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Effects of climatic and time-related variables on dung beetle communities: A case study in Central Spain

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Abstract

Dung beetles are considered a key element in ecosystems as they are involved in many ecological processes, being one of the main decomposers of organic matter in the landscape. They can be classified into 3 subfamilies: Aphodiinae, Geotrupinae and Scarabaeinae, with each subfamily exhibiting specific adaptations and evolutionary strategies that have developed over time. The global patterns of dung beetle diversity are influenced by ecological factors, such as climatic (temperature, humidity, atmospheric pressure) and time-related variables. Thus, the aim of the study is to see how these variables affect a dung beetle community and whether there are different responses among the subfamilies. The study was carried out in Mataelpino, a town located in Central Spain (Madrid, Spain). Monthly sampling was conducted from May 2018 to February 2020. According to the results the variables considered exert an effect on dung beetles, with differences observed among the subfamilies. To our knowledge, atmospheric pressure has been considered for the first time in a study of this type, with a greater effect being observed in the Aphodiinae subfamily than in the rest of the dung beetle groups. Regarding the other subfamilies, it has been observed that temperature is a determining factor for Scarabaeinae species, whereas humidity seems to have a greater effect on Geotrupinae species.

Key words: Central Spain, climatic variables, diversity patterns, dung beetles, Scarabaeoidea, time-related variables

Introduction

Insects constitute most of the known biodiversity on Earth and dominate virtually all ecosystems. In recent years, several studies attempting to determine the impact of environmental conditions and climate change on organisms have used insects as the object of study (Halsch *et al.* 2021; Jaworski & Hilszczanski 2013; Kingsolver *et al.* 2011; Lobo 2016; Palumbo 2010; Pureswaran *et al.* 2018; Raza *et al.* 2014; Sangle *et al.* 2015; Spector 2006). Moreover, being ectotherms makes them more dependent on environmental conditions and, therefore, very useful as indicators (McGeoch 1998, 2007; Saleh *et al.* 2014).

Within the group, dung beetles (Coleoptera, Scarabaeoidea) are considered an excellent focal group for studying species diversity patterns, owing to their well-known taxonomy, wide geographic distribution, ease of sampling, habitat specialization, response to small-scale habitat heterogeneity and importance in ecosystem function (Agoglitta *et al.* 2012; Carvalho *et al.* 2020; Nichols *et al.* 2008; Raine & Slade 2019; Spector 2006; Tonelli 2021). Also, they play important roles in ecosystems, participating in the ecological processes of nutrient cycling, secondary seed dispersal, bioturbation, the biological control of flies and livestock parasites, and pollination, among others (Nichols *et al.* 2008).

The superfamily Scarabaeoidea comprises a large and diverse group of insects, with around 31,000 species described worldwide. This superfamily is characterized as having enormous ecological plasticity, being able to exploit a wide spectrum of food resources from all types of organic matter of both animal and plant origin (Martín-Piera & López-Colón 2000). Within this superfamily are the commonly known dung beetles, which feed mainly on mammalian dung and also use dung as a breeding chamber for their larvae (Halffter & Edmonds 1982; Halffter & Matthews 1966). Dung beetles comprise species of the subfamily Geotrupinae, within the Geotrupidae family, and members of Aphodiinae and Scarabaeinae subfamilies, within the Scarabaeidae family (Browne & Scholtz 1999; Halffter & Edmonds 1982; Scholtz 1990; Villalba *et al*. 2002). They are distributed worldwide and are mainly associated with tropical and temperate forests, savannas and grasslands (Halffter & Matthews 1966; Hanski & Cambefort 1991). More specifically, most of the Aphodiinae and Geotrupinae species are found in temperate to temperate–cold climates (Cabrero-Sañudo & Lobo 2009), whereas the Scarabaeinae are typically found in hot and arid climates (Davis & Scholtz 2001). These ecological differences, which have arisen from different evolutionary histories, segregate dung beetles according to their preferences for specific environmental conditions (Davis & Scholtz 2001; Errouissi *et al*. 2004).

Over the years, the effect of ecological factors on the spatial and temporal distribution of dung beetles has been studied. Temperature and precipitation are considered the most influential climatic factors (Ambrozova *et al*. 2022; Calatayud *et al*. 2021; Dortel *et al*. 2013; Ferreira *et al*. 2018; Halffter & Edmonds 1982; Labidi *et al*. 2012; Lobo *et al*. 2002; Lumaret & Kirk 1991; Numa *et al*. 2012). In the Spanish Mediterranean Region, Scarabaeinae species have been found to be more active under warm conditions (Errouissi *et al*. 2009; Halffter & Edmonds 1982; Jay-Robert, Errouissi, & Lumaret 2008). However, there is a progressive replacement with Aphodiinae and Geotrupinae species as conditions become wetter and cooler (Errouissi *et al*. 2004, 2009; Halffter & Edmonds 1982; Jay-Robert, Errouissi, & Lumaret 2008; Lumaret & Kirk 1987). In addition, the seasonal pattern of each subfamily is adjusted to the moments of the year when their ideal climatic conditions occur (Agoglitta *et al*. 2012; Jay-Robert, Errouissi, & Lumaret 2008; Lobo 1982; Lumaret & Kirk 1987, 1991; Senyüz *et al*. 2019).

On the other hand, atmospheric pressure is a factor that has not yet been explicitly considered. The few studies that have been carried out relating insects and atmospheric pressure have used other groups, such as flies or parasitoid wasps, and most of them have been carried out under laboratory conditions (Adonyeva *et al*. 2021; Ankney 1984; Austin *et al*. 2014; Dagaeff *et al*. 2016; Fournier *et al*. 2005; Marchand & McNeil 2000; Pellegrino *et al*. 2013; Rousse *et al*. 2009). Depending on the weather patterns, calm, dry and sunny climates are associated with high atmospheric pressure levels. In contrast, low atmospheric pressure levels are often accompanied by precipitation and high-speed winds (Wellington 1946). In general, most of the individuals used in these studies showed increased activity when atmospheric pressure levels were high (in good weather), whereas at low atmospheric pressure levels their activity rates were reduced (in bad weather) (Adonyeva *et al*. 2021; Ankney 1984; Austin *et al*. 2014; Dagaeff *et al*. 2016; Fournier *et al*. 2005; Marchand & McNeil 2000; Pellegrino *et al*. 2013; Rousse *et al*. 2009). This shows that detecting atmospheric pressure fluctuations allows individuals to identify imminent changes in weather conditions that may represent a threat to their survival (Pellegrino *et al*. 2013).

The growing concern about the consequences of climate change makes these studies even more important (Cuesta *et al*. 2021; Cuesta & Lobo 2019; Dortel *et al*. 2013; Menéndez *et al*. 2014; Menéndez & Gutiérrez 2004). Knowing how dung beetle species will respond to different ecological changes could help find solutions and reduce the effects of their decline in the coming years (Batilani-Filho & Hernández 2017; Carpaneto *et al*. 2007; Fuzessy *et al*. 2021; Lobo 2001; Nichols *et al*. 2007, 2009), beyond the elimination or changes of certain livestock techniques that also influence these species, such as the use of ivermectin, housing livestock indoors or the progressive abandonment of transhumance (Lobo *et al*. 2006; Martínez *et al*. 2017; Numa *et al*. 2020; Verdú *et al*. 2015, 2020).

Therefore, the purpose of this study was to determine the effect of ecological factors on a dung beetle community from a locality of Central Spain during the continuous monitoring of more than one annual cycle. We seek to answer three main questions: (i) are there climatic and time-related variables that affect dung beetles; (ii) what importance will these have on their diversity patterns; and (iii) how will representatives of each of the subfamilies respond to them? To answer these questions, we focused on several variables ($N = 60$) related to temperature, humidity, atmospheric pressure and time, seeking to determine whether the temporal distribution of dung beetles has been mediated by these ecological factors.

Material and methods

Study area

The study was carried out in Mataelpino, a town located in the north-west of the Madrid Autonomous Community (Spain). A semi-open plot of 1.16 ha with frequent livestock use located on the outskirts of the city, on its western side, has been used for the study. It is located at an altitude of 1140 m a.s.l. (40.73°N, −3.96°W) (Fig. 1). The study area is located in the vicinity of the Guadarrama Mountain Range National Park and the Biosphere Reserve of the Upper Basins of the Manzanares, Lozoya and Guadarrama rivers.

