



A comparison of dung beetle assemblages (Coleoptera, Scarabaeoidea) collected 34 years apart in an Iberian mountain locality

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Abstract

Knowing how recent environmental changes may have affected species diversity is a major objective to estimate the consequences of habitat alteration and climate change. In this study two dung beetle inventories made in the same locality of the Sierra de Guadarrama (Madrid, Spain) 34 years apart (1983–2017) are compared. Changes in diversity, species richness, abundances and composition were analysed and species replacements described considering the three main functional dung beetle groups: large paracoprids, small paracoprids and small endocoprids. In addition, changes in vegetation cover and climate between the two periods were also analysed to examine their association with the detected faunistic changes. Both the vegetation and climatic data show that the surveyed locality would have experienced an increase in the area covered by bushes and forest and an increase in temperature and warm conditions during the 34 years. These changes are associated with a probable increase in species richness and species dominance, a decrease in diversity and an important change in composition that would have positively affected small paracoprids but negatively affected large paracoprids.

Keywords Sierra de Guadarrama · Intertemporal variation · Climate change · Land use change · Chao estimator

Introduction

The comparison of species inventories collected at different times is a difficult task due not only to the frequent inability to replicate the survey conditions that existed in studies carried out many years ago, but also to the idiosyncratic and contingent characteristics of any faunistic collection. For insect species, these difficulties are even more pronounced due to the lack of reliable past inventories and the hyperdiverse nature of many insect groups. As a consequence, there are few studies describing temporal trends or intertemporal comparisons in insects (Ashton et al. 2015; Dirzo

et al. 2015; Thomas 2016; Loboda et al. 2018). Recent evidence suggests that when these data come from taxonomically and temporally exhaustive surveys, they unequivocally show a general decline in insect fauna (Hallmann et al. 2017). Several factors have been proposed as causes of this decline, with habitat alterations and climatic changes being the main causal factors mentioned (Conrad et al. 2002; Fox et al. 2014) without ruling out the negative effects of the increasing use of chemical compounds (Benton et al. 2002).

Dung beetles are a species-rich indicator group specialized in the consumption of mammal faeces with important ecological functions linked to, for instance, the removal and burial of these faeces in the soils, nutrient cycling, aeration, seed dispersal or nematode and fly control (Nichols et al. 2008). Nonetheless, there are no studies showing long term trends in dung beetle assemblages due to the lack of standardized surveys repeated over time, even in countries with a long entomological tradition such as Great Britain (Lane and Mann 2016). Thus, the decline of dung beetle species and the changes in species compositions have been inferred by inter-temporal comparisons that, at most, use two or three surveys carried out in different years. Most of these studies have been carried out in the American continent at times

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usually not separated for more than 10 years (Howden and Howden 2001; Escobar et al. 2008; Touroult et al. 2017). These studies carried out in Texas, Costa Rica and French Guiana show both a decline in the number of species and a shift in the composition of dung beetle assemblages, which have been associated with vegetation changes and/or habitat disturbances. These and other Neotropical studies (Howden and Scholtz 1986; Lobo and Morón 1993; Beiroz et al. 2017) thus suggest that a moderate faunistic change is the rule in these inter-temporal comparisons but also that the detected changes are influenced by the differences in collection efforts, as well as climatic and vegetation modifications.

In Europe, the available studies on inter-temporal comparisons are scarcer. Sometimes, a significant change in species richness is not detected but a moderately compositional turnover (Agoglitto et al. 2012). When elevational gradients are studied, the uphill of some dung beetle species is verified which is associated with compositional changes due to the increase of the temperature experienced in the region (Menéndez et al. 2014; Birkett et al. 2018). As a result, climate change, habitat degradation and cessation of grazing and traditional land management practices are considered the main drivers responsible of the detected declines and changes in dung beetle assemblages (Lobo 2001; Lane and Mann 2016), although the increasing use of parasiticides (Verdú et al. 2018) would be accelerating this process more recently. Additionally, the increase in temperature can also modify the seasonal occurrence of dung beetle species (Menéndez 2007; Menéndez and Gutiérrez 2004) causing an earlier appearance of the adult stages and probably an acceleration in the development of larvae stages (Menéndez 2007). Here, we present a comparison of the species richness and faunistic composition of dung beetles collected 34 years apart in a locality of the Iberian Central System to examine the modifications in these assemblages, and their association with the climatic and habitat changes experienced in this locality.

Materials and methods

Study area and sampling

The study area is located in a mountain grassland area near the “El Ventorrillo” Biological Station (1,450 m a.s.l.) in the Sierra de Guadarrama (Madrid, Spain). The sampling was carried out every two weeks from May to September in both 1983 and 2017; thus, a total of 16 effective days of collection were carried out during 1983 and 23 days were carried out during 2017. This period covers almost the complete activity period of dung beetle species in the mountain areas of the Iberian Central System (Martín-Piera et al. 1992). During these two periods, surveys were carried out in the same pasture; an open area of approximately 1 hectare (see Fig. 1)

surrounded by a supra-Mediterranean vegetation type (Rivas-Martínez 1982) currently dominated by forests of *Pinus sylvestris* Linnaeus, 1753. Regarding the density of livestock in the survey area, data derived from the Anuario Estadístico de la Comunidad de Madrid 1985–2017 (<http://www.madrid.org/iestadis/fijas/estructu/general/anuario/descarga/anu11-1-10.xls>) and some studies (Arroyo et al. 1993), suggest that the number of head of cattle would not have experienced large changes between the two considered periods.

