UNIVERSIDAD COMPLUTENSE DE MADRID
FACULTAD DE CIENCIAS BIOLÓGICAS

TESIS DOCTORAL

Estudio temporal de la biodiversidad y composición de las comunidades de escarabajos coprófagos (Coleoptera, Scarabaeoidea) presentes en un sistema agropecuario, en las cercanías del Parque Nacional de la Sierra de Guadarrama

Temporal study of the biodiversity and composition of dung beetle communities (Coleoptera, Scarabaeoidea) present in an agricultural system, near the Sierra de Guadarrama National Park

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

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D9BA - DOCTORADO EN BIOLOGÍA

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Quien me conozca sabe que este es con diferencia el apartado que más se me ha atragantado de toda la tesis, ya que no soy mucho de expresar mis sentimientos en público. Además, estoy segura de que, si empiezo con los agradecimientos a toda la gente que se ha topado por mi camino durante la tesis, alguien se me olvida fijo. Por eso, voy a ser breve y voy a hacer un agradecimiento general, para que todo el mundo se sienta incluido.

Para mí la tesis, más que un viaje, de cómo lo suele definir la gente, ha sido una montaña rusa, con sus momentos buenos en las subidas y sus momentos malos en las bajadas. Han sido más de 6 años de montaña rusa, en la que me ha acompañado mucha gente, tanto del mundo de la ciencia como de fuera. Algunos solo han tenido que soportarme un poquito, mientras que otros han aguantado día tras día mi turra. No obstante, todos han aportado su granito de arena aún sin saberlo para que esta tesis saliera adelante. Para mí, esta tesis es tan suya como mía, yo solo le he dado el último retoque. Solo espero que una vez que se acabe esta etapa de mi vida, no salgan de ella, que el "hasta luego" no se convierta en un "hasta nunca".

Y, como reflexión final, estos últimos días previos al depósito de la tesis, se me ha estado pasando por la cabeza una y otra vez la pregunta de que, si tuviese la oportunidad de volver atrás en el tiempo justo al día en que me matriculé, de si lo volvería a hacer o no; y, la respuesta no puede ser otra que un SÍ, me volvería a matricular en el doctorado.

Es cierto que no ha sido para nada fácil, hacer una tesis sin beca no es un camino de rosas, a veces te toca currar por las noches por unos miseros eurillos para seguir adelante o correr detrás de mariposas por diferentes parques de la ciudad de Madrid, eso ya os lo dejo a vuestra elección. Tampoco la tesis entiende de emociones… ¿Quién me iba a decir a mí que íbamos a estar encerrados en nuestras casas por una pandemia mundial o por la nevada del siglo en Madrid (Filomena) durante meses? Por mucho que uno quiera, hay cosas en la vida que no se pueden predecir y, lo peor, es que tienes que aprender a enfrentarte a ello si no quieres quedarte atrás. Creo que no hay mejor definición que la "*Hipótesis de la Reina Roja*", que viene a decir que debes saber adaptarte a las situaciones que se te presenten y correr más que tu oponente si quieres seguir evolucionando.

Así que, si estas leyendo esto ahora mismo y se te ha pasado por la cabeza la idea loca de hacer una tesis, que sepas que no te lo van a poner nada fácil, vas a recibir por todos los lados, pero lo que de verdad vale la pena es toda la gente que va a estar ahí a tu lado apoyándote y ayudándote a dar un paso más cada día. Y, al final, si eres persistente e igual de burra que yo, ya verás como SÍ se puede hacer una tesis; solo hay que estar *focused*.

Ahora sólo me quedaría por decir:

¡Muchas gracias – Dziękuję bardzo – Thank you– Merci beaucoup – Arigato gozaimasu!

En memoria de todos los pequeñajos de cuatro patas que nos dejaron antes de tiempo

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RESUMEN

La tesis que lleva por título "*Estudio temporal de la biodiversidad y composición de las comunidades de escarabajos coprófagos (Coleoptera, Scarabaeoidea) presentes en un sistema agropecuario, en las cercanías del Parque Nacional de la Sierra de Guadarrama*" tiene como objetivo estudiar una comunidad de escarabajos coprófagos de la Sierra de Guadarrama en relación a diferentes aspectos ecológicos, como pueden ser el recurso trófico o las variables climáticas y aquellas relacionadas con el tiempo, así como evaluar la metodología que tradicionalmente se emplea para muestrear a los mismos.

Los escarabajos coprófagos son un grupo de insectos que pertenecen a la superfamilia Scarabaeoidea, considerada una de las mejor estudiadas dentro de los coleópteros (Coleoptera). Dentro de la superfamilia, hay catalogadas alrededor de unas 200 especies en la península ibérica, repartidas entre las subfamilias Geotrupinae, Aphodiinae y Scarabaeinae. Sus patrones de distribución son globales, estando asociados principalmente a bosques templados y tropicales, sabanas y pastizales.

Los escarabajos coprófagos poseen todas las características para ser considerados un excelente grupo bioindicador. Además, al alimentarse y criar dentro de los excrementos, tienen un papel crucial en los ecosistemas, participando en multitud de procesos ecológicos, como el reciclado de los nutrientes, la aireación y fertilización del suelo, la bioturbación, la dispersión secundaria de semillas, el control biológico de moscas y parásitos del ganado o la polinización, entre otros. Por todas estas razones, han sido utilizados en multitud de investigaciones ecológicas y estudios de biodiversidad en todo el mundo.

Existen multitud de factores ecológicos, geográficos o históricos que han ido configurando las distribuciones de los escarabajos, tanto a una escala espacial como temporal. Además, los escarabajos coprófagos han estado siempre muy asociados a los mamíferos, al alimentarse de sus excrementos, de ahí que sus historias evolutivas estén ligadas. Como resultado de todo esto, las especies de escarabajos coprófagos van a mostrar unos requerimientos ecológicos específicos, que van a determinar sus patrones de diversidad.

La metodología empleada para muestrear escarabajos coprófagos tiene la ventaja de ser económica y muy fácil de usar, además de ser bastante efectiva a la hora de capturar escarabajos coprófagos. No obstante, no existe una metodología estandarizada, encontrando una gran cantidad de variantes dependiendo del estudio realizado. Por tanto, el desarrollo, en la medida de lo posible, de una metodología universal permitiría que los estudios pudiesen compararse y encontrar soluciones a su conservación de forma conjunta.

Por ello, los objetivos principales de la tesis son: 1) determinar la existencia de preferencias tróficas en los escarabajos coprófagos cuando son expuestos a diferentes tipos de excremento (**Capítulo 1**); 2) analizar el efecto de diferentes variables climáticas y aquellas relacionadas con el tiempo sobre los escarabajos (**Capítulo 2**); y, 3) evaluar la metodología comúnmente utilizada para los escarabajos coprófagos, en relación con el tiempo óptimo que deben permanecer activas las trampas en el campo para que los resultados obtenidos sean significativos (**Capítulo 3**).

Los resultados del capítulo 1 han determinado que los escarabajos coprófagos tienden a ser generalistas, alimentándose de cualquier tipo de excremento. No obstante, si se les expone a excrementos con diferentes características fisicoquímicas, pueden mostrar preferencias. De entre todos los excrementos, el de elefante resultó ser el que albergaba una mayor diversidad y abundancia de escarabajos coprófagos. Otros excrementos como el de jabalí o el de búfalo, tambien tuvieron bastante éxito, aunque en menor medida que el de elefante. El hecho de encontrar escarabajos en excrementos de animales no autóctonos indica que la procedencia del excremento no influye en su proceso de selección.

Los resultados del capítulo 2 han visto un efecto de las condiciones climáticas y aquellas relacionadas con el tiempo sobre los escarabajos coprófagos. En general, las variables relacionadas con el tiempo han sido las que más variabilidad han explicado, lo que da a entender que las especies de escarabajos coprófagos van a ajustar sus ciclos vitales a los momentos que mejor se ajusten a sus preferencias climáticas. En cambio, las variables de temperatura y humedad no han resultado ser muy explicativas, al igual que la presión atmosférica, una variable nunca antes estudiada en los escarabajos coprófagos.

Los resultados del capítulo 3 han demostrado que no hay diferencias significativas en exponer las trampas en el medio 24, 48 o 72 horas. Las comunidades resultantes son

prácticamente iguales, a excepción de unas pocas especies que no fueron tenidas en cuenta al obtener unos registros muy bajos. Por ello, se sugiere que el tiempo óptimo que deba permanecer una trampa en el campo para conseguir resultados significativos sea de 24 horas. En la medida de lo posible, sería conveniente buscar soluciones conjuntas a la problemática de la heterogeneidad de las metodologías para capturar escarabajos coprófagos.

En resumen, los escarabajos coprófagos son capaces de alimentarse de excrementos procedentes de diferentes animales, incluso de aquellos que son exóticos a la zona de estudio. No obstante, cuando son expuestos a excrementos con cualidades fisicoquímicas diferentes tienen ciertas preferencias tróficas, como, por ejemplo, el excremento de elefante. Las diferentes variables climáticas y aquellas relacionadas con el tiempo parecen ejercer un efecto sobre las comunidades de escarabajos coprófagos, siendo las más explicativas las variables relacionadas con el tiempo. Aunque los primeros resultados de la presión atmosférica no han sido los esperables, no habría que descartar su efecto como posible factor y seguir investigando al respecto. Aparte de los factores estudiados, existen otros que no se han tenido en cuenta para este estudio, que también son responsables de los patrones de diversidad actuales de los escarabajos coprófagos. Al evaluar el tiempo de exposición, se aconseja mantener las trampas un máximo de 24 horas, ya que no se observan diferencias significativas entre los tres tiempos de exposición. En la medida de lo posible, sería conveniente hallar un método universal que permita la comparación de estudios y proponer actuaciones conjuntas en pro de los escarabajos coprófagos.

ABSTRACT

The thesis entitled "*Temporal study of the biodiversity and composition of dung beetles communities (Coleoptera, Scarabaeoidea) present in an agricultural system, near the Sierra de Guadarrama National Park*" aims to study a community of dung beetles from the Sierra de Guadarrama, in relation to different ecological aspects, such as trophic resources or climatic variables and those related to time, as well as evaluating the methodology that is traditionally used to sample them.

Dung beetles are a group of insects that belong to the superfamily Scarabaeoidea, considered one of the best studied among beetles (Coleoptera). Within the superfamily, there are around 200 species in the Iberian Peninsula, distributed among the subfamilies Geotrupinae, Aphodiinae and Scarabaeinae. Its distribution patterns are global, being mainly associated with temperate and tropical forests, savannahs and grasslands.

Dung beetles have all the characteristics to be considered an excellent bioindicator group. Furthermore, by feeding and reproducing in excrements, they play a crucial role in ecosystems, participating in a multitude of ecological processes, such as nutrient recycling, soil aeration and fertilization, bioturbation, secondary seed dispersal, biological control of flies and parasites of livestock or pollination, among others. For all these reasons, they have been used in many ecological research and biodiversity studies around the world.

There are many ecological, geographical or historical factors that have shaped the distribution of dung beetles, both on a spatial and temporal scale. Furthermore, dung beetles have always been closely associated with mammals, feeding on their excrements, hence their evolutionary histories are linked. As a result of all this, dung beetle species show specific ecological requirements, which determine their diversity patterns.

The methodology used to sample dung beetles has the advantage of being cheap and very easy to use, as well as being quite effective in capturing dung beetles. However, there is no standardized methodology, and a large number of variants are found depending on the study carried out. Therefore, the development, to the extent possible, of a universal methodology would make it possible to compare studies and find solutions for their conservation together.

Therefore, the main objectives of the thesis are: 1) determine the existence of trophic preferences in dung beetles when exposed to different types of excrement (**Chapter 1**); 2) analyse the effect of different climatic variables and those related to time on dung beetles (**Chapter 2**); and, 3) evaluate the methodology commonly used for dung beetles, in relation to the optimal time that traps must remain active in the field for the results obtained to be significant (**Chapter 3**).

The results of **Chapter 1** have determined that dung beetles tend to be generalists and feed on any type of excrement. However, if they are exposed to excrements with different physicochemical characteristics, they may show preferences. Of all the dung, elephant dung turned out to be the one that harboured the greatest diversity and abundance of dung beetles. Other dung, such as wild boar or buffalo dung, was also quite successful, although to a lesser extent than elephant dung. Finding beetles in excrements from non-native animals indicates that the origin of the excrements does not influence their selection process.

The results from **Chapter 2** have seen an effect of climatic and time-related variables on dung beetles. In general, time-related variables have been the ones that have explained the most variability, suggesting that dung beetle species will adjust their life cycles to the times that best fit their climatic preferences. On the other hand, the variables of temperature and humidity have not been very explanatory, as has atmospheric pressure, a variable never before studied in dung beetles.

The results of **Chapter 3** have shown that there are no significant differences when exposing the traps for 24, 48 or 72 hours. The resulting communities are practically the same, except for some species that were not taken into account as very low records were obtained. Therefore, it is suggested that the optimal time a trap should remain in the field to achieve significant results is 24 hours. To the extent possible, it would be advisable to seek joint solutions to the problem of heterogeneity in dung beetle sampling methodologies.

In summary, dung beetles are capable of feeding on excrement from different animals, even those that are exotic to the study area. However, when exposed to dung with different physicochemical qualities, they have certain trophic preferences, such as elephant dung. The different climatic and time-related variables seem to have an effect on dung beetle communities, with time-related variables being the most explanatory. Although the first results of atmospheric pressure have not been as expected, its effect should not be ruled out as a possible factor and research should continue in this regard. Apart from the factors studied, there are others that have not been taken into account for this study and that are also responsible for the current diversity patterns of dung beetles. When evaluating the exposure time, it is advisable to keep the traps for a maximum of 24 hours, since no significant differences are observed between the three exposure times. As far as possible, it would be advisable to find a universal method that allows studies to be compared and joint actions to be proposed in support of dung beetles.

INTRODUCCIÓN GENERAL

La Sierra de Guadarrama es un espacio de gran valor natural en donde se puede distinguir una enorme diversidad de hábitats y ecosistemas de montaña, desde las crestas y cumbres con sus pastizales y matorrales de montaña, pasando por los pinares y robledales que tapizan las laderas hasta las formaciones adehesadas de los fondos de valle. En estos fondos de valle, los ecosistemas presentes son el resultado de las actividades y aprovechamientos agropecuarios que durante siglos han ido moldeando el paisaje hasta lo que es hoy. Entre ellos, destacan los prados de siega, tierras llanas y de bajo relieve destinadas a dejar crecer la hierba, para servir de alimento al ganado, tanto en época de pastos como en el periodo invernal en forma de heno. Paralelamente, estos prados ofrecen multitud de servicios ecosistémicos, al intervenir en el ciclo de los nutrientes y del agua, en la formación y retención del suelo, o en el provisionamiento de hábitat para gran cantidad de especies florales y faunísticas. En este contexto, uno de los componentes más característicos y singulares de estos paisajes son las deyecciones procedentes de los animales, principalmente del ganado.

Cada excremento constituye un microhábitat efímero, delimitado y heterogéneo con respecto al medio circundante, en el que se produce un relevo faunístico a medida que éste se homogeniza con el suelo (Lobo, 1992a; Tonelli, 2021). Cuando un excremento aparece en el medio manifiesta una microsucesión o sucesión heterotrófica, en la que participan principalmente diferentes taxones de insectos (Hanski, 1980; Kessler & Balsbaugh, 1972; Lobo, 1992a; Menéndez & Gutiérrez, 1999; Mohr, 1943; Valiela, 1974). Se pueden distinguir 4 sucesiones o escuadras principales: una primera, constituida por diversas especies de dípteros (Diptera); una segunda, representada por diversos grupos de coleópteros; una tercera, en la que se distinguen algunas especies de ácaros y nematodos; y, una última, formada por especies típicas de la fauna edáfica, como enquitreidos, lombrices de tierra y colémbolos (Lobo, 1992a). Dentro de los coleópteros, se pueden distinguir dos grupos diferentes: los escarabajos coprófilos, aquellos que se encuentran en el excremento, pero se no se alimentan de este, sino que son depredadores de otros grupos de insectos; y, los escarabajos coprófagos, aquellos que usan el excremento como fuente de alimento, asi como cámara de cría para sus larvas (Halffter & Matthews, 1966; Halffter & Edmonds, 1982).

Los escarabajos coprófagos pertenecen a la superfamilia Scarabaeoidea, considerada una de las mejor estudiadas dentro del orden Coleoptera, con más de 30.000 especies distribuidas por todas las regiones del planeta (Martín-Piera & López-Colón, 2000). Los miembros de este grupo se caracterizan por tener una enorme plasticidad ecológica y el potencial de colonizar una gran variedad de hábitats, desde las zonas áridas a los bosques tropicales y desde el nivel del mar hasta zonas alpinas. Asimismo, son capaces de explotar un amplio espectro de recursos alimenticios procedentes de todo tipo de materia orgánica de origen animal y vegetal, ya sean excrementos, cadáveres, humus, madera, hojas, etc. Dentro de esta superfamilia, se encuentran los que comúnmente se denominan escarabajos coprófagos o peloteros, habiendo catalogadas alrededor de unas 200 especies en la península ibérica. Están repartidos entre la subfamilia Geotrupinae, incluida dentro de la familia Geotrupidae, y las subfamilias Aphodiinae y Scarabaeinae, dentro de la familia Scarabaeidae (Halffter & Edmonds, 1982; Scholtz, 1990; Browne & Scholtz, 1999; Villalba *et al.*, 2002). Sus patrones de distribución son globales, estando asociados principalmente a bosques templados y tropicales, sabanas y pastizales (Halffter & Matthews, 1966; Hanski & Cambefort, 1991). Los escarabajos coprófagos se caracterizan por tener unas pautas de comportamiento, en relación con la utilización del excremento y la reproducción, bastante complejas. De hecho, los escarabajos coprófagos se pueden dividir en diferentes grupos funcionales en función de su comportamiento de nidificación (Halffter & Mathews, 1966; Bornemissza, 1976; Halffter & Edmonds, 1982). Existen muchas clasificaciones al respecto, aunque la más extendida y utilizada es la que formuló Bornemissza (1976), tal vez por su sencillez y porque recoge las tres estrategias básicas de comportamiento. Por un lado, se encuentran los paracópridos (subfamilias Geotrupinae y Scarabaeinae), los cuales van a recolocar una porción de excremento en sentido vertical hacia el interior del suelo donde tienen construidas sus galerías; los telecópridos (Scarabaeinae), los cuales van a rodar una porción de excremento a cierta distancia de la fuente original y la van a enterrar en un nido simple, y, por último, los endocópridos (subfamilia Aphodiinae), los cuales viven y se reproducen en el propio excremento (**Figura 1**). Existiría un cuarto comportamiento denominado cleptoparasitismo (Paulian, 1943), que hace referencia a aquellas especies de escarabajos coprófagos que utilizan los nidos y las reservas de excremento de otros escarabajos, para su propia alimentación y reproducción. Esta estrategia es poco común en las regiones templadas, pero muy extendida en las regiones tropicales y subtropicales, donde la competencia por el alimento es más intensa, al igual que en las zonas áridas, donde la escasez del alimento es severa (Martín-Piera & López-Colón, 2000).

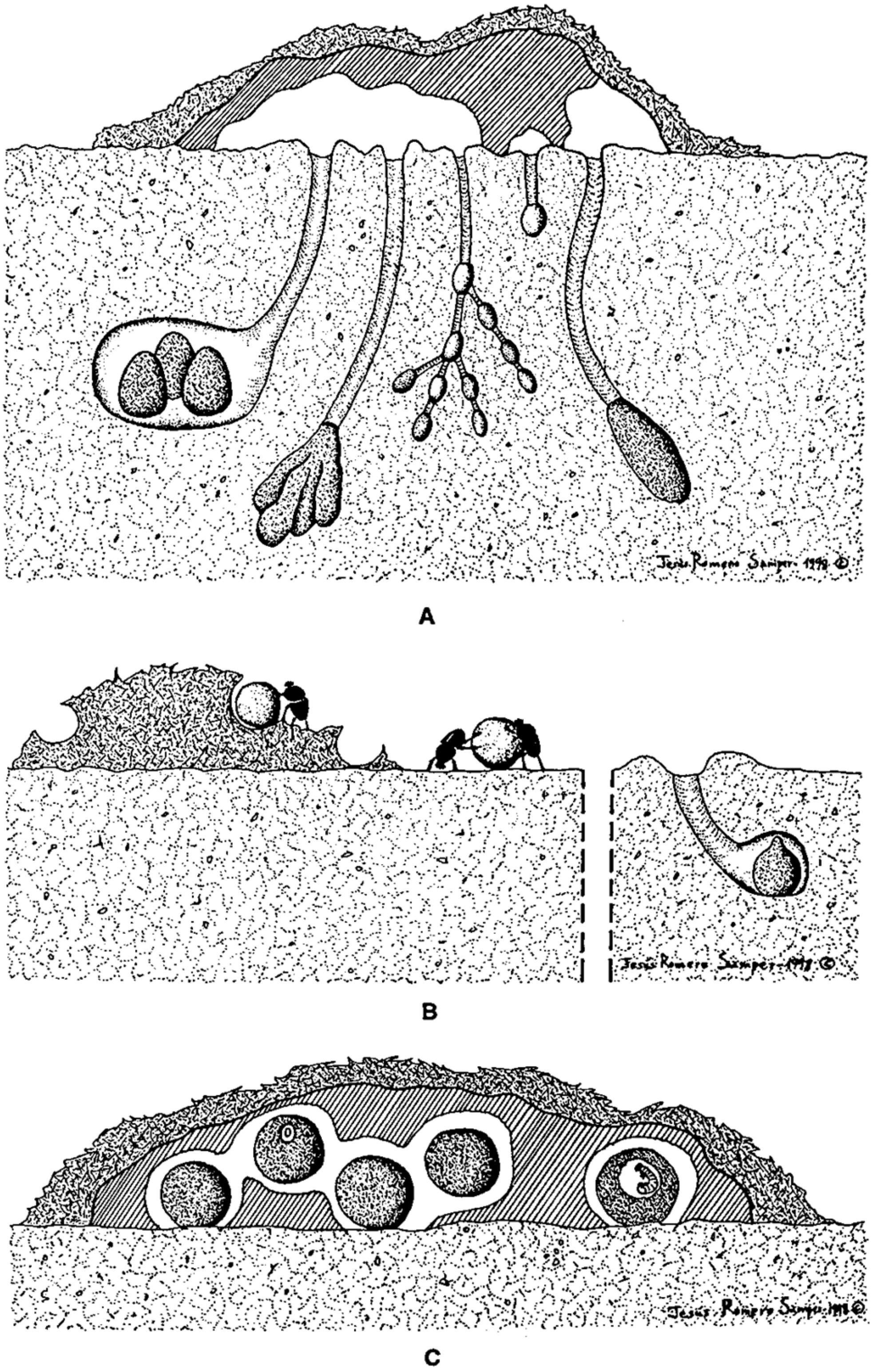


Figura 1. Comportamientos reproductivos de los escarabajos coprófagos, en donde se puede diferenciar la estrategia paracóprida (A), telecóprida (B) y endocóprida (C). La estrategia cleptoparásita no se muestra en la imagen. Fuente: Imagen tomada de Martín-Piera & López-Colón, 2000.

Los escarabajos coprófagos se consideran uno de los taxones más estudiados dentro de los artrópodos terrestres (Spector, 2006; Raine & Slade, 2019; Giménez-Gómez *et al.*, 2020). Han sido utilizados en multitud de investigaciones ecológicas y estudios de biodiversidad en todo el mundo como bioindicadores (Spector, 2006; Agoglitta *et al.*, 2012; Bourg *et al.*, 2016; Raine & Slade, 2019; Carvalho *et al.*, 2020). Los escarabajos coprófagos poseen todas las características para ser considerados un excelente grupo bioindicador: son conspicuos y fáciles de observar en el campo; son susceptibles de ser estudiados mediante muestreos estandarizables; tienen una buena accesibilidad taxonómica; poseen una amplia distribución geográfica, así como una gran diversidad morfológica, ecológica y etológica; responden frente a cambios ambientales y sus abundancias y riquezas se correlacionan con otros grupos de insectos; y, han demostrado tener importancia ecológica y económica (Spector, 2006). Además, al alimentarse y criar dentro los excrementos, tienen un papel crucial en los ecosistemas, participando en multitud de procesos ecológicos, como el reciclado de los nutrientes, la aireación y fertilización del suelo, la bioturbación, la dispersión secundaria de semillas, el control biológico de moscas y parásitos del ganado o la polinización, entre otros (Andressen, 2002; Nichols *et al.*, 2008; Nichols & Gómez, 2014).

Con base en los coprolitos descubiertos, el origen de la coprofagia se estima que tuvo lugar con la aparición de los grandes dinosaurios que habitaron la Tierra durante la era Mesozoica (Chin & Gill, 1996). Seguramente el antecesor de los escarabajos coprófagos tuviese una alimentación saprófaga, pudiéndose alimentar de cualquier materia orgánica en descomposición, ya fuese de origen animal o vegetal. La llegada de los dinosaurios a los ecosistemas y, por ende, de sus excrementos, les dio la oportunidad de explotar un nuevo nicho trófico, desarrollándose así la coprofagia (Chin & Gill, 1996). Con la extinción de los dinosaurios al final del periodo Cretácico, los escarabajos se verían desprovistos de sus principales fuentes de alimento, viéndose forzados a alimentarse de otros recursos si querían sobrevivir (Halffter & Matthews, 1966; Scholtz *et al.*, 2009). No obstante, la desaparición de los dinosaurios permitió que los mamíferos se diversificaran, por lo que sus excrementos empezaron a ser más frecuentes en el ecosistema, pudiendo servir de alimento para los escarabajos coprófagos (Cabrero-Sañudo & Lobo, 2009). En la actualidad, la coprofagia sigue siendo la estrategia trófica predominante entre los escarabajos coprófagos (Scholtz *et al.*, 2009; Ebert *et al.*, 2019), salvo en los bosques tropicales, donde los escarabajos coprófagos no se limitan a alimentarse solamente de excrementos. En estas regiones, donde la competencia es muy elevada, los escarabajos coprófagos presentan una mayor diversidad de hábitos alimenticios, ya sean excrementos de pájaros o reptiles, fruta podrida, carroña, hongos, etc. (Gill, 1991; Hanski & Cambefort, 1991; Estrada *et al.*, 1993; Hill, 1996; Scholtz *et al.*, 2009; da Silva *et al.*, 2012; Salomão *et al.*, 2014, 2018; Stavert *et al.*, 2014; Bourg *et al.*, 2016; Ebert *et al.*, 2019; Giménez-Gómez *et al.*, 2020).