With the continental nature of the interior of the peninsula, together with the inherent characteristics of the study area

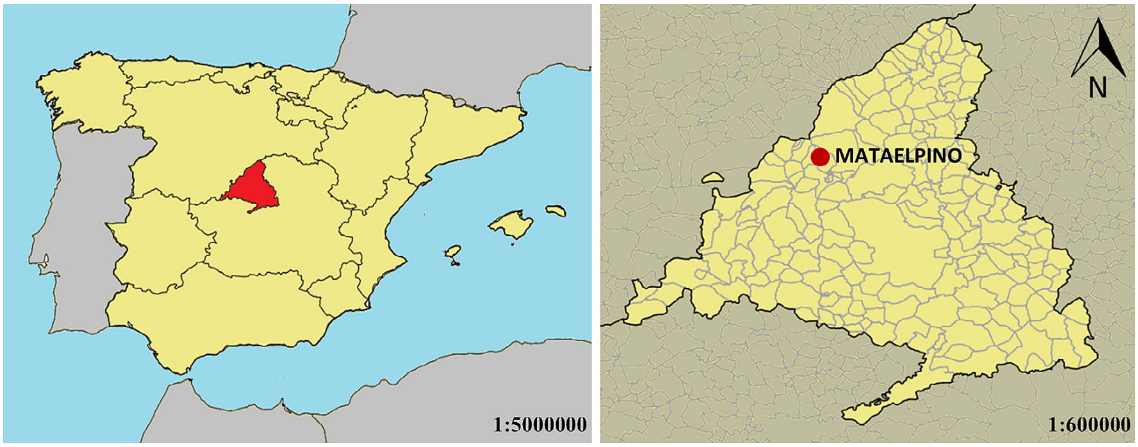

Figure 1 Location maps of the sampling area. The study was carried out in the town of Mataelpino, in the north-west of the Madrid Autonomous Community, Central Spain (40.73°N, –3.96°W). Black or grey lines represent administrative boundaries.

(altitude, slope, orientation, etc.), the climate is characterized by large diurnal and annual thermal oscillations and a marked summer drought. Winters are particularly cold and wet, with possible frosts from November to April, whereas summers are hot and dry (Rivas-Martínez 1983). The average annual temperature is between 8°C and 15°C, although values of down to −7°C have been recorded during the coldest months and up to 38°C has been recorded in the warmest months (Meteoclimatic 2020). The average annual values of atmospheric pressure vary between 1012.45 and 1017.59 hPa, with the daily fluctuations of atmospheric pressure being greater in winter than in summer (Meteoclimatic 2020). In terms of rainfall, the pluviometric regime is characterized as seasonal. The periods of greatest precipitation are associated with autumn and spring, whereas the driest period is associated with the summer months. Average annual rainfall records are usually around 700 mm (Meteoclimatic 2020).

These climatic conditions determine the plant communities and the existing fauna in the study area. The predominant vegetation is a forest of *Quercus ilex* spp. *ballota* (Desf.) Samp. (holm oak) and *Quercus pyrenaica* Willd. (Pyrenean oak), frequently mixed with a landscape of pastures and bushes. In addition, pine forests of *Pinus sylvestris* (European red pine), including *Pteridium aquilinum* (L.) Kuhn (eagle fern) and *Genista florida* L. (Iberian silver-leaved broom), can be found. Among the bushes, the most representative plants are brooms, junipers and rock roses. In the herbaceous stratum, grazing meadows for livestock predominate (Rivas-Martínez & Cantó 1987). These climatic and vegetation characteristics place the study area in the lower supramediterranean bioclimatic floor (Rivas-Martínez 1983).

It is important to highlight the livestock and wildlife that may be present in the study area, as the local dung beetle biodiversity could depend on their excrement. Fundamentally, there is a high level of livestock activity in the area, especially cattle (*Bos taurus* Linnaeus, 1758) and horses (*Equus ferus caballus* Linnaeus, 1758). Moreover, dung beetles usually also demonstrate a predilection for the excrement of herbivorous animals, such as those of *Capreolus capreolus* (Linnaeus, 1758) (roe deer), *Dama dama* (Linnaeus, 1758) (fallow deer) and *Oryctolagus cuniculus* (Linnaeus, 1758) (rabbit). However, they can also be attracted to the excrement of omnivorous animals, such as those of *Sus scrofa* (Linnaeus, 1758) (wild boar) or *Vulpes vulpes* (Linnaeus, 1758) (fox), and to those of carnivores, such as *Canis lupus signatus* (Cabrera, 1907) (the Iberian wolf) (Viejo-Montesinos 2013).

Data collection

Sampling was conducted once a month from May 2018 to February 2020. Permits for sampling and collecting dung beetles were obtained from the Department of the Environment, Territorial Planning and Sustainability of the Madrid Autonomous Community (refs 10/065982.9/18 and 10/135977.9/20) for the entire sampling period. Although we intended to carry out a 24-month study, sanitary confinement during the COVID-19 pandemic interrupted the final 2 months of the study. The sampling consisted of 12 pitfall traps that were set and checked monthly, following the method recommended by Lobo *et al*. (1988) and Veiga *et al*. (1989). The pitfall traps were distributed evenly throughout the sampling area, with a minimum distance of 50 m between each pair. The pitfall traps were baited with 250 g of fresh dung from different untreated animals, including ruminant and non-ruminant herbivores, as well as omnivores, in similar proportions (Grzechnik & Cabrero-Sañudo, in press) and the dung beetles attracted were collected after 72 h. For each month, the combined information from all 12 traps was used for the statistical analysis.

The climatic data were obtained from a meteorological station located in the town of El Boalo (Madrid, Spain), which is less than 5 km in a straight line from the study area. It is located at an altitude of 945 m a.s.l. (40.72°N, −3.92°W). Data are available online, upon request (Meteoclimatic 2020).

Sample processing

The collected dung beetles (coprophagous Scarabaeoidea) were kept separately in individual traps and preserved in 70% alcohol until identification. The individuals were subsequently identified using a binocular magnifier and the use of dichotomous keys (Martín-Piera & López-Colón 2000; Veiga 1998). Once dry-prepared, representatives of each species found in the samplings were incorporated into the Entomology Collection of Complutense University (UCME) collection (Madrid, Spain).

Analytical procedures

Analyses were performed to determine the influence of climatic and time-related variables on the diversity patterns of dung beetles. They were conducted for the dung beetles as a whole (coprophagous Scarabaeoidea) and then for each subfamily separately (Aphodiinae, Geotrupinae and Scarabaeinae).

At first, an estimate of biological diversity was carried out for each study unit using the estimation method proposed by Chao and Jost (2015). Based on Hill numbers (Chao *et al*. 2021, 2023; Hill 1973), this method allows one to quantify the species diversity of an assemblage by calculating continuous diversity profiles estimated as a function of q. The diversity profiles calculated include, among others, the potential species richness (q_0), the exponential Shannon index diversity, which can be interpreted as the effective number of abundant species in the assemblage (q_1 = effective species), and the inverse Simpson index diversity, interpreted as the effective number of highly abundant species in the assemblage (q_2 = dominant species) (Chao *et al*. 2014, 2020, 2021, 2023; Chao & Jost 2015). Using the data for potential and observed species richness, it is possible to establish a relationship to validate the sampling effort, with >70% considered a good representation of the data regarding the diversity present in the study area (Jiménez-Valverde & Hortal 2003). Analyses were conducted using the R package SpadeR 0.1.1 with the *Diversity* function to compute diversity estimates (Chao *et al*. 2016). The diversity profiles, the observed abundance of individuals and the species richness obtained (R_0) from the field data were considered dependent variables.

For this study, 60 ecological variables were used and considered as independent variables. All of them have been grouped into 4 sets according to their similarities (18 variables related to temperature, 21 variables related to humidity, 19 variables related to atmospheric pressure and 2 time-related variables) (Appendix, Table A3). Variables related to temperature, humidity and atmospheric pressure have been obtained directly from the raw data provided by the meteorological station. Variables considered to be cyclical, such as time-related variables, were transformed into both sine and cosine (where each day represents a portion of the complete 360° circular range) (Cuesta *et al*. 2021; Lobo & Cuesta 2021). Owing to the possibility that dung beetle communities may differ from one study year to the next, a variable related to the year of study was included in the analyses.

To explore the degree of correlation among all the ecological variables and within each set, Spearman's correlation analyses were performed.

Generalized linear models (GLMs) were then used to model how the dependent variables varied with each of the 60 ecological variables (Crawley 1993; McCullagh & Nelder 1989). Continuous variables were standardized to remove the effect of differences in measurement scale. Statistically significant relationships between dependent and independent variables were explored to determine whether a linear, quadratic or cubic function for each selected variable increased the explanatory capacity of the model (Dobson 1999). In cases where there was more than one significant independent variable per set, a backward removal procedure was used to find the best predictive model per set of variables and for the global models (Hsieh & Lu 2006). The goodness of fit for the models obtained was measured using the deviance statistic and the change in deviance was tested using the *F*-ratio test (Dobson 1999; McCullagh & Nelder 1989) with a 5% significance level. The percentage of explained deviance was calculated for each model (Dobson 1999).