The sampling methodology was similar in both years, using 15 pitfall traps of recognized efficiency (Lobo et al. 1988; Veiga et al. 1989) baited with 250 g of cattle dung in 2017 and with cattle and equine dung during 1983. Traps were placed for periods of 24 h, with a minimum distance between them of 15 meters. Additionally, all existing specimens in cow droppings present in the sampling area were also collected manually in 1983. However, the use of the same kind of pitfall trap in both periods and the capacity of this trap to collect the beetles that naturally inhabit excrement 48–72 h after its deposition (Lobo et al. 1988; Veiga et al. 1989) allow us to assume that the influence of the sampling technique on this comparison is marginal.

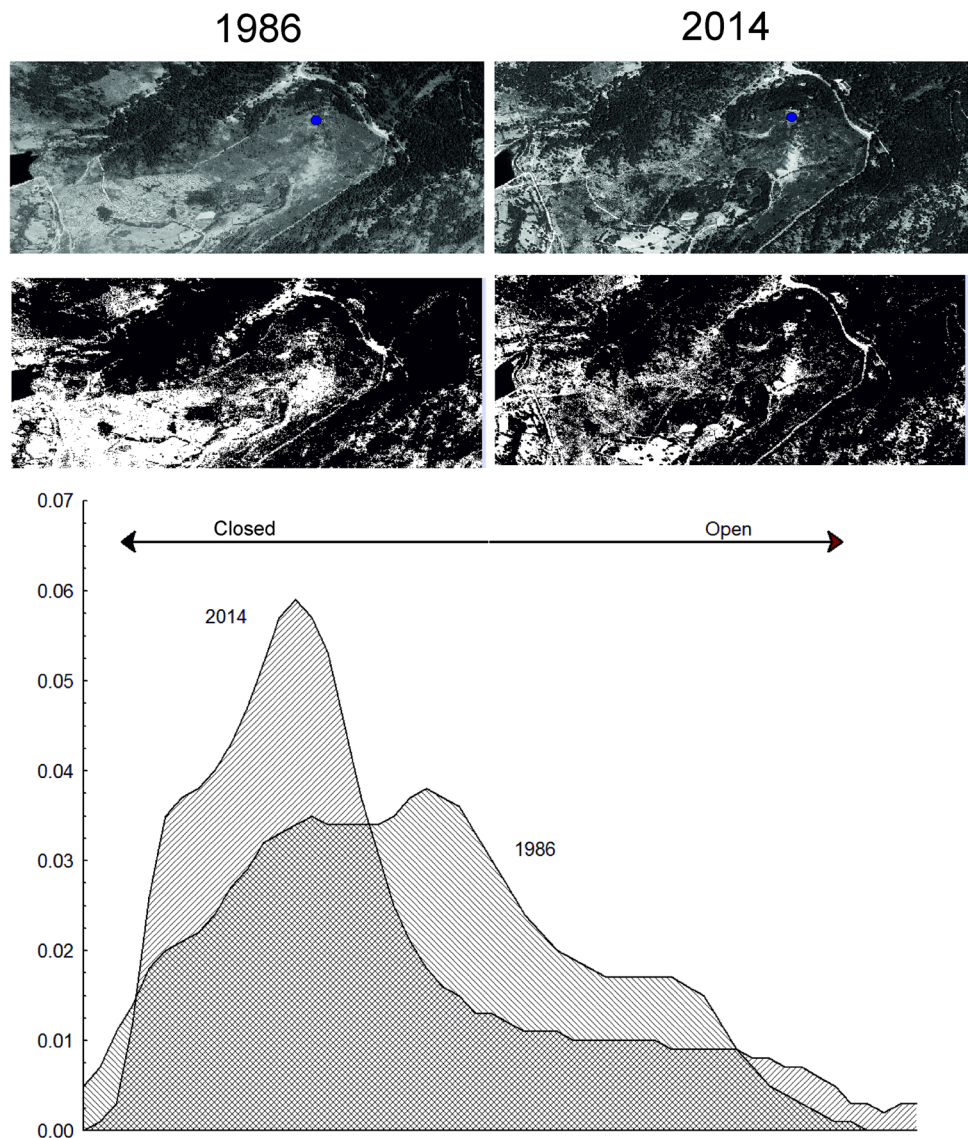
Change in vegetation cover

To estimate the degree of change in the vegetation cover of the study area, two aerial digital photographs corresponding to the years 1986 and 2014 were compared. These photographs were downloaded from the Instituto Geográfico Nacional of Spain (<http://centrodedescargas.cnig.es/>) and encompassed an area of 2.41 km² from $-4^{\circ}2'10''$ to $-4^{\circ}0'40''$ in longitude and from $40^{\circ}44'43''$ to $40^{\circ}45'19''$ in latitude, including the sampling site (Fig. 1). Both photographs were transformed to the same greyscale oscillating between 0 (black) and 255 (white) corresponding to a gradient from “closed” (forest) to “open” vegetation cover (pastures). The distribution of these values was compared between the photographs of both years to estimate the change in the degree of afforestation in the region. To do so, the Wald-Wolfowitz non-parametric test (WW test) was calculated because it is based on both the comparison of mean values and the shape of the complete distribution of these values (Sprent and Smeeton 2007). Relative pixel frequencies in classes of 5 ($255/5=51$) were used in these calculations.