En general, los escarabajos coprófagos se alimentan de diferentes excrementos de mamíferos, mostrando un carácter generalista y oportunista al respecto (Hanski & Cambefort, 1991; Martín-Piera & Lobo, 1996; Simmons & Ridsdill-Smith, 2011; Frank *et al.*, 2017, 2018a, 2018b; Wurmitzer *et al.*, 2017; Raine & Slade, 2019). Aunque algunos estudios han señalado que los escarabajos coprófagos pueden mostrar preferencias por ciertos tipos de excremento (Sánchez-Piñero & Ávila, 1991; Wassmer, 1995; Lumaret & Iborra, 1996; Gittings & Giller, 1998; Verdú, 1998; Barbero *et al.*, 1999; Galante & Cartagena, 1999; Finn & Giller, 2002; Verdú & Galante, 2002; Tonelli *et al.*, 2021), estas preferencias se observan cuando los escarabajos coprófagos son expuestos a excrementos con diferentes características fisicoquímicas. Esto no significa que los escarabajos coprófagos estén especializados en explotar ese excremento en concreto, sino que cuando se les da la opción van a elegir el excremento que para ellos resulta más atractivo (Dormont *et al.*, 2004, 2007; Frank *et al.*, 2018a; Urrutia *et al.*, 2022). De hecho, existen muy pocos casos en los que se haya visto una clara especialización de los escarabajos coprófagos a alimentarse de un solo tipo de excremento (Tonelli *et al.*, 2021). Por ejemplo, algunas especies endémicas de la península iberica, parecen haber tenido un proceso de coevolución con el conejo europeo (*Oryctolagus cuniculus* L.), ya que se les ha visto alimentarse casi exclusivamente de las deyecciones de este animal. Incluso, han modificado partes de su aparato bucal para poder alimentarse de este excremento tan seco y compacto (Sánchez-Piñero & Ávila, 1991; Verdú, 1998; Galante & Cartagena, 1999; Verdú & Galante, 2002).

El proceso de elección de un excremento del medio por parte de los escarabajos coprófagos va a depender de señales olfativas, concretamente de los compuestos orgánicos volátiles que emiten los excrementos, así como de la distancia a la que se encuentra el excremento y de su calidad nutricional (Hanski & Cambefort, 1991; Dormont *et al.*, 2004, 2007, 2010; Holter & Scholtz, 2007; Urrutia *et al.*, 2022). Cada excremento está definido por unas características fisicoquímicas únicas, ligadas principalmente a los diferentes regímenes alimenticios de los mamíferos de los que procede (herbívoros, carnívoros u omnívoros). En general, los excrementos de los herbívoros son los más utilizados por los escarabajos coprófagos, debido a su gran disponibilidad en los ecosistemas resultado de las prácticas tradicionales ganaderas (Holter & Scholtz, 2007). Incluso, dentro de los herbívoros, suelen tener predilección por los excrementos de mamíferos rumiantes, como la vaca, frente a los no rumiantes, como el caballo. Esto se debe a que los excrementos de los rumiantes están más procesados, al tener éstos una digestión mucha más compleja que la de los no rumiantes, los cuales son incapaces de digerir la celulosa de las plantas, lo que hace que sus excrementos sean menos nutritivos (Finn & Giller, 2002; Frank *et al.*, 2018b). No obstante, si se hace una comparación entre los excrementos de herbívoros con los de los otros regímenes alimenticios, éstos suelen quedar en última posición. Por ejemplo, los excrementos de carnívoros se caracterizan por tener altas concentraciones de nitrógeno, procedente del consumo de carne animal, lo que les hace tener una calidad nutricional elevada, al ser el nitrógeno un elemento indispensable para el correcto desarrollo de los insectos (Al-Houty & Al-Musalam, 1997; Hewavithana *et al.*, 2016; Frank *et al.*, 2017). Irónicamente, no suelen tener un gran poder de atracción, por lo que suelen pasar desapercibidos en el campo (Martín-Piera & Lobo, 1996; Frank *et al.*, 2018b). En el caso de los excrementos de omnívoros, al tener una dieta mucho más variada, hace que también sus excrementos tengan una calidad nutricional considerable (Dormont *et al.*, 2004, 2007; Bogoni & Hernández, 2014). Además, se ha visto que algunos animales omnívoros, como el jabalí, desprenden compuestos orgánicos volátiles con un gran poder atractor sobre los escarabajos coprófagos (Frank *et al.*, 2018a). De hecho, en las regiones tropicales, a diferencia de las zonas templadas, el excremento de omnívoro es el más utilizado en los estudios con escarabajos coprófagos, ya que su éxito ha sido más que contrastado (Estrada *et al.*, 1993, Filgueiras *et al.*, 2009, Amézquita & Favila, 2010; Marsh *et al.*, 2013; Bogoni & Hernández, 2014; Correa *et al.*, 2016; Giménez-Gómez *et al.*, 2020; Sathiandran *et al.*, 2021). Hay que tener presente que las diferencias en la selección de excrementos no solo dependen de las cualidades intrínsecas de los excrementos, sino que entran en juego otros factores, ya sean ecológicos, geográficos o históricos, que tambien ejercen un efecto sobre los escarabajos coprófagos (Barbero *et al.*, 1999).

Estos mismos factores han sido los responsables de moldear los patrones de distribución que presentan los escarabajos coprófagos en la actualidad. Eventos como la dispersión o la vicarianza, las glaciaciones o las extinciones locales, fueron configurando las distribuciones de los escarabajos, tanto a una escala espacial como temporal (Davis & Scholtz, 2001; Hortal *et al.*, 2011), sin olvidar que la historia evolutiva de los escarabajos coprófagos está ligada a la historia evolutiva de los mamíferos, al depender de sus excrementos para subsistir (Davis *et al.*, 2002; Cabrero-Sañudo & Lobo, 2009). La división de Pangea en dos continentes, Laurasia y Gondwana dio lugar a la formación de nuevas especies mediante procesos de dispersión y vicarianza, al verse impedido el contacto entre las poblaciones ancestrales. Se cree que el origen de las especies de la subfamilia Scarabaeinae está en Gondwana (Davis & Scholtz, 2001), de ahí que estén adaptadas a vivir en zonas donde el clima es mucho más cálido y seco (Halffter & Edmonds, 1982; Jay-Roberts *et al.*, 2008a; Errouissi *et al.*, 2009), encontrando su máxima diversidad en las regiones tropicales y subtropicales. En cambio, muestran limitaciones fisiológicas para sobrevivir en condiciones frías (Hortal *et al.*, 2011). Por el contrario, la mayoría de los representantes de las subfamilias Geotrupinae y Aphodiinae tendrían su origen en Laurasia (Martín-Piera & López-Colón, 2000; Cabrero-Sañudo & Lobo, 2009), de ahí que muestren una clara preferencia por climas fríos y húmedos (Halffter & Edmonds, 1982; Lumaret & Kirk, 1987; Errouissi *et al.*, 2004, 2009; Jay-Roberts *et al.*, 2008a; Cabrero-Sañudo & Lobo, 2009).

Como resultado de estos procesos pasados, los escarabajos coprófagos se encuentran distribuidos acorde a unas condiciones ambientales concretas (Davis & Scholtz, 2001; Errouissi *et al.*, 2004), rigiéndose principalmente por la temperatura y las precipitaciones (Halffter & Edmonds, 1982; Lumaret & Kirk, 1987, 1991; Lobo *et al.*, 2002; Errouissi *et al.*, 2004, 2009; Andresen, 2005; Davis *et al.*, 2008; Labidi *et al.*, 2012; Numa *et al.*, 2012; Dortel *et al.*, 2013; Cajaiba *et al.*, 2017; Ferreira *et al.*, 2018; Calatayud *et al.*, 2021; Correa *et al.*, 2021; Ambrozova *et al.*, 2022). En la región Mediterránea, los escarabajos coprófagos van a tener picos de mayor o menor diversidad dependiendo de la estación del año (Lobo, 1982; Lumaret & Kirk, 1987, 1991; Jay-Roberts *et al.*, 2008a; Agoglitta *et al.*, 2012; Senyüz *et al.*, 2019). Aphodiinae sigue el clásico patrón bimodal, encontrando una mayor diversidad y abundancia de adultos después de las lluvias típicas de los meses de primavera y otoño (Lumaret & Kirk, 1987, 1991; Lumaret, 1995; Errouissi *et al.*, 2004, 2009; Jay-Roberts *et al.*, 2008a; Senyüz *et al.*, 2019). Al ser endocópridos, es decir, el vivir dentro del excremento les hace vulnerables a las sequias y heladas de los meses de verano e invierno, respectivamente (Lumaret, 1995; Jay-Roberts *et al.*, 2008a), por eso los adultos no están tan activos en estos meses del año. En cambio, Scarabaeinae y Geotrupinae presentan un patrón unimodal. Los Scarabaeinae son más activos en el periodo estival, ya que están bien adaptados a las condiciones cálidas, estando prácticamente ausentes durante el invierno (Jay-Roberts *et al.*, 2008a; Errouissi *et al.*, 2009; Hortal *et al.*, 2011). En Geotrupinae, el pico de mayor actividad se produce a finales de año, especialmente en los meses de otoño (Lumaret & Kirk, 1987; Jay-Roberts *et al.*, 2008a; Errouissi *et al.*, 2004, 2009). Su estrategia es salir y reproducirse después de las primeras lluvias de otoño, para luego sobrevivir a las inclemencias del tiempo invernal como huevo, larva o pupa (Lumaret, 1995).

Asimismo, algunos estudios apuntan a que existen otros factores capaces de influir sobre los patrones de distribución de los escarabajos coprófagos, como puede ser la altitud (Martín-Piera *et al.*, 1992; Jay-Robert *et al.*, 1997, 2008a; Errouissi *et al.*, 2004; Labidi *et al.*, 2012) o el tipo de hábitat (Halffter & Edmonds, 1982; Lumaret & Kirk, 1987; Martín-Piera *et al.*, 1992; Jay-Roberts *et al.*, 2008b), viendo claros gradientes de diversidad al respecto. En las zonas bajas, caracterizadas por un paisaje abierto de pastos y donde el clima es mucho más suave, las comunidades de escarabajos coprófagos están constituidas principalmente por especies de la subfamilia Scarabaeinae. No obstante, a medida que la altitud va en aumento y el paisaje se va transformando de una zona abierta de pasto a una de bosque cerrado, las especies de Scarabaeinae van a ir siendo sustituidas por miembros de las subfamilias Aphodiinae y Geotrupinae (Lumaret & Kirk, 1987; Martín-Piera *et al.*, 1992; Jay-Roberts *et al.*, 2008b), mucho mejor adaptados a los climas fríos y húmedos.

Durante los últimos años, la preocupación por el descenso de la biodiversidad ha encabezado los esfuerzos de conservación en todo el mundo (Savard *et al.*, 2000; Mora-Aguilar *et al.*, 2023). La diversidad de muchas formas de vida, entre ellas la de los escarabajos coprófagos, se está viendo reducida año tras año, debido a diversos factores, como el cambio climático, la introducción de especies invasoras, la caza o captura ilegal, la contaminación del agua, etc. (Dirzo & Raven, 2003). Por ello, conocer los mecanismos por los cuales se rigen los patrones de diversidad de los escarabajos coprófagos, así como desarrollar una metodología estandarizada que permita que los estudios sean comparables, hará que se esté un paso por delante a la hora de encontrar soluciones que consigan reducir al máximo su declive (Lobo, 2001; Carpaneto *et al.*, 2007; Nichols *et* *al.*, 2007, 2009; Tocco *et al.*, 2016; Batilani-Filho & Hernández, 2017; Fuzessy *et al.*, 2021).

Una de las metodologías más utilizada para capturar escarabajos coprófagos son las trampas *piftall* o de caída (Lobo *et al.*, 1988; Veiga *et al.*, 1989; Halffter & Favila, 1993; Tocco *et al.*, 2016; Mora-Aguilar *et al.*, 2023). Su éxito y popularidad se debe a que no solo son económicas y relativamente sencillas de fabricar y usar, sino que además está probada su efectividad a la hora de capturar una gran diversidad y abundancia de individuos de escarabajos coprófagos (Siewers *et al.*, 2014; Mora-Aguilar *et al.*, 2023). No obstante, no hay una metodología estandarizada a la hora de usar las trampas *pitfall*, encontrando una gran cantidad de variantes dependiendo del estudio realizado. A esto se le suma, la diversidad encontrada entre las diferentes regiones del planeta. Por ejemplo, en la región Paleártica, la trampa se deja a ras del suelo sin tapar, mientras que en las regiones tropicales y subtropicales es habitual tapar las trampas para protegerlas de la precipitación o de la acumulación de las hojas (Siewers *et al.*, 2014).

Otro aspecto a tener en cuenta es la efectividad de las trampas, las cuales pueden verse influenciadas por diversos factores, como el tipo de hábitat, las condiciones climáticas, o incluso a cómo está diseñado el experimento. Los pocos estudios que se han llevado a cabo en relacion a este aspecto, se han centrado generalmente en la efectividad del cebo utilizado y de si los escarabajos coprófagos pueden desarrollar una preferencia por alguno de ellos (Hanski & Cambefort, 1991; Wassmer, 1995; Lumaret & Iborra, 1996; Martín-Piera & Lobo, 1996; Barbero *et al.*, 1999; Finn & Giller, 2002; Verdú & Galante, 2002; Frank *et al.*, 2018a, 2018b; Wurmitzer *et al.*, 2017; Tonelli *et al.*, 2021). En cambio, otros aspectos han tenido menor repercusión, como pueden ser: la distancia necesaria que hay que dejar entre las trampas para evitar solapamientos de información (Larsen & Forsyth, 2005; da Silva & Hernández, 2015; Marsh *et al.*, 2018; Moctezuma, 2021), el uso de diferentes modelos de trampas *pitfall* para ver cuál es la mejor (Lobo *et al.*, 1988; Veiga *et al.*, 1989; Doube & Giller, 1990), la cantidad de cebo que hay que colocar (Mora-Aguilar *et al.*, 2023), el tiempo que deben permanecer activas las trampas en el campo (Lobo *et al.*, 1988; Veiga *et al.*, 1989), el esfuerzo de muestreo (Tocco *et al.*, 2016), entre otros. Por ello, es importante invertir más tiempo en buscar una forma de muestrear escarabajos coprófagos, que, a ser posible, sea lo más universal para todas las regiones del planeta y que permita hacer comparaciones de los datos obtenidos, con el fin de que sirva para alcanzar soluciones globales para la conservación de los escarabajos coprófagos.

Estructura de la tesis

A lo largo de esta tesis se ha estudiado el efecto que tienen varios factores ecológicos, entre ellos, el recurso trófico, diferentes variables climáticas y aquellas relacionadas con el tiempo, sobre una comunidad de escarabajos coprófagos de la Sierra de Guadarrama. Por otro lado, se ha analizado un aspecto del diseño experimental para determinar su eficacia a la hora de capturar escarabajos coprófagos.

Aunque el estudio de las preferencias tróficas en escarabajos coprófagos esté bien documentado en la península ibérica, nunca antes se habían utilizado excrementos procedentes de animales no autóctonos. Asimismo, el estudio de los factores que pueden influir sobre los patrones de distribución de los escarabajos coprófagos ha sido tratado en estudios previos. No obstante, nunca antes se habían incluido variables relacionadas con la presión atmosférica, un factor poco estudiado en insectos y que parece ser crucial para ellos. Por último, la falta de una metodología estandarizada para los escarabajos coprófagos ha dado lugar a la aparición de multitud de variantes, que suponen un problema a la hora de querer proponer medidas de actuación conjuntas. Debido a ello, se ha evaluado cual es el tiempo óptimo que deben permanecer las trampas en el medio para obtener resultados significativos.

En el primer capítulo, se aborda el tema de las preferencias tróficas en una comunidad de escarabajos coprófagos del Sistema Central (Madrid, España). Mediante el uso de excrementos procedentes de mamíferos con diferentes tipos de alimentación y orígenes, se pudo determinar que la tendencia general de los escarabajos coprófagos era tener una dieta variada, alimentándose de diferentes excrementos indistintamente. Algo que tendría sentido al tratarse el excremento de un recurso efímero y limitado en el ecosistema, lo que restringe la aparición de especies que puedan tener una especificidad hacia un excremento en concreto. No obstante, las especies pueden tener preferencias por ciertos excrementos al verse expuestos a ellos. Por ejemplo, la comunidad obtenida del excremento de elefante ha resultado ser la más rica en especies y abundancia de individuos de escarabajos coprófagos. Otros excrementos como los del búfalo o jabalí tambien han resultado ser bastante exitosos, aunque en menor medida que el elefante. Al no influir la procedencia del excremento en el proceso de selección de los escarabajos coprófagos, deben ser las características intrínsecas de los excrementos los que determinen dicha selección.

El segundo capítulo trata sobre el efecto que pueden tener diferentes variables climáticas y aquellas relacionadas con el tiempo sobre los patrones de diversidad de los escarabajos coprófagos. De entre todas las variables utilizadas, las relacionadas con el tiempo fueron las más explicativas, dando a entender que los escarabajos coprófagos ajustan sus ciclos biológicos a los momentos del año que les favorecen. En cambio, variables como la temperatura y humedad no han tenido mucho efecto sobre los escarabajos coprófagos, algo que coincide con estudios previos. Aunque este haya sido un tema del que se tiene bastante información, nunca antes se había estudiado el efecto de la presión atmosférica, aunque parece ser crucial a la hora de detectar cambios ambientales en el medio. A pesar de no haber obtenido los resultados esperables, habría que seguir profundizando en el tema.

El último capítulo evalúa el tiempo optimo que hay que dejar las trampas activas para que la información obtenida de ellas sea significativa. En base a los resultados se puede observar que no existen diferencias entre los tiempos de exposición. Aunque podría parecer que existen diferencias, las comunidades resultantes son prácticamente idénticas, a excepción de unas pocas especies que no fueron tenidas en cuenta al obtener unos registros muy bajos. Por tanto, la opción más recomendable sería dejar las trampas un máximo de 24 horas en el campo. Las discrepancias observadas con la literatura se deben a la falta de una estandarización del método, lo que ha dado lugar a la existencia de multitud de variantes del diseño experimental. Por ello, sería conveniente buscar soluciones conjuntas a la problemática de la heterogeneidad de las metodologías para la captura de escarabajos coprófagos.

Objetivos generales

El objetivo general de esta tesis es determinar cómo varía la diversidad de una comunidad de escarabajos coprófagos de la Sierra de Guadarrama en relación con diferentes aspectos ecológicos, como puede ser el recurso trófico o las variables climáticas y aquellas relacionadas con el tiempo, así como examinar la metodología que se emplea tradicionalmente para muestrear escarabajos coprófagos. Mas concretamente, en este estudio se busca responder a las siguientes cuestiones:

I. Determinar la existencia de preferencias tróficas en una comunidad de escarabajos coprófagos cuando son expuestos a diferentes tipos de excremento. Para ello, se han utilizado seis excrementos procedentes de mamíferos con diferentes regímenes alimenticios, siendo algunos exóticos para la zona de estudio (**Capítulo 1** - Estudio de las preferencias tróficas en una comunidad de escarabajos coprófagos (Coleoptera, Scarabaeoidea) de la Sierra de Guadarrama (Madrid, España) al ser expuestos a excrementos de mamíferos autóctonos y exóticos).

II. Analizar el efecto de diferentes variables climáticas y aquellas relacionadas con el tiempo sobre una comunidad de escarabajos coprófagos (Coleoptera, Scarabaeoidea) de la Sierra de Guadarrama (Madrid, España) (**Capítulo 2** – Efecto de diversas variables climáticas y relacionadas con el tiempo sobre una comunidad de escarabajos coprófagos (Coleoptera, Scarabaeoidea) de la Sierra de Guadarrama (Madrid, España)).

III. Evaluar la metodología comúnmente utilizada para los escarabajos coprófagos, en relación con el tiempo óptimo que deben permanecer activas las trampas en el campo para que los resultados obtenidos sean significativos (**Capítulo 3** – Optimización de la metodología empleada para escarabajos coprófagos con base en el tiempo que deben estar expuestas las trampas en el medio (24, 48 o 72 horas)).

General objectives

The general objective of this study is to determine how the diversity of a community of dung beetles in the Sierra de Guadarrama varies in relation to different ecological factors, such as trophic resources or climatic and time-related variables, as well as to test the methodology traditionally used to sample dung beetles. More specifically, this study seeks to answer the following questions:

I. Determine the existence of trophic preferences in a dung beetle community when exposed to different types of excrement. For this, six excrements from mammals with different trophic guilds have been used, some exotic for the study area (**Chapter 1** - Study of trophic preferences in a community of dung beetles (Coleoptera, Scarabaeoidea) from the Sierra de Guadarrama (Madrid, Spain) when exposed to excrements from native and exotic mammals).

II. Analyze the effect of different climatic and time-related variables on a dung beetle community (Coleoptera, Scarabaeoidea) of the Sierra de Guadarrama (Madrid, Spain) (**Chapter 2** – Effect of various climatic and time-related variables on a community of dung beetles (Coleoptera, Scarabaeoidea) from the Sierra de Guadarrama (Madrid, Spain)).

III. Test the methodology commonly used for dung beetles, in relation to the optimal time that traps must remain active in the field for the results obtained to be significant (**Chapter 3** – Optimization of the methodology used for dung beetles based on the time that the traps must be exposed to the environment (24, 48 or 72 hours)).

MATERIAL Y MÉTODOS

Área de estudio

El estudio se llevó a cabo en Mataelpino, una localidad situada a unos 60 kilómetros de la ciudad de Madrid, en dirección noroeste desde la capital. Más concretamente, el estudio se realizó en una parcela semiabierta de uso ganadero que se encuentra a las afueras de la localidad, en su lado oeste (**Figura 1**). Las dimensiones de la finca de estudio son de 1.16 hectáreas, encontrándose a una altitud de 1.140 metros sobre el nivel del mar y cuyas coordenadas son 40.73ºN, 3.96ºO. El área de estudio se encuentra próxima al Parque Nacional de la Sierra de Guadarrama y a la Reserva de la Biosfera Cuencas altas de los ríos Manzanares, Lozoya y Guadarrama.

La zona de estudio presenta un clima mediterráneo continental, propio del interior peninsular. Los inviernos son particularmente fríos y húmedos, con posibles heladas de noviembre a abril, mientras que los veranos son calurosos y secos con algunos meses de sequía (Rivas-Martínez, 1983). La temperatura media anual oscila entre los 8ºC y los 15ºC, aunque se han registrado valores de hasta -7ºC durante los meses más fríos y 38ºC en los más cálidos. En cuanto a las precipitaciones, el régimen pluviométrico se caracteriza por ser estacional. Los periodos de mayor precipitación se asocian a los meses de otoño y primavera, mientras que el periodo más seco se asocia a los meses de verano. Los registros de precipitaciones promedio anuales suelen rondar los 700 milímetros (Meteoclimatic, 2020).

El paisaje del área de estudio tiene un carácter puramente forestal, predominando las masas arbóreas sobre los matorrales y pastizales herbáceos. Las formaciones vegetales predominantes son bosques de encinas (*Quercus ilex* spp. *ballota* (Desf.) Samp.) y rebollos (*Quercus pyrenaica* Willd.), frecuentemente mezclados con un paisaje de pastos y matorrales. Además, se pueden encontrar pinares de pino silvestre (*Pinus sylvestris* L.), acompañados de helecho águila (*Pteridium aquilinum* (L.) Kuhn) y retama ibérica (*Genista florida* L.). Entre los arbustos, los más representativos son las retamas, los enebros y las jaras. En el estrato herbáceo predominan las praderas de pastoreo para uso ganadero (Rivas-Martínez & Cantó, 1987). Estas características climáticas y vegetales sitúan la zona de estudio en el piso bioclimático supramediterráneo inferior (Rivas-Martínez, 1983).

Es importante resaltar la comunidad faunística de la zona de estudio ya que los excrementos de estos animales son la principal fuente de alimento de los escarabajos coprófagos. La zona de estudio se caracteriza por tener un alto nivel de actividad ganadera, especialmente bovina (*Bos taurus* Linnaeus, 1758) y equina (*Equus ferus caballus* Linnaeus, 1758). Además de estos excrementos, los escarabajos coprófagos pueden utilizar excrementos de animales salvajes con diferentes regímenes tróficos, aunque estos recursos son, en su mayoría, más esporádicos. Por ejemplo, los escarabajos coprófagos pueden alimentarse de excrementos de herbívoros salvajes, como el corzo (*Capreolus capreolus* (Linnaeus, 1758)), la cabra montesa (*Capra pyrenaica* Schinz, 1838) o el conejo europeo (*Oryctolagus cuniculus* (Linnaeus, 1758)). Por otro lado, también pueden verse atraídos por excrementos de omnívoros, como los del jabalí (*Sus scrofa* Linnaeus, 1758) o del zorro (*Vulpes vulpes* (Linnaeus, 1758)), y por los de carnívoros, como los del lobo ibérico (*Canis lupus signatus* Cabrera, 1907) (Viejo, 2013).

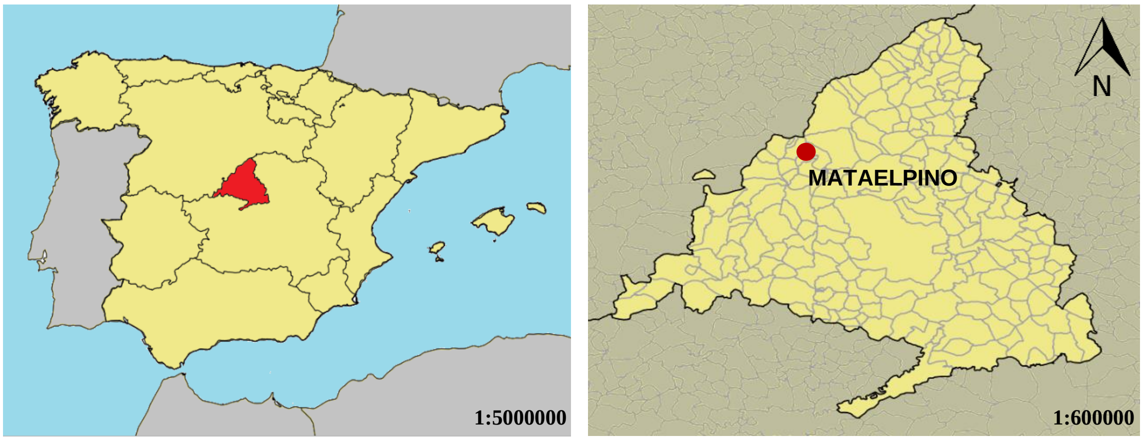


Figura 1. Mapas de localización del área de estudio. El estudio se llevó a cabo en la localidad de Mataelpino, en el noroeste de la Comunidad Autónoma de Madrid. Las coordenadas son 40.73°N, 3.96°W. Las líneas negras y grises representan límites administrativos.

Diseño experimental

Los muestreos se realizaron durante un periodo de casi dos años, realizando una visita por mes desde mayo de 2018 hasta febrero de 2020. Aunque se pretendía realizar un estudio de 24 meses, la situación de confinamiento sanitario lo interrumpió durante los dos últimos meses.