Subsequently, the pure and combined effects of the different groups of variables considered in the study were quantified by applying the techniques of variation partitioning (Anderson & Gribble 1998; Borcard *et al*. 1992; Legendre & Legendre 1998; Qinghong & Brakenhielm 1995) and hierarchical decomposition (MacNally 2000). This allowed us to estimate how much of the variation of the response variable can be attributed exclusively to one independent variable, and to calculate the fraction of the variation accounted for by the joint effect of the variables considered (Cabrero-Sañudo & Lobo 2003). Thanks to this, the effects of certain groups of variables in which there may be some autocorrelation (possible temporal autocorrelation in time-related variables) can be separated, allowing the effect of other groups of variables to be independently evaluated. All the statistical analyses were carried out with R 4.2.1 (R Core Team 2022) and STATISTICA 10 (StatSoft Inc 2011).

Results

In total, 59,264 dung beetles belonging to 46 species were collected (Appendix, Table A1). Twenty-four species and 52,959 individuals of the subfamily Aphodiinae, 18 species and 6216 individuals of Scarabaeinae, and 4 species and 89 individuals of Geotrupinae were recorded. Aphodiinae represents 52% of the dung beetle species found and 89% of the individuals collected, being the most diverse and abundant taxa. Scarabaeinae represents 39% of the species found and 11% of the individuals collected. For both species richness and individual abundance, Geotrupinae was the least represented taxon, representing only 9% and less than 1%, respectively.

The diversity profiles (q_0, q_1 and q_2) and their graphical representations are shown in Appendix, Table AA2 and Figure 2, respectively. Likewise, the values for the abundance of individuals (*Ab*) and the species richness obtained (R_0) from the field data were graphically represented over time (Fig. 2).

In general, it is observed that species richness reaches its maximum during the spring months, with some peaks observed in the autumn months, whereas it reaches its minimum in the summer and winter months. This same general pattern can be observed in the results for Aphodiinae. In contrast, the richness and abundance of Geotrupinae reaches its maximum in the autumn months, with some peaks in late summer or early winter. Scarabaeinae reaches a greater richness and abundance of individuals in the summer months, with some peaks in late spring and early autumn.

As all the values of the ratios were higher than 70.00%, it can be assumed that the representation of the data is good (Appendix, Table A2). As a whole (coprophagous Scarabaeoidea), the dung beetle community is well represented, with more than 78% of extant species found in the study area. Geotrupinae was the best represented, with all possible species found in the study area, followed by Scarabaeinae, with a representation of 94.74%, and Aphodiinae, with a representation of 75.00%.

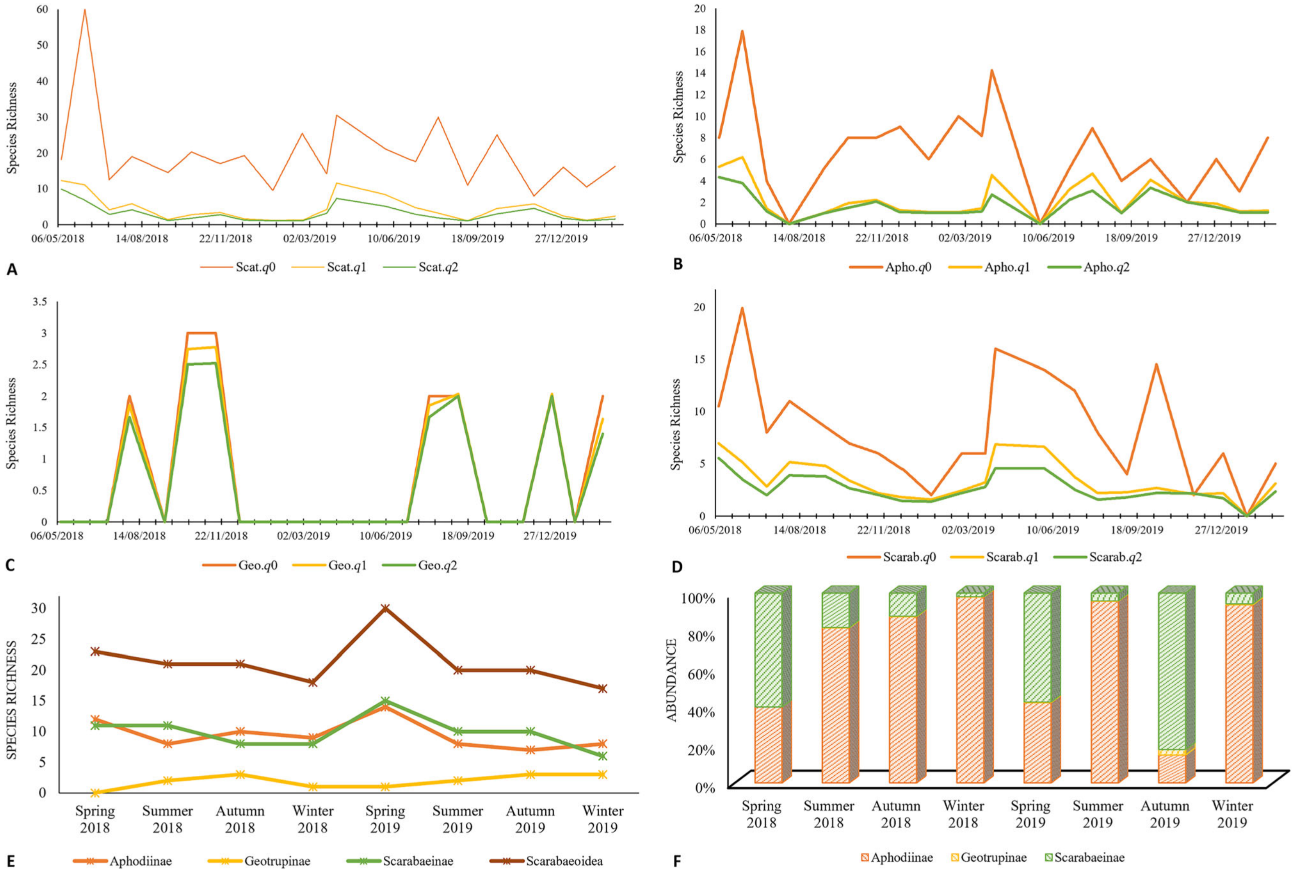

Figure 2 Representation of the estimation method. The dung beetles were considered as (A) a whole (coprophagous Scarabaeoidea) and by subfamilies separately: (B) Aphodiinae; (C) Geotrupinae; and (D) Scarabaeinae. Diversity profiles are potential species richness (q_0), exponential Shannon index diversity (q_1) and inverse Simpson index diversity (q_2). In addition, species richness (E) and abundance of individuals (F) obtained from the field data are represented by seasons. Abbreviations: Scarabaeoidea (Scat.); Aphodiinae (Apho.); Geotrupinae (Geo); Scarabaeinae (Scarab.).

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The results of the Spearman's correlation analyses, used to determine the degree of relationship among all the ecological variables and within each set, have been explored (Table - SA1). In general, it can be observed that the relationships among the variables included within the same set of variables present high positive correlations, whereas correlations among sets of variables, if present, are usually negative.

The results of the GLMs analysis have revealed the independent variables that exert an effect on the diversity patterns of dung beetles. In a first step, some previous analyses were used to determine whether the study year had any effect on the data, but these did not show any significant results. The predictive models per set of variables and for the global models resulting from the GLMs analysis are shown in Table 1, along with data for the *F*-statistic with a significant *P*-value ($P < 0.05$) and its explained variance (R^2). Differences can be observed in terms of the effect that each model per set of variables exerts on the dependent variables. In fact, it can be seen that some models have no effect on certain dependent variables. The effects also vary depending on whether the dung beetle community is considered as a whole or separately. All the statistically significant relationships between dependent and independent variables are shown (Appendix, Table A4).

According to the results, the temperature model has had an almost exclusive effect on the Scarabaeinae subfamily. When the rest of the subfamilies or dung beetles as a whole are taken into account, no temperature effect is observed, except when analyzing R_0 in the Geotrupinae, where temperature variables explain up to 64.15% of the deviance. In the case of the Scarabaeinae, for q_0, q_1, q_2 and R_0, the temperature variables explain 51.07%, 19.94%, 20.56% and 34.79% of the deviance, respectively.

Something similar happens with the humidity model, as no effect of humidity on dung beetles was observed, except in two cases. The first exception was for R_0 and *Ab* in Geotrupinae, explaining up to 71.13% and 29.65% of the deviance, respectively. The other case was in the Scarabaeinae, where the humidity variables explain 20.15%, 19.50% and 32.95% of the deviance observed for q_0, q_1 and R_0, respectively.

