	0,156	2,289	0,181	0,023
		Average number of eggs	Min. T	0,432	0,186	0,051	1,375	0,286	28,071
			Max. T	0,347	0,120	-0,026	0,822	0,400	33,518
			Precip.	0,325	0,105	-0,044	0,706	0,433	14,220
BASAL	*Hegeter tristis*	Activity density	Min. T	0,162	0,026	-0,136	0,161	0,702	-0,009
			Max. T	0,114	0,013	-0,151	0,080	0,787	-0,017
			Precip.	0,004	0,000	-0,167	0,000	0,993	0,028
		Average dry weight	Min. T	0,149	0,022	-0,467	0,046	0,851	0,071
			Max. T	0,187	0,035	-0,448	0,073	0,813	0,030
			Precip.	0,856	0,733	0,599	5,485	0,144	0,075

		Average number of eggs	Min. T	0,934	0,873	0,809	13,724	0,066	-9,214
			Max. T	0,914	0,835	0,753	10,127	0,086	-23,646
			Precip.	0,271	0,073	-0,390	0,158	0,729	18,305
BASAL	*Arthrodeis obesus*	Activity density	Min. T	0,250	0,062	-0,094	0,400	0,551	-0,636
			Max. T	0,252	0,064	-0,093	0,407	0,547	-1,792
			Precip.	0,386	0,149	0,007	1,049	0,345	1,241
		Average dry weight	Min. T	0,629	0,396	0,275	3,279	0,130	0,107
			Max. T	0,615	0,378	0,254	3,041	0,142	0,132
			Precip.	0,544	0,295	0,155	2,097	0,207	0,067
		Average number of eggs	Min. T	0,333	0,111	-0,037	0,750	0,420	28,909
			Max. T	0,376	0,141	-0,002	0,988	0,359	46,137
			Precip.	0,373	0,139	-0,004	0,972	0,362	12,172
BASAL	*Zophosis bicarinata*	Activity density	Min. T	0,066	0,004	-0,162	0,026	0,877	0,320
			Max. T	0,115	0,013	-0,151	0,081	0,786	0,184
			Precip.	0,627	0,393	0,292	3,886	0,096	0,455
		Average dry weight	Min. T	0,701	0,491	0,406	5,791	0,053	0,012
			Max. T	0,710	0,504	0,422	6,102	**0,048**	0,016
			Precip.	0,697	0,486	0,400	5,665	0,055	0,008
		Average number of eggs	Min. T	0,894	0,800	0,766	23,972	**0,003**	24,369
			Max. T	0,909	0,825	0,796	28,361	**0,002**	37,392
			Precip.	0,649	0,421	0,324	4,360	0,082	7,670
BASAL	*Pimelia canariensis*	Activity density	Min. T	0,069	0,005	-0,161	0,029	0,872	0,077
			Max. T	0,087	0,008	-0,158	0,046	0,837	0,097
			Precip.	0,515	0,265	0,143	2,164	0,192	0,046
		Average dry weight	Min. T	0,951	0,904	0,880	37,483	**0,004**	0,484
			Max. T	0,940	0,883	0,854	30,278	**0,005**	0,708
			Precip.	0,980	0,961	0,951	97,795	**0,001**	0,208
		Average number of eggs	Min. T	0,550	0,303	0,186	2,603	0,158	62,771
			Max. T	0,572	0,327	0,215	2,917	0,139	98,373
			Precip.	0,303	0,092	-0,060	0,606	0,466	18,738
CLOUDY MONTANE	*Carabus interruptus*	Activity density	Min. T	0,381	0,145	-0,026	0,850	0,399	1,507
			Max. T	0,336	0,113	-0,065	0,634	0,462	1,652
			Precip.	0,412	0,170	0,004	1,024	0,358	0,426
		Average dry weight	Min. T	0,024	0,001	-0,499	0,001	0,976	0,113
			Max. T	0,248	0,061	-0,408	0,131	0,752	0,182
			Precip.	0,662	0,438	0,157	1,558	0,338	0,125
		Average number of eggs	Min. T	0,274	0,075	-0,387	0,163	0,726	35,867
			Max. T	0,629	0,395	0,093	1,306	0,372	122,057
			Precip.	0,875	0,766	0,649	6,541	0,125	16,706

Table 5. R, R squared, regression values of the analysis of the variance and regressions coefficients values. (Abbreviations: R – ANOVA F-test; Sig – probability; Beta – standardized coefficients; bold values indicate statistical significance at the 95% level or higher.