El diseño experimental consistió en la colocación de 36 trampas *pitfall* en la parcela de estudio, siguiendo el método recomendado por Lobo *et al.* (1988) y Veiga *et al.* (1989). Cada trampa consistía en un barreño de plástico enterrado a ras de suelo, rellenado hasta la mitad con una solución de agua y jabón (para romper la tensión superficial del agua). Encima de cada recipiente se colocaba una rejilla, y sobre ésta se dejaba la cantidad de 250 gramos de estiércol fresco (siempre medido con el mismo recipiente) (**Figura 2**).

Las trampas se organizaron en seis hexágonos, colocados aleatoriamente a lo largo del área de muestreo, con una separación mínima de 50 metros entre ellos. Dentro de cada hexágono, las trampas estaban separadas con una distancia mínima de 10 m. (Lobo *et al.*, 1988; Lobo, 1992a, 1992b; Martín-Piera & Lobo, 1996). Además, se colocaron dos trampas sin cebar a modo de trampas control. Las trampas *pitfall* fueron cebadas con excrementos de mamíferos con diferentes regímenes alimenticios y diferentes propiedades y composición de los mismos (ver capítulo 1): búfalo rojo (*Syncerus caffer nanus* (Boddaert, 1785)), elefante asiático (*Elephas maximus* Linnaeus, 1758), oso pardo (*Ursus arctos* Linnaeus, 1758), cabra (*Capra hircus* Linnaeus, 1758), gamo (*Dama dama* (Linnaeus, 1758)) y jabalí (*Sus scrofa* Linnaeus, 1758). Todos los excrementos fueron suministrados por el Zoológico-Acuario de Madrid. Los animales involucrados en el estudio no habían recibido previamente ningún tratamiento veterinario.

Figura 2. Fotografía de una trampa *pitfall*. En la imagen se puede ver como quedaría colocada una trampa *pitfall* en el campo, aún sin cebar, el cual se pondría encima de la rejilla en medio.

Una vez al mes, se colocaban las trampas en el área de estudio y se recogían en los días consecutivos a su puesta. Para cada tiempo de exposición de las trampas (24, 48 y 72 horas), se seleccionaban aleatoriamente dos hexágonos, incluyendo todas sus trampas *pitfall*, para hacer un total de 12 trampas por tiempo de exposición. Los escarabajos coprófagos recogidos de cada trampa se mantenían individualizados en un bote con alcohol al 70% para su conservación. Posteriormente, se identificaba cada individuo recolectado mediante una lupa binocular y el uso de claves dicotómicas del grupo (Veiga, 1998; Martín-Piera & López-Colón 2000). Una vez preparados en seco, un representante de cada especie encontrada en los muestreos era incorporado a la colección UCME (Museo de Entomología de la Universidad Complutense de Madrid).

Análisis estadísticos

Una vez terminada la época bianual de muestreos, se realizaron diferentes análisis estadísticos con el fin de poder responder a las hipótesis planteadas. Todos los análisis estadísticos se llevaron a cabo a diferentes niveles taxonómicos, es decir, representando a los escarabajos coprófagos como su conjunto (Scarabaeoidea coprófagos) o separándolos en sus respectivas subfamilias (Aphodiinae, Geotrupinae y Scarabaeinae).

En primer lugar, para determinar si el esfuerzo de muestreo realizado fue significativo se llevó a cabo una estimación de la diversidad para cada excremento utilizando el método de estimación propuesto en Chao & Jost (2015). Basado en la serie numérica de Hill (Hill, 1973; Chao *et al.*, 2021, 2023), este método permite cuantificar la diversidad de especies de una comunidad mediante el cálculo de perfiles de diversidad continua estimados en función de q. Los perfiles de diversidad calculados son, entre otros, la riqueza potencial de especies (q_0), el exponencial del índice de Shannon, que puede interpretarse como el número efectivo de especies abundantes en el conjunto (q_1 = especies efectivas), y el inverso del índice de Simpson, interpretado como el número efectivo de especies altamente abundantes en el conjunto (q_2 = especies dominantes) (Chao & Jost, 2015; Chao *et al.*, 2014, 2020, 2021, 2023). Con los datos de la riqueza potencial y observada se pudo establecer una relación para validar el esfuerzo de muestreo, considerando por encima del 70% una buena representación de los datos en relacion a la diversidad presente en el área de estudio (Jiménez-Valverde & Hortal, 2003). Los análisis se realizaron utilizando el paquete SpadeR versión 0.1.1 de R con la función *Diversidad* para calcular las estimaciones de la diversidad (Chao *et al.*, 2016). Así, los perfiles de diversidad (q_0, q_1 y q_2), la abundancia observada de individuos y la riqueza de especies obtenidos de los datos de campo, todas ellas cuantitativas, fueron consideradas como variables dependientes para el presente estudio.

Para determinar la existencia de preferencias tróficas en la comunidad de escarabajos coprófagos (**Capítulo 1**), se utilizaron pruebas no paramétricas, ya que no todas las variables del estudio estaban distribuidas normalmente, para comparar los parámetros de diversidad obtenidos para cada uno de los excrementos utilizados. Al ser los datos muestras dependientes en función de la fecha, se llevó a cabo una prueba de Friedman (Friedman, 1937, 1940), la cual permite analizar tres o más mediciones repetidas de los datos ordinales. Luego se realizó una prueba de Wilcoxon para detectar diferencias entre pares de datos de nivel ordinal (Wilcoxon, 1945), con la corrección de Bonferroni. De esta forma, se pudo determinar si las comunidades de escarabajos coprófagos mostraban preferencias por un tipo específico de excremento o si estaban distribuidas homogéneamente entre los diferentes excrementos. Todos los análisis estadísticos se realizaron con el paquete STATISTICA versión 10 (StatSoft Inc., 2011).

Específicamente, se utilizaron análisis de interacción de redes para ilustrar y cuantificar las asociaciones tróficas de los escarabajos coprófagos entre los diferentes excrementos utilizados. Para ello, se emplearon tres índices: densidad de enlaces (Bersier *et al.*, 2002), índice de especialización H_2' (Blüthgen *et al.*, 2006) e índice de anidamiento WNODF (Almeida-Neto & Ulrich, 2011). La densidad de enlaces es el número promedio de enlaces por especie. Para H_2', el nivel mínimo ($H_2'= 0$) se produce cuando cada una de las especies de escarabajos coprófagos utiliza diferentes tipos de excremento en proporciones similares. Por el contrario, el máximo ($H_2'= 1$) se alcanza si todos los tipos de excremento son utilizados de forma exclusiva por diferentes especies de escarabajos. Los valores de WNODF oscilan entre 0 y 100, siendo 100 una comunidad perfectamente anidada. Se realizó un análisis de modelo nulo para comprobar si las redes obtenidas diferían en estructura de una red generada aleatoriamente con propiedades estructurales similares. Los índices de cada red se compararon con 10.000 redes generadas aleatorias mediante el paquete *bipartite* (Dormann *et al.*, 2008), en donde se limitó la abundancia total de especies y los enlaces, y se compararon con las redes obtenidas empíricamente utilizando una prueba t de una muestra (Dormann *et al.*, 2009).

Finalmente, se realizó un estudio comparativo de los excrementos empleados en el estudio para determinar cuál albergaba una mayor diversidad filogenética de especies de escarabajos coprófagos. Se utilizó la metodología descrita en Vane-Wright *et al.* (1991). Este método se utiliza en programas de conservación para identificar qué áreas deben protegerse con base a la diversidad que albergan. Primero, a cada especie se le asigna una puntuación basada en su posición en la filogenia y las relaciones filogenéticas con otras especies. Luego, se realiza la suma de cada excremento con base a las especies que se han encontrado en él. De esta forma, si un excremento llega al 100%, esto indica que alberga el total de especies encontradas en el estudio y, por tanto, es el que alberga una mayor diversidad. En el caso de que ninguno de los excrementos llegue al 100%, se establecerá una escala de prioridades. Se repetirían los mismos cálculos, pero esta vez sin tener en cuenta el excremento que mejores resultados ha obtenido. De esta forma se obtendrán los excrementos que secundariamente albergan una mayor diversidad de especies y, así sucesivamente, hasta que la suma de los excrementos llegue al 100%. Para obtener la filogenia consenso se utilizaron filogenias de estudios previos (Martín-Piera & López-Colón, 2000; Martín-Piera, 2001; Villalba *et al.*, 2002; Cabrero-Sañudo & Zardoya, 2004; Verdú *et al.*, 2004; Pizzo *et al.*, 2006, 2013; Cabrero-Sañudo, 2007; Cunha *et al.*, 2011; Macagno *et al.*, 2011).

Para evaluar la influencia de las variables climáticas y aquellas relacionadas con el tiempo en los patrones de diversidad de los escarabajos coprófagos, se utilizaron 60 variables ecológicas que fueron consideradas como variables independientes (**Capítulo 2**). Todas ellas se han agrupado en 4 conjuntos según sus similitudes (18 variables relacionadas con la temperatura, 21 con la humedad, 19 con la presión atmosférica y 2 variables relacionadas con el tiempo). Las variables relacionadas con temperatura, humedad y presión atmosférica se obtuvieron directamente de los datos brutos proporcionados por la estación meteorológica. Aquellas variables consideradas cíclicas, como las relacionadas con el tiempo, se transformaron tanto en seno como en coseno (cada día representa una porción del rango circular completo de 360º) (Cuesta *et al.*, 2021; Lobo & Cuesta, 2021). Debido a la posibilidad de que las comunidades de escarabajos coprófagos puedan ser diferentes de un año para otro, se incluyó en los análisis una variable relacionada con el año de estudio. Para explorar el grado de correlación entre todas las variables utilizadas y dentro de cada conjunto, se realizaron análisis de correlación de Spearman.

Luego se utilizaron modelos lineales generalizados para evaluar el efecto de cada una de las 60 variables ecológicas sobre las variables dependientes (McCullagh & Nelder, 1989; Crawley, 1993). Las variables continuas se estandarizaron para eliminar el efecto de las diferencias en la escala de medición. Se exploraron relaciones estadísticamente significativas entre variables dependientes e independientes para determinar si una función lineal, cuadrática o cúbica de cada variable seleccionada aumentaba el poder explicativo del modelo (Dobson, 1999). En los casos en los que había más de una variable independiente significativa por conjunto, se utilizó el procedimiento *backward removal* para encontrar el mejor modelo predictivo total y por conjunto de variables (Hsieh & Lu, 2006). La bondad de ajuste de los modelos obtenidos se midió mediante el estadístico de desviación y el cambio en la desviación se probó mediante la prueba del índice F (McCullagh & Nelder, 1989; Dobson 1999) con un nivel de significancia del 5%. Se calculó el porcentaje de desviación explicada para cada modelo (Dobson, 1999).

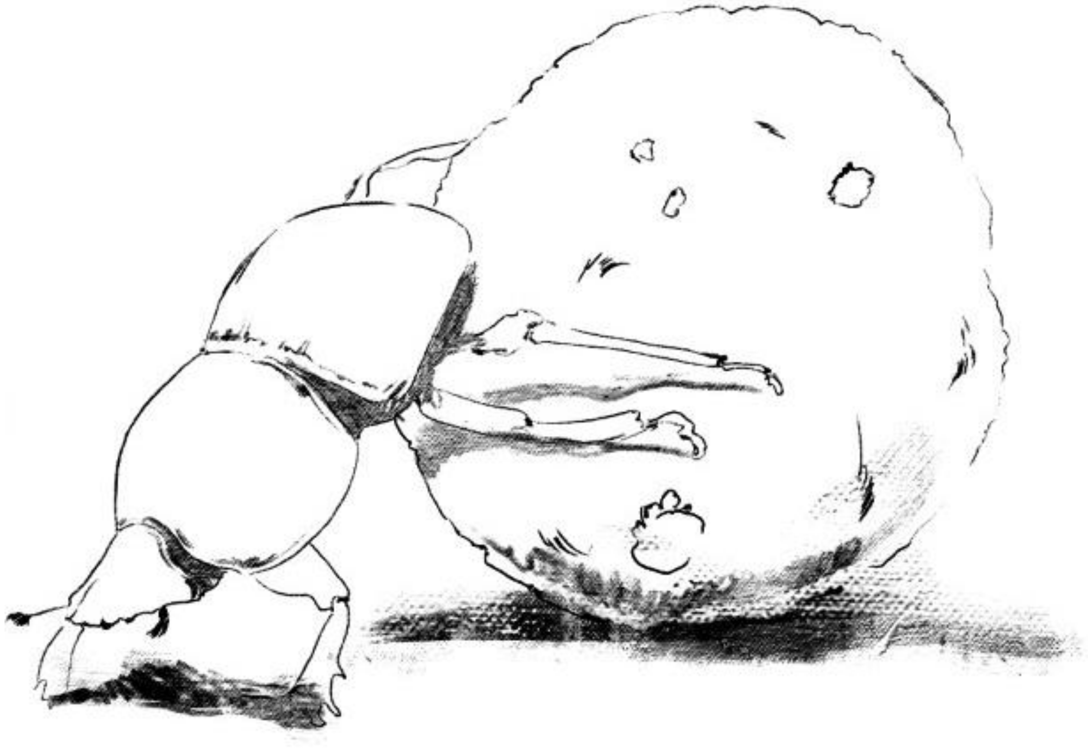
Posteriormente, se cuantificaron los efectos puros y combinados de los diferentes grupos de variables considerados en el estudio aplicando técnicas de partición y descomposición jerárquica de la varianza (Borcard *et al.*, 1992; Qinghong & Brakenhielm, 1995; Anderson & Gribble, 1998; Legendre & Legendre, 1998; MacNally, 2000). Esto permitió estimar qué parte de la varianza de la variable respuesta puede atribuirse exclusivamente a una sola variable independiente, y calcular la fracción de la varianza explicada por el efecto conjunto de las variables consideradas (Cabrero-Sañudo & Lobo, 2003). Gracias a ello, se pudieron separar los efectos de determinados grupos de variables en los que puede haber cierta autocorrelación (posible autocorrelación temporal en las variables relacionadas con el tiempo), permitiendo así evaluar de forma independiente el efecto de otros grupos de variables. Todos los análisis estadísticos se realizaron utilizando R versión 4.2.1 (R Core Team, 2022) y el paquete STATISTICA versión 10 (StatSoft Inc., 2011).

Se realizaron varios análisis estadísticos para establecer cuánto tiempo se deben dejar las trampas para conseguir la mayor cantidad de información sobre la diversidad de escarabajos coprófagos en el menor tiempo de exposición posible (**Capítulo 3**). Como las variables de estudio no estaban distribuidas normalmente, se utilizaron pruebas no paramétricas para comparar los parámetros de diversidad obtenidos para cada tiempo de exposición. Al ser los datos muestras dependientes en función de la fecha, se realizó una prueba de Friedman (Friedman, 1937, 1940), ya que permite analizar tres o más mediciones repetidas de datos ordinales. Luego se realizó una prueba de Wilcoxon para detectar diferencias entre pares de datos de nivel ordinal (Wilcoxon, 1945), con una corrección de Bonferroni. De esta manera, se pudo determinar si el tiempo que una trampa permanece en el ecosistema podría estar afectando a la diversidad de escarabajos coprófagos del área de estudio. Todos los análisis estadísticos se realizaron con el paquete STATISTICA versión 10 (StatSoft Inc., 2011).

Para cuantificar el efecto que tiene la variable independiente (tiempo de exposición) sobre las diferentes variables dependientes se realizaron modelos lineares generalizados (McCullagh & Nelder, 1989; Crawley, 1993). Como el experimento se realizó en diferentes épocas del año, se incluyó el día de muestreo como variable independiente adicional. Al considerarse cíclica, se transformó tanto en seno como en coseno (cada día representa una porción del rango circular completo de 360º) (Cuesta *et al.*, 2021; Lobo & Cuesta, 2021), considerándose dos variables diferentes relacionadas con el tiempo. Las variables continuas se estandarizaron para eliminar el efecto de las diferencias en la escala de medición. Se exploraron relaciones estadísticamente significativas entre variables dependientes e independientes para determinar si una función lineal, cuadrática o cúbica de cada variable seleccionada aumentaba el poder explicativo del modelo (Dobson, 1999). En los casos en los que tanto el seno como el coseno eran significativos, se utilizó el procedimiento *backward removal* para encontrar el mejor modelo predictivo global (Hsieh & Lu, 2006). Cuando hubo un efecto de cualquiera de las variables relacionadas con el tiempo, los residuos se utilizaron para discernir el efecto que se debió únicamente a la variable del tiempo de exposición (Pierce & Schafer, 1986). La bondad de ajuste de los modelos obtenidos se midió mediante el estadístico de desviación y el cambio en la desviación se probó mediante la prueba del índice F (McCullagh & Nelder, 1989; Dobson, 1999) con un nivel de significancia del 5%. Se calculó el porcentaje de desviación explicada para cada modelo (Dobson, 1999). Todos los análisis estadísticos se realizaron utilizando R versión 4.2.1 (R Core Team, 2022) y el paquete STATISTICA versión 10 (StatSoft Inc., 2011).

Por otro lado, se llevaron a cabo varios análisis cualitativos para respaldar los resultados obtenidos de los análisis cuantitativos. En primer lugar, se realizó una comparación de los valores de la riqueza observada para cada tiempo de exposición. Para cada período de muestreo se calculó la riqueza observada total, la cual se utilizó para determinar la proporción de especies encontradas en cada tiempo de exposición. La comparación también se realizó a escala temporal, para comprobar cómo variaban los resultados de cada tiempo de exposición a lo largo del tiempo. En segundo lugar, se estudiaron y compararon las comunidades resultantes para cada tiempo de exposición, con el fin de encontrar similitudes, así como reconocer especies que puedan mostrar preferencia por un tiempo de exposición específico.

CHAPTER 1: STUDY OF TROPHIC PREFERENCES IN A COMMUNITY OF DUNG BEETLES (COLEOPTERA, SCARABAEOIDEA) FROM THE SIERRA DE GUADARRAMA (MADRID, SPAIN) WHEN EXPOSED TO EXCREMENTS FROM NATIVE AND EXOTIC MAMMALS



This chapter is based on the manuscript: Grzechnik, S., & Cabrero-Sañudo, F.J. A taste for dung: dung beetles ‘foodie’ habits uncovered. *Under review*.

Abstract

Dung beetles (Coleoptera, Scarabaeoidea: Aphodiinae, Scarabaeinae, Geotrupinae) are a group of insects specialized in feeding mainly on excrements, preferably from large herbivorous mammals. In the Iberian Peninsula, dung beetles usually feed on different types of dung. However, if they have different types of excrement at their disposal, it is possible that they show preferences for a specific one. In addition, studies using non-native dungs are lacking. Thus, the aim of the study is to determine if an Iberian dung beetle community develops preferences for specific dungs and whether there are dung beetles attracted to exotic dungs. The study was carried out in Mataelpino, a town located in Central Spain (Madrid, Spain). A total of six different dungs were used, from animals with different origin and feeding strategies: African forest buffalo, Asian elephant, brown bear, goat, fallow deer and wild boar. To determine whether dung beetles develop preferences for a dung type, different statistical analyzes were carried out with the information collected from the field sampling. The results show that dung beetle species have a generalist character, being found in all the excrement used. However, it was observed that there were preferences for some types of excrement, such as that of the elephant, being this an exotic dung. Buffalo and wild boar dungs were quite accepted among dung beetle species. In contrast, goat excrement was the least preferred. To conclude, dung beetles have a general diet although they can develop preferences for some specific excrements.

Resumen

Los escarabajos coprófagos (Coleoptera, Scarabaeoidea: Aphodiinae, Scarabaeinae, Geotrupinae) son un grupo de insectos especializados en alimentarse de diferentes excrementos, preferentemente de grandes herbívoros mamíferos. En la península ibérica, los escarabajos coprófagos suelen alimentarse de diferentes tipos de excremento. Sin embargo, pueden desarrollar preferencias tróficas cuando son expuestos a diferentes excrementos. Además, no existen estudios en donde se hayan utilizado excrementos procedentes de animales no autóctonos. Por ello, el objetivo del estudio es determinar si una comunidad de escarabajos coprófagos ibéricos puede desarrollar preferencias por un tipo concreto de excremento y de si existen escarabajos coprófagos que puedan verse atraídos por excrementos exóticos. El estudio se llevó a cabo en Mataelpino, una localidad situada en el Sistema Central (Madrid, España). Se utilizaron un total de seis excrementos diferentes, procedentes de animales con diferentes orígenes y estrategias de alimentación: búfalo rojo, elefante asiático, oso pardo, cabra, gamo y jabalí. Para determinar si los escarabajos coprófagos pueden desarrollar preferencias por un excremento concreto, se realizaron diferentes análisis estadísticos con la información recopilada de los muestreos de campo. Los resultados mostraron que las especies de escarabajos coprófagos tienen un carácter generalista, encontrándose en todos los excrementos utilizados. Sin embargo, se observó que existían preferencias por algunos tipos de excrementos, como el de elefante, siendo éste un excremento exótico. Los excrementos de búfalo y jabalí también tuvieron bastante éxito entre las especies de escarabajos coprófagos. Por otro lado, el excremento de cabra fue el menos seleccionado. En resumen, los escarabajos coprófagos tienen una dieta generalista, aunque pueden desarrollar preferencias por ciertos excrementos.

Introduction

Dung beetles (Scarabaeoidea: Aphodiinae, Scarabaeinae, Geotrupinae) are considered one of the most studied taxa among terrestrial arthropods (Spector, 2006; Raine & Slade, 2019; Giménez-Gómez *et al.*, 2020). Possessing all of the characteristics of an ideal focal taxon, they have been used in many ecological research and biodiversity studies around the world (Halffter & Favila, 1993; Spector, 2006; Raine & Slade, 2019). Also, they play many important ecological functions in both natural and anthropogenic land-use areas, particularly in livestock pastures (Hanski & Cambefort, 1991; Andresen & Feer, 2005; Nichols *et al.*, 2008; Verdú *et al.*, 2018; Giménez-Gómez *et al.*, 2020). Key ecosystem services provided by these insects include, nutrient recycling, soil aeration, control of parasites and pest flies, and secondary seed dispersal (Andressen, 2002; Nichols *et al.*, 2008; Nichols & Gómez, 2014).

Dung beetles are mainly coprophagous, feeding preferably on the excrements of large herbivorous mammals (Scholtz, Davis & Kryger, 2009). However, it has been seen that they can feed on other resources, such as rotting fruits, decomposing fungi, or vertebrate carrion and invertebrate carcasses (Halffter & Matthews, 1966; Hanski & Cambefort, 1991; Verdú *et al.*, 2007; Scholtz *et al.*, 2009; Stavert *et al.*, 2014; Ebert *et al.*, 2019; Giménez-Gómez *et al.*, 2020; Weithmann *et al.*, 2020). It is likely that coprophagy derived from a saprophagous ancestor that evolved into a dung-feeding specialist to exploit the waste of large dinosaurs (Chin & Gill, 1996). Following the extinction of these large vertebrates at the end of the Cretaceous, increased competition among species for lower food availability probably led to the use of alternatives to dung (Halffter & Matthews, 1966; Scholtz *et al.*, 2009), until the emergence of mammals and their excrements, which, when the dinosaurs disappeared, occupied their niche and thrived (Cabrero-Sañudo & Lobo, 2009).

In both temperate and cold-temperate regions of the planet coprophagy remains the dominant feeding strategy (Ebert *et al.*, 2019). In these habitats, the dung beetle community is primarily sustained by the excrement of several species of herbivorous mammals (Hanski & Cambefort, 1991; Simmons & Ridsdill-Smith, 2011; Raine & Slade, 2019). In the Iberian Peninsula, several research have investigated the possible existence of dung beetles' preference for different dung types (Sánchez-Piñero & Ávila, 1991; Martín-Piera & Lobo, 1996; Verdú, 1998; Galante & Cartagena, 1999; Verdú & Galante, 2002). However, species linked exclusively to one type of dung seem to be very rare

(Sánchez-Piñero & Ávila, 1991; Verdú, 1998; Galante & Cartagena, 1999; Verdú & Galante, 2002). Furthermore, non-native mammal dungs have not been previously examined.

In recent decades, numerous studies have focused on the effects of various factors, such as climate change, habitat fragmentation or anthropogenic disturbances, have on dung beetle species (Menéndez & Gutiérrez, 2004; Dortel *et al.*, 2013; Menéndez *et al.*, 2014; Cuesta & Lobo, 2019; Cuesta *et al.*, 2021). Nevertheless, little is known about the effect of these factors in dung beetle–mammal associations (Raine *et al.*, 2018). It is possible that the disappearance or reduction in the number of mammals could cause a cascading effect on dung beetles, with serious consequences on the ecosystem structure and function (Colwell, Dunn & Harris, 2012; Nichols *et al.*, 2016; Raine *et al.*, 2018). Hence evaluating the resource use and flexibility of dung beetle species is crucial, especially under changing environmental conditions (Raine *et al.*, 2018).

Therefore, the purpose of this study was to determine if: 1) an Iberian dung beetle community develops preferences for a specific type of dung; and 2) dung beetles are attracted to exotic dungs. According to the null hypothesis: 1) there would be a tendency towards generalist dung selection among dung beetles; 2) there would be no difference in attraction between native and exotic dungs.

Material and methods

Study area

The study was carried out in the village of Mataelpino, located in the northwest of the Madrid Autonomous Community (Spain). More specifically, the sampling area is a semi-open plot for livestock use located on the outskirts of the village (**Figure 1**). The dimension of the semi-open plot is 1.16 hectares, located at an altitude of 1,140 metres above sea level and at coordinates 40.73ºN, 3.96ºW. The study area has a continental Mediterranean climate, with particularly cold and humid winters, with possible frosts, and hot and dry summers with some months of drought (Rivas-Martínez, 1983).

The landscape of the study area has a purely forest character, predominantly holm oaks (*Quercus ilex* spp. *ballota* (Desf.) Samp.) and Pyrenean oaks (*Quercus pyrenaica* Willd.) forests. Among the bushes, the most representative are brooms, junipers, and rock roses.

In the herbaceous stratum, grazing meadows for livestock use 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 faunal community of the study area since the excrements of these animals are the main source of food for the dung beetles. The study area is characterized by having a high level of livestock activity, especially cattle (*Bos taurus* Linnaeus, 1758) and horses (*Equus ferus caballus* Linnaeus, 1758). In addition to these dungs, dung beetles can use wild animal dungs with different trophic guilds. For example, dung beetles can feed on dung from herbivores, such as roe deer (*Capreolus capreolus* (Linnaeus, 1758)), Iberian ibex (*Capra pyrenaica* Schinz, 1838) or European rabbit (*Oryctolagus cuniculus* (Linnaeus, 1758)). In addition, they can also be attracted by omnivorous excrements, such as those of the wild boar (*Sus scrofa* Linnaeus, 1758) or the fox (*Vulpes vulpes* (Linnaeus, 1758)), and by those of carnivores, such as those of the Iberian wolf (*Canis lupus signatus* Cabrera, 1907) (Viejo, 2013). The presence of these excrements and these conditions of livestock use is a situation not very different from what could be found in most of the Iberian Peninsula, especially in the central area and close to mountain ranges.