When dung beetles as a whole (coprophagous Scarabaeoidea) are considered, the variables related to atmospheric pressure explain 32.40% and 29.78% of the deviance in q_1 and q_2, respectively. For Scarabaeinae, the atmospheric pressure variables explain 21.08% (q_0), 24.33% (q_1), 20.30% (q_2) and 28.93% (R_0) of the deviance. In Aphodiinae, atmospheric variables are responsible for explaining 24.83% and 20.32% of the deviance in q_1 and q_2, respectively. The atmospheric pressure model does not appear to have any effect on the species diversity of Geotrupinae.

Dung beetle diversity, both when studied as a whole and by subfamily, has been described with the time-related model. If dung beetles are studied as a whole, it has been observed that the time-related variables explain 31.07% and 24.27% of the deviance in q_1 and q_2, respectively. In the case of Aphodiinae, these explain 28.44% of the deviance in R_0. In Geotrupinae, time-related variables explain part of the deviance in q_0 (27.39%), q_1 (27.09%), q_2 (26.69%), R_0 (58.75%),and abundance (26.91%). Regarding Scarabaeinae, the time-related variables explain 45.28%, 44.10%, 34.56% and 52.94% of the deviance observed in q_0, q_1, q_2 and R_0, respectively.

When a single group of variables explains part of the observed deviance of a dependent variable, the global model matches. However, if there are several groups of variables capable of explaining part of the deviance, the global model can coincide with the effect of some of these groups, but it can also be a combination of several of them, increasing their explanatory power. This can be observed in R_0 and *Ab* in Geotrupinae, as well as in q_0 in Scarabaeinae, explaining up to 90.79%, 47.53% and 62.20% of the deviance observed, respectively. Moreover, it should be noted that practically none of the ecological variables has had an effect on the abundance of dung beetles, except in the two cases in Geotrupinae already described above.

The deviance partition analysis revealed the contribution of the pure effects of the different groups of variables and their combined effect (Fig. 3). In almost all the models there was a percentage of deviance that was not explained by our studied variables (unknown). However, this does not mean that the experimental design was incorrect or that the variables selected were not appropriate. It must be taken into account that the diversity patterns that can be seen today are the result of the joint effect of geographical, historical and ecological factors, which have been shaping dung beetle populations over time. In this case, the study has only focused on ecological factors. In coprophagous Scarabaeoidea, the variation is explained by the pure effect of atmospheric pressure variables (1.33% for q_1 and 5.51% for q_2) and the combined effect of atmospheric pressure variables and time-related variables (31.07% for q_1 and 24.27% for q_2). The relationship between the dependent variables and the variables related to atmospheric pressure was negative. As pressure increases, the dependent variables decreases and vice versa. The trend observed when studying the combined effect of the time-related variables and those of atmospheric pressure on the dependent variables (q_1 and q_2) was that there is an increase in dung beetle diversity when the minimum pressure also increases during the warm months of the year (Fig. 4).

In Aphodiinae, the variation was explained by the pure effect of atmospheric pressure variables (24.83% for q_1 and 20.32% for q_2) and the pure effect of time-related variables

Table 1 Results of GLMs analysis. Data for $F_{(1,19)}$-statistic with a significant P-value ($P < 0.05$) and explained variance (R^2) for the sets of variables are shown. Dependent variables are potential species richness (q_0), exponential Shannon index diversity (q_1), inverse Simpson index diversity (q_2), observed abundance of individuals (Ab) and species richness obtained (R_0). The superscript letters refer to the independent variable or variables that have been selected in each set of variables: ^{a}tr; ^{b}TM + TM15; ^{c}td; ^{d}taRat; ^{e}TM7; ^{f}hm3; ^{g}hr; ^{h}hm7; ^{i}hm10; ^{j}HM; ^{k}psm; ^{l}PsM; ^{m}PsM30; ^{n}psd; ^{o}CDSin; ^{p}CDCos; ^{q}CDSin + CDCos; ^{r}hm3 + CDSin + CDCos; ^{s}hr + CDCos; ^{t}CDSin + TM15

	Coprophagous Scarabaeoidea					Aphodiinae					Geotrupinae					Scarabaeinae				
	q_0	q_1	q_2	R_0	Ab	q_0	q_1	q_2	R_0	Ab	q_0	q_1	q_2	R_0	Ab	q_0	q_1	q_2	R_0	Ab
Temperature model	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 32.21^{a}$ 64.15%	–	$F = 17.74^{b}$ 51.07%	$F = 4.48^{c}$ 19.94%	$F = 4.66^{d}$ 20.56%	$F = 9.60^{e}$ 34.79%	–
Humidity model	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 39.41^{f}$ 71.13%	$F = 7.59^{g}$ 29.65%	$F = 4.54^{h}$ 20.15%	$F = 4.44^{i}$ 19.78%	–	$F = 8.85^{j}$ 32.95%	–
Atmospheric pressure model	–	$F = 8.63^{k}$ 32.40%	$F = 7.63^{k}$ 29.78%	–	–	–	$F = 5.94^{l}$ 24.83%	$F = 4.59^{l}$ 20.32%	–	–	–	–	–	–	–	$F = 4.81^{m}$ 21.08%	$F = 5.79^{k}$ 24.33%	$F = 4.59^{n}$ 20.30%	$F = 7.33^{l}$ 28.93%	–
Time-related model	–	$F = 8.11^{o}$ 31.07%	$F = 5.77^{o}$ 24.27%	–	–	–	–	–	$F = 7.15^{p}$ 28.44%	–	$F = 6.79^{p}$ 27.39%	$F = 6.69^{p}$ 27.09%	$F = 6.55^{p}$ 26.69%	$F = 24.21^{q}$ 58.75%	$F = 6.63^{p}$ 26.91%	$F = 14.90^{o}$ 45.28%	$F = 14.20^{o}$ 44.10%	$F = 9.50^{o}$ 34.56%	$F = 20.25^{o}$ 52.94%	–
Global model	–	$F = 8.63^{k}$ 32.40%	$F = 7.63^{k}$ 29.78%	–	–	–	$F = 5.94^{l}$ 24.83%	$F = 4.59^{l}$ 20.32%	$F = 7.15^{p}$ 28.44%	–	$F = 6.79^{p}$ 27.39%	$F = 6.69^{p}$ 27.09%	$F = 6.55^{p}$ 26.69%	$F = 137.94^{r}$ 90.79%	$F = 15.40^{s}$ 47.53%	$F = 28.46^{t}$ 62.20%	$F = 14.20^{o}$ 44.10%	$F = 9.50^{o}$ 34.56%	$F = 20.25^{o}$ 52.94%	–