Climate change

To estimate the changes in temperature between the two considered periods, meteorological data from the station Puerto de Navacerrada near the sampling area ($40^{\circ}47'35''$ N, and $4^{\circ}0'38''$ W) were analysed. These data were obtained from the Agencia Estatal de Meteorología

Fig. 1 Aerial photographs of the years 1986 and 2014 in the region at which the sampling was carried out in both periods (blue dot). The greyscale from 0 (black) to 255 (white) corresponds to a gradient from “closed” to “open” vegetation cover. The area covered by the two photographs is 2.41 km² (from $-4^{\circ}2'10''$ to $-4^{\circ}0'40''$ in longitude and from $40^{\circ}44'43''$ to $40^{\circ}45'19''$ in latitude). The middle images represent the pixels with values below the mean (closed vegetation in black) and above the mean (open vegetation in white). The lower figure represents the distribution of greyscale frequencies in both periods. (Color figure online)



(<http://www.aemet.es>) and included variation from January of 1983 to December of 2016 (34 years or 408 months) in the mean monthly temperature, mean maximum monthly temperature, mean minimum monthly temperature, monthly total precipitation, monthly days with appreciable rainfall, monthly percentage of insolation and monthly days of frost. These data were used to generate nine annual climatic variables ($n = 34$) including mean monthly temperature (in $^{\circ}\text{C}$), maximum mean monthly temperature (in $^{\circ}\text{C}$), minimum mean monthly temperature (in $^{\circ}\text{C}$), temperature of the warmest month (in $^{\circ}\text{C}$), temperature of the coldest month (in $^{\circ}\text{C}$), annual precipitation (in mm), annual days with appreciable precipitation (more than 0.1 mm), % of monthly time with sunny conditions, and annual days of frost. Annual rates of change in these climatic variables were estimated using linear regressions. The slope of this regression represents the rate of change

($\pm 95\%$ confidence interval), and whether it is significantly different from zero was estimated by a t test.

Species richness, completeness, undetected species and diversity

The increase in the number of species with an increase in sampling effort (measured as the number of collected individuals) and non-parametric estimators were used to examine the completeness of both inventories (Chao and Jost 2012). Thus, the increase in the number of species as a function of the number of individuals (accumulation curve) was plotted and the slope at the end of this curve or “coverage” calculated (Chao and Jost 2012). Derived species richness estimates for both periods were compared at the same coverage as recommended by using the iNEXT application (Hsieh et al. 2016). Hill numbers or “true” diversity values

of different orders (q) are also used to examine assemblage differences in evenness and dominance (see Jost 2007; Chao et al. 2013; Chao and Jost 2015). Predicted but undetected species in each one of the two periods were estimated using the Good-Turing application recently proposed by Chao et al. (2017) (see <https://chao.shinyapps.io/GoodTuring/>). Good-Turing allows estimating both the number of species that remain undetected in any assemblage according to the non-parametric Chao1 richness estimator, and the number of undetected species shared by two different assemblages.

Faunal change

The abundances of the collected species during 1983 were linearly regressed against the abundances of the species obtained in 2017. First, the abundance data were transformed by $\text{Log}(N + 1)$, and the obtained values were standardized by dividing them by the maximum value attained by a species in each period (0 to 1 scale). In this way, a positive and significant regression slope between the standardized abundance values of both periods would indicate that the relative abundance of the species covary and that the assemblages are congruent. This congruence will be very high if this slope does not significantly differ from one according to a t test, while slopes significantly greater or lower than one would indicate that the abundances of the collected species are higher in one of the two periods. The residuals of this linear regression can be considered a measure of the departure of each species from the general congruence pattern. Once calculated including the 99% confidence interval of the regression line, these residuals were used to discriminate those species that preferentially appear in each period as well as to estimate by one-way ANOVA whether these residuals significantly differ among the three main functional groups: (i) endocoprids or small-sized dwelling species living and feeding inside the dung whose larvae usually are free-living (Aphodiinae), (ii) small (< 1 cm) paracoprid or tunnelling species that bury dung portions in the soil under the excrement used for feeding or nesting, and (iii) large paracoprid species with a body size greater than 1 cm. Only two individuals of one species of roller or telecoprid dung beetle have been collected in 2017, so that this functional group was obviated in the analyses.