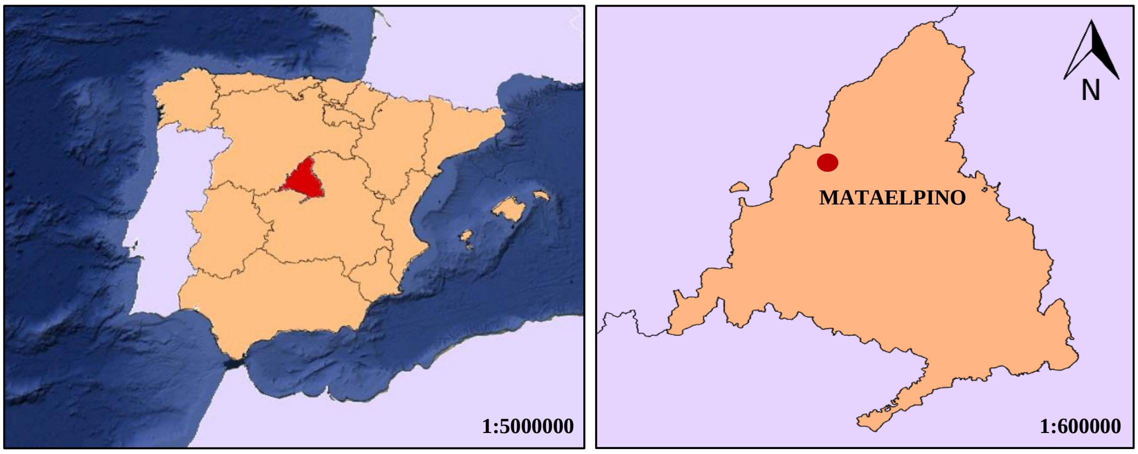


Figure 1. Location maps of the sampling area. The study was carried out in the city of Mataelpino, in the northwest of the Madrid Autonomous Community, Central Spain. The coordinates are 40.73ºN, 3.96ºW. Black lines represent administrative boundaries.

Sampling design

To determine the existence of trophic preferences in dung beetles, a sampling was designed in which pitfall traps baited with dung from different animals were used. A total of six different dungs were used: African forest buffalo (*Syncerus caffer nanus* (Boddaert, 1785)), Asian elephant (*Elephas maximus* Linnaeus, 1758), brown bear (*Ursus arctos* Linnaeus, 1758), goat (*Capra hircus* Linnaeus, 1758), fallow deer (*Dama dama* (Linnaeus, 1758)) and wild boar (*Sus scrofa* Linnaeus, 1758). All excrements were supplied by The Zoo-Aquarium of Madrid. Animals involved in the study had not previously received any veterinary treatment.

The selection of these excrements was the result of a bibliographic research based on the physicochemical characteristics of different dungs used in similar works (Folin & Wentworth, 1910; Dougall, 1963; Gaur, Neelakantan & Dargan, 1971; Hansen, 1978; Grenet, Chenost & Martin-Rosset, 1984; Leslie & Starkey, 1985; Brody & Pelton, 1988; Howery & Pfister, 1990; Abdouli, Khorchani & Nefzaoui, 1992; Kirchmann & Witter, 1992; Alhadhrami & Yousif, 1994; Williams & Haynes, 1995; Leeming *et al.*, 1996; Al-Houty & Al-Musalam, 1997; Chen *et al.*, 1998; Dierenfeld, Wildman & Romo, 2000; Moore & Bower, 2001; Kannan, Guruswamy & Kumar, 2003; Portejoie *et al.*, 2004; Garg *et al.*, 2005, 2006; O'Connell, Callan & O’Doherty, 2006; Holter & Scholtz, 2007; Shah *et al.*, 2007; Moe & Wegge, 2008; Schwarm *et al.*, 2009; Okoroigwe, Ibeto & Ezema, 2010; Barfuss *et al.*, 2011; Ngo *et al.*, 2011; Yadav & Garg, 2011; Yadav, Tare & Ahammed, 2011; Rai & Singh, 2012; Steyaert *et al.*, 2012; Whipple & Hoback, 2012; Irshad *et al.*, 2013; Doan *et al.*, 2014; Okoroigwe, Ibeto & Okpara, 2014; Sahito, Mahar & Ahmed, 2014; Cu *et al.*, 2015; Dhamodharan, Kumar & Kalamdhad, 2015; Abdulyekeen *et al.*, 2016; Holter, 2016; Vodounnou *et al.*, 2016; Frank *et al.*, 2017; Kheira *et al.*, 2017; Pan-in & Sukasem, 2017; Pérez-Godínez *et al.*, 2017; Somorin *et al.*, 2017). With the extracted physicochemical information, a database was configured with 15 descriptive variables for 18 types of excrement (**Appendix 1. Table 1**). A comparison among all the dungs considered was made using the Gower similarity coefficient (Gower, 1971) and a cluster analysis using a UPGMA amalgamation rule, together with a SIMPROF analysis. This analysis has been carried out with the Primer-E version 7.0 program (Clarke & Gorley, 2015). Thus, thanks to the dendrogram obtained through the cluster, representative excrements were selected from each of the resulting groups (**Appendix 2. Figure 1**).

Due to the need to test the effectiveness of the six selected types of dung, the traps were organised in hexagons, placing a different dung at each vertex. Although in some studies the distance between traps was less than three metres to simulate a real situation in nature (Filgueiras *et al.*, 2009; Martínez *et al.*, 2012; Rangel-Acosta *et al.*, 2012), for this sampling the distances among the traps were big enough to avoid overlaps among dungs of the same hexagon or between adjacent hexagons (Larsen & Forsyth, 2005). In total, 12 traps organised in two hexagons were randomly placed throughout the meadow, with a minimum separation of 50m between each of them. Within each hexagon, the traps were randomly placed and separated with a minimum distance of 10m (Lobo, Martín-Piera & Veiga, 1988; Lobo, 1992a, 1992b; Martín-Piera & Lobo, 1996). In addition, two traps without dung were placed in the meadow as control traps.

Following the method recommended by Lobo *et al.* (1988) and Veiga, Lobo & Martín-Piera (1989), each trap consisted of a buried plastic basin, filled with a soapy water solution. A grid was placed on top of each basin, on which an amount of 250 grams of fresh dung (always measured with the same container) was placed (**Figure 2**). Samplings were conducted once a month from May 2018 to February 2020. Although a 24-month study was planned initially, the situation of sanitary confinement interrupted it for the last two months. The traps remained in the field for 72 hours (Lobo *et al.*, 1988; Veiga *et al.*, 1989). After that, the attracted dung beetles were collected from the pitfall traps and preserved in 70% alcohol until their identification in the laboratory.

Figure 2. A photograph of a *pitfall* trap. In the photography it can be seen an example of what a *pitfall* trap placed in the field would look like. The only thing left would be to place the manila paper and the dung on top of the grid.

Analytical procedures

Analyses were performed to determine the existence of trophic preferences in the dung beetle community. The combined information from the two monthly traps for each excrement was used. They were conducted for all dung beetles as a whole (coprophagous Scarabaeoidea) and for each subfamily separately (Aphodiinae, Geotrupinae and Scarabaeinae).

At first, an estimate of biological diversity was carried out for each excrement using the estimation method proposed in Chao & Jost (2015). Based on Hill series of numbers (Hill, 1973; Chao *et al.*, 2021, 2023), this method allows to quantify the species diversity of an assemblage by calculating continuous diversity profiles estimated as a function of q. The diversity profiles calculated are, among others, the potential species richness (q_0), the exponential Shannon index diversity, that 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 & Jost, 2015; Chao *et al.*, 2014, 2020, 2021, 2023). With the data of the potential and observed richness, it has been possible to establish a relationship to validate the sampling effort, considering above 70% 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 version 0.1.1 with the Diversity function to compute diversity estimates (Chao *et al.*, 2016). Thus, diversity profiles, the observed abundance of individuals (Ab) and the species richness obtained (R_0) from the field data, all of them quantitative variables, were considered as the study variables.

Non-parametric tests were used to compare the diversity parameters obtained for each dung, as not all the study variables were normally distributed. Since the data were dependent samples according to dates, a Friedman Anova test was performed (Friedman, 1937, 1940), as it allows three or more repeated measurements of ordinal data to be analysed. Then, a Wilcoxon signed rank test was performed to detect differences between pairs of ordinal-level data (Wilcoxon, 1945), with a Bonferroni correction. In this way, it was possible to determine if the dung beetle communities showed preferences for a specific type of dung or if they were homogeneously distributed among the different excrements used. All the statistical analyses were carried out with STATISTICA 10 (StatSoft Inc., 2011).

On the other hand, interaction network analyses were used to illustrate and quantify the feeding associations of dung beetles among the different dungs. Three indices were used: linkage density (Bersier, Banašek-Richter & Cattin, 2002), network-level measure H_2’ (Blüthgen, Menzel & Blüthgen, 2006), and WNODF (Weighted Nestedness metric based on Overlap and Decreasing Fill; Almeida-Neto & Ulrich, 2011). Linkage density is the mean number of links per species. For H_2’, the minimum level (H_2’= 0) occurs when each of the dung beetle species uses different dung types in similar proportions. In contrast, the maximum (H_2’= 1) is reached if all dung types are used as exclusively as possible by different beetle species. WNODF values range from 0 to 100 where 100 is perfectly nested. A null model analysis was performed to test whether the observed networks differed in structure from a random network with similar structural properties. The indices were compared between the observed network and 10,000 random networks. Random networks were simulated using the *bipartite* package (Dormann, Gruber & Fründ, 2008), constraining the total species abundance and links, and compared to the empirically observed networks using a one-sample t-test (Dormann *et al.*, 2009).

Finally, a comparative study of the dungs used in the study was carried out to determine which one holds a greater phylogenetic diversity of dung beetle species. The methodology described by Vane-Wright, Humphries & Williams (1991) was used. First of all, each species is assigned a score based on its position in the phylogeny and the phylogenetic relationships with other species. Then the sum for each excrement is made based on the species that have been found in it. In this way, if an excrement reaches 100%, this indicates that it houses the total number of species found in the study and, therefore, it is the one that harbour the greatest diversity. If none of the excrement reaches 100%, a priority scale will be established. The same calculations would be repeated, but this time without taking into account the excrement that have obtained the best results. In this way, the excrement that secondarily harbour the greatest diversity of species will be obtained and so on until the sum of the excrements reaches the 100%. Phylogenies from previous studies have been used (Martín-Piera & López-Colón, 2000; Martín-Piera, 2001; Villalba *et al.*, 2002; Cabrero-Sañudo & Zardoya, 2004; Verdú *et al.*, 2004; Pizzo *et al.*, 2006, 2013; Cabrero-Sañudo, 2007; Cunha *et al.*, 2011; Macagno *et al.*, 2011).

Results

In total, 59,264 dung beetles belonging to 46 species were collected (**Appendix 1. Table 2**). Twenty-four species and 52,959 individuals of the subfamily Aphodiinae, 18 species and 6,216 individuals of Scarabaeinae, and four species and 89 individuals of Geotrupinae were recorded. No representative of the Geotrupinae subfamily was found in goat dung. When comparing the dungs, it can be seen that elephant excrement has been the one that has obtained the best results, followed by buffalo and wild boar dungs. On the other hand, goat excrement has obtained the lowest values. The most heterogeneous results have been observed in bear dung (**Table 1** and **Appendix 2. Figure 2**).

Regarding validation of the sample effort, almost all the ratios were equal to or higher than 70.00%, except for goat dung (**Table 1**). However, since it was very close to 70%, it was assumed that, like the rest of the dungs, the representation of the data was good. The best represented dungs were those of fallow deer and bear, having found more than 90% of the possible species for the study area. Then, there were followed by the buffalo and wild boar dungs with a representation of 86.67% and 83.22% respectively. Finally, elephant and goat dung have obtained the lowest representation values.

	q_0	**q_1**	**q_2**	**Richness Obtained (R_0)**	**Abundance (Ab)**	**R_0/ q_0 Ratio**
Buffalo	45.000	5.263	3.214	39	9,265	86.67%
Elephant	60.000	4.150	3.147	42	27,547	70.00%
Goat	32.120	2.277	1.586	22	1,979	68.49%
Fallow deer	31.785	2.759	1.878	30	3,482	94.38%
Wild boar	37.250	3.229	2.187	31	15,086	83.22%
Bear	27.000	7.862	5.215	25	1,905	92.59%

Table 1. **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 significance of the sampling effort is assumed when the values of the ratios are equal to or higher than 70.00% (marked in red).

Figure 3 shows the results of the non-parametric analyses that were carried out to compare the different dungs and see whether there are differences among them. The results of the abundance and richness obtained in the field are shown for all dung beetles as a whole (coprophagous Scarabaeoidea) and for each subfamily separately (Aphodiinae, Geotrupinae and Scarabaeinae). Regardless of the excrement being studied, the results obtained for the diversity profiles are similar to those obtained for the richness obtained.

In most cases, elephant dung has proven to be one of the best dung used, closely followed by buffalo dung. On the other hand, goat dung has obtained the worst results. Likewise, bear and fallow deer dungs have obtained quite low values, especially for abundance.

When comparing dung with each other, some interesting relationships can be observed. In any of the cases, no significant differences have been found between elephant and buffalo dungs, except for the abundance of Geotrupinae, where elephant dung has stood out above the rest. In turn, between these two dungs and those of goat and fallow deer, significant differences have been observed in most cases. For wild boar and bear dungs, the results have been more heterogeneous. In general, no significant differences were found among them. These excrements tended to differ from those of buffalo and elephant, although for the Scarabaeinae subfamily no significant differences were observed among them.

The dung beetle interaction networks included the 46 recorded species of dung beetles (grouped as coprophagous Scarabaeoidea and by subfamilies) and all six types of dungs (**Figure 4**). Regardless of the taxonomic level at which the species has been studied, low values of H_2’ were recorded. The linkage density values are quite high, with the highest values being obtained in the community of the Scarabaeinae subfamily. The community of the subfamily Aphodiinae has obtained the highest WNODF value, indicating that it is nested. Except for the subfamily Geotrupinae, linkage density and H_2’ were significantly different from the null model expectation under random association. In contrast, WNODF index did not differ significantly from the null model expectation (**Appendix 1. Table 3**).

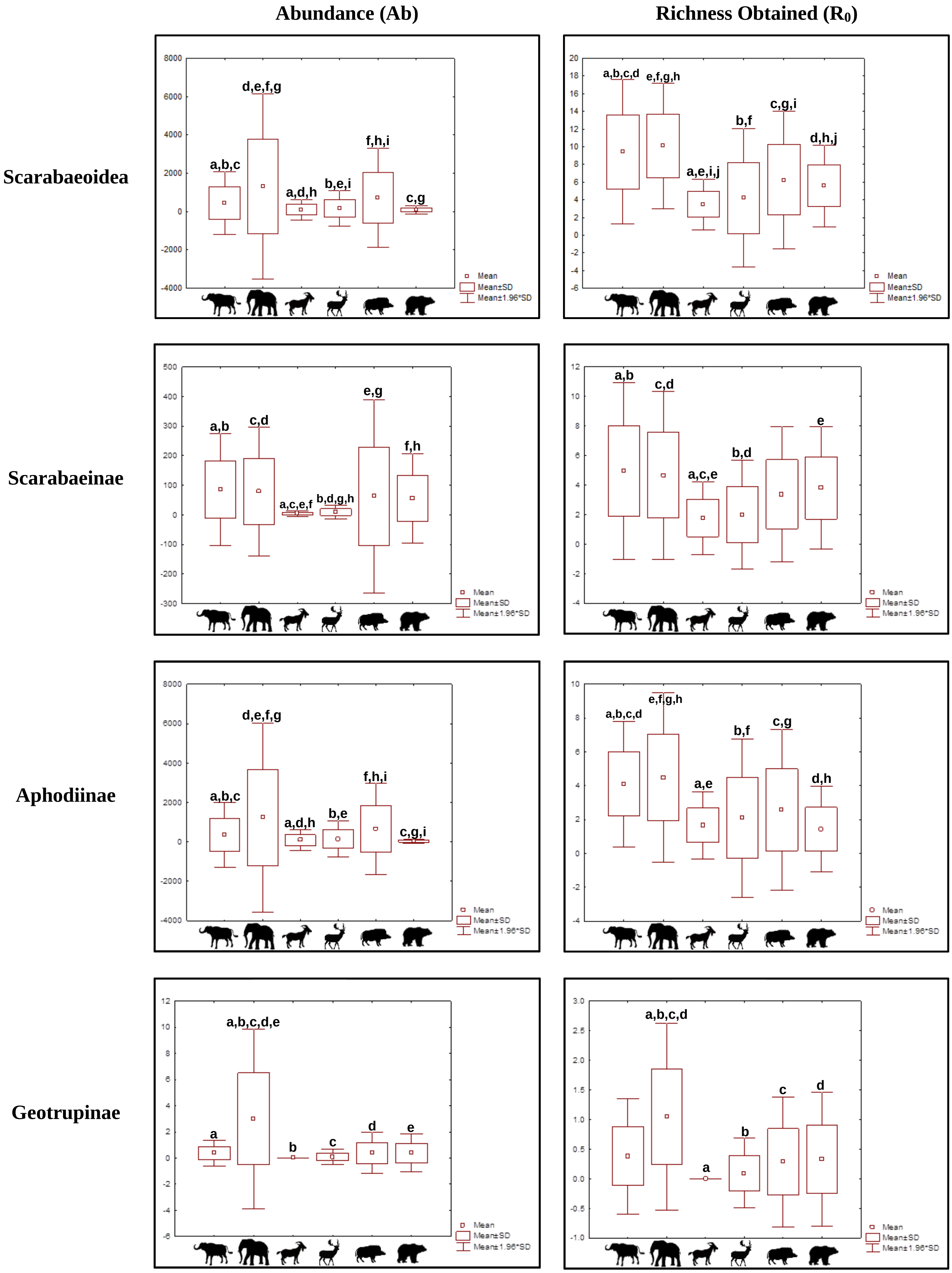


Figure 3. Graphical representation of non-parametric analyses. The results of the abundance (Ab) and richness observed (R_0) in the field are shown for all dung beetles as a whole (coprophagous Scarabaeoidea) and for each subfamily separately (Aphodiinae, Geotrupinae and Scarabaeinae). The lowercase letter identifies the pair of excrements where there were significant.

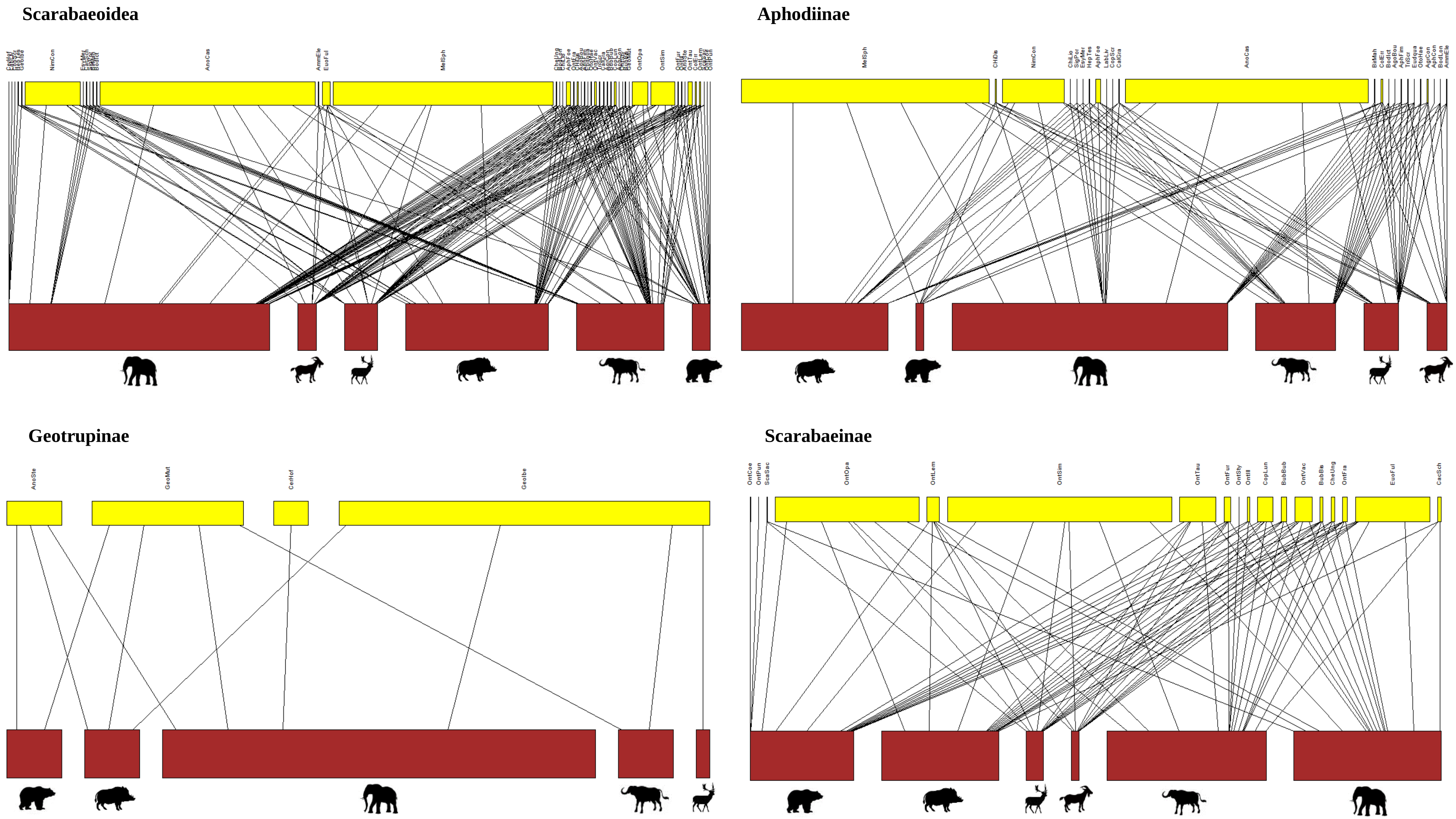


Figure 4. Dung beetle interaction networks. The results were performed for all dung beetles (coprophagous Scarabaeoidea) and for each subfamily separately (Aphodiinae, Geotrupinae and Scarabaeinae). Networks represent interactions between dung beetle species and dung types based on dung beetle abundance. Connecting bars represent the links between the dung beetle species and the different dungs used. Top level: bar size scaled by the abundance of dung beetle species; bottom level: bar size proportional to the number of visits of the dung beetle species to the different dungs used. Each of the images identifies the excrement in question. Species abbreviation: *Agolius bonvouloiri* (AgoBou); *Agrilinus constans* (AgrCon); *Aphodius conjugatus* (AphCon); *Aphodius fimetarius* (AphFim); *Aphodius foetidus* (AphFoe); *Ammoecius elevatus* (AmmEle); *Anomius castaneus* (AnoCast); *Biralus mahunkaorum* (BirMah); *Bodiloides ictericus* (BodIct); *Calamosternus granarius* (CalGra); *Chilothorax distinctus* (ChiDis); *Chilothorax lineolatus* (ChiLin); *Colobopterus erraticus* (ColErr); *Coprimorphus scrutator* (CopScr); *Esymus merdarius* (EsyMer); *Eudolus quadriguttatus* (EudQua); *Heptaulacus testudinarius* (HepTes); *Labarrus lividus* (LabLiv); *Melinopterus sphacelatus* (MelSph); *Nimbus contaminatus* (NimCon); *Otophorus haemorrhoidalis* (OtoHae); *Sigorus porcus* (SigPor); *Trichonotulus scrofa* (TriScr); *Bubas bison* (BubBis); *Bubas bubalus* (BubBub); *Caccobius schreberi* (CacSch); *Cheironitis ungaricus* (CheUng); *Copris lunaris* (CopLun); *Euoniticellus fulvus* (EuoFul); *Onthophagus coenobita* (OntCoe); *Onthophagus fracticornis* (OntFra); *Onthophagus furcatus* (OntFur); *Onthophagus illyricus* (OntIll); *Onthophagus lemur* (OntLem); *Onthophaugus opacicollis* (OntOpa); *Onthophagus punctatus* (OntPun); *Onthophagus similis* (OntSim); *Onthophagus stylocerus* (OntSty); *Onthophagus taurus* (OntTau); *Onthophagus vacca* (OntVac); *Scarabaeus sacer* (ScaSac); *Anoplotrupes stercorosus* (AnoSte); *Geotrupes ibericus* (GeoIbe); *Geotrupes mutator* (GeoMut); *Ceratophyus hoffmannseggi* (CerHof).

Finally, the results from the comparative study are shown to see which dung or dungs host a greater diversity of dung beetle species (**Table 2** and **Appendix 2. Figure 3 and 4**). In all cases, elephant dung has turned out to hold the greatest diversity of species, always getting the highest score. In fact, all representatives of the Geotrupinae subfamily have been found in this excrement (100%). In the case of the subfamily Aphodiinae, all recorded species were found in elephant dung (96.94%) with one species missing, *Aphodius conjugatus* Mulsant, 1842, which is specific to buffalo dung (3.06%). According to the Vane-Wright diversity analyses, the greatest diversity would be found in elephant dung and for greater representation of all taxa, this could be complemented by buffalo dung. For the subfamily Scarabaeinae, almost 90% of the species found were collected from elephant dung. Only the species *Onthophagus punctatus* (Illiger, 1803) and *Onthophagus coenobita* (Herbst, 1783) were missing, which were exclusive to bear excrement (8.39%), as well as *Onthophagus stylocerus* Graëlls, 1851, which was found only in buffalo dung (3.23%). In this case, elephant dung would have the greatest diversity but would be best complemented by bear dung and finally buffalo dung, for greater representation of all taxa.

	Buffalo	Elephant	Goat	Fallow deer	Wild boar	Bear
Scarabaeinae	78.69%	88.38%	60.15%	70.91%	75.46%	83.00%
	3.23%	-	-	-	-	8.39%
Aphodiinae	89.80%	96.94%	50.00%	71.43%	52.04%	30.61%
	3.06%	-	-	-	-	-
Geotrupinae	30.77%	100%	0%	15.38%	53.85%	38.46%

Table 2. Results of the comparative study. The method described in Vane-Wright *et al.* (1991) was used. Based on the phylogeny, each species is assigned to a score. Adding all the scores, the dung or dungs with the greatest diversity of dung beetles have been obtained. Dungs that have been significant for the study are marked in red. The percentages indicate the order on the scale of priorities, with 100% being the excrement that houses the greatest diversity of species.