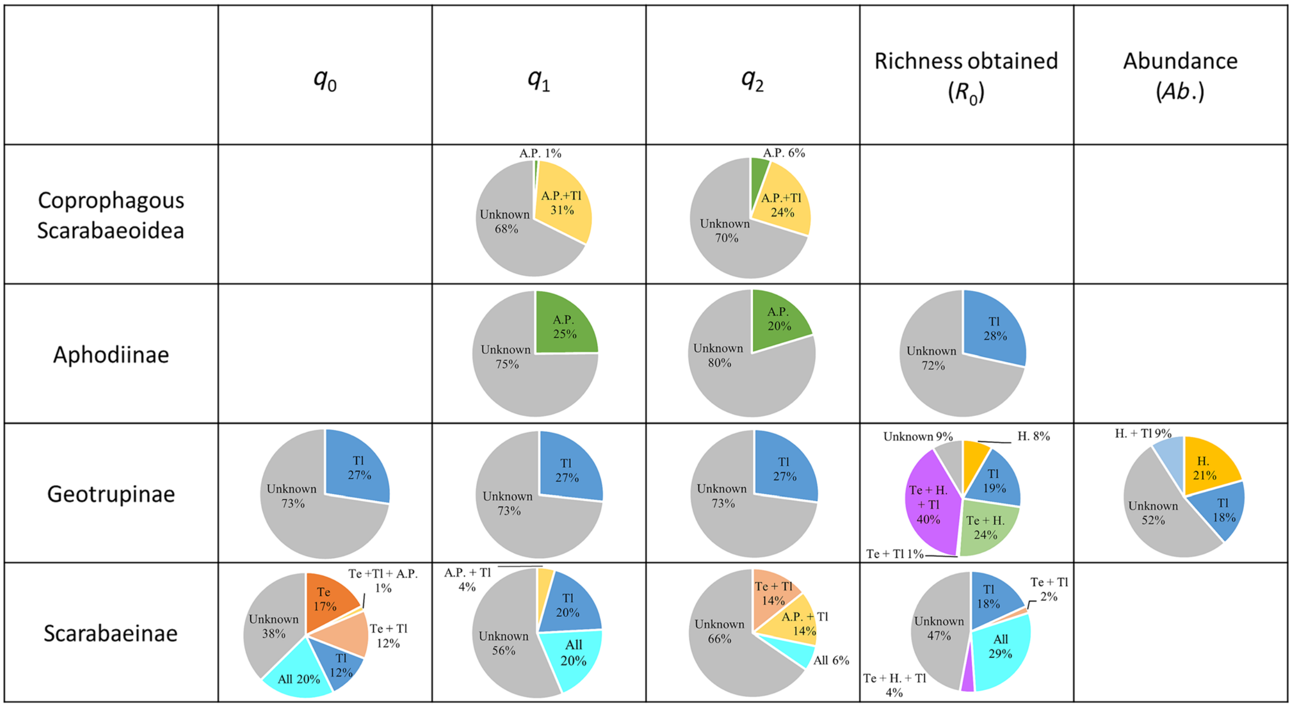

Figure 3 Results of the variation partitioning analysis. The significant independent variables were studied to determine their effect on dependent variables. The percentages of pure and combined effects of the variables are shown. Abbreviations: temperature related variables (Te), humidity related variables (H.), atmospheric pressure related variables (A.P.), and time-related variables (Tl). The variance not explained by the ecological factors is shown in gray (unknown). To facilitate the interpretation of the figure, the descriptive names of each group of variables have been used. To know which variable is being treated, refer to the information contained in the text and Table A2.

(28.44% for R_0) (Fig. 3). In the case of atmospheric pressure-related variables, their relationships with the dependent variables were inversely proportional, whereas the relationships of the time-related variables with the dependent variables were directly proportional.

In Geotrupinae, the variation of q_0, q_1 and q_2 was explained by the pure effect of the time-related variables (27.39%, 27.09% and 26.69%, respectively). For the abundance, 17.88% of the deviance is explained by the pure effect of time-related variables, 20.62% is explained by the pure effect of humidity variables and 9.03% is explained by the combined effect of both groups of variables. For R_0, a percentage of the deviance is explained by both the pure and the combined effect of all groups of significant variables, as observed in the GLMs analyses (Table 1). About 27% of the deviance is explained by the pure effects of the groups of significant variables (8.30% by the humidity variables and 19.05% by the time-related variables). The combined effect of temperature, humidity and time-related variables explained the most (39.81%) (Fig. 3). The combined effect of temperature and humidity also accounted for explaining the deviance (23.73%). If pure effects are studied, a positive relationship can be observed between humidity-related variables and abundance, whereas a negative relationship can be observed between time-related variables and dependent variables (q_0, q_1 and q_2). If the combined effect of humidity and time-related variables is considered, an interaction between them can be observed. For example, the abundance of Geotrupinae will be favored at times of the year associated with rain, such as the autumn months, and when there are no large fluctuations in the levels of humidity (Fig. 4).

In Scarabaeinae, the pure and combined effects of the different groups of variables explain some of the observed deviance. In almost all cases, the pure effects of the time-related variables turned out to be those that explained the most among the pure effects of the other groups of variables (11.87% in q_0, 19.77% in q_1 and 18.15% in R_0) (Fig. 3). Regarding the combined effects, the interaction between time-related and temperature variables is the one that has explained the most deviance (12.33% in q_0, 14.25% in q_2 and 1.84% in R_0). Temperature and time-related variables positively influence Scarabaeinae species diversity, whereas humidity and atmospheric pressure-related variables have the opposite effect. When the combined effect of humidity and temperature-related variables was studied, an interaction between these independent variables was observed. It was

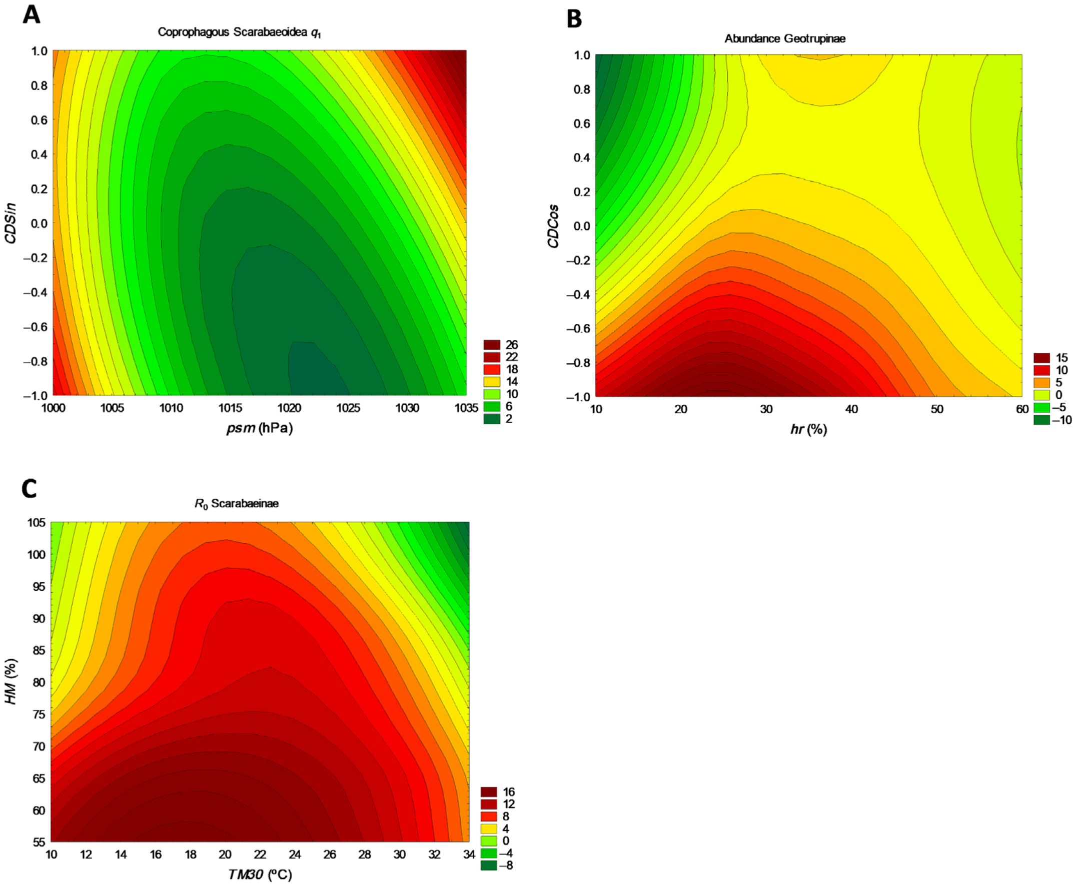

Figure 4 Contour plots of the predicted dung beetle diversity. These predictions are associated with interactions between two selected independent variables. In coprophagous Scarabaeoidea, there is an increase of q_1 when *psm* also increases during the warm months of the year (A). In Geotrupinae, the abundance is associated with the autumn months and periods in which there are no large fluctuations in humidity levels (B). In Scarabaeinae, R_0 is favoured when *HM* is low and *TM30* is high (C). Positive–negative scores are represented as red–green.

observed that Scarabaeinae species richness is greater when the maximum humidity values were low and the maximum temperature values were high (Fig. 4).

Discussion

The results of the study showed that climatic and time-related variables exert an effect on the diversity patterns of the Mataelpino dung beetle community. The different groups of variables studied have managed to explain some of the variability observed in the selected dependent variables. In fact, differences have been observed depending on the treatment of the variables (separately or combined effect per set of variables), as well as on the taxonomic level in which the dung beetles have been represented (as a whole or separated by subfamilies).

Among all the variables, the only group that has exerted an effect at all taxonomic levels has been the time-related variables. Furthermore, much of the deviance observed in the results has been explained using these variables, even by themselves. Altogether, this indicates that the diversity of the dung beetles is adjusted to the climatic conditions that occur over time in the study area. In general, it has been seen that the dung beetle diversity was much higher during spring and autumn, whereas in summer and winter the diversity decreased. This is consistent with other studies carried out in the Mediterranean region, where peaks of greater or lesser diversity can be distinguished depending on the season of the year (Agoglitta *et al.* 2012; Jay-Robert, Errouissi, & Lumaret 2008; Lobo 1982; Lumaret & Kirk 1987, 1991; Senyüz *et al.* 2019). However, if the subfamilies are studied separately, clear differences can be noted in the seasonal patterns of each one.