Finally, the possible change in the phenology of the species shared by the two periods ($n = 25$) was examined. For this, we estimated the mean seasonal occurrence of each species in each period, taking into account the number of specimens collected on each date and considering that day 1 corresponds to the winter solstice (December 21st) and day 276 to the autumn equinox (September 22nd). A linear regression is used to relate the mean seasonal occurrence during 2017 to those of 1983. Only shared species between the two periods are used for this purpose. Again, a positive

regression slope not significantly different from one would suggest a similar pattern of emergence in the two periods. Alternatively, a slope significantly different from zero but higher or lower than one would imply that this seasonal advance or delay varies throughout the year (e.g., a seasonal advance during 2017 in the spring occurrence but a similar occurrence during autumn in both periods). The statistical significance and the sign of the intercept were also examined because it may also indicate an advance or delay in the seasonal occurrence of the species.

Results

The analysis of the vegetational changes showed that “closed” vegetation covered 71% of the territory during 1986 but that this percentage increased to 80% in 2014 (Fig. 1). The distribution of frequencies corresponding to the open-closed vegetation gradient (greyscale) differed significantly between the two periods (Fig. 1; WW test = 2.56, $p = 0.01$, $n_1 = n_2 = 51$).

The climatic conditions also seem to have changed between the two periods (Table 1). The mean monthly temperatures significantly increased during the examined period (approximately 1 °C). These temperature changes seem to have mainly affected the mean maximum monthly temperatures (approximately 1.5 °C in total) and temperatures experienced during the warmest month (1.7 °C). The annual frost days also decreased significantly (almost 20 fewer days of frost). None of the remaining variables related to minimum temperatures and precipitation values showed statistically significant changes during the analysed period.

A total of 1,134 individuals and 34 species were collected in 1983, and 4733 individuals belonging to 41 species were collected during 2017. Although the 2017 assemblage was richer in species (Table 2), confidence intervals indicate that both estimates of species richness do not differ significantly. Alternatively, the values of the Chao1 species richness estimator suggest that the 2017 assemblage could be slightly richer. The number of equally common species ($q = 1$) was approximately 73% greater in the 1983 assemblage (Table 2), a pattern that is repeated when the q order is 2 and 3. In 1983, the number of equally common species oscillated from 9.9 to 11.6 (95% confidence interval) for $q = 2$ and from 8.0 to 9.5 for $q = 3$, while these values varied from 5.0 to 5.4 and from 4.0 to 4.4 in the case of 2017. Thus, the diversity of the 1983 assemblage was higher than the diversity of the 2017 assemblage due to the higher evenness of species abundances during 1983, and the higher dominance of a few species in the 2017 assemblage. In 1983, the four most abundant species (*Geotrupes ibericus*, *Aphodius fimetarius*, *Coloboptyerus erraticus* and *Teuchestes fossor*) accounted for approximately half of the total number of individuals, while

Table 1 Annual rates ($\pm 95\%$ confidence intervals) and total change in the nine considered annual climatic variables from 1983 to 2016 (34 years)

	Annual rates	Total change
Mean monthly temperature ($^{\circ}\text{C}$)	$0.031 \pm 0.020^{**}$	1.033
Maximum mean monthly temperature ($^{\circ}\text{C}$)	$0.046 \pm 0.022^{***}$	1.515
Minimum mean monthly temperature ($^{\circ}\text{C}$)	0.015 ± 0.018	0.502
Temperature of the warmest month ($^{\circ}\text{C}$)	$0.050 \pm 0.044^{*}$	1.666
Temperature of the coldest month ($^{\circ}\text{C}$)	0.003 ± 0.042	0.099
Annual precipitation (mm)	6.46 ± 10.33	213.15
Annual days with appreciable precipitation	0.07 ± 0.48	2.41
% of monthly time with sunny conditions	0.05 ± 0.13	1.52
Annual days of frost	$-0.60 \pm 0.62^{*}$	-19.87

A t test was used to test whether the slope of the regression line for each variable differs from zero over time

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Table 2 Species richness and total abundance of both periods; estimated species richness of 1000, 5000 and 10,000 individuals by extrapolating accumulation curves; equally common species ($q = 1$); number of species estimated by the non-parametric estimator Chao1; uncollected species in each period; and observed and estimated number of shared species

	1983	2017
Observed number of individuals	1134	4733
Observed species richness	34	41
Number of species predicted at 1000 individuals	33.6 (31.3–35.8)	31.4 (29.9–32.9)
Number of species predicted at 5000 individuals	34.7 (27.1–42.4)	41.3 (36.9–45.8)
Number of species predicted at 10,000 individuals	34.7 (27.3–42.2)	45.7 (39.0–52.4)
Equally-common species ($q = 1$)	15.6 (14.6–16.5)	9.0 (8.6–9.3)
Estimated richness (Chao1)	35 (34–41)	50 (43–94)
Number of undetected species	1	9
Observed shared species richness		25
Estimated shared species richness		34 (26–84)

Calculations were made with the iNEXT and Good-Turing applications (Chao et al. 2013 and 2017). In all parentheses, confidence interval values are 95%

the four most abundant species during 2017 (*C. erraticus*, *Onthophagus similis*, *Euoniticellus fulvus* and *Otophorus haemorrhoidalis*) accounted for three quarters of the total abundance (see Table 3). Interestingly, the Good-Turing application suggests that the difference between estimated and observed shared species richness values ($34 - 25 = 9$) is equal to the number of undetected species in the 2017 survey (Table 2). Thus, undetected species in 2017 would have been shared with those of the 1983 inventory, and approximately one-third of the predicted species in 2017 (16 of the 50 species) would have been specific to this period (Table 2).