Discussion

In this study, the results confirm that dung beetles are characterized by feeding on various types of excrement, with most species exhibiting generalist tendencies. Neither the feeding strategy of the mammals used, nor the origin of the excrement have been an impediment for the dung beetles of the study area to colonize them. Nevertheless, some excrements have stood out for having harbored a greater abundance and richness of dung beetle species.

In Palearctic temperate biomes, dung beetle species show an opportunistic and generalized use of a wide range of herbivorous dungs (Hanski & Cambefort, 1991; Simmons & Ridsdill-Smith, 2011; Raine & Slade, 2019). The results of this study confirm this general pattern by finding that the communities resulting from each excrement were quite homogeneous. These communities shared a high percentage of dung beetle species, resulting in high linkage density values and low H_2’ index values. In addition, the WNODF index indicated that there was some nesting among the communities, reaffirming the idea that dung beetles have low specialization and resource partitioning. It should be noted that the results obtained for Scarabaeoidea have been similar to the Aphodiinae. In comparison, Aphodiinae have been much more abundant than the subfamilies Scarabaeinae and Geotrupinae, which may have overshadowed them when the community as a whole is studied.

Some species were found only in one dung type, but all of them were represented by very few individuals. In some cases, even for a single record. Furthermore, all those species are characterized by having a relatively polyphagous trophic spectrum, being able to colonize dung from various types of animals (Martín-Piera & López-Colón, 2000). Dung beetle species linked exclusively to one type of dung have been reported in a very few cases in Mediterranean areas (Sánchez-Piñero & Ávila, 1991; Lumaret & Iborra, 1996; Verdú, 1998; Galante & Cartagena, 1999; Verdú & Galante, 2002, 2004). The ephemeral and limited nature of dung as a food source may explain why extreme specialization in dung beetles is considered very unlikely (Halffter & Matthews, 1966; Hanski & Cambefort, 1991; Lobo, 1992a; Finn & Giller 2002).

Despite the general tendency toward generalism, some types of dung stood out above others. This is consistent with the hypothesis of *choosy generalism*, proposed for dung beetles (Dormont, Epinat & Lumaret, 2004; Dormont *et al.*, 2007; Frank *et al.*, 2018a; Urrutia, Cortez & Verdú, 2022). According to this hypothesis, when dung beetles are exposed to different types of resources, they are able to select the most valuable resource. In this study, elephant dung has accumulated the most dung beetles and where the greatest diversity of species has been found. Similar studies determined that elephant dung had attracted more taxonomically diverse assemblages of dung beetles and in greater proportion than other dungs studied (Vinod & Sabu, 2007, Hewavithana *et al.*, 2016). Buffalo dung has recorded much lower abundance values than elephant dung. Still, buffalo dung has proven to be similar to elephant dung (Hewavithana *et al.*, 2016), sharing many of the recorded dung beetle species. Buffalo dung could be compared to cow dung as it has similar qualities. This could explain its great success among dung beetles, since in this area of the central Iberian Peninsula they are well adapted to this type of excrement (Martín-Piera & Lobo, 1996; Galante & Cartagena, 1999; Errouissi *et al.*, 2004). Fallow deer droppings have had an intermediate appealing power, which it has been reflected in the results. Other studies in which fallow deer dung have been included, confirm the results of this study (Martín-Piera & Lobo, 1996; Dormont *et al.*, 2007). In comparison, goat excrement has obtained the lowest diversity values. Studies carried out in more humid and cold climates, goat excrement or its analogue (sheep dung), are quite successful (Finn & Giller, 2002; Errouissi *et al.*, 2004, Dormont *et al.*, 2007, 2010). On the other hand, in the Mediterranean region it has been seen that goat excrement dries out more quickly in the environment (Errouissi *et al.*, 2004). Unlike other dungs, it does not form a compact protective crust on the surface that protects against water loss (Lumaret & Kirk, 1987). As it becomes a dry and hard dung, its appealing power decreases, hence these results.

Unlike the excrements of herbivores, those of omnivores have not had as much impact in the Palearctic temperate biomes. Furthermore, there are discrepancies among the different studies. In some of them, it has been observed that dung beetle species occur only sporadically in wild omnivorous dung (Carpaneto & Fabbri, 1983; Martín-Piera & Lobo, 1996; Barbero, Palestrini & Rolando, 1999; Frank *et al.*, 2018b). In contrast, in other studies a strong attraction to omnivorous dung has been noted (Martín-Piera & Lobo, 1996; Frank *et al.*, 2018a, 2018b). In this study, both aspects have been observed. On one hand, wild boar dung has been quite successful, hosting a diverse and abundant community of dung beetles. In fact, it has been the second excrement that has accumulated the greatest abundance of dung beetles. This coincides with other studies in which it has seen that wild boar dungs turned out to be one of the most attractive dungs (Frank *et al.*, 2018a; Sathiandran, Vineesh & Thomas, 2021). In contrast, the bear dung community has been quite poor, both in species richness and individual abundance. Probably, its appealing power is much lower compared to the rest of excrements, which explains these results (Hewavithana *et al.*, 2016; Frank *et al.*, 2018b). It is interesting to note that in other regions of the planet, omnivorous excrements are one of the most used resources, as they are very effective in capturing dung beetles (Filgueiras *et al.*, 2009; Carpaneto, Mazziotta & Ieradi, 2010; Whipple & Hoback, 2012; Giménez-Gómez *et al.*, 2020; Sathiandran *et al.*, 2021).

As previously mentioned, the study of trophic preferences in dung beetles has been widely researched in the Iberian Peninsula. However, excrement from non-native animals had never been used before. In accordance with other international studies, where both exotic and native animals were used (Gittings & Giller, 1998; Whipple & Hoback, 2012), the origin of the excrement does not seem to affect the dung beetles at the study site. These results are supported by our comparative study, which confirmed that elephant dung held the greatest diversity of dung beetle species. In fact, all the recorded species of Geotrupinae subfamily, almost all of Aphodiinae species and more than the 85% of Scarabaeinae species were found in this excrement. Greater abundance and richness of dung beetle species were expected in ruminant mammal dungs (buffalo, fallow deer and goat), since they digest food better than non-ruminants herbivores (elephant) (Holter, 2016). Furthermore, it has been seen that the nutrient quality of the excrements is usually lower in proportion to that of ruminant excrements (Finn & Giller, 2002). The C/N ratio (an index that describe the quality of organic substrates) (Holter & Scholtz, 2007), is usually quite high in non-ruminant excrements, indicating a low proportion of nitrogen and, therefore, amino acids. These are crucial for the insect development, such as the emergence from the pupal skin, they are precursors of pigments or promote growth in larvae and adults (Frank *et al.*, 2017). Therefore, the amount and composition of volatile organic compounds and other organoleptic properties of dung must play a key role (Frank *et al.*, 2017). For example, horse dung, analogous to elephant dung, has been observed to give off a strong odour, which could explain the success of elephant dung (Finn & Giller, 2002).

In the case of omnivorous excrements, no notable results were expected to be obtained. In general, they tend to be excrements that have an intermediate nutritional quality, with C/N ratio values between those of herbivores and carnivores (Frank *et al.*, 2017). Unlike the bear, wild boar dung has been a revelation. Although both are omnivores and their diet varies with the seasons, the bear usually consumes more animal foods than the wild boar. Therefore, its dung would be more similar to those of a carnivore, while wild boar excrements would be more similar to those of herbivores. Frank *et al.* (2017) observed that although carnivore excrements are the richest in nutrients (high C/N ratio), they could contain pathogenic bacteria, which are perceived by the dung beetles via olfactory cues. This would explain the low results obtained for bear dung (Martín-Piera & Lobo, 1996; Frank *et al.*, 2018b). However, the results of the comparative study chose it as the second dung with the greatest diversity of Scarabaeinae species held. Therefore, it would be interesting to include this type of excrement in future studies. It is possible that something similar to elephant droppings happens with wild boar droppings. Frank *et al.* (2018a) observed that some of the volatile organic compounds emanating from wild boar dungs were among the most attractive to dung beetles, which would explain the results of this study.

It is important to remember that the observed differences are not only due to intrinsic qualities of the excrement (Dormont *et al.*, 2004, 2007, 2010; Stavert *et al.*, 2014; Holter, 2016; Frank *et al.*, 2017, 2018a), but also to other factors, such as the type of habitat in which the excrement is found (Barbero *et al.*, 1999) or, even a biological demand of the considered beetle (Dormont *et al.*, 2004). Therefore, the selection among different dung types is conditioned by various factors, whether historical, geographical or ecological, which should be taken into account in future studies (Barbero *et al.*, 1999). In addition, there is uncertainty about the consequences that changing environmental conditions will have on ecosystem food webs. The disappearance of large herbivorous mammals would negatively impact dung beetle communities and, consequently, the ecosystem functions they perform (Raine *et al.*, 2018). Therefore, understanding the feeding habits of dung beetles and their trophic plasticity could be very helpful in the future.

Conclusions

This study is the first in the Iberian Peninsula to utilize excrements from both native and exotic fauna. Dung beetle species have great trophic plasticity, being able to feed on various types of excrement. However, they can develop preferences when exposed to different dung types. Among all the dung types, elephant dung has obtained the highest diversity indices, demonstrating that the origin of the dung does not influence the selection of dung beetle species. It is important to highlight that the observed preferences are not due to a fixed species trait, but rather to the joint effect of several ecological, geographical and historical factors. Dung beetles are essential for the proper functioning of ecosystems, making it crucial to initiate conservation initiatives for them.

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Appendix 1

Table 1. Summary table of the literature search. In total, information on 18 different dungs was collected. The table showed 15 descriptive variables based on the physicochemical characteristics of the dungs.

Excrements	Water content (%)	Dry weight (%)	C/N ratio	Fats (%/mg)	Proteins (%/mg)	Sterols (%/mg)	pH	Ash (%)	Size	Shape	Texture	Colour	Diet	Habitat	Domestic/Wild
Horse	70.73	29.27	21.13	0.28	4.15	0.49	7.53	3.46	Big	Dungpat	Fibrous	Light brown	Herbivorous	Meadow	Domestic
Camel	60.00	40.00	18.00	0.38	4.04	-	8.48	16.84	Big	Dungpat	Fibrous	Light brown	Herbivorous	Meadow	Domestic
Sheep	73.56	26.44	15.09	0.21	3.61	3.20	8.24	6.81	Small	Pellet	Fibrous	Dark brown	Herbivorous	Meadow	Domestic
Dog	27.00	73.00	17.00	0.15	2.19	4.10	7.70	1.50	Medium	Stool	Partially digested	Variable	Omnivorous	Meadow	Domestic
Fox	51.00	49.00	6.60	0.30	12.09	1.04	-	-	Small	Stool	Partially digested	Brown	Carnivorous	Forest	Wild
Lynx	62.00	38.00	5.40	1.38	-	10.26	-	-	Small	Stool	Partially digested	Brown	Carnivorous	Forest	Wild
Wolf	39.00	61.00	11.30	0.67	-	0.61	-	-	Medium	Stool	Partially digested	Variable	Carnivorous	Forest	Wild
Bear	78.00	22.00	16.30	0.53	20.71	2.42	-	2.23	Big	Stool	Partially digested	Variable	Omnivorous	Forest	Wild
Rabbit	69.00	31.00	19.29	0.34	3.75	1.62	8.16	11.04	Small	Pellet	Fibrous	Dark brown	Herbivorous	Forest	Wild
Wild boar	48.62	51.38	16.20	0.50	5.85	1.24	6.65	13.27	Medium	Dungpat	Fibrous	Variable	Omnivorous	Forest	Wild

Cow	78.29	21.71	37.05	0.37	1.95	0.91	7.95	5.69	Big	Dungpat	No fibrous	Brown	Herbivorous	Meadow	Domestic
Fallow deer	63.00	37.00	13.90	0.43	6.40	0.74	7.80	13.41	Small	Pellet	Fibrous	Dark brown	Herbivorous	Forest	Wild
Donkey	65.20	34.80	59.20	0.31	4.46	0.58	8.10	-	Big	Dungpat	Fibrous	Light brown	Herbivorous	Meadow	Domestic
Elephant	78.07	21.93	26.60	0.57	1.52	0.69	7.35	2.91	Big	Dungpat	Fibrous	Light brown	Herbivorous	Meadow	Wild
Goat	31.90	68.10	25.70	0.86	6.93	3.48	7.83	-	Small	Pellet	Fibrous	Dark brown	Herbivorous	Meadow	Domestic
Buffalo	80.64	19.36	24.00	0.31	2.42	0.6	8.10	7.49	Big	Dungpat	No fibrous	Brown	Herbivorous	Forest	Wild
African buffalo	78.30	21.70	33.28	0.47	3.18	0.11	8.57	3.28	Big	Dungpat	No fibrous	Brown	Herbivorous	Meadow	Wild
Human	74.44	25.56	4.43	5.09	7.64	4.61	9.10	3.69	Medium	Stool	Partially digested	Variable	Omnivorous	Meadow	Domestic

Table 2. 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 per dung are indicated.

List of species	**Abundance of individuals per dung**					
	Buffalo	**Elephant**	**Goat**	**Fallow deer**	**Wild boar**	**Bear**
Subfamily Aphodiinae						
Agolius bonvouloiri (Harold, 1860)	1	1	0	0	0	0
Agrilinus constans (Duftschmid, 1805)	61	19	1	3	0	1
Aphodius conjugatus (Panzer, 1795)	1	0	0	0	0	0
Aphodius fimetarius (Linnaeus, 1758)	18	12	0	6	3	0
Aphodius foetidus (Herbst, 1783)	67	236	16	16	73	25
Ammoecius elevatus (Olivier, 1789)	8	9	10	20	0	0
Anomius castaneus (Illiger, 1803)	4,491	11,293	1,540	2,424	2,801	205
Biralus mahunkaorum Adam, 1983	14	33	0	1	0	0
Bodiloides ictericus (Laicharting, 1781)	3	7	0	1	0	0
Bodilus longispina (Küster 1854)	2	1	1	3	0	0
Calamosternus granarius (Linnaeus, 1767)	6	32	1	13	5	9
Chilothorax distinctus (Müller, 1776)	10	61	1	2	37	8
Chilothorax lineolatus (Illiger, 1803)	1	1	0	0	1	0
Colobopterus erraticus (Linnaeus, 1758)	58	3	1	21	12	46
Coprimorphus scrutator (Herbst, 1789)	0	1	0	0	0	0
Esymus merdarius (Fabricius, 1775)	2	12	0	0	2	0
Eudolus quadriguttatus (Herbst, 1783)	7	2	0	2	1	0
Heptaulacus testudinarius (Fabricius, 1775)	2	24	0	1	3	0
Labarrus lividus (Olivier, 1789)	0	1	0	0	0	0
Melinopterus sphacelatus (Panzer, 1798)	2,390	9,682	309	755	9,713	382
Nimbus contaminatus (Herbst, 1783)	256	4,375	7	13	1,102	54
Otophorus haemorrhoidalis (Linnaeus, 1758)	31	13	0	2	0	0
Sigorus porcus (Fabricius, 1792)	1	3	0	0	1	0
Trichonotulus scrofa (Fabricius, 1787)	36	9	1	3	5	0
Subfamily Scarabaeinae						
Bubas bison (Linnaeus, 1767)	12	12	1	1	1	5
Bubas bubalus (Olivier, 1811)	29	17	0	2	8	5
Caccobius schreberi (Linnaeus, 1767)	7	26	0	0	3	0

Cheironitis ungaricus **(Herbst, 1789)**	10	19	1	0	8	0
Copris lunaris **(Linnaeus, 1758)**	27	61	9	12	34	30
Euoniticellus fulvus **(Goeze,1777)**	242	558	2	5	21	9
Onthophagus coenobita **(Herbst, 1783)**	0	0	0	0	0	7
Onthophagus fracticornis **(Preyssler, 1790)**	5	33	1	2	6	4
Onthophagus furcatus **(Fabricius, 1781)**	7	23	2	3	16	24
Onthophagus illyricus **(Scopoli, 1763)**	8	8	0	0	3	8
Onthophagus lemur **(Fabricius, 1781)**	31	29	2	6	18	52
Onthophagus opacicollis **Reitter, 1892**	454	271	31	76	527	254
Onthophagus punctatus **(Illiger, 1803)**	0	0	0	0	0	1
Onthophagus similis **(Scriba, 1790)**	650	489	28	73	630	651
Onthophagus stylocerus **Graëlls, 1851**	1	0	0	0	0	0
Onthophagus taurus **(Schreber, 1759)**	232	42	12	11	6	104
Onthophagus vacca **(Linnaeus, 1767)**	76	65	2	2	38	11
Scarabaeus sacer **Linnaeus, 1758**	0	1	0	1	0	2
Subfamily Geotrupinae						
Anoplotrupes stercorosus **(Scriba, 1791)**	0	4	0	0	1	3
Geotrupes ibericus **Baraud, 1958**	7	43	0	2	2	0
Geotrupes mutator **(Marsham, 1802)**	1	11	0	0	5	5
Ceratophyus hoffmannseggi **Fairmaire, 1856**	0	5	0	0	0	0

Table 3. Results of the interaction network analyses. The values of linkage density, network-level measure H_2' and WNODF are shown. Index values that were significantly different from the null model expectation are marked in red.

	Linkage density	**H_2'**	**WNODF (%)**
Scarabaeoidea	3.80	0.13	60.00
Aphodiinae	3.12	0.11	65.85
Geotrupinae	2.33	0.25	57.29
Scarabaeinae	4.54	0.11	55.22

Appendix 2

Figure 1. Dendrogram of clustering based on the Gower similarity coefficient. Similarity relationships are shown between the 19 excrements studied using 15 descriptive variables based on the physicochemical characteristics of the excrements. If the dungs are grouped in the same clade (marked in red) it means that there is no statistical evidence that the dungs are different. Based on these relationships, the selection of excrements for the study was carried out.

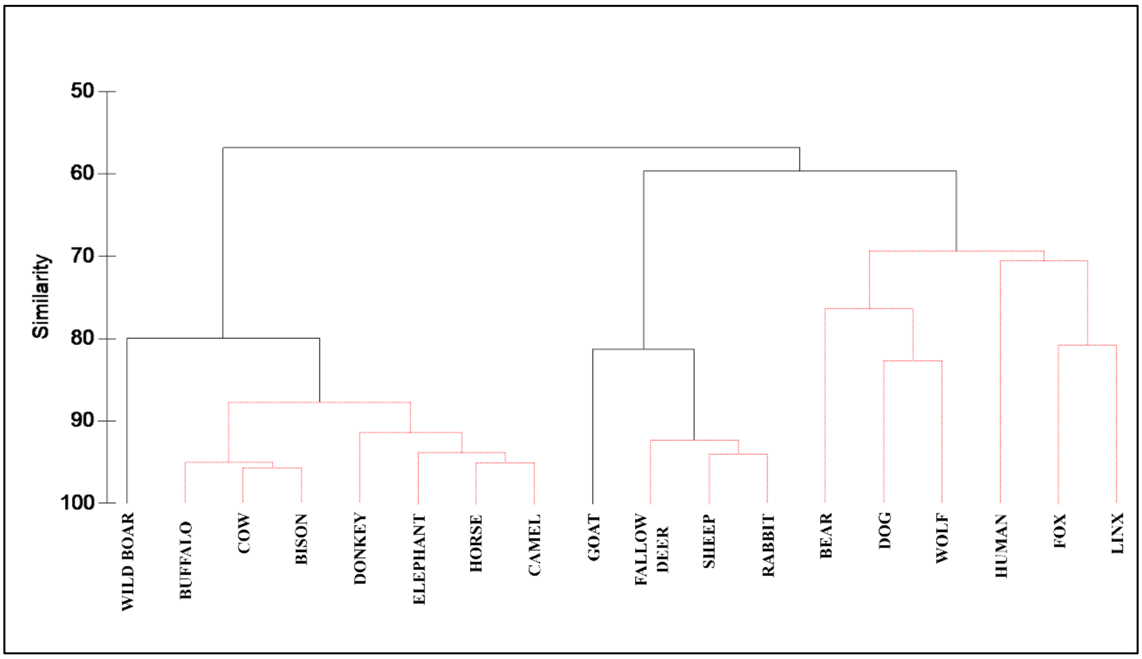
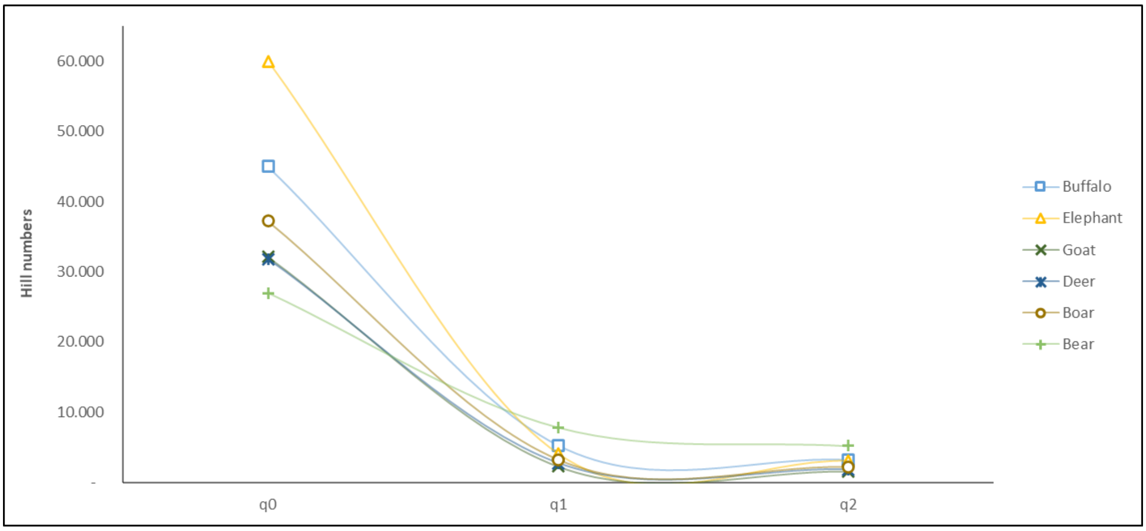


Figure 2. Graphical representation of Hill numbers. The values of the diversity profiles: potential species richness (q_0), exponential Shannon index diversity (q_1), and inverse Simpson index diversity (q_2) for each dung used are shown.



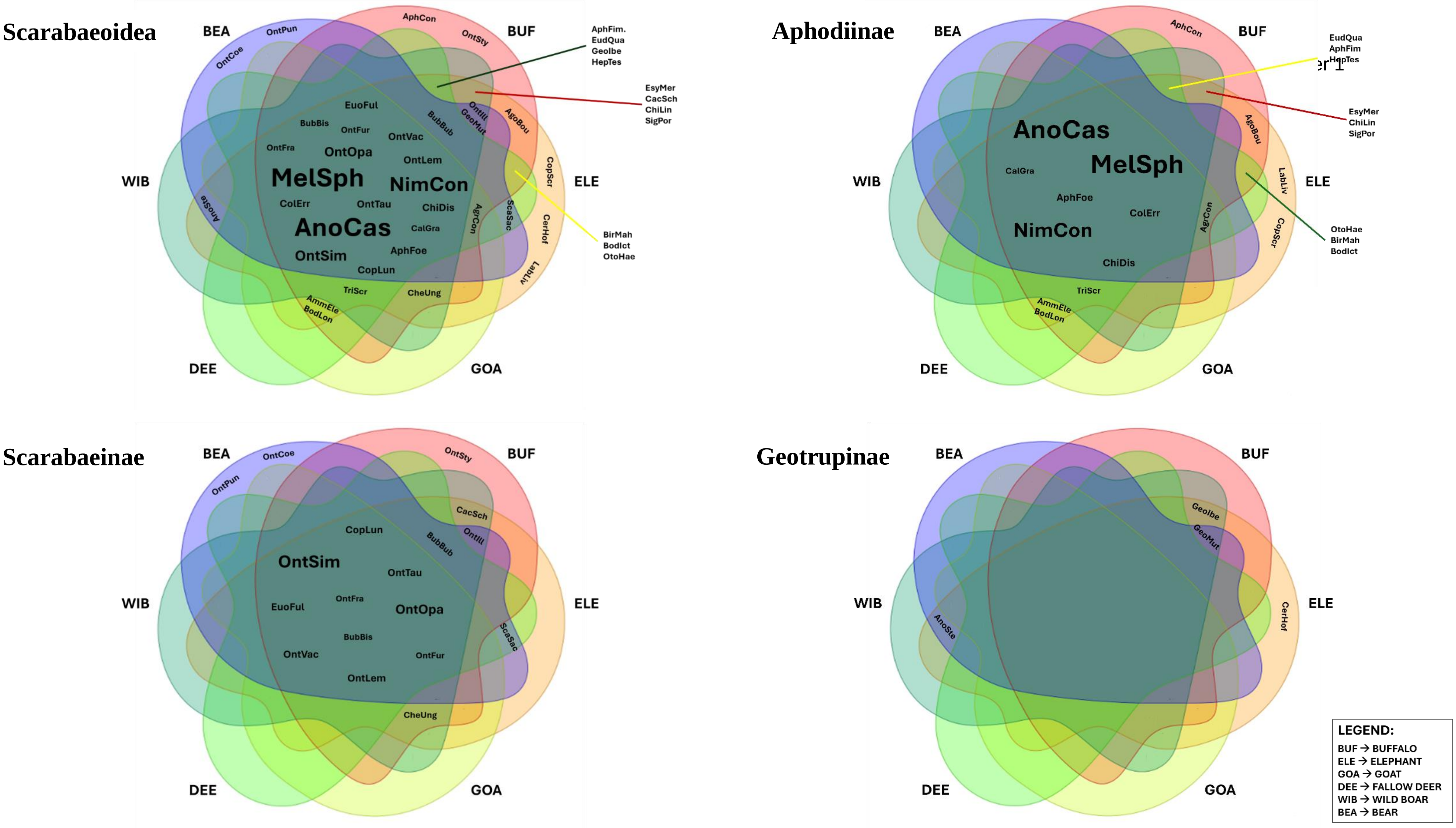
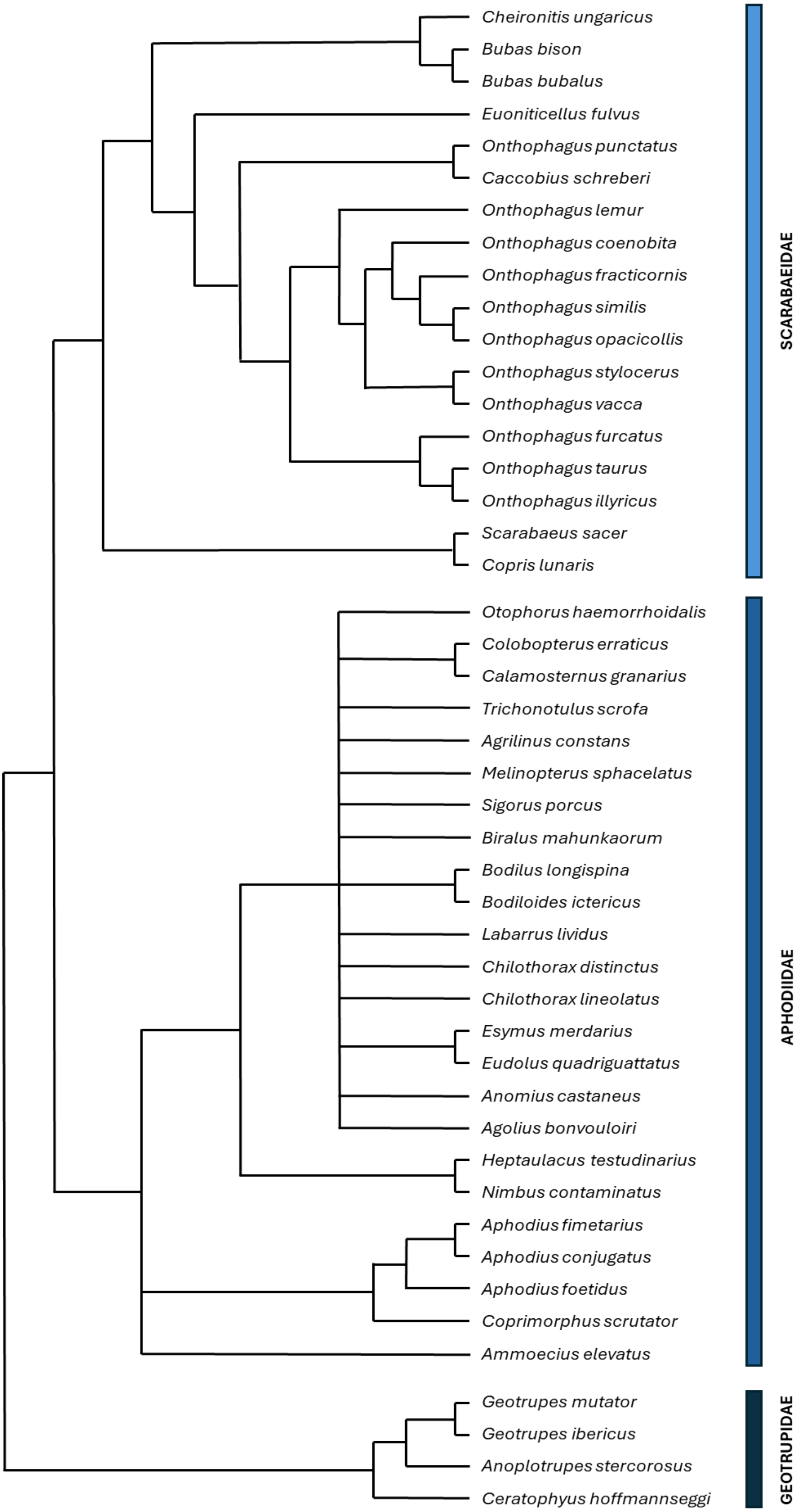