Aphodiinae followed the classic Mediterranean bimodal pattern (Lumaret & Kirk 1991; Senyüz *et al.* 2019), with the highest species richness and abundance values recorded in spring and autumn. In fact, the results showed a positive relationship between the *CDCos* variable (this variable refers to the day of trap collection transformed into cosine) and R_0, suggesting that the greatest diversity of Aphodiinae species can be found in the autumn months. Being dwellers inside excrement makes them vulnerable to the droughts and the frosts that are typical of the summer and the winter months, respectively (Jay-Robert, Errouissi, & Lumaret 2008; Lumaret 1995). Therefore, there was a reduction in Aphodiinae representation during these times of the year.

On the other hand, Scarabaeinae and Geotrupinae presented a unimodal pattern. In Scarabaeinae, a positive relationship has been observed between the dependent variables (q_0 and q_1) and the *CDSin* variable (this variable refers to the day of trap collection transformed into sine). This suggests that the highest Scarabaeinae species richness will be found mainly in the summer months. This agrees with other studies in which it was seen that the members of this subfamily were more active in the summer period, as they are well adapted to warm conditions, and are practically absent during winter (Errouissi *et al*. 2009; Jay-Robert, Errouissi, & Lumaret 2008). They overcome droughts by burying the dung in the ground, preventing it from desiccation (Jay-Robert, Errouissi, & Lumaret 2008; Labidi *et al*. 2012).

In Geotrupinae, the peak of greatest activity occurs at the end of the year, especially in the autumn months (Errouissi *et al*. 2004, 2009; Jay-Robert, Errouissi, & Lumaret 2008; Lumaret & Kirk 1987). Their strategy is to come out and breed after the first autumn rains, and to survive periods of inclement weather as an egg, larva or pupa (Lumaret 1995). However, the results show the opposite. A negative relationship can be observed between Geotrupinae species richness and the autumn months (*CDCos*). A possible explanation for this result could be associated with the species *Ceratophyus hoffmannseggi* Fairmaire, 1856 and *Anoplotrupes stercorosus* (Scriba, 1791). Although both present the typical phenological pattern of Geotrupinae, it has been observed that they need drier environments for their larvae to develop correctly (Galante & Rodríguez 1988; Marczak & Mroczynski 2018). It is possible that the presence of these two species, with different ecological requirements from the rest of Geotrupinae, is interfering in the global results.

Another interesting result has been to see that atmospheric pressure seems to have an effect on dung beetle communities. The results of this study showed that atmospheric pressure was always inversely proportional to the dependent variables. This means that when atmospheric pressure levels are high (good weather), the dung beetle diversity is negatively affected. This might make sense for Aphodiinae, which typically shows a peak of greater activity after rainy periods (spring and autumn) (Lumaret & Kirk 1991; Senyüz *et al*. 2019). These factors could explain why its diversity values are associated with low atmospheric pressure conditions. In fact, a direct effect of this variable can be seen on the species of Aphodiinae. The *PsM* variable (this variable refers to the maximum pressure of the day) has turned out to be the only variable from the atmospheric pressure group that has influenced the Aphodiinae. In addition, it seemed to have an effect mainly on the abundant (q_1) and highly abundant (q_2) species of the assemblage. These species are *Anomius castaneus* (Illiger, 1803), *Melinopterus sphacelatus* (Panzer, 1798) and *Nimbus contaminatus* (Herbst, 1783), which have a markedly autumnal phenology (Agoiz-Bustamante 2008; Errouissi *et al*. 2009; Veiga 1998). Therefore, it could be said that Aphodiinae, specifically the abundant species, are negatively affected by high records of atmospheric pressure.

Although pressure does not seem to exert an effect on Geotrupinae, the same response as seen in Aphodiinae would have been expected, as both have similar temperate preferences and peaks in the activity of species recorded in the autumn (Errouissi *et al*. 2004; Lobo & Halffter 2000; Lumaret & Kirk 1991; Martín-Piera & López-Colón 2000; Mena 2001).

On the other hand, a positive relationship between Scarabaeinae diversity and atmospheric pressure levels would have been expected, as these dung beetles are adapted to hot and dry climates and their activity usually takes place during the central hours of the day (Errouissi *et al*. 2004, 2009; Jay-Robert, Errouissi, & Lumaret 2008; Lumaret & Kirk 1991; Martín-Piera & López-Colón 2000). However, the atmospheric variables do not seem to have a great effect on Scarabaeinae. Two species have been found, *Bubas bison* (Linnaeus, 1767) and *Bubas bubalus* (Olivier, 1811), which show a seasonal pattern similar to that of Aphodiinae and Geotrupinae (Martín-Piera & López-Colón 2000). However, it is unlikely that the results that have been observed are associated with them as they do not even represent 2% of the Scarabaeinae community. Most likely there is an effect that is not being noticed because it is masked or because of the interaction with other variables that have a greater weight on Scarabaeinae diversity, such as time-related or temperature variables.

Regarding temperature and humidity, their effects have been widely studied and have always been considered the most influential factors in dung beetles (Ambrozova *et al*. 2022; Dortel *et al*. 2013; Errouissi *et al*. 2004, 2009; Ferreira *et al*. 2018; Lobo *et al*. 2002; Lumaret & Kirk 1987, 1991; Numa *et al*. 2012). However, in this study they have turned out to be the least relevant as they have only affected the Geotrupinae and Scarabaeinae subfamilies. Neither of these two factors seemed to influence Aphodiinae, although it was expected that they would have the same response as Geotrupinae, as they have the same preference for cooler and wetter climates (Cabrero-Sañudo & Lobo 2009; Errouissi *et al*. 2004; Jay-Robert, Lumaret, & Lebreton 2008; Lobo & Halffter 2000; Lumaret & Kirk 1991).

The results showed that Scarabaeinae diversity was positively influenced by temperature-related variables. In fact, temperature has had an almost exclusive effect on the diversity of Scarabaeinae. However, this effect has not been especially large, except in q_0 where the interaction between *TM* (this variable refers to the maximum temperature of the day) and *TM15* (this variable refers to the average of the maximum temperatures of 15 days) alone manages to explain 17% of the observed deviance. It can be observed that most of these variables are related to the maximum temperature reached during the day. This would agree with the fact that most of the recorded species are diurnal, showing a peak of activity in the middle of the day. For example, *Onthophagus similis* (Scriba, 1790), *Onthophagus opacicollis* Reitter, 1893 and *Euoniticellus fulvus* Goeze, 1777, which turned out to be the most abundant species, showed this pattern (Ávila & Pascual 1988; Lumaret & Kirk 1987; Martín-Piera & López-Colón 2000; Mena *et al*. 1989). Even other species that were not so well represented, such as *Onthophagus lemur* (Fabricius, 1781), *Onthophagus taurus* (Schreber, 1759) or *Onthophagus vacca* (Linnaeus, 1767), are also thermophiles (Ávila & Pascual 1988; Baz 1988; Lumaret & Kirk 1987; Martín-Piera & López-Colón 2000; Mena *et al*. 1989; Wassmer 1995).

In the Geotrupinae, the factor that seems most important between the two is humidity. It is observed that humidity-related variables (*hr* and *hm3*) have a negative effect on the dependent variables. However, humidity was expected to exert a positive influence on Geotrupinae species, as they usually appear after the spring and autumn rains (Errouissi *et al*. 2004; Lobo & Halffter 2000; Lumaret & Kirk 1991; Martín-Piera & López-Colón 2000; Mena 2001). As previously mentioned, it is possible that the occurrence of two species with different ecological requirements from the rest of the Geotrupinae is interfering with the global results.

On the other hand, when the dung beetles were represented together (coprophagous Scarabaeoidea), the results were confusing. *CDSin* and *psm* were the only variables that explain the deviance observed in the dependent variables. However, the variables *CDCos* and *PsM* were expected to have greater importance, as Aphodiinae was the most representative subfamily, both in terms of the abundance of individuals and richness of species. It is possible that the joint representation of taxonomic groups with different adaptations could lead to a misinterpretation of the data, as there are mixed responses that could sometimes even be contradictory. Therefore, it is better to consider the effects of variables by analyzing the dung beetles as separated subfamilies.

It was expected to observe an effect of the ecological variables on the abundance of dung beetle individuals. However, the results do not show any relationship except in Geotrupinae, where a negative effect of two variables (*hr* and *CDCos*) has been observed. This could be associated with the heterogeneity of the data collected for Aphodiinae and Scarabaeinae, as there were months in which outbreaks of certain species occurred and the number of individuals collected considerably exceeded the values in other months. On the other hand, the values for Geotrupinae were more stable in comparison, which could indicate a relationship between ecological factors and the abundance of individuals. In fact, this relationship was expected to be positive, considering that the abundance of Geotrupinae species should increase during the autumn months. Therefore, this could be a sign that the abundance of individuals depends on other non-climatic factors, such as the characteristics of the microhabitats, the availability of food (Bogoni *et al*. 2016) or the properties of the dung (Treitler *et al*. 2017).