The slope of the linear regression (b) between the relative abundances of 1983 and 2017 dung beetles was positive and statistically significant ($b = 0.255$; $t = 2.12$, $p = 0.04$, 95% confidence interval from 0.013 to 0.496). The interspecific variation in the relative abundance in 1983 only explained a small amount of the interspecific variation observed during 2017 ($R^2 \times 100 = 8.6\%$) and a high portion of the total collected species (68%) is outside the 99% confidence intervals (Fig. 2). A total of 18 species were relatively more abundant in 1983 than in 2017 and only 6 of them represented more

than 1% of the total collected individuals (Table 3) and can be considered characteristic of the 1983 dung beetle assemblage: *Calamosternus granarius*, *Aphodius coniugatus*, *Agriolus constans*, *Melinopterus sphacelatus*, *Teuchestes fossor* and *Geotrupes mutator*. During 2017, 16 species occurred at a higher comparative relative abundance than in the 1983 period, with 10 of them representing more than 1% of the total individuals: *Colobopterus erraticus*, *Nimbus contaminatus*, *Chilo thorax sticticus*, *Otophorus haemorrhoidalis*, *Aphodius foetidus*, *Euoniticellus fulvus*, *Onthophagus lemur*, *O. similis*, *O. taurus* and *O. vacca* (Table 3).

The residuals of the relationship between the relative abundance of species in the two periods differed significantly among the three functional groups ($F = 8.91$, $p = 0.0005$, $R^2 = 27.9\%$). Thus, these residuals did not differ between endocoprids and large paracoprids functional groups (mean $\pm 95\%$ CI: -0.07 ± 0.08 and -0.15 ± 0.20 , respectively), but its negative signs indicate that these two groups of species appear more abundantly during 1983. However, the residuals for the small paracoprids were positive and significantly higher than those for the

Table 3 Number of individuals of each species collected during 1983 and 2017, the family to which they belong and their functional group (FG; *E* endocoprid, *SP* small paracoprid, *LP* large paracoprid, *T* telecoprid)