Figure 3. Graphical representation of dung selection by dung beetle species. The results were performed for all dung beetles (coprophagous Scarabaeoidea) and for each subfamily separately (Aphodiinae, Geotrupinae and Scarabaeinae). Each figure shows the distribution of the species according to the dungs where they were found. If a species has been recorded in all the excrements studied, it has been located in the center of the graph. As a species becomes more restrictive it moves away from the centre. At the extremes are the species that have been specific to a specific excrement. The font size is proportional to the recorded abundance of each species. Dung abbreviations: BUF: Buffalo; ELE: Elephant; GOA: Goat; DEE: Fallow deer; WIB: Wild boar; and BEA: Bear. Species abbreviation: APHODIINAE: *Agolius bonvouloiri* (AgoBou); *Agrilinus constans* (AgrCon); *Aphodius conjugatus* (AphCon); *Aphodius fimetarius* (AphFim); *Aphodius foetidus* (AphFoe); *Ammoecius elevatus* (AmmEle); *Anomius castaneus* (AnoCast); *Biralus mahunkaorum* (BirMah); *Bodilus longispina* (BodLon); *Bodiloides ictericus* (BodIct); *Calamosternus granarius* (CalGra); *Chilothorax distinctus* (ChiDis); *Chilothorax lineolatus* (ChiLin); *Colobopterus erraticus* (ColErr); *Coprimorphus scrutator* (CopScr); *Esymus merdarius* (EsyMer); *Eudolus quadriguttatus* (EudQua); *Heptaulacus testudinarius* (HepTes); *Labarrus lividus* (LabLiv); *Melinopterus sphacelatus* (MelSph); *Nimbus contaminatus* (NimCon); *Otophorus haemorrhoidalis* (OtoHae); *Sigorus porcus* (SigPor); *Trichonotulus scrofa* (TriScr). SCARABAEINAE: *Bubas bison* (BubBis); *Bubas bubalus* (BubBub); *Caccobius schreberi* (CacSch); *Cheironitis ungaricus* (CheUng); *Copris lunaris* (CopLun); *Euoniticellus fulvus* (EuoFul); *Onthophagus coenobita* (OntCoe); *Onthophagus fracticornis* (OntFra); *Onthophagus furcatus* (OntFur); *Onthophagus illyricus* (OntIll); *Onthophagus lemur* (OntLem); *Onthophaugus opacicollis* (OntOpa); *Onthophagus punctatus* (OntPun); *Onthophagus similis* (OntSim); *Onthophagus stylocerus* (OntSty); *Onthophagus taurus* (OntTau); *Onthophagus vacca* (OntVac); *Scarabaeus sacer* (ScaSac). GEOTRUPINAE: *Anoplotrupes stercorosus* (AnoSte); *Geotrupes ibericus* (GeoIbe); *Geotrupes mutator* (GeoMut); *Ceratophyus hoffmannseggi* (CerHof).

Figure 4. Phylogenetics relationships of the dung beetles. The phylogenetic relationships of the species collected in the study area are shown, differentiating the three subfamilies. This phylogeny is the result of previous studies (Martín-Piera & López-Colón, 2000; Martín-Piera, 2001; Villalba *et al.*, 2002; Cabrero-Sañudo & Zardoya, 2004; Verdú *et al.*, 2004; Pizzo *et al.*, 2006, 2013; Cabrero-Sañudo, 2007; Cunha *et al.*, 2011; Macagno *et al.*, 2011).



CHAPTER 2: EFFECT OF VARIOUS CLIMATIC AND TIME-RELATED VARIABLES ON A COMMUNITY OF DUNG BEETLES (COLEOPTERA, SCARABAEOIDEA) FROM THE SIERRA DE GUADARRAMA (MADRID, SPAIN)

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Abstract

Dung beetles are considered a key element in ecosystems since 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, Scarabaeinae and Geotrupinae, 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 samplings were conducted from May 2018 to February 2020. According to the results, the considered variables exert an effect on dung beetles, with differences 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, while humidity seems to have a greater effect on Geotrupinae species.

Resumen

Los escarabajos coprófagos son considerados un elemento clave en los ecosistemas ya que intervienen en multitud de procesos ecológicos, siendo uno de los principales descomponedores de materia orgánica del paisaje. Se pueden clasificar en 3 subfamilias: Aphodiinae, Scarabaeinae y Geotrupinae, cada una con adaptaciones particulares y estrategias evolutivas que se han desarrollado a lo largo del tiempo. Los patrones globales de diversidad de los escarabajos coprófagos están influenciados por factores ecológicos, como las variables climáticas (temperatura, humedad, presión atmosférica) y aquellas relacionadas con el tiempo. Así, el objetivo del estudio es ver cómo afectan estas variables a una comunidad de escarabajos coprófagos y si existen diferentes respuestas entre las subfamilias. El estudio se llevó a cabo en Mataelpino, una localidad situada del Sistema Central (Madrid, España). Los muestreos mensuales se realizaron desde mayo de 2018 hasta febrero de 2020. Según los resultados, las variables consideradas tienen un efecto sobre los escarabajos coprófagos, existiendo diferencias entre las subfamilias. Hasta donde sabemos, la presión atmosférica ha sido considerada por primera vez en un estudio de este tipo, observándose un mayor efecto en la subfamilia Aphodiinae que en el resto de grupos de escarabajos coprófagos. Respecto al resto de subfamilias, se ha observado que la temperatura es un factor determinante para las especies Scarabaeinae, mientras que la humedad parece tener un efecto mayor para las especies Geotrupinae.

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 them as the object of study (Spector, 2006; Palumbo, 2010; Kingsolver *et al.*, 2011; Jaworski & Hilszczanski, 2013; Raza *et al.*, 2014; Sangle *et al.*, 2015; Lobo, 2016; Pureswaran *et al.*, 2018; Halsch *et al.*, 2021). Besides, being ectotherms makes them more dependent on environmental conditions and, therefore, very useful as indicators (McGeoch, 1998, 2007; Saleh *et al.*, 2014).

Within them, dung beetles (Coleoptera, Scarabaeoidea) are considered an excellent focal group for studying species diversity patterns, due to their well-known taxonomy, wide geographic distribution, ease of sampling, habitat specialization, response to small-scale habitat heterogeneity and importance in ecosystem function (Spector, 2006; Nichols *et al.*, 2008; Agoglitta *et al.*, 2012; Raine & Slade, 2019; Carvalho *et al.*, 2020; Tonelli, 2021). Also, they play important roles in those ecosystems, participating in the ecological processes of nutrient cycling, secondary seed dispersal, bioturbation, 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. It is characterized by having enormous ecological plasticity, being able to exploit a wide spectrum of food resources from all types of organic matter of animal and plant origin (Martín-Piera & Colón, 2000). Within this superfamily are the commonly called dung beetles, which feed mainly on mammalian dung and also use dung as a breeding chamber for their larvae (Halffter & Matthews, 1966; Halffter & Edmonds, 1982). Dung beetles comprise species of the subfamily Geotrupinae, within the Geotrupidae family, and members of Aphodiinae and Scarabaeinae subfamilies, within the Scarabaeidae family (Halffter & Edmonds, 1982; Scholtz, 1990; Browne & Scholtz, 1999; Villalba *et al.*, 2002). They are worldwide distributed, mainly associated to 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), while Scarabaeinae are typical of hot and arid ones (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 one of the most influential climatic factors (Halffter & Edmonds, 1982; Lumaret & Kirk, 1991; Lobo *et al.*, 2002; Labidi *et al.*, 2012; Numa *et al.*, 2012; Dortel *et al.*, 2013; Ferreira *et al.*, 2018; Calatayud *et al.*, 2021; Ambrozova *et al.*, 2022). In the Spanish Mediterranean Region, Scarabaeinae species have been found to be more active under warm conditions (Halffter & Edmonds, 1982; Jay-Roberts *et al.*, 2008a; Errouissi *et al.*, 2009). However, there is a progressive replacement by Aphodiinae and Geotrupinae species as conditions become wetter and cooler (Halffter & Edmonds, 1982; Lumaret & Kirk, 1987; Jay-Roberts *et al.*, 2008a; Errouissi *et al.*, 2004, 2009). In addition, the seasonal pattern of each subfamily is adjusted to the moments of the year when their ideal climatic conditions occur (Lobo, 1982; Lumaret & Kirk, 1987, 1991; Jay-Roberts *et al.*, 2008a; Agoglitta *et al.*, 2012; 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 (Ankney, 1984; Marchand & McNeil, 2000; Fournier *et al.*, 2005; Rousse *et al.*, 2009; Pellegrino *et al.*, 2013; Austin *et al.*, 2014; Dagaeff *et al.*, 2016; Adonyeva *et al.*, 2021). Depending on weather patterns, calm, dry, and sunny climate is 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 (good weather), while at low atmospheric pressure levels their activity rates were reduced (bad weather) (Ankney, 1984; Marchand & McNeil, 2000; Fournier *et al.*, 2005; Rousse *et al.*, 2009; Pellegrino *et al.*, 2013; Austin *et al.*, 2014; Dagaeff *et al.*, 2016; Adonyeva *et al.*, 2021). 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 (Menéndez & Gutiérrez, 2004; Dortel *et al.*, 2013; Menéndez *et al.*, 2014;

Cuesta & Lobo, 2019; Cuesta *et al.*, 2021). 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 (Lobo, 2001; Carpaneto *et al.*, 2007; Nichols *et al.*, 2007, 2009; Batilani-Filho & Hernández, 2017; Fuzessy *et al.*, 2021), 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; Verdú *et al.*, 2015, 2020; Martínez *et al.*, 2017; Numa *et al.*, 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 a 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 if 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 northwest of the Madrid Autonomous Community (Spain). A semi-open plot of 1.16 hectares 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 1,140 metres above sea level and at coordinates 40.73ºN, -3.96ºW (**Figure 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 (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, while summers are hot and dry (Rivas-Martínez, 1983). The average annual temperature is between 8ºC and 15ºC, although values of up to -7ºC have been recorded during the coldest months and 38ºC in the warmest (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 by being seasonal. The periods of greatest precipitation are associated with the autumn and spring months, while the driest period is associated with the summer months. Average annual rainfall records are usually around 700 millimetres (Meteoclimatic, 2020).

These climatic conditions determine the plant communities and the existing fauna in the study area. The predominant vegetation is a forest of holm oaks (*Quercus ilex* spp. *ballota* (Desf.) Samp.) and Pyrenean oaks (*Quercus pyrenaica* Willd.), frequently mixed with a landscape of pastures and bushes. In addition, pine forests of European red pine, accompanied by eagle fern (*Pteridium aquilinum* (L.) Kuhn) and Iberian silver-leaved broom (*Genista florida* L.) can be found. Among the bushes, the most representative are brooms, junipers, and rock roses. In the herbaceous stratum, grazing meadows predominate for livestock use (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 since the local dung beetle biodiversity could depend on their excrements. 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 by omnivorous excrements, 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).

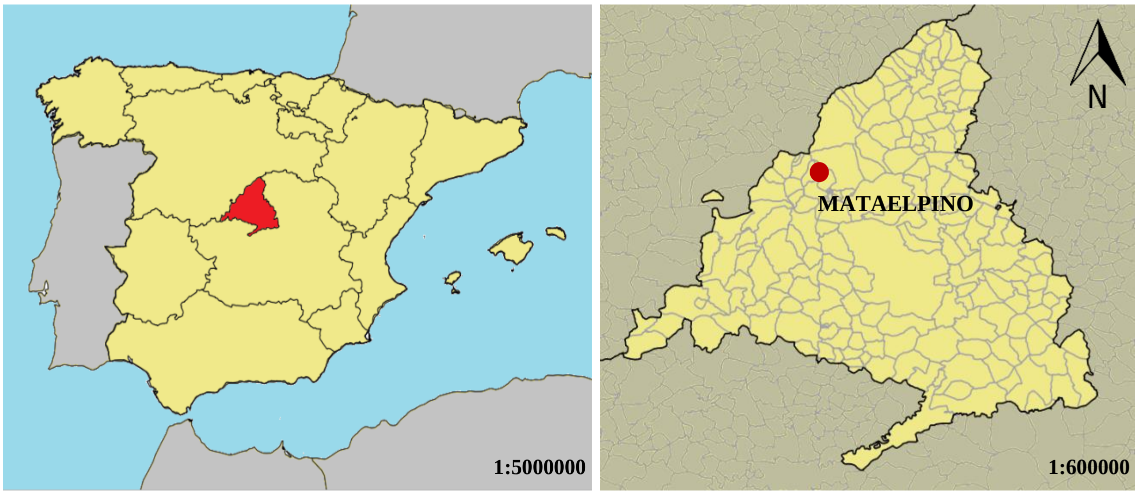

Figure 1. Location maps of the sampling area. The study was carried out in the town of Mataelpino, in the northwest of the Madrid Autonomous Community, Central Spain. The coordinates are 40.73ºN, -3.96ºW. Black or grey lines represent administrative boundaries.

Data collection

Samplings were 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 (References 10/065982.9/18 and 10/135977.9/20) for the entire sampling period. Although it was intended to carry out a 24-month study, the situation of sanitary confinement interrupted it for the last two months. The sampling consisted of 12 *pitfall* traps that were set and recollected monthly, following the method recommended by Lobo *et al.* (1988) and Veiga *et al.* (1989). The *pitfall* traps were evenly distributed throughout the sampling area, with a minimum distance of 50m between each pair. The *pitfall* traps were baited with 250 grams 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 attracted dung beetles were collected after 72 hours. 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 kilometres in a straight line from the study area. It is located at an altitude of 945m.a.s.l. and at coordinates 40.72ºN, -3.92ºW. 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 (Veiga, 1998; Martín-Piera & López-Colón, 2000). Once dry-prepared, representatives of each species found in the samplings were incorporated into the UCME collection (Entomology Museum at the Complutense University, Madrid).

Analytical procedures

Analyses were performed to determine the influence of climatic and time-related variables on diversity patterns of dung beetles. They were conducted for all dung beetles as a whole (coprophagous Scarabaeoidea) and 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 in Chao & Jost (2015). Based on Hill numbers (Hill, 1973; Chao *et al.*, 2021, 2023), this method allows to quantify the species diversity of an assemblage by calculating continuous diversity profiles estimated as a function of *q*. The diversity profiles calculated are, among others, the potential species richness (q_0), the exponential Shannon index diversity, that 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 & Jost, 2015; Chao *et al.*, 2014, 2020, 2021, 2023). 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 packages *SpadeR version 0.1.1* with the *Diversity* function to compute diversity estimates (Chao *et al.*, 2016). Diversity profiles, the observed abundance of individuals and the species richness obtained (R_0) from the field data were considered as 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 to humidity, 19 to atmospheric pressure and 2 time-related variables) (**Appendix, Table 3**). Temperature, humidity, and atmospheric pressure related variables have been obtained directly from the raw data provided by the meteorological station. Those variables considered cyclical, such as the time-related ones, were transformed into both sine and cosine (each day represents a portion of the complete 360º circular range) (Cuesta *et al.*, 2021; Lobo & Cuesta, 2021). Due to the possibility that dung beetle communities may be different 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 (McCullagh & Nelder, 1989; Crawley, 1993). 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 of each selected variable increased the explanatory capacity of the model (Dobson, 1999). In cases in 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 of the obtained models was measured using the deviance statistic and the change in deviance was tested using the F-ratio test (McCullagh & Nelder, 1989; Dobson 1999) 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 (Borcard *et al.*, 1992; Qinghong & Brakenhielm, 1995; Anderson & Gribble, 1998; Legendre & Legendre, 1998) and hierarchical decomposition (MacNally, 2000). This allowed to estimate how much of the variation of the response variable can be exclusively attributed 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 version 4.2.1 (R Core Team, 2022) and the STATISTICA package version 10 (StatSoft Inc, 2011).

Results

In total, 59,264 dung beetles belonging to 46 species were collected (**Appendix. Table 1**). Twenty-four species and 52,959 individuals of the subfamily Aphodiinae, 18 species and 6,216 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 2** and in **Figure 2**, respectively. Likewise, the values of the abundance of individuals (Ab) and the species richness obtained (R_0) from the field data were graphically represented over time (**Figure 2**). In general, it can be observed that species richness reaches its maximum during the spring months, with some peaks in the autumn months, while in summer and winter it reaches its minimum. 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 certain 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 2**). As a whole (coprophagous Scarabaeoidea), the dung beetle community is well represented, having found more than 78% of extant species in the study area. Geotrupinae was the best represented, having found all possible species for the study area. Then, it was followed by Scarabaeinae with a representation of 94.74% and Aphodiinae with a 75.00% representation.

The results of the Spearman's correlation analyse, used to determine the degree of relationship among all the ecological variables and within each set have been explored (**Appendix**. **Table 4**). In general, it can be observed that the relationships among the variables included within the same set of variables present high positive correlations, while correlations among sets of variables, if present, are usually negative.

The results of the GLMs analysis have shown the independent variables that exert an effect on 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 the data of 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 5**).

According to the results, 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 analysing the R_0 in Geotrupinae, where temperature variables explain up to 64.15% of the deviance. In the case of 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 the dung beetles as a whole (coprophagous Scarabaeoidea) are taken into account, 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). In Aphodiinae, atmospheric variables are responsible for explaining 24.83% and 20.32% of the deviance in q_1 and q_2, respectively. 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 of 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 deviances observed in q_0, q_1, q_2 and R_0, respectively.

When a single group of variables is able to explain 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. The latter 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, respectively. Besides, it should be noted that practically none of the ecological variables has had an effect on the abundance of dung beetles, except in 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 (**Figure 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 it 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 the atmospheric pressure variables (1.33% for q_1 and 5.51% for q_2) and the combined effect of the atmospheric pressure variables and those time-related ones (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 of dung beetle diversity when the minimum pressure also increases during the warm months of the year (**Figure 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 (28.44% for R_0) (**Figure 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 abundance, there is a 17.88% of deviance explained by the pure effect of the time-related variables, a 20.62% by the pure effect of the humidity variables and a 9.03% by the combined effect of both groups of variables. For R_0, there is a percentage of the deviance explained by both the pure and 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%) (**Figure 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, while 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 favoured at times of the year associated with rains, such as the autumn months, and when there are no large fluctuations in humidity levels (**Figure 4**).

In Scarabaeinae, the pure and combined effects of the different groups of variables explain a part of the observed deviance. In almost all cases, the pure effects of the time-related variables turned out to be the ones 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) (**Figure 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, while humidity and atmospheric pressure related variables have the opposite effect. When the combined effect between humidity and temperature related variables was studied, an interaction between these independent variables was observed. It was observed that Scarabaeinae species richness is greater when the maximum humidity values were low and the maximum temperature values were high (**Figure 4**).

	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%	-

Table 1. Results of GLMs analysis. Data of F ($_{1,19}$) statistic with a significant p-value ($p<0.05$) and explained variance (R^2) for sets of variables are shown. Dependant 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 refers 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.

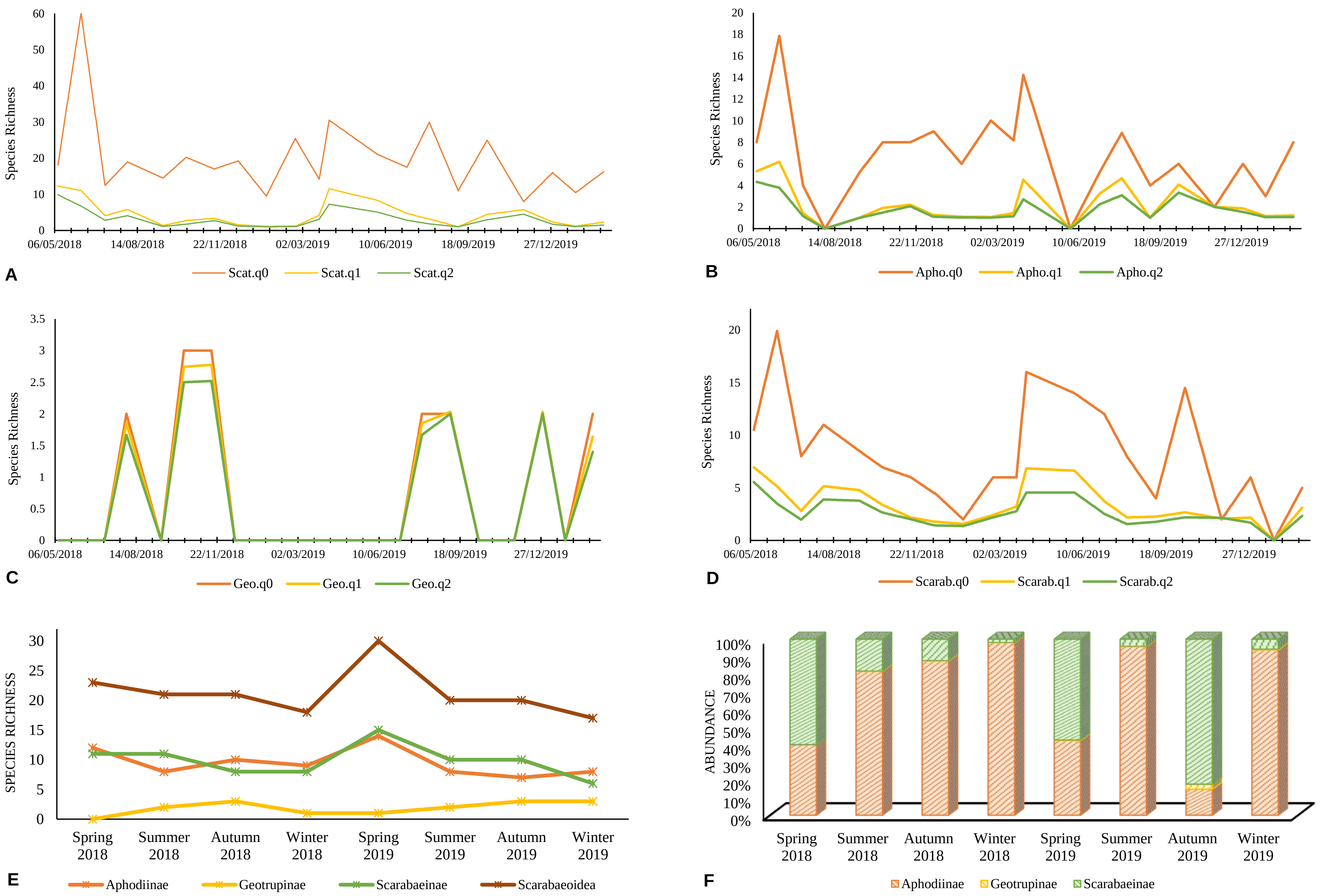

Figure 2. Representation of the estimation method. The dung beetles were considered as a whole (coprophagous Scarabaeoidea (**A**)) and by subfamilies separately (Aphodiinae (**B**), Geotrupinae (**C**) and Scarabaeinae (**D**)). Diversity profiles are potential species richness (q_0), exponential Shannon 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.).