Finally, it should be noted that this study has focused solely on determining the effect that climatic and time-related variables have on the diversity patterns of a dung beetle community. The limitation introduced by not taking into account other factors was reflected in the results, as in many cases there has been a percentage of the deviance that could not be explained by the variables studied. In fact, there are other ecological factors, both abiotic and biotic, as well as geographical and historical events that have not been taken into account in this study. For example, several investigations have noted an effect of other ecological factors, such as altitude (Errouissi *et al*. 2004; Jay-Robert et al. 1997; Jay-Robert, Errouissi, & Lumaret 2008; Labidi *et al*. 2012; Martín-Piera *et al*. 1992) or habitat type (Halffter & Edmonds 1982;Jay-Robert, Lumaret, & Lebreton 2008 ; Lumaret & Kirk 1987 ; Martín-Piera *et al*. 1992), on dung beetles, distinguishing diversity gradients. Scarabaeinae species are more restricted to lowlands and open pastures where the climate is warmer. In contrast, Aphodiinae and Geotrupinae species prefer woodlands and highlands, where climatic conditions are better suited to their preferences (Jay-Robert, Lumaret, & Lebreton 2008; Lumaret & Kirk 1987; Martín-Piera *et al*. 1992). Other studies have observed that the development of preferences for a specific type of dung can also influence the diversity patterns of dung beetles (Dormont *et al*. 2004, 2007; Raine & Slade 2019; Tonelli *et al*. 2021). Even the development of different nesting strategies (Halffter & Edmonds 1982; Halffter & Matthews 1966), as well as the development of parental care (Klemperer 1982; Martín-Piera & López-Colón 2000; Thotagamuwa *et al*. 2023), are factors to take into account when studying dung beetles. Nor should we forget that several historical events (dispersal and vicariance, local extinctions and glaciations) have influenced the configuration of the spatial distribution of dung beetles over time (Davis & Scholtz 2001). These and other factors are responsible for the dung beetle diversity patterns that are observed today. Therefore, when studies of this type are carried out, it must be noted that they have their limitations and that the factors studied will not be the only ones responsible for the observed diversity.

Conclusion

In summary, the results showed that climatic and time-related variables have an effect on the Mataelpino dung beetle community. Specifically, time-related variables have been shown to have a greater effect on the diversity variables studied. Therefore, the composition of the Mataelpino dung beetle community varies throughout the year, with peaks of greater or lesser richness and abundance of individuals depending on the ecological requirements of the species. Another factor that has turned out to be significant, and that has never been studied before in dung beetles, is atmospheric pressure. Although not all the results have turned out as expected, research should continue in this direction. Regarding temperature and humidity, they have turned out to be the least relevant variables. It must also be noted that there are other factors, both ecological and historical, which have not been considered for this study and are responsible for the dung beetle diversity patterns that are observed today. Therefore, ecological variables will only be able to explain some of these results.

Author contributions

Both authors contributed equally to the development of this study.

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Conflict of interest statement

The authors have no conflict of interest to declare.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Appendix

Table A1 List of the 46 dung beetle species registered in Mataelpino. A list of the species grouped by subfamilies is shown. In addition, the collected individuals of each species are indicated

List of species	Abundance of individuals
Subfamily Aphodiinae	
Agolius bonvouloiri (Harold, 1860)	2
Agrilinus constans (Duftschmid, 1805)	85
Aphodius conjugatus (Panzer, 1795)	1
Aphodius fimetarius (Linnaeus, 1758)	39
Aphodius foetidus (Herbst, 1783)	433
Ammoecius elevatus (Olivier, 1789)	47
Anomius castaneus (Illiger, 1803)	22,754
Biralus mahunkaorum Adam, 1983	48
Bodiloides ictericus (Laicharting, 1781)	11
Bodilus longispina (Küster, 1854)	7
Calamosternus granarius (Linnaeus, 1767)	66
Chilothorax distinctus (Müller, 1776)	119
Chilothorax lineolatus (Illiger, 1803)	3
Colobopterus erraticus (Linnaeus, 1758)	141
Coprimorphus scrutator (Herbst, 1789)	1
Esymus merdarius (Fabricius, 1775)	16
Eudolus quadriguttatus (Herbst, 1783)	12
Heptaulacus testudinarius (Fabricius, 1775)	30
Labarrus lividus (Olivier, 1789)	1
Melinopterus sphacelatus (Panzer, 1798)	23,231
Nimbus contaminatus (Herbst, 1783)	5807
Otophorus haemorrhoidalis (Linnaeus, 1758)	46
Sigorus porcus (Fabricius, 1792)	5
Trichonotulus scrofa (Fabricius, 1787)	54
Subfamily Scarabaeinae	
Bubas bison (Linnaeus, 1767)	32
Bubas bubalus (Olivier, 1811)	61
Caccobius schreberi (Linnaeus, 1767)	36
Cheironitis ungaricus (Herbst, 1789)	38
Copris lunaris (Linnaeus, 1758)	173
Euoniticellus fulvus (Goeze,1777)	837
Onthophagus coenobita (Herbst, 1783)	7
Onthophagus fracticornis (Preyssler, 1790)	51
Onthophagus furcatus (Fabricius, 1781)	75
Onthophagus illyricus (Scopoli, 1763)	27
Onthophagus lemur (Fabricius, 1781)	138
Onthophagus opacicollis Reitter, 1892	1613
Onthophagus punctatus (Illiger, 1803)	1
Onthophagus similis (Scriba, 1790)	2521
Onthophagus stylocerus Graëlls, 1851	1
Onthophagus taurus (Schreber, 1759)	407
Onthophagus vacca (Linnaeus, 1767)	194
Scarabaeus sacer Linnaeus, 1758	4
Subfamily Geotrupinae	
Anoplotrupes stercorosus (Scriba, 1791)	8
Geotrupes ibericus Baraud, 1958	54
Geotrupes mutator (Marsham, 1802)	22
Ceratophyus hoffmannseggi Fairmaire, 1856	5

Table A2 Results of the estimation method. The values of the diversity profiles: potential species richness (q_0), exponential Shannon index diversity (q_1) and inverse Simpson index diversity (q_2) are shown. Also, observed abundance of individuals (*Ab*) and species richness obtained (R_0) from the field data are shown. The validation of the sampling effort is represented as the ratio between R_0 and q_0. The statistical significance of the sampling effort is assumed when the values of the ratios are higher than 70.00% (marked in red)

	q_0	q_1	q_2	Richness obtained (R_0)	Abundance (*Ab*)	R_0/q_0
Coprophagous Scarabaeoidea	58.500	4.535	3.189	46	59,264	78.63%
Aphodiinae	32.000	2.996	2.568	24	52,959	75.00%
Geotrupinae	4.000	2.841	2.304	4	89.000	100.00%
Scarabaeinae	19.000	5.604	3.894	18	6,216	94.74%

Table A3 List of the 60 ecological variables included in the study. The variables are grouped into 4 sets: temperature, humidity, atmospheric pressure and time-related variables. The time-related variables were analyzed using circular statistics (Cuesta *et al*. 2021; Lobo & Cuesta 2021)

Independent variables	Abbreviations	Description/formulae
Temperature		
Max. temperature of the day	*TM*	Raw data from the weather station
Min. temperature of the day	*tm*	Raw data from the weather station
Daily average temperature	*td*	Raw data from the weather station
Daily temperature range	*tr*	Raw data from the weather station
3-day average max. temperature	*TM3*	(Sum (max. temperature of the first 3 days)/3)
7-day average max. temperature	*TM7*	(Sum (max. temperature of the first 7 days)/7)
10-day average max. temperature	*TM10*	(Sum (max. temperature of the first 10 days)/10)
15-day average max. temperature	*TM15*	(Sum (max. temperature of the first 15 days)/15)
30-day average max. temperature	*TM30*	(Sum (max. temperature of the first 30 days)/30)
3-day average min. temperature	*tm3*	(Sum (min. temperature of the first 3 days)/3)
7-day average min. temperature	*tm7*	(Sum (min. temperature of the first 7 days)/7)
10-day average min. temperature	*tm10*	(Sum (min. temperature of the first 10 days)/10)
15-day average min. temperature	*tm15*	(Sum (min. temperature of the first 15 days)/15)
30-day average min. temperature	*tm30*	(Sum (min. temperature of the first 30 days)/30)
Monthly average temperature	*taM*	(Sum (daily average temperature of the first 30 days)/30)
Temperature average ratio	*taRat*	Monthly average temperature/monthly temperature range
Monthly absolute min. temperature	*tmAM*	Raw data from the weather station
Monthly absolute max. temperature	*TMAM*	Raw data from the weather station
Humidity		
Max. humidity of the day	*HM*	Raw data from the weather station
Min. humidity of the day	*hm*	Raw data from the weather station
Daily average humidity	*hd*	Raw data from the weather station
Daily humidity range	*hr*	Raw data from the weather station
3-day average max. humidity	*HM3*	(Sum (max. humidity of the first 3 days)/3)
7-day average max. humidity	*HM7*	(Sum (max. humidity of the first 7 days)/7)
10-day average max. humidity	*HM10*	(Sum (max. humidity of the first 10 days)/10)
15-day average max. humidity	*HM15*	(Sum (max. humidity of the first 15 days)/15)
30-day average max. humidity	*HM30*	(Sum (max. humidity of the first 30 days)/30)
3-day average min. humidity	*hm3*	(Sum (min. humidity of the first 3 days)/3)
7-day average min. humidity	*hm7*	(Sum (min. humidity of the first 7 days)/7)
10-day average min. humidity	*hm10*	(Sum (min. humidity of the first 10 days)/10)
15-day average min. humidity	*hm15*	(Sum (min. humidity of the first 15 days)/15)
30-day average min. humidity	*hm30*	(Sum (min. humidity of the first 30 days)/30)
Monthly average humidity	*haM*	(Sum (daily average humidity of the first 30 days)/30)
Humidity average ratio	*haRat*	Monthly average humidity/monthly humidity range