Species	Family	1983	2017	FG
<i>Acanthobodilus immundus</i> (Creutzer, 1799)	Aphodiidae	1	0	E
<i>Acrossus carpetanus</i> (Gräells, 1847)	Aphodiidae	2	0	E
<i>Acrossus depressus</i> (Kugelann, 1792)	Aphodiidae	9	1	E
<i>Agolius bonvouloiri</i> (Harold, 1860)	Aphodiidae	0	3	E
<i>Agrilinus constans</i> (Duftschmid, 1805)	Aphodiidae	42	1	E
<i>Agrilinus scybalarius</i> Fabricius, 1781	Aphodiidae	35	37	E
<i>Ammoecius elevatus</i> (Olivier, 1789)	Aphodiidae	6	0	E
<i>Anomius annamariae</i> (Baraud, 1982)	Aphodiidae	1	5	E
<i>Aphodius coniugatus</i> (Panzer, 1795)	Aphodiidae	26	0	E
<i>Aphodius fimetarius</i> (Linnaeus, 1758)	Aphodiidae	232	74	E
<i>Aphodius foetidus</i> (Herbst, 1783)	Aphodiidae	2	108	E
<i>Biralus satellitius</i> (Herbst, 1789)	Aphodiidae	2	0	E
<i>Bodilus ictericus</i> (Laicharting, 1781)	Aphodiidae	2	1	E
<i>Calamosternus granarius</i> (Linnaeus, 1767)	Aphodiidae	31	0	E
<i>Chilothorax sticticus</i> (Panzer, 1798)	Aphodiidae	0	173	E
<i>Colobopterus erraticus</i> (Linnaeus, 1758)	Aphodiidae	98	1715	E
<i>Coprimorphus scrutator</i> (Herbst, 1789)	Aphodiidae	6	0	E
<i>Esymus merdarius</i> (Fabricius, 1775)	Aphodiidae	5	0	E
<i>Esymus pusillus</i> (Herbst, 1789)	Aphodiidae	1	3	E
<i>Heptalaucus testudinarius</i> (Fabricius, 1775)	Aphodiidae	0	1	E
<i>Melinopterus prodromus</i> (Brahm, 1790)	Aphodiidae	0	2	E
<i>Melinopterus sphaelatus</i> (Panzer, 1798)	Aphodiidae	34	3	E
<i>Nialus varians</i> (Duftschmid, 1805)	Aphodiidae	0	3	E
<i>Nimbus contaminatus</i> (Herbst, 1783)	Aphodiidae	22	78	E
<i>Nimbus proximus</i> Ádám, 1994	Aphodiidae	0	34	E
<i>Otophorus haemorrhoidalis</i> (Linnaeus, 1758)	Aphodiidae	61	334	E
<i>Phalacronotus biguttatus</i> (Germar, 1824)	Aphodiidae	0	1	E
<i>Planolinus borealis</i> (Gyllenhal, 1827)	Aphodiidae	0	10	E
<i>Sigorus porcus</i> (Fabricius, 1792)	Aphodiidae	0	5	E
<i>Teuchestes fossor</i> (Linnaeus, 1758)	Aphodiidae	98	8	E
<i>Trichonotulus scrofa</i> (Fabricius, 1787)	Aphodiidae	5	15	E
<i>Geotrupes ibericus</i> Baraud, 1958	Geotrupidae	152	25	LP
<i>Geotrupes mutator</i> (Marsham, 1802)	Geotrupidae	26	5	LP
<i>Bubas bubalus</i> (Olivier, 1811)	Scarabaeidae	3	1	LP
<i>Caccobius schreberi</i> (Linnaeus, 1758)	Scarabaeidae	2	18	SP
<i>Copris lunaris</i> (Linnaeus, 1758)	Scarabaeidae	59	22	LP
<i>Euoniticellus fulvus</i> (Goeze, 1777)	Scarabaeidae	14	646	SP
<i>Onitis belial</i> Fabricius, 1798	Scarabaeidae	2	0	LP
<i>Onthophagus coenobita</i> (Herbst, 1783)	Scarabaeidae	0	23	SP
<i>Onthophagus fracticornis</i> (Preyssler, 1790)	Scarabaeidae	32	46	SP
<i>Onthophagus grossepunctatus</i> Reitter, 1905	Scarabaeidae	0	29	SP
<i>Onthophagus joannae</i> Goljan, 1953	Scarabaeidae	0	22	SP
<i>Onthophagus lemur</i> (Fabricius, 1781)	Scarabaeidae	0	67	SP
<i>Onthophagus opacicollis</i> Reitter, 1893	Scarabaeidae	0	28	SP
<i>Onthophagus ovatus</i> (Linnaeus, 1767)	Scarabaeidae	0	26	SP
<i>Onthophagus similis</i> (Scriba, 1790)	Scarabaeidae	17	869	SP
<i>Onthophagus stylocerus</i> Gräells, 1851	Scarabaeidae	3	3	SP
<i>Onthophagus taurus</i> (Schreber, 1759)	Scarabaeidae	9	147	SP
<i>Onthophagus vacca</i> (Linnaeus, 1767)	Scarabaeidae	94	139	SP
<i>Sisyphus schaefferi</i> (Linnaeus, 1758)	Scarabaeidae	0	2	T

Table 3 (continued)

The abundance of the species that preferentially appear in each period (Fig. 2) and represent more than 1% of the total individuals in each period are in bold

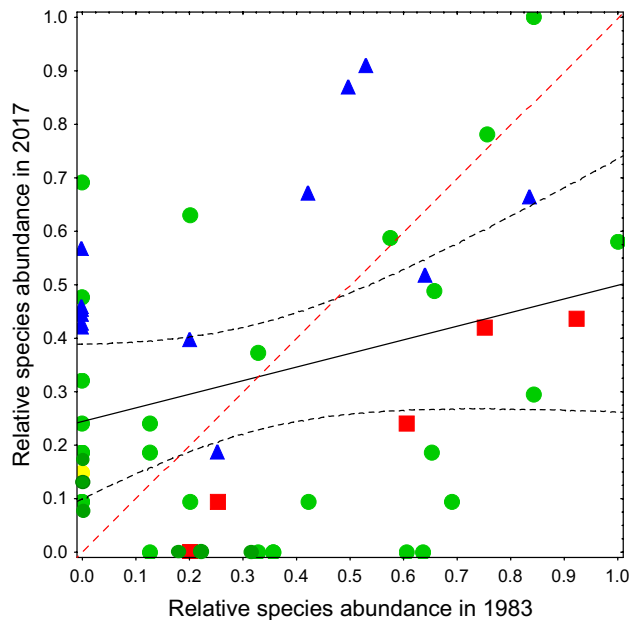


Fig. 2 Variation between 1983 and 2017 in the relative abundance of the different species. The raw abundance values of each species were Log transformed ($\log(N + 1)$) and subsequently standardized by the maximum abundance attained for a species in each period. The continuous line represents the linear regression, and the black broken lines are 99% confidence intervals. Species outside these confidence intervals are considered those preferentially appear in each period. Red broken line is the equality line. Red squares are large paracoprid species, blue triangles are small paracoprids, green dots are endocoprid species, and the yellow point is the only collected telecoprid or roller species. (Color figure online)

other two functional groups (0.23 ± 0.13). Thus, small paracoprids species seem to have increased their relative abundances during 2017 while large paracoprids and endocoprids would have reduced it (Fig. 2).