6. Discussion

In the period of study during the last 34 years, the average temperatures have increased both in the Malpaís of Güímar and in the Ravine of Badajoz, while the average precipitations have decreased. This kind of short-term thermal fluctuations affects the life-cycle of the different species sampled in both elevational strata. The annual rhythms of activity, reproduction and development of the terrestrial soil-surface beetle populations, in the two elevational strata studied, show marked differences between and within each of the different families studied.

The period of reproduction of most darkling-beetle populations in the basal stratum seems to be during the spring, due to its maximum peak in that season of population parameters. However, *Pimelia canariensis* presents its reproduction period during the winter. Seasonal patterns of those species are affected by climatic conditions. Two species showed to be more linked to climatic variables: *Zophosis bicarinata* and *Pimelia canariensis*, in which temperature was the main parameter that determines its life cycle, especially its average number of eggs and average dry weight. Also, in *P. canariensis* the precipitation influences its average dry weight, being this climatic variable essential for hatching larvae.

It seems that most of darkling-beetle populations activity density in the basal stratum have decreased due to a temperature increase and a precipitation decrease. Although most of darkling-beetle species presents their maximum activity density during the period of higher temperature and lower precipitation (summer), these conditions of increased dryness and aridity are affecting these populations negatively. It is reflected in a clear decrease in the surface activity of all the species studied in the Malpaís de Güímar. Activity density of *Hegeter amaroides, Hegeter tristis, Zophosis bicarinata* and *Pimelia canariensis,* have significantly changed throughout the study period. Also, it seems that this populations have decreased, comparing the results of average number of species captured per sampling plot in the three sampling periods. Highlight the great decrease of the number of individuals captured of *Hegeter amaroides* in the basal stratum during the sampling period of 2018/19.

In the cloudy-montane stratum, *Carabus interruptus*, a winter-breeder, was analyzed. This species is characteristic of this elevational stratum and its linked to humidity conditions. *C. interruptus* presents activity surface mainly during the winter, when surface temperature is lower, and precipitation is higher. Maximum and minimum of the average number of eggs and dry weight remain constant throughout the study periods, so life histories features have not changed.

During the 1980's, ground-beetle populations were well represented in this stratum but, in the last years, most species has not been found during the sampling periods. The absence of most ground-beetle populations during late winter and spring could be explained because of soil dryness, due to the decrease of precipitation and the increase of temperature. Ravine of Badajoz has suffered a clear defaunation of most ground-beetle species, with the exception of *Carabus interruptus* that remains nowadays.

This displacement would have stimulated *Orthomus berytensis* to colonize Ravine of Badajoz. It is a species widely distributed in the Mediterranean basin and it is preferably xerophilous and inhabits the sub-desert landscapes, but it is also found in meadows and nitrophilous environments from the coast to the summit at 1800 m altitude. It does not live in areas of shrubs or forests, where its dispersion capacity is reduced (Machado, 1992). The colonization of this species may be explained by a progressive warming of the study site.

Both the activity density and the number of individuals of the species analyzed have decreased, since the temperature and precipitation parameters have varied throughout the period of 2018/19, becoming increasingly inadequate for them. Despite this, there are still seasonal periods in which life-cycles are carried out and completed. Also, it can be expected that these species will end up being displaced from this habitat to other more favorable in a medium-long term of time, as it has happened with other species in the past very abundant as *Calathus depressus* and *Hegeter proximus* at the cloudy montane stratum. However, it's crucial to understand that those results are partial, as we need to have a global view of a one-year life cycle to get more representative conclusions.

7. Conclusions

From the results obtained, the following conclusions can be drawn:

1. There's evidence of short-term thermal fluctuation during the sampling years in the last 34 years: temperature have increased, while precipitation has decreased in both strata.
2. These climatic fluctuations affect both ground-beetle as darkling-beetle populations.
3. Temperature is one of the main factors that affects terrestrial soil-surface beetle populations seasonal patterns of activity density and life histories features.
4. In the last 34 years, average number of darkling-beetle and ground-beetle populations have decreased significantly at the basal stratum and at the cloudy montane stratum.
5. It seems that the reproduction of most darkling-beetles is during the spring, except *Pimelia canariensis* which reproduction is during the winter.
6. Within the reproductive types of ground-beetles, *Carabus interruptus* is a winter-breeder, typical of these latitudes.
7. A new species (*Orthomus berytensis*) has appeared in both elevational strata, occupying the ecological niches that have remained empty.
8. A global view of a one-year life-cycle will be more representative about the soil-surface beetles species status, especially darkling-beetles.

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