(*Continues*)

Table A3 (continued)

Independent variables	Abbreviations	Description/formulae
Monthly absolute min. humidity	*hmAM*	Raw data from the weather station
Monthly absolute max. humidity	*HMAM*	Raw data from the weather station
Precipitations	*Pp*	Raw data from the weather station
Monthly average precipitations	*PpaM*	(Sum (precipitations of the first 30 days)/30)
Precipitation average ratio	*PpaRat*	Precipitations/Monthly average precipitations
Atmospheric pressure		
Max. pressure of the day	*PsM*	Raw data from the weather station
Min. pressure of the day	*psm*	Raw data from the weather station
Daily average pressure	*psd*	Raw data from the weather station
Daily pressure range	*psr*	Raw data from the weather station
3-day average max. pressure	*PsM3*	(Sum (max. pressure of the first 3 days)/3)
7-day average max. pressure	*PsM7*	(Sum (max. pressure of the first 7 days)/7)
10-day average max. pressure	*PsM10*	(Sum (max. pressure of the first 10 days)/10)
15-day average max. pressure	*PsM15*	(Sum (max. pressure of the first 15 days)/15)
30-day average max. pressure	*PsM30*	(Sum (max. pressure of the first 30 days)/30)
3-day average min. pressure	*psm3*	(Sum (min. pressure of the first 3 days)/3)
7-day average min. pressure	*psm7*	(Sum (min. pressure of the first 7 days)/7)
10-day average min. pressure	*psm10*	(Sum (min. pressure of the first 10 days)/10)
15-day average min. pressure	*psm15*	(Sum (min. pressure of the first 15 days)/15)
30-day average min. pressure	*psm30*	(Sum (min. pressure of the first 30 days)/30)
Monthly average pressure	*psaM*	(Sum (daily average pressure of the first 30 days)/30)
Pressure average ratio	*psaRat*	Monthly average pressure/Monthly pressure range
Monthly absolute min. pressure	*psAm*	Raw data from the weather station
Monthly absolute max. pressure	*PsAM*	Raw data from the weather station
Wind	*W*	Raw data from the weather station
Time-related		
Collection day (SEN)	*CDSin*	Analyzed with circular statistics
Collection day (COS)	*CDCos*	Analyzed with circular statistics

Table A4 Results of the generalized linear models (GLMs). Data for the $F_{(1,19)}$-statistic and explained variance (R^2) are shown, but only results where the F-statistic offers values with a significant P-value ($P < 0.05$) are listed. Only the independent variables that have had an effect on the dependent variables are shown. Dependent variables are potential species richness (q_0), exponential Shannon index diversity (q_1), inverse Simpson index diversity (q_2), observed abundance of individuals (Ab.) and species richness obtained (R_0)

	Coprophagous Scarabaeoidea					Aphodiinae					Geotrupinae					Scarabaeinae				
	q_0	q_1	q_2	R_0	*Ab*	q_0	q_1	q_2	R_0	*Ab*	q_0	q_1	q_2	R_0	*Ab*	q_0	q_1	q_2	R_0	*Ab*
Atmospheric pressure																				
PsM	–	$F = 7.27$ 28.77%	$F = 6.23$ 25.71%	–	–	–	$F = 5.94$ 24.83%	$F = 4.59$ 20.32%	–	–	–	–	–	–	–	$F = 5.06$ 21.93%	$F = 5.70$ 24.05%	$F = 4.47$ 19.90%	$F = 7.33$ 28.93%	–
psm	–	$F = 8.63$ 32.40%	$F = 7.63$ 29.78%	–	–	–	$F = 5.05$ 21.90%	–	–	–	–	–	–	–	–	–	$F = 5.79$ 24.33%	–	$F = 6.26$ 25.81%	–
psd	–	$F = 8.31$ 31.57%	$F = 7.22$ 28.63%	–	–	–	$F = 5.71$ 24.10%	$F = 4.39$ 19.61%	–	–	–	–	–	–	–	$F = 4.67$ 20.60%	$F = 6.00$ 24.99%	$F = 4.59$ 20.30%	$F = 7.08$ 28.23%	–
PsM3	–	$F = 5.26$ 22.62%	$F = 4.82$ 21.13%	–	–	–	$F = 4.73$ 20.82%	–	–	–	–	–	–	–	–	–	–	–	–	–
PsM15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 4.65$ 20.53%	–	–	$F = 5.20$ 22.42%	–
PsM30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 4.81$ 21.08%	–	–	$F = 5.28$ 22.68%	–
psaM	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 4.46$ 19.87%	–	–	$F = 5.04$ 21.87%	–
Temperature																				
TM	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 5.52$ 23.48%	–	–	$F = 8.487$ 32.03%	–
tm	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 4.74$ 20.84%	–	–	$F = 7.00$ 28.00%	–
td	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 5.88$ 24.63%	$F = 4.48$ 19.94%	–	$F = 9.03$ 33.40%	–
TM3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 13.79$ 44.78%	–	–	$F = 16.03$ 48.53%	–
TM7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 14.80$ 46.54%	–	–	$F = 17.41$ 50.60%	–
TM10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 13.35$ 43.99%	–	–	$F = 15.73$ 48.06%	–
TM15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 17.29$ 50.42%	–	–	$F = 17.88$ 51.26%	–
TM30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 22.81$ 57.30%	–
tm3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 5.48$ 23.33%	–
tm7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 4.11$ 18.59%	–
taRat	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 4.66$ 20.56%	$F = 5.14$ 22.21%	–
tr	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 35.52$ 67.63%	–	–	–	–	–	–
TMAM	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 11.78$ 40.93%	–
Humidity																				
hr	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 5.22$ 22.47%	$F = 7.59$ 29.65%	–	–	–	–	–
hm3	–	–	–	–	–	–	–	–	–	–	–	–	–	$F = 42.02$ 72.42%	–	–	–	–	$F = 6.74$ 27.23%	–

(*Continues*)

Table A4 (continued)

	Coprophagous Scarabaeoidea					Aphodiinae					Geotrupinae					Scarabaeinae				
	q_0	q_1	q_2	R_0	*Ab*	q_0	q_1	q_2	R_0	*Ab*	q_0	q_1	q_2	R_0	*Ab*	q_0	q_1	q_2	R_0	*Ab*
hm7	–	–	–	–	–	–	–	–	–	–	–	–	–	*F* = 13.37 44.03%	–	*F* = 4.549 20.15%	*F* = 4.410 19.69%	–	*F* = 8.22 31.35%	–
hm10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*F* = 4.44 19.78%	–	*F* = 7.46 29.30%	–
hm15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*F* = 7.56 29.58%	–
hm30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*F* = 6.72 27.19%	–
haM	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*F* = 5.54 23.53%	–
HM	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*F* = 8.85 32.95%	–
hm	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*F* = 4.91 21.42%	–	–	–	–	–
hd	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*F* = 5.74 24.19%	–
Time-related																				
CDSin	–	*F* = 8.11 31.07%	*F* = 5.77 24.27%	–	–	–	–	–	–	–	–	–	–	*F* = 8.28 31.52%	–	*F* = 14.90 45.28%	*F* = 14.20 44.10%	*F* = 9.50 34.56%	*F* = 20.25 52.94%	–
CDCos	–	–	–	–	–	–	–	–	*F* = 7.15 28.44%	–	*F* = 6.79 27.39%	*F* = 6.69 27.09%	*F* = 6.56 26.69%	*F* = 6.06 25.17%	*F* = 6.63 26.91%	–	–	–	–	–

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