The mean seasonal occurrence of the species in the study area oscillates from late spring to autumn (Fig. 3). Common species collected both in 1983 and 2017 have mean seasonal occurrences that are positively correlated ($r = 0.84$, $p < 0.0001$, $n = 25$). The intercept of this relationship was significantly higher than zero (64.26 ± 38.01 ; $t = 7.41$; $p = 0.002$) and the slope was significantly lower than one ($b = 0.73 \pm 0.20$; $t = 7.41$, $p < 0.0001$). As consequence, spring beetles tended to appear later during 2017 while some summer-autumn species tend to appear comparatively early in 2017 than in 1983 (Fig. 3): *Agrilus scybalarius*, *Onthophagus taurus*, *Bodilus ictericus*, and to a lesser extent, the autumnal *Nimbus contaminatus*.

Discussion

Climate change and land-use modifications are generally recognized as the main major forces responsible of the detected decline of insect species and changes in faunal compositions (Fox et al. 2014; Ashton et al. 2015; Hallmann et al. 2017; Loboda et al. 2018). Similar arguments have been put forward in the case of dung beetles (Howden and Howden 2001; Escobar et al. 2008; Menéndez et al. 2014; Lane and Mann 2016; Birkett et al. 2018) although the general lack of reliable long term data does not provide powerful evidence.

According to our results, both the vegetation and climatic data suggested that the surveyed region would have experienced an increase in the area covered by bushes and forest and an increase in temperature and warm conditions during the 34 years examined. These changes are in accordance with previous studies indicating the replacement of grasslands by shrubs in these mountains between the 1950s and 1990s (Sanz-Elorza et al. 2003) and with studies showing very similar variation in the climatic conditions observed in our study (Sanz-Elorza et al. 2003; Menéndez et al. 2014; Wilson et al. 2007).

These changes in climatic and habitat conditions are associated with the probable modifications in species richness and composition of dung beetle assemblages. Although the results may not be conclusive, species richness could have been increased slightly according to Chao1 results, and the remaining uncollected species during 2017 could have been shared with those in 1983. Thus, the most likely scenario is one in which the increase in species, if anything, has arisen as a consequence of colonization by new warm-adapted species that increase the dominance of the whole assemblage and thus diminish diversity. Other studies have detected inter-temporal elevational shifts in the occurrence of dung beetles (Birkett et al. 2018; Menéndez et al. 2014) or predicted extensive latitudinal changes in composition (Dortel et al. 2013) in response to climatic changes. In our case, the local dung beetle assemblages inhabiting the pasturelands of the Sierra de Guadarrama would have increased from 1983 to 2017, and this rise was mainly a consequence of the addition of new elements (rare species). The consequence of all these changes is that the abundances of the species inhabiting both periods are only relatively congruent; dung beetle species show different relative abundances between the two years. Among the species only collected during 2017, there are two species associated with the presence of forest habitats, *Onthophagus coenobita* and *Chilo thorax sticticus* (Martín-Piera and López-Colón 2000; Veiga 1998), the occurrence of which may be due to the increase in closed

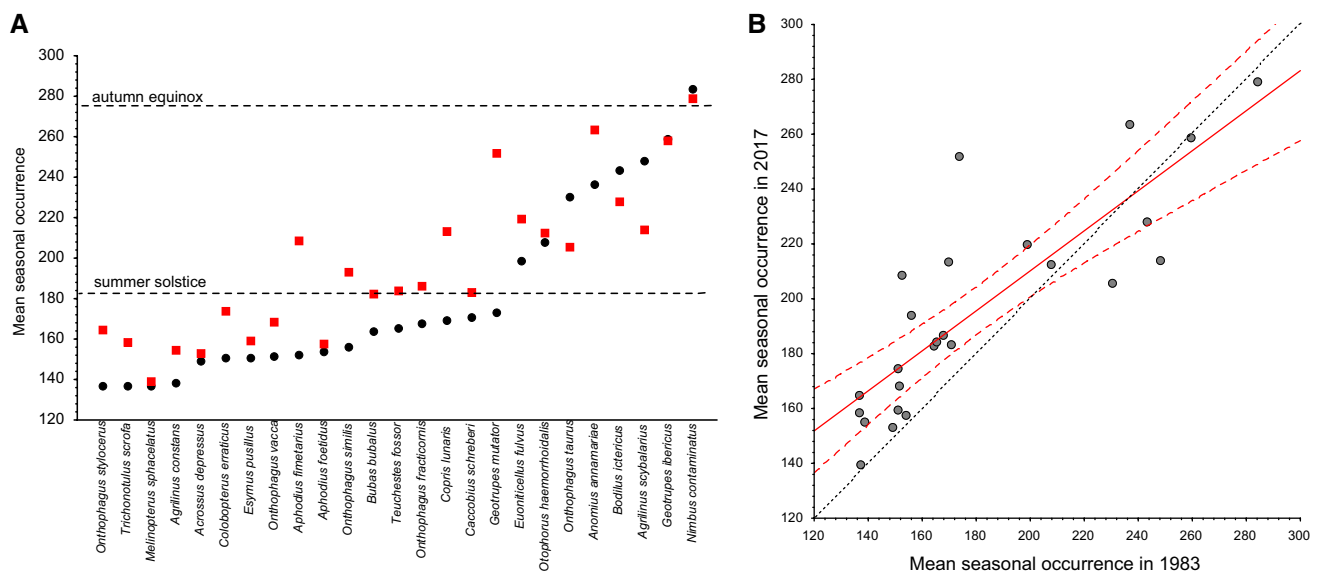


Fig. 3 **A** Mean seasonal occurrence of the 25 common species in 1983 (black circles) and 2017 (red squares). Day 1 corresponds to the winter solstice (December 21st), and the two horizontal, broken lines correspond to the summer solstice (June 21st) and autumn equinox