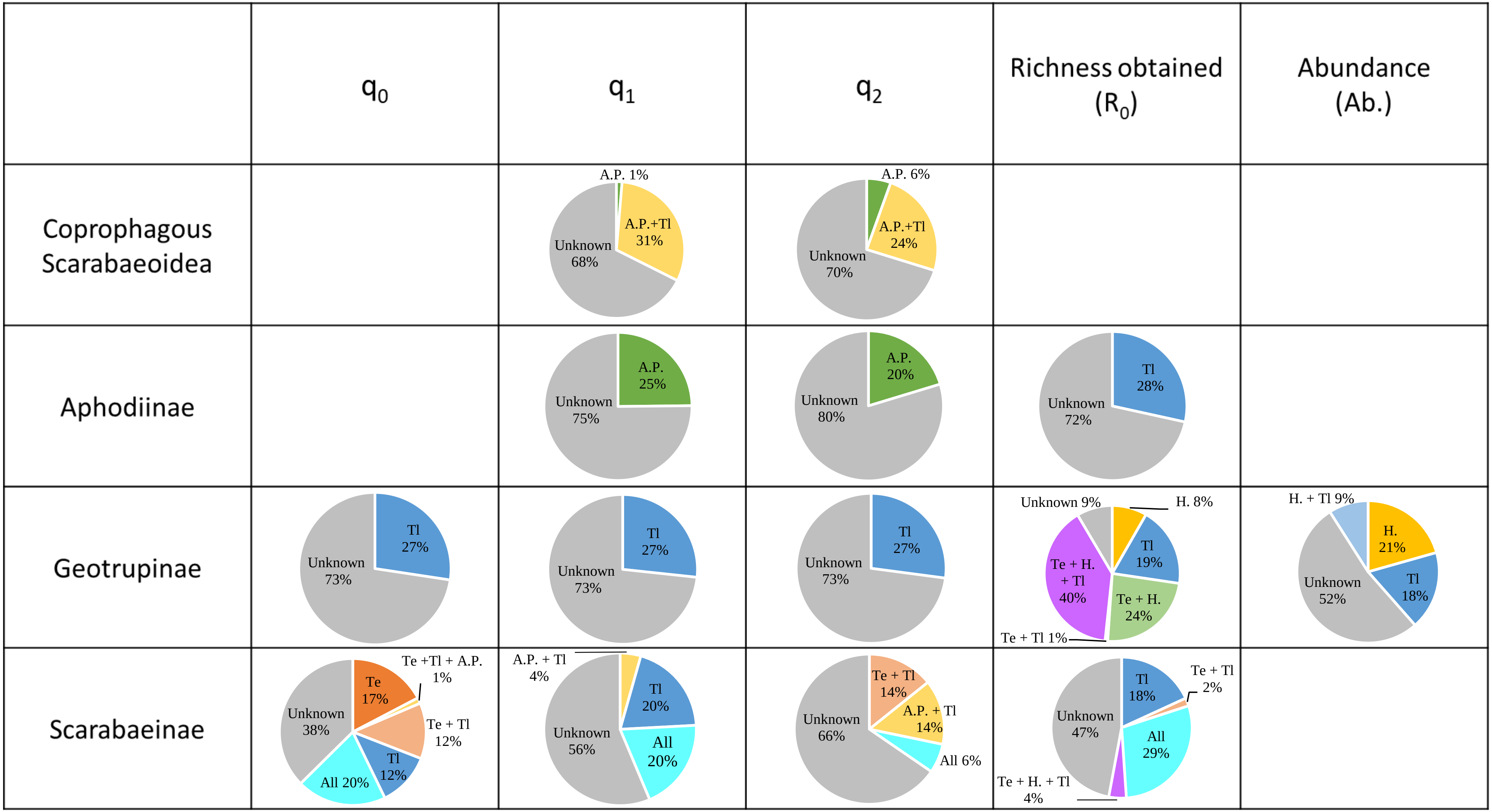

Figure 3. Results of the variation partitioning analysis. The significant independent variables were studied to determine their effect on dependent variables. The percentages of pure and combined effects of the variables are shown. Abbreviations: temperature related variables (Te), humidity related variables (H.), atmospheric pressure related variables (A.P.), and time-related variables (Tl). The variance not explained by the ecological factors is shown in grey (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 2.

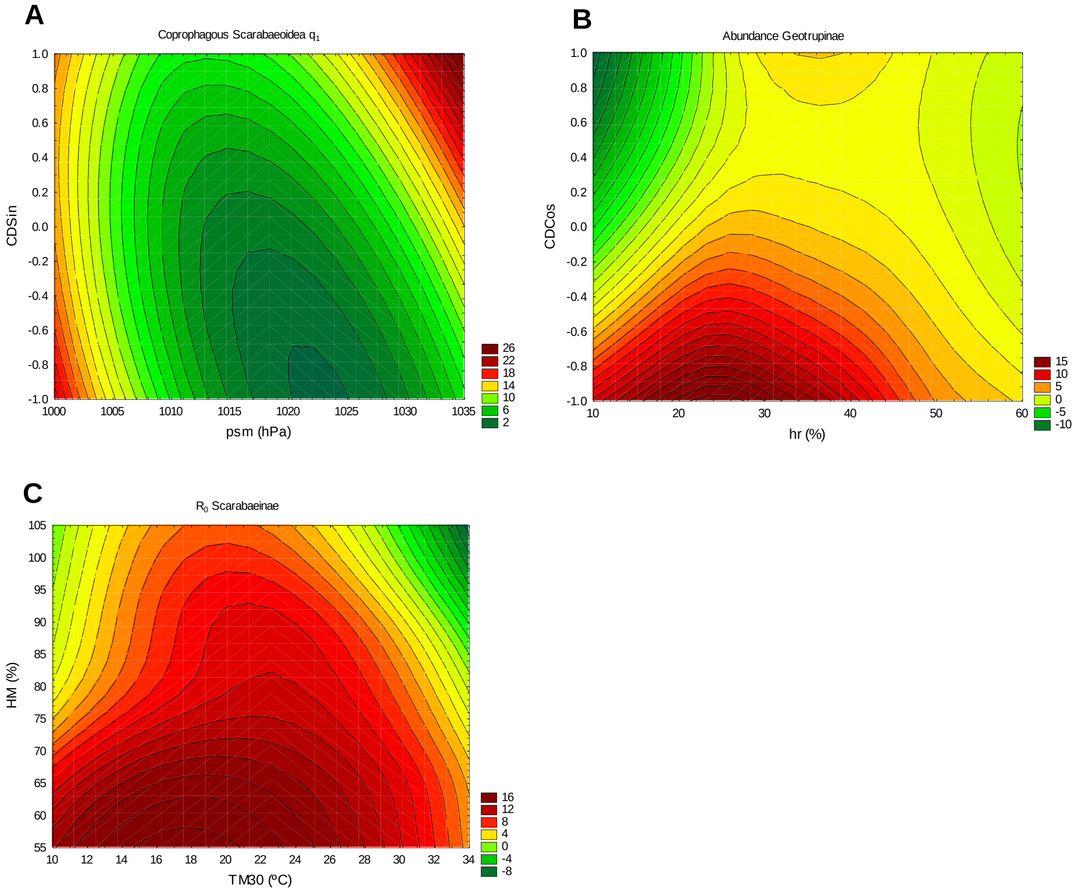

Figure 4. Contour-plots of the dung beetle diversity predicted. These predictions are due to the interactions between two selected independent variables. In coprophagous Scarabaeoidea, there is an increase of q_1 when psm also increases during the warm months of the year (A). In Geotrupinae, the abundance is associated with autumn months and when 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 *versus* negative scores are represented in a red to green gradient.

Discussion

The results of the study showed that climatic and time-related variables exert an effect on the diversity patterns of Mataelpino dung beetle community. The different groups of variables studied have managed to explain part 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 thanks to 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, while 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 (Lobo, 1982; Lumaret & Kirk, 1987, 1991; Jay-Roberts *et al.*, 2008a; Agoglitta *et al.*, 2012; Senyüz *et al.*, 2019). However, if the subfamilies are studied separately, clear differences can be noticed 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 and R_0, suggesting that the greatest diversity of Aphodiinae species can be found in the autumn months. Being dwellers inside excrements makes them vulnerable to the droughts and frosts typical of the summer and winter months respectively (Lumaret, 1995; Jay-Roberts *et al.*, 2008a). Therefore, there was a reduction in its 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 suggests that the highest Scarabaeinae species richness will be found mainly in the summer months. This coincides with other studies in which it was seen that the members of this subfamily were more active in the summer period, since they are well adapted to warm conditions, being practically absent during the winter (Jay-Roberts *et al.*, 2008a; Errouissi *et al.*, 2009). They overcome droughts by burying the dung in the ground, preventing it from desiccation (Jay-Roberts *et al.*, 2008a; Labidi *et al.*, 2012).

In Geotrupinae, the peak of greatest activity occurs at the end of the year, especially in the autumn months (Lumaret & Kirk, 1987; Errouissi *et al.*, 2004, 2009; Jay-Roberts *et al.*, 2008a). Their strategy is to come out and breed after the first autumn rains, to survive the 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 due to these two 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 so that their larvae can 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 the rainy periods (spring and autumn) (Lumaret & Kirk, 1991; Senyüz *et al.*, 2019). These 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 has turned out to be the only variable of the atmospheric pressure group that has influenced on 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 have turned out to be *Anomius castaneus* (Illiger, 1803), *Melinopterus sphacelatus* (Panzer, 1798) and *Nimbus contaminatus* (Herbst, 1783), which have a markedly autumnal phenology (Veiga, 1998; Agoiz-Bustamante, 2008; Errouissi *et al.*, 2009). 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 (Lumaret & Kirk, 1991; Lobo & Halffter, 2000; Martín-Piera & López-Colón, 2000; Mena, 2001; Errouissi *et al.*, 2004).

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 (Lumaret & Kirk, 1991; Martín-Piera & López-Colón, 2000; Errouissi *et al.*, 2004, 2009; Jay-Roberts *et al.*, 2008a). 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 due to them since 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 (Lumaret & Kirk, 1987, 1991; Lobo *et al.*, 2002; Errouissi *et al.*, 2004, 2009; Numa *et al.*, 2012; Dortel *et al.*, 2013; Ferreira *et al.*, 2018; Ambrozova *et al.*, 2022). However, in this study they have turned out to be the least relevant since they have only had effects on 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 (Lumaret & Kirk, 1991; Lobo & Halffter, 2000; Errouissi *et al.*, 2004; Jay-Roberts *et al.*, 2008b; Cabrero-Sañudo & Lobo, 2009).

The results showed that Scarabaeinae diversity were 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 and TM15 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 central hours 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, showed this pattern (Lumaret & Kirk, 1987; Ávila & Pascual, 1988; Mena *et al.*, 1989; Martín-Piera & López-Colón, 2000). Even other species that have not been so representative, such as *Onthophagus lemur* (Fabricius, 1781), *Onthophagus taurus* (Schreber, 1759) or *Onthophagus vacca* (Linnaeus, 1767) are also thermophiles (Lumaret & Kirk, 1987; Ávila & Pascual, 1988; Baz, 1988; Mena *et al.*, 1989; Wassmer, 1995; Martín-Piera & López-Colón, 2000).

In 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 the

Geotrupinae species, since they usually appear after the spring and autumn rains (Lumaret & Kirk, 1991; Lobo & Halffter, 2000; Martín-Piera & López-Colón, 2000; Mena, 2001; Errouissi *et al.*, 2004). As previously mentioned, it is possible that the occurrence of two species with different ecological requirements from the rest of Geotrupinae is interfering in 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 CDCos and PsM variables were expected to have greater importance, since Aphodiinae was the most representative subfamily, both in terms of 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, since there are mixed responses that could sometimes even be contradictory. Therefore, it is better to consider the effects of variables by analysing 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 due to the heterogeneity of the data collected for Aphodiinae and Scarabaeinae, since there were months in which outbreaks of certain species occurred and the number of individuals collected considerably exceeded the values of the 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 (Martín-Piera *et al.*, 1992; Jay-Robert *et al.*, 1997, 2008a; Errouissi *et al.*, 2004; Labidi *et al.*, 2012) or habitat type (Halffter & Edmonds, 1982; Lumaret & Kirk, 1987; Martín-Piera *et al.*, 1992; Jay-Roberts *et al.*, 2008b) 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 (Lumaret & Kirk, 1987; Martín-Piera *et al.*, 1992; Jay-Roberts *et al.*, 2008b). 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 & Matthews, 1966; Halffter & Edmonds, 1982), 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 taken into account that they have their limitations and that the factors studied will not be the only ones responsible for the observed diversity.

Conclusions

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, finding 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 taken into account that there are other factors, both ecological and historical, which have not been taken into account 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 a part of these results.

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Appendix

Table 1. 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)	5,807
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	1,613
Onthophagus punctatus (Illiger, 1803)	1
Onthophagus similis (Scriba, 1790)	2,521
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 2. 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 Ratio**
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 3. List of the 60 ecological variables included in the study. The variables are grouped into 4 sets based on their similarities: temperature, humidity, atmospheric pressure and time-related ones. The time-related variables were analysed using circular statistics (Cuesta *et al.*, 2021; Lobo & Cuesta, 2021).

Independent variables	Abbreviations	Description/Formulas
TEMPERATURE		
Maximum temperature of the day	TM	Raw data from the weather station
Minimum 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
Three-day average maximum temperature	TM3	(Sum(maximum temperature of the first 3 days)/3)
Seven-day average maximum temperature	TM7	(Sum(maximum temperature of the first 7 days)/7)
Ten-day average maximum temperature	TM10	(Sum(maximum temperature of the first 10 days)/10)
Fifteen-day average maximum temperature	TM15	(Sum(maximum temperature of the first 15 days)/15)
Thirty-day average maximum temperature	TM30	(Sum(maximum temperature of the first 30 days)/30)
Three-day average minimum temperature	tm3	(Sum(minimum temperature of the first 3 days)/3)
Seven-day average minimum temperature	tm7	(Sum(minimum temperature of the first 7 days)/7)
Ten-day average minimum temperature	tm10	(Sum(minimum temperature of the first 10 days)/10)
Fifteen-day average minimum temperature	tm15	(Sum(minimum temperature of the first 15 days)/15)
Thirty-day average minimum temperature	tm30	(Sum(minimum 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 minimum temperature	tmAM	Raw data from the weather station
Monthly absolute maximum temperature	TMAM	Raw data from the weather station
HUMIDITY		
Maximum humidity of the day	HM	Raw data from the weather station
Minimum 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
Three-day average maximum humidity	HM3	(Sum(maximum humidity of the first 3 days)/3)
Seven-day average maximum humidity	HM7	(Sum(maximum humidity of the first 7 days)/7)
Ten-day average maximum humidity	HM10	(Sum(maximum humidity of the first 10 days)/10)
Fifteen-day average maximum humidity	HM15	(Sum(maximum humidity of the first 15 days)/15)
Thirty-day average maximum humidity	HM30	(Sum(maximum humidity of the first 30 days)/30)
Three-day average minimum humidity	hm3	(Sum(minimum humidity of the first 3 days)/3)
Seven-day average minimum humidity	hm7	(Sum(minimum humidity of the first 7 days)/7)
Ten-day average minimum humidity	hm10	(Sum(minimum humidity of the first 10 days)/10)
Fifteen-day average minimum humidity	hm15	(Sum(minimum humidity of the first 15 days)/15)

Thirty-day average minimum humidity	hm30	(Sum(minimum 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
Monthly absolute minimum humidity	hmAM	Raw data from the weather station
Monthly absolute maximum 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		
Maximum pressure of the day	PsM	Raw data from the weather station
Minimum 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
Three-day average maximum pressure	PsM3	(Sum(maximum pressure of the first 3 days)/3)
Seven-day average maximum pressure	PsM7	(Sum(maximum pressure of the first 7 days)/7)
Ten-day average maximum pressure	PsM10	(Sum(maximum pressure of the first 10 days)/10)
Fifteen-day average maximum pressure	PsM15	(Sum(maximum pressure of the first 15 days)/15)
Thirty-day average maximum pressure	PsM30	(Sum(maximum pressure of the first 30 days)/30)
Three-day average minimum pressure	psm3	(Sum(minimum pressure of the first 3 days)/3)
Seven-day average minimum pressure	psm7	(Sum(minimum pressure of the first 7 days)/7)
Ten-day average minimum pressure	psm10	(Sum(minimum pressure of the first 10 days)/10)
Fifteen-day average minimum pressure	psm15	(Sum(minimum pressure of the first 15 days)/15)
Thirty-day average minimum pressure	psm30	(Sum(minimum 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 minimum pressure	psAm	Raw data from the weather station
Monthly absolute maximum pressure	PsAM	Raw data from the weather station
Wind	W	Raw data from the weather station
TIME-RELATED		
Collection day (SEN)	CDSin	Analysed with circular statistics
Collection day (COS)	CDCos	Analysed with circular statistics

Table 4. Results of the regression analysis using Spearman's correlation. The degree of relationship among all the environmental variables is shown. Each relationship receives a value between -1 and 1, where values greater than 0 indicate a positive relationship between the variables, values close to 0 indicate that there is no association between the variables, and values less than 0 indicate a negative relationship.