(September 22nd). **B** Linear regression (red, continuous line) and 95% CI (red, broken lines) between the mean seasonal occurrence of species in 1983 and 2017. The grey, broken line is the identity line or line of equality. (Color figure online)

vegetation areas and the role played by shaded habitats in buffering temperature changes (Menéndez and Gutiérrez 2004). *O. lemur*, *O. grossepunctatus* and *O. opacicolis* are now also present in these mid-mountain areas, although they are generally considered lowland and warm-adapted species (Martín-Piera and López-Colón 2000). This uphill shift has also been observed in other insect groups of the Sierra de Guadarrama (Wilson et al. 2005, 2007; Nieto-Sánchez et al. 2015), and the increase in the thermophily of the dung beetle fauna of this locality is also supported by the dominance of other warm-adapted species such as *Colobopterius erraticus* and *Euoniticellus fulvus* (Martín-Piera and López-Colón 2000).

One of the most interesting results of this faunistic comparison is that small paracoprids increased in their relative abundance. Small tunnellers belonging to the Scarabaeinae subfamily are comparatively more abundant and frequent than are endocoprid Aphodiinae in Iberian localities with a lower number of species, making their occurrence generally more homogeneous among different habitat types (Hortal et al. 2000). This has been associated with their capacity to be insensitive to environmental conditions because both larvae and adults eat the dung in underground chambers safe from changes in external environmental conditions. This characteristic, and especially their good dispersal ability, might have favoured the colonization by small tunnellers with a change in climatic conditions. In contrast, large tunneller species seem to have been disadvantaged in our temporal study. These species could have declined as a consequence of a reduction in cattle numbers, as other studies

demonstrate (Lumaret et al. 1992; Halffter and Arellano 2002). Although there is no concrete information, the available data suggest that cattle numbers have not substantially changed in the survey area. The negative impact of widely used veterinary products on large-bodied dung beetles (Verdú et al. 2018) may also help explain this decline (these products were not applied in Spain during 1983).

Finally, a relatively surprising result is the delay in the occurrence of most part of dung beetle species during 2017 except in the case of some summer-autumnal species (Fig. 3). This is an *a priori* contradictory result if one considers that the increase in temperatures should generate earlier emergence of imaginal stages (Menéndez 2007). We consider this result to be a consequence of the important role played by precipitation in facilitating the emergence of these insect species (Hanski and Cambefort 1991; Davis 1997). Precipitation was abnormally scarce during April in 2017, thus delaying the spring emergence of individuals after unfavourable winter conditions (Fig. 4). Although temperature affects developmental rates and brood emergence, phenological traits are complex (Tobin et al. 2008), and explanations of shifts in insect phenology should take both temperature and precipitation values into account (Ellwood et al. 2012).

The data provided by this study must be treated as an indication of a trend that should prompt additional studies directed to check if this pattern is maintained over time, and/or if other groups experience a similar trend in the region. In spite of the difficulties in comparing collected inventories made at different times, the provided results suggest that mid-mountain dung beetle assemblages are changing due

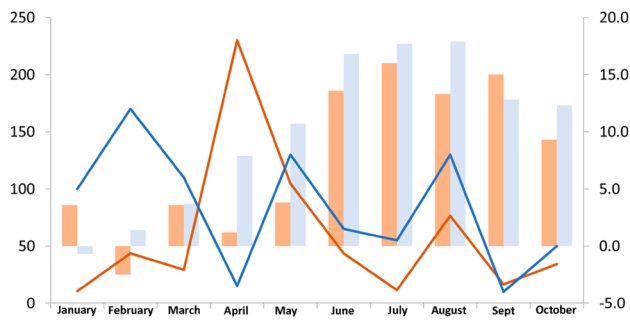


Fig. 4 Mean monthly temperature (bars) and precipitation (lines) during 1983 (orange) and 2017 (blue) from January to October (data from the Spanish Agencia Estatal de Meteorología). (Color figure online)

mainly to the incorporation of species inhabiting lowland places or preferring forests habitats and to a lesser extent as a consequence of the decline in some species, especially those that are large-bodied. Being aware of the provisional character of the detected patterns, more exhaustive studies examining the population trends of the endemic orophilous species surviving in the high mountain pasturelands of the Iberian Central System will be necessary.

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Compliance with ethical standards

Conflict of interest There is no conflict of interest that could be perceived to bias the work.

Ethical approval Beetle collection was conducted with relevant permissions provided by the Comunidad de Madrid (Dirección General de Medio Ambiente), considering all applicable international and national guidelines for the care and use of animals.

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