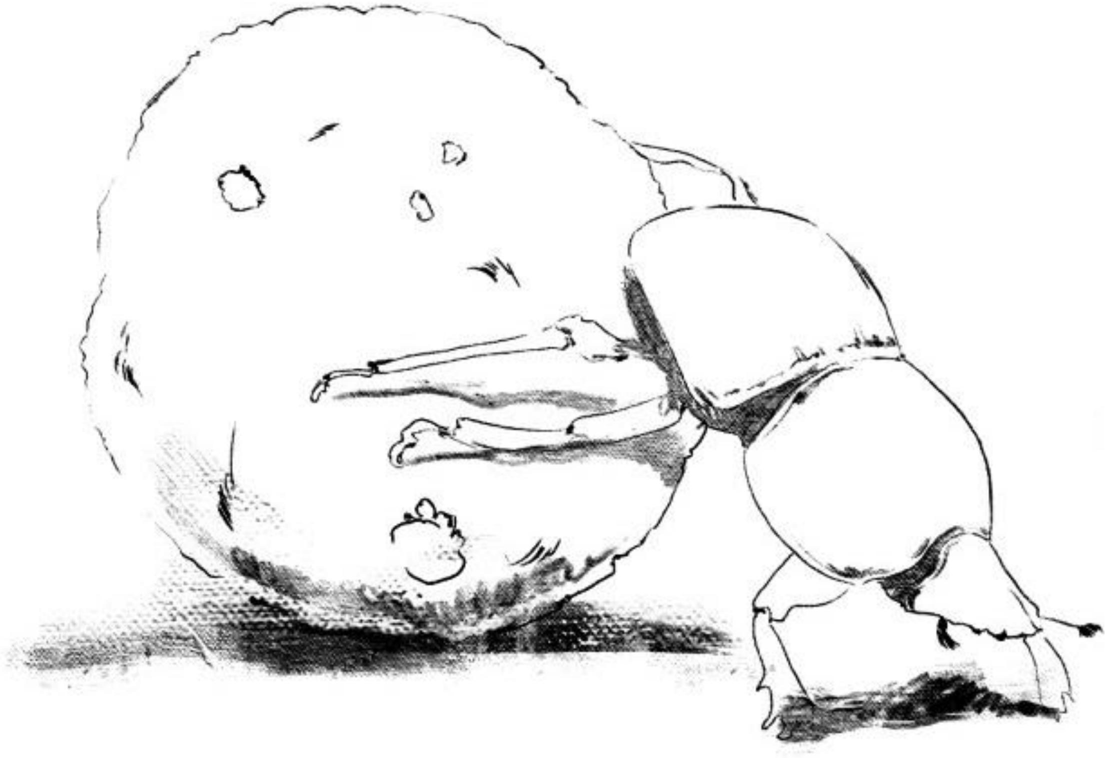
	TM	tm	td	tr	HM	hm	hd	hr	PsM	psm	psd	psr	W	Pp	TM3	TM7	TM10	TM15	TM30	tm3	tm7	tm10	tm15	tm30	taM	taRat	HM3	HM7	HM10	HM15	HM30	HMAM	hmAM	hm3	hm7	hm10	hm15	hm30	haM	haRat	PsM3	PsM7	PsM10	PsM15	PsM30	PsAM	psAm	psm3	psm7	psm10	psm15	psm30	psaM	psaRat	PpaM	PpaRat	tmAM	TMAM	CDSin	CDCos
TM	1.00	0.81	0.97	0.76	-0.66	-0.63	-0.67	0.36	-0.42	-0.25	-0.34	-0.45	-0.50	-0.14	0.94	0.91	0.89	0.89	0.89	0.82	0.86	0.86	0.88	0.85	0.89	0.53	-0.66	-0.58	-0.57	-0.60	-0.68	-0.53	-0.46	-0.73	-0.67	-0.64	-0.67	-0.74	-0.74	-0.25	-0.35	-0.66	-0.71	-0.78	-0.79	-0.85	0.06	-0.15	-0.53	-0.55	-0.64	-0.68	-0.74	0.30	-0.67	-0.14	0.87	0.86	0.79	-0.46
tm	0.81	1.00	0.93	0.23	-0.43	-0.17	-0.28	-0.17	-0.67	-0.54	-0.61	-0.35	-0.30	0.18	0.77	0.75	0.76	0.79	0.83	0.91	0.86	0.84	0.86	0.87	0.87	0.46	-0.41	-0.46	-0.49	-0.53	-0.56	-0.42	-0.20	-0.34	-0.34	-0.38	-0.48	-0.58	-0.57	0.11	-0.63	-0.83	-0.86	-0.87	-0.86	-0.85	0.08	-0.52	-0.78	-0.76	-0.78	-0.78	-0.83	0.08	-0.79	0.18	0.87	0.79	0.64	-0.66
td	0.97	0.93	1.00	0.57	-0.60	-0.47	-0.54	0.15	-0.55	-0.39	-0.47	-0.43	-0.44	-0.01	0.92	0.89	0.88	0.89	0.91	0.90	0.90	0.89	0.91	0.90	0.92	0.52	-0.58	-0.55	-0.56	-0.60	-0.66	-0.51	-0.37	-0.60	-0.56	-0.56	-0.63	-0.71	-0.71	-0.11	-0.48	-0.77	-0.81	-0.86	-0.86	-0.89	0.07	-0.31	-0.66	-0.66	-0.73	-0.75	-0.81	0.22	-0.75	-0.01	0.91	0.87	0.77	-0.57
tr	0.76	0.23	0.57	1.00	-0.62	-0.87	-0.81	0.79	0.05	0.18	0.12	-0.36	-0.50	-0.43	0.70	0.67	0.64	0.61	0.55	0.34	0.46	0.49	0.50	0.44	0.51	0.37	-0.64	-0.45	-0.40	-0.42	-0.51	-0.41	-0.54	-0.84	-0.74	-0.64	-0.58	-0.59	-0.60	-0.55	0.13	-0.17	-0.21	-0.32	-0.36	-0.47	0.01	0.33	-0.01	-0.06	-0.18	-0.27	-0.31	0.41	-0.24	-0.43	0.47	0.55	0.60	-0.02
HM	-0.66	-0.43	-0.60	-0.62	1.00	0.82	0.93	-0.31	0.37	0.26	0.32	0.29	0.14	0.35	-0.69	-0.68	-0.69	-0.61	-0.55	-0.51	-0.52	-0.54	-0.53	-0.44	-0.52	-0.35	0.74	0.75	0.72	0.71	0.73	0.72	0.44	0.76	0.74	0.71	0.64	0.64	0.72	0.60	0.19	0.34	0.39	0.45	0.49	0.48	0.19	0.06	0.26	0.31	0.38	0.47	0.49	-0.09	0.46	0.35	-0.57	-0.44	-0.61	0.03
hm	-0.63	-0.17	-0.47	-0.87	0.82	1.00	0.97	-0.80	0.09	-0.03	0.03	0.34	0.27	0.58	-0.60	-0.58	-0.56	-0.50	-0.43	-0.31	-0.40	-0.42	-0.43	-0.34	-0.40	-0.37	0.64	0.50	0.43	0.43	0.53	0.49	0.37	0.79	0.68	0.60	0.52	0.53	0.57	0.79	-0.04	0.18	0.24	0.32	0.38	0.43	0.25	-0.17	0.08	0.15	0.24	0.35	0.36	-0.29	0.33	0.58	-0.40	-0.41	-0.57	-0.10
hd	-0.67	-0.28	-0.54	-0.81	0.93	0.97	1.00	-0.64	0.21	0.09	0.15	0.33	0.23	0.51	-0.67	-0.65	-0.64	-0.57	-0.50	-0.40	-0.47	-0.49	-0.49	-0.40	-0.47	-0.38	0.71	0.63	0.56	0.56	0.64	0.61	0.41	0.81	0.74	0.67	0.59	0.60	0.66	0.75	0.05	0.25	0.31	0.39	0.44	0.47	0.24	-0.08	0.16	0.22	0.31	0.41	0.43	-0.23	0.40	0.51	-0.49	-0.44	-0.62	-0.05
hr	0.36	-0.17	0.15	0.79	-0.31	-0.80	-0.64	1.00	0.23	0.31	0.27	-0.25	-0.29	-0.60	0.28	0.24	0.20	0.19	0.14	-0.01	0.11	0.14	0.16	0.10	0.13	0.24	-0.28	-0.05	0.04	0.03	-0.11	-0.06	-0.15	-0.51	-0.36	-0.24	-0.19	-0.20	-0.19	-0.68	0.25	0.07	0.01	-0.06	-0.12	-0.20	-0.21	0.34	0.15	0.08	0.00	-0.09	-0.09	0.39	-0.07	-0.60	0.08	0.23	0.30	0.19
PsM	-0.42	-0.67	-0.55	0.05	0.37	0.09	0.21	0.23	1.00	0.94	0.98	0.14	-0.19	0.07	-0.50	-0.48	-0.48	-0.52	-0.56	-0.71	-0.59	-0.56	-0.57	-0.57	-0.57	-0.04	0.26	0.40	0.43	0.49	0.51	0.38	0.03	0.19	0.24	0.31	0.43	0.50	0.51	-0.13	0.84	0.80	0.77	0.68	0.59	0.65	-0.17	0.74	0.77	0.71	0.61	0.52	0.59	0.55	0.56	0.07	-0.62	-0.50	-0.59	0.33
psm	-0.25	-0.54	-0.39	0.18	0.26	-0.03	0.09	0.31	0.94	1.00	0.98	-0.22	-0.42	0.07	-0.34	-0.34	-0.35	-0.37	-0.41	-0.56	-0.42	-0.39	-0.39	-0.41	-0.42	0.08	0.12	0.28	0.31	0.37	0.37	0.27	-0.01	0.07	0.17	0.23	0.33	0.36	0.36	-0.16	0.81	0.67	0.61	0.51	0.45	0.48	-0.15	0.75	0.66	0.55	0.44	0.39	0.45	0.68	0.42	0.07	-0.46	-0.37	-0.48	0.23
psd	-0.34	-0.61	-0.47	0.12	0.32	0.03	0.15	0.27	0.98	0.98	1.00	-0.04	-0.31	0.07	-0.42	-0.41	-0.42	-0.45	-0.49	-0.64	-0.52	-0.48	-0.48	-0.50	-0.50	0.02	0.20	0.35	0.38	0.44	0.45	0.33	0.01	0.13	0.21	0.27	0.39	0.44	0.44	-0.15	0.84	0.74	0.70	0.61	0.53	0.57	-0.16	0.76	0.73	0.64	0.53	0.46	0.53	0.63	0.50	0.07	-0.55	-0.44	-0.54	0.28
psr	-0.45	-0.35	-0.43	-0.36	0.29	0.34	0.33	-0.25	0.14	-0.22	-0.04	1.00	0.66	0.02	-0.44	-0.38	-0.36	-0.40	-0.40	-0.41	-0.45	-0.46	-0.47	-0.41	-0.42	-0.32	0.39	0.32	0.33	0.33	0.39	0.31	0.10	0.36	0.18	0.19	0.27	0.38	0.39	0.08	0.05	0.33	0.42	0.44	0.38	0.44	-0.03	-0.05	0.30	0.42	0.45	0.37	0.37	-0.38	0.35	0.02	-0.41	-0.35	-0.29	0.27
W	-0.50	-0.30	-0.44	-0.50	0.14	0.27	0.23	-0.29	-0.19	-0.42	-0.31	0.66	1.00	-0.09	-0.36	-0.33	-0.28	-0.29	-0.28	-0.28	-0.33	-0.33	-0.34	-0.30	-0.30	-0.66	0.12	0.04	0.04	0.03	0.13	0.13	0.19	0.28	0.16	0.10	0.10	0.22	0.20	0.11	-0.11	0.17	0.22	0.33	0.35	0.32	0.09	-0.24	0.07	0.14	0.29	0.33	0.33	-0.64	0.30	-0.09	-0.24	-0.27	-0.31	0.10
Pp	-0.14	0.18	-0.01	-0.43	0.35	0.58	0.51	-0.60	0.07	0.07	0.07	0.02	-0.09	1.00	-0.16	-0.09	-0.04	0.01	0.11	0.03	-0.04	-0.06	-0.01	0.09	0.10	-0.17	0.21	0.04	-0.05	-0.04	0.00	0.05	0.00	0.36	0.18	0.07	0.02	-0.03	0.01	0.72	-0.20	-0.11	-0.02	0.02	0.07	0.10	0.17	-0.23	-0.16	-0.05	0.01	0.08	0.08	0.01	0.08	1.00	0.09	-0.01	-0.16	-0.26
TM3	0.94	0.77	0.92	0.70	-0.69	-0.60	-0.67	0.28	-0.50	-0.34	-0.42	-0.44	-0.36	-0.16	1.00	0.98	0.97	0.96	0.92	0.85	0.88	0.88	0.89	0.86	0.92	0.32	-0.76	-0.68	-0.67	-0.72	-0.76	-0.56	-0.58	-0.83	-0.77	-0.75	-0.78	-0.79	-0.80	-0.18	-0.36	-0.63	-0.67	-0.73	-0.75	-0.84	0.18	-0.14	-0.48	-0.50	-0.58	-0.62	-0.70	0.17	-0.62	-0.16	0.91	0.87	0.77	-0.50
TM7	0.91	0.75	0.89	0.67	-0.68	-0.58	-0.65	0.24	-0.48	-0.34	-0.41	-0.38	-0.33	-0.09	0.98	1.00	0.99	0.98	0.93	0.86	0.89	0.88	0.89	0.86	0.92	0.27	-0.79	-0.73	-0.71	-0.74	-0.77	-0.60	-0.57	-0.82	-0.81	-0.78	-0.80	-0.81	-0.82	-0.14	-0.38	-0.62	-0.64	-0.70	-0.73	-0.82	0.18	-0.16	-0.48	-0.46	-0.54	-0.60	-0.68	0.16	-0.60	-0.09	0.92	0.86	0.79	-0.48
TM10	0.89	0.76	0.88	0.64	-0.69	-0.56	-0.64	0.20	-0.48	-0.35	-0.42	-0.36	-0.28	-0.04	0.97	0.99	1.00	0.99	0.95	0.86	0.89	0.89	0.90	0.86	0.93	0.21	-0.81	-0.77	-0.76	-0.78	-0.80	-0.65	-0.58	-0.81	-0.82	-0.80	-0.82	-0.82	-0.84	-0.10	-0.39	-0.63	-0.63	-0.68	-0.71	-0.80	0.22	-0.18	-0.48	-0.45	-0.51	-0.57	-0.65	0.12	-0.57	-0.04	0.93	0.86	0.77	-0.50
TM15	0.89	0.79	0.89	0.61	-0.61	-0.50	-0.57	0.19	-0.52	-0.37	-0.45	-0.40	-0.29	0.01	0.96	0.98	0.99	1.00	0.97	0.88	0.90	0.90	0.92	0.90	0.96	0.18	-0.76	-0.73	-0.73	-0.77	-0.80	-0.63	-0.55	-0.76	-0.77	-0.77	-0.82	-0.83	-0.84	-0.02	-0.44	-0.68	-0.67	-0.70	-0.72	-0.83	0.26	-0.22	-0.53	-0.49	-0.53	-0.57	-0.66	0.09	-0.57	0.01	0.95	0.89	0.77	-0.55
TM30	0.89	0.83	0.91	0.55	-0.55	-0.43	-0.50	0.14	-0.56	-0.41	-0.49	-0.40	-0.28	0.11	0.92	0.93	0.95	0.97	1.00	0.90	0.91	0.90	0.93	0.94	0.99	0.17	-0.70	-0.68	-0.69	-0.75	-0.81	-0.62	-0.51	-0.65	-0.67	-0.68	-0.76	-0.84	-0.84	0.08	-0.50	-0.73	-0.72	-0.73	-0.73	-0.85	0.29	-0.30	-0.60	-0.56	-0.58	-0.59	-0.67	0.07	-0.59	0.11	0.97	0.94	0.73	-0.63
tm3	0.82	0.91	0.90	0.34	-0.51	-0.31	-0.40	-0.01	-0.71	-0.56	-0.64	-0.41	-0.28	0.03	0.85	0.86	0.86	0.88	0.90	1.00	0.97	0.95	0.95	0.93	0.93	0.30	-0.58	-0.60	-0.58	-0.63	-0.70	-0.58	-0.32	-0.47	-0.46	-0.47	-0.56	-0.68	-0.69	0.06	-0.65	-0.85	-0.85	-0.84	-0.84	-0.89	0.20	-0.48	-0.75	-0.71	-0.72	-0.73	-0.80	0.01	-0.74	0.03	0.94	0.85	0.71	-0.64
tm7	0.86	0.86	0.90	0.46	-0.52	-0.40	-0.47	0.11	-0.59	-0.42	-0.52	-0.45	-0.33	-0.04	0.88	0.89	0.89	0.90	0.91	0.97	1.00	0.99	0.99	0.94	0.94	0.30	-0.65	-0.61	-0.57	-0.60	-0.68	-0.58	-0.37	-0.55	-0.49	-0.46	-0.54	-0.66	-0.67	-0.03	-0.53	-0.79	-0.81	-0.83	-0.83	-0.91	0.21	-0.35	-0.68	-0.68	-0.71	-0.72	-0.79	0.15	-0.72	-0.04	0.95	0.88	0.72	-0.65
tm10	0.86	0.84	0.89	0.49	-0.54	-0.42	-0.49	0.14	-0.56	-0.39	-0.48	-0.46	-0.33	-0.06	0.88	0.88	0.89	0.90	0.90	0.95	0.99	1.00	0.99	0.94	0.93	0.27	-0.67	-0.62	-0.57	-0.60	-0.68	-0.59	-0.39	-0.57	-0.50	-0.46	-0.53	-0.64	-0.67	-0.07	-0.49	-0.76	-0.80	-0.82	-0.82	-0.90	0.23	-0.31	-0.65	-0.67	-0.70	-0.70	-0.77	0.17	-0.71	-0.06	0.94	0.88	0.71	-0.64
tm15	0.88	0.86	0.91	0.50	-0.53	-0.43	-0.49	0.16	-0.57	-0.39	-0.48	-0.47	-0.34	-0.01	0.89	0.89	0.90	0.92	0.93	0.95	0.99	0.99	1.00	0.97	0.96	0.27	-0.65	-0.60	-0.56	-0.60	-0.68	-0.56	-0.36	-0.58	-0.51	-0.48	-0.55	-0.66	-0.68	-0.05	-0.52	-0.78	-0.82	-0.85	-0.85	-0.92	0.19	-0.34	-0.68	-0.69	-0.73	-0.73	-0.80	0.19	-0.74	-0.01	0.95	0.91	0.71	-0.67
tm30	0.85	0.87	0.90	0.44	-0.44	-0.34	-0.40	0.10	-0.57	-0.41	-0.50	-0.41	-0.30	0.09	0.86	0.86	0.86	0.90	0.94	0.93	0.94	0.94	0.97	1.00	0.98	0.22	-0.59	-0.54	-0.52	-0.58	-0.67	-0.49	-0.30	-0.51	-0.46	-0.45	-0.54	-0.62	-0.64	0.04	-0.55	-0.78	-0.82	-0.83	-0.85	-0.93	0.17	-0.41	-0.70	-0.70	-0.72	-0.75	-0.81	0.19	-0.75	0.09	0.93	0.96	0.61	-0.79
taM	0.89	0.87	0.92	0.51	-0.52	-0.40	-0.47	0.13	-0.57	-0.42	-0.50	-0.42	-0.30	0.10	0.92	0.92	0.93	0.96	0.99	0.93	0.94	0.93	0.96	0.98	1.00	0.21	-0.66	-0.63	-0.63	-0.69	-0.76	-0.58	-0.43	-0.61	-0.60	-0.60	-0.68	-0.76	-0.77	0.06	-0.53	-0.77	-0.78	-0.79	-0.80	-0.90	0.24	-0.35	-0.66	-0.63	-0.65	-0.67	-0.74	0.12	-0.67	0.10	0.97	0.96	0.70	-0.70
taRat	0.53	0.46	0.52	0.37	-0.35	-0.37	-0.38	0.24	-0.04	0.08	0.02	-0.32	-0.66	-0.17	0.32	0.27	0.21	0.18	0.17	0.30	0.30	0.27	0.27	0.22	0.21	1.00	0.03	0.04	0.06	0.06	-0.01	-0.07	0.05	-0.16	-0.06	-0.03	-0.01	-0.10	-0.08	-0.44	-0.03	-0.27	-0.36	-0.48	-0.52	-0.35	-0.53	0.01	-0.25	-0.33	-0.48	-0.58	-0.54	0.52	-0.55	-0.17	0.22	0.18	0.39	0.02
HM3	-0.66	-0.41	-0.58	-0.64	0.74	0.64	0.71	-0.28	0.26	0.12	0.20	0.39	0.12	0.21	-0.76	-0.79	-0.81	-0.76	-0.70	-0.58	-0.65	-0.67	-0.65	-0.59	-0.66	0.03	1.00	0.93	0.88	0.85	0.82	0.70	0.56	0.78	0.82	0.79	0.75	0.73	0.79	0.25	0.19	0.39	0.37	0.38	0.37	0.53	-0.29	0.01	0.26	0.25	0.25	0.26	0.32	-0.07	0.26	0.21	-0.68	-0.61	-0.51	0.31
HM7	-0.58	-0.46	-0.55	-0.45	0.75	0.50	0.63	-0.05	0.40	0.28	0.35	0.32	0.04	0.04	-0.68	-0.73	-0.77	-0.73	-0.68	-0.60	-0.61	-0.62	-0.60	-0.54	-0.63	0.04	0.93	1.00	0.98	0.95	0.89	0.84	0.54	0.64	0.79	0.82	0.80	0.79	0.85	0.09	0.34	0.47	0.40	0.36	0.33	0.45	-0.30	0.16	0.36	0.28	0.24	0.22	0.28	0.13	0.22	0.04	-0.68	-0.51	-0.53	0.23
HM10	-0.57	-0.49	-0.56	-0.40	0.72	0.43	0.56	0.04	0.43	0.31	0.38	0.33	0.04	-0.05	-0.67	-0.71	-0.76	-0.73	-0.69	-0.58	-0.57	-0.57	-0.56	-0.52	-0.63	0.06	0.88	0.98	1.00	0.98	0.90	0.83	0.56	0.62	0.78	0.84	0.85	0.83	0.87	-0.02	0.35	0.47	0.39	0.35	0.30	0.43	-0.34	0.18	0.37	0.28	0.22	0.18	0.25	0.19	0.19	-0.05	-0.68	-0.50	-0.51	0.24
HM15	-0.60	-0.53	-0.60	-0.42	0.71	0.43	0.56	0.03	0.49	0.37	0.44	0.33	0.03	-0.04	-0.72	-0.74	-0.78	-0.77	-0.75	-0.63	-0.60	-0.60	-0.60	-0.58	-0.69	0.06	0.85	0.95	0.98	1.00	0.94	0.84	0.60	0.64	0.79	0.86	0.88	0.88	0.92	-0.05	0.38	0.51	0.43	0.39	0.34	0.48	-0.36	0.21	0.41	0.31	0.26	0.22	0.30	0.22	0.23	-0.04	-0.74	-0.56	-0.55	0.29
HM30	-0.68	-0.56	-0.66	-0.51	0.73	0.53	0.64	-0.11	0.51	0.37	0.45	0.39	0.13	0.00	-0.76	-0.77	-0.80	-0.80	-0.81	-0.70	-0.68	-0.68	-0.68	-0.67	-0.76	-0.01	0.82	0.89	0.90	0.94	1.00	0.89	0.60	0.64	0.75	0.80	0.84	0.92	0.96	0.00	0.39	0.54	0.47	0.44	0.43	0.57	-0.31	0.22	0.43	0.34	0.30	0.30	0.38	0.15	0.31	0.00	-0.79	-0.67	-0.59	0.34
HMAM	-0.53	-0.42	-0.51	-0.41	0.72	0.49	0.61	-0.06	0.38	0.27	0.33	0.31	0.13	0.05	-0.56	-0.60	-0.65	-0.63	-0.62	-0.58	-0.58	-0.59	-0.56	-0.49	-0.58	-0.07	0.70	0.84	0.83	0.84	0.89	1.00	0.52	0.48	0.61	0.64	0.65	0.77	0.83	0.09	0.28	0.42	0.34	0.31	0.30	0.38	-0.21	0.13	0.32	0.23	0.20	0.21	0.27	0.12	0.22	0.05	-0.64	-0.44	-0.51	0.15
hmAM	-0.46	-0.20	-0.37	-0.54	0.44	0.37	0.41	-0.15	0.03	-0.01	0.01	0.10	0.19	0.00	-0.58	-0.57	-0.58	-0.55	-0.51	-0.32	-0.37	-0.39	-0.36	-0.30	-0.43	0.05	0.56	0.54	0.56	0.60	0.60	0.52	1.00	0.64	0.69	0.66	0.64	0.65	0.65	-0.04	-0.15	-0.01	-0.01	0.04	-0.01	0.12	-0.52	-0.41	-0.19	-0.18	-0.12	-0.16	-0.09	0.09	-0.17	0.00	-0.46	-0.39	-0.36	0.06
hm3	-0.73	-0.34	-0.60	-0.84	0.76	0.79	0.81	-0.51	0.19	0.07	0.13	0.36	0.28	0.36	-0.83	-0.82	-0.81	-0.76	-0.65	-0.47	-0.55	-0.57	-0.58	-0.51	-0.61	-0.16	0.78	0.64	0.62	0.64	0.64	0.48	0.64	1.00	0.91	0.84	0.78	0.69	0.71	0.44	-0.01	0.22	0.29	0.38	0.43	0.53	-0.08	-0.22	0.06	0.13	0.25	0.33	0.38	-0.20	0.31	0.36	-0.60	-0.59	-0.67	0.10
hm7	-0.67	-0.34	-0.56	-0.74	0.74	0.68	0.74	-0.36	0.24	0.17	0.21	0.18	0.16	0.18	-0.77	-0.81	-0.82	-0.77	-0.67	-0.46	-0.49	-0.50	-0.51	-0.46	-0.60	-0.06	0.82	0.79	0.78	0.79	0.75	0.61	0.69	0.91	1.00	0.97	0.91	0.82	0.83	0.24	0.14	0.27	0.22	0.27	0.30	0.42	-0.19	-0.10	0.10	0.03	0.09	0.17	0.24	0.01	0.16	0.18	-0.60	-0.52	-0.69	0.02
hm10	-0.64	-0.38	-0.56	-0.64	0.71	0.60	0.67	-0.24	0.31	0.23	0.27	0.19	0.10	0.07	-0.75	-0.78	-0.80	-0.77	-0.68	-0.47	-0.46	-0.46	-0.48	-0.45	-0.60	-0.03	0.79	0.82	0.84	0.86	0.80	0.64	0.66	0.84	0.97	1.00	0.97	0.87	0.87	0.12	0.20	0.32	0.24	0.26	0.28	0.40	-0.21	-0.01	0.16	0.06	0.08	0.15	0.22	0.10	0.14	0.07	-0.62	-0.51	-0.66	0.05
hm15	-0.67	-0.48	-0.63	-0.58	0.64	0.52	0.59	-0.19	0.43	0.33	0.39	0.27	0.10	0.02	-0.78	-0.80	-0.82	-0.82	-0.76	-0.56	-0.54	-0.53	-0.55	-0.54	-0.68	-0.01	0.75	0.80	0.85	0.88	0.84	0.65	0.64	0.78	0.91	0.97	1.00	0.93	0.92	-0.02	0.31	0.44	0.35	0.34	0.33	0.48	-0.31	0.09	0.28	0.16	0.15	0.18	0.27	0.19	0.18	0.02	-0.70	-0.58	-0.69	0.15
hm30	-0.74	-0.58	-0.71	-0.59	0.64	0.53	0.60	-0.20	0.50	0.36	0.44	0.38	0.22	-0.03	-0.79	-0.81	-0.82	-0.83	-0.84	-0.68	-0.66	-0.64	-0.66	-0.62	-0.76	-0.10	0.73	0.79	0.83	0.88	0.92	0.77	0.65	0.69	0.82	0.87	0.93	1.00	0.99	-0.06	0.39	0.55	0.45	0.44	0.40	0.56	-0.36	0.15	0.40	0.27	0.26	0.24	0.33	0.18	0.24	-0.03	-0.80	-0.65	-0.76	0.20
haM	-0.74	-0.57	-0.71	-0.60	0.72	0.57	0.66	-0.19	0.51	0.36	0.44	0.39	0.20	0.01	-0.80	-0.82	-0.84	-0.84	-0.84	-0.69	-0.67	-0.67	-0.68	-0.64	-0.77	-0.08	0.79	0.85	0.87	0.92	0.96	0.83	0.65	0.71	0.83	0.87	0.92	0.99	1.00	0.00	0.38	0.55	0.47	0.45	0.42	0.57	-0.32	0.16	0.41	0.30	0.29	0.28	0.36	0.16	0.28	0.01	-0.81	-0.66	-0.73	0.23
haRat	-0.25	0.11	-0.11	-0.55	0.60	0.79	0.75	-0.68	-0.13	-0.16	-0.15	0.08	0.11	0.72	-0.18	-0.14	-0.10	-0.02	0.08	0.06	-0.03	-0.07	-0.05	0.04	0.06	-0.44	0.25	0.09	-0.02	-0.05	0.00	0.09	-0.04	0.44	0.24	0.12	-0.02	-0.06	0.00	1.00	-0.24	-0.12	0.02	0.13	0.23	0.14	0.58	-0.23	-0.12	0.04	0.16	0.31	0.26	-0.40	0.29	0.72	0.06	0.00	-0.21	-0.28
PsM3	-0.35	-0.63	-0.48	0.13	0.19	-0.04	0.05	0.25	0.84	0.81	0.84	0.05	-0.11	-0.20	-0.36	-0.38	-0.39	-0.44	-0.50	-0.65	-0.53	-0.49	-0.52	-0.55	-0.53	-0.03	0.19	0.34	0.35	0.38	0.39	0.28	-0.15	-0.01	0.14	0.20	0.31	0.39	0.38	-0.24	1.00	0.89	0.78	0.68	0.59	0.63	-0.10	0.94	0.89	0.73	0.60	0.53	0.59	0.40	0.56	-0.20	-0.55	-0.42	-0.52	0.35
PsM7	-0.66	-0.83	-0.77	-0.17	0.34	0.18	0.25	0.07	0.80	0.67	0.74	0.33	0.17	-0.11	-0.63	-0.62	-0.63	-0.68	-0.73	-0.85	-0.79	-0.76	-0.78	-0.78	-0.77	-0.27	0.39	0.47	0.47	0.51	0.54	0.42	-0.01	0.22	0.27	0.32	0.44	0.55	0.55	-0.12	0.89	1.00	0.95	0.88	0.80	0.86	-0.09	0.77	0.97	0.87	0.80	0.72	0.78	0.12	0.74	-0.11	-0.79	-0.67	-0.69	0.50
PsM10	-0.71	-0.86	-0.81	-0.21	0.39	0.24	0.31	0.01	0.77	0.61	0.70	0.42	0.22	-0.02	-0.67	-0.64	-0.63	-0.67	-0.72	-0.85	-0.81	-0.80	-0.82	-0.82	-0.78	-0.36	0.37	0.40	0.39	0.43	0.47	0.34	-0.01	0.29	0.22	0.24	0.35	0.45	0.47	0.02	0.78	0.95	1.00	0.98	0.89	0.91	0.01	0.69	0.94	0.96	0.94	0.84	0.88	-0.03	0.86	-0.03	-0.80	-0.71	-0.65	0.58
PsM15	-0.78	-0.87	-0.86	-0.32	0.45	0.32	0.39	-0.06	0.68	0.51	0.61	0.44	0.33	0.02	-0.73	-0.70	-0.68	-0.70	-0.73	-0.84	-0.83	-0.82	-0.85	-0.83	-0.79	-0.48	0.38	0.36	0.35	0.39	0.44	0.31	0.04	0.38	0.27	0.26	0.34	0.44	0.45	0.13	0.68	0.88	0.98	1.00	0.95	0.93	0.10	0.59	0.87	0.93	0.96	0.91	0.94	-0.19	0.92	0.02	-0.81	-0.73	-0.69	0.57
PsM30	-0.79	-0.86	-0.86	-0.36	0.49	0.38	0.44	-0.12	0.59	0.45	0.53	0.38	0.35	0.07	-0.75	-0.73	-0.71	-0.72	-0.73	-0.84	-0.83	-0.82	-0.85	-0.85	-0.80	-0.52	0.37	0.33	0.30	0.34	0.43	0.30	-0.01	0.43	0.30	0.28	0.33	0.40	0.42	0.23	0.59	0.80	0.89	0.95	1.00	0.95	0.25	0.53	0.78	0.82	0.90	0.97	0.99	-0.32	0.98	0.07	-0.78	-0.76	-0.66	0.60
PsAM	-0.85	-0.85	-0.89	-0.47	0.48	0.43	0.47	-0.20	0.65	0.48	0.57	0.44	0.32	0.10	-0.84	-0.82	-0.80	-0.83	-0.85	-0.89	-0.91	-0.90	-0.92	-0.93	-0.90	-0.35	0.53	0.45	0.43	0.48	0.57	0.38	0.12	0.53	0.42	0.40	0.48	0.56	0.57	0.14	0.63	0.86	0.91	0.93	0.95	1.00	0.00	0.51	0.79	0.81	0.84	0.87	0.92	-0.21	0.87	0.10	-0.87	-0.87	-0.73	0.64
psAm	0.06	0.08	0.07	0.01	0.19	0.25	0.24	-0.21	-0.17	-0.15	-0.16	-0.03	0.09	0.17	0.18	0.18	0.22	0.26	0.29	0.20	0.21	0.23	0.19	0.17	0.24	-0.53	-0.29	-0.30	-0.34	-0.36	-0.31	-0.21	-0.52	-0.08	-0.19	-0.21	-0.31	-0.36	-0.32	0.58	-0.10	-0.09	0.01	0.10	0.25	0.00	1.00	0.10	0.04	0.12	0.23	0.43	0.32	-0.48	0.41	0.17	0.22	0.25	0.05	-0.23
psm3	-0.15	-0.52	-0.31	0.33	0.06	-0.17	-0.08	0.34	0.74	0.75	0.76	-0.05	-0.24	-0.23	-0.14	-0.16	-0.18	-0.22	-0.30	-0.48	-0.35	-0.31	-0.34	-0.41	-0.35	0.01	0.01	0.16	0.18	0.21	0.22	0.13	-0.41	-0.22	-0.10	-0.01	0.09	0.15	0.16	-0.23	0.94	0.77	0.69	0.59	0.53	0.51	0.10	1.00	0.86	0.72	0.59	0.54	0.56	0.33	0.57	-0.23	-0.37	-0.26	-0.29	0.37
psm7	-0.53	-0.78	-0.66	-0.01	0.26	0.08	0.16	0.15	0.77	0.66	0.73	0.30	0.07	-0.16	-0.48	-0.48	-0.48	-0.53	-0.60	-0.75	-0.68	-0.65	-0.68	-0.70	-0.66	-0.25	0.26	0.36	0.37	0.41	0.43	0.32	-0.19	0.06	0.10	0.16	0.28	0.40	0.41	-0.12	0.89	0.97	0.94	0.87	0.78	0.79	0.04	0.86	1.00	0.93	0.84	0.74	0.78	0.10	0.77	-0.16	-0.70	-0.56	-0.56	0.51
psm10	-0.55	-0.76	-0.66	-0.06	0.31	0.15	0.22	0.08	0.71	0.55	0.64	0.42	0.14	-0.05	-0.50	-0.46	-0.45	-0.49	-0.56	-0.71	-0.68	-0.67	-0.69	-0.70	-0.63	-0.33	0.25	0.28	0.28	0.31	0.34	0.23	-0.18	0.13	0.03	0.06	0.16	0.27	0.30	0.04	0.73	0.87	0.96	0.93	0.82	0.81	0.12	0.72	0.93	1.00	0.96	0.82	0.84	-0.06	0.85	-0.05	-0.66	-0.57	-0.48	0.56
psm15	-0.64	-0.78	-0.73	-0.18	0.38	0.24	0.31	0.00	0.61	0.44	0.53	0.45	0.29	0.01	-0.58	-0.54	-0.51	-0.53	-0.58	-0.72	-0.71	-0.70	-0.73	-0.72	-0.65	-0.48	0.25	0.24	0.22	0.26	0.30	0.20	-0.12	0.25	0.09	0.08	0.15	0.26	0.29	0.16	0.60	0.80	0.94	0.96	0.90	0.84	0.23	0.59	0.84	0.96	1.00	0.91	0.91	-0.24	0.92	0.01	-0.68	-0.60	-0.53	0.55
psm30	-0.68	-0.78	-0.75	-0.27	0.47	0.35	0.41	-0.09	0.52	0.39	0.46	0.37	0.33	0.08	-0.62	-0.60	-0.57	-0.57	-0.59	-0.73	-0.72	-0.70	-0.73	-0.75	-0.67	-0.58	0.26	0.22	0.18	0.22	0.30	0.21	-0.16	0.33	0.17	0.15	0.18	0.24	0.28	0.31	0.53	0.72	0.84	0.91	0.97	0.87	0.43	0.54	0.74	0.82	0.91	1.00	0.99	-0.39	1.00	0.08	-0.66	-0.63	-0.55	0.54
psaM	-0.74	-0.83	-0.81	-0.31	0.49	0.36	0.43	-0.09	0.59	0.45	0.53	0.37	0.33	0.08	-0.70	-0.68	-0.65	-0.66	-0.67	-0.80	-0.79	-0.77	-0.80	-0.81	-0.74	-0.54	0.32	0.28	0.25	0.30	0.38	0.27	-0.09	0.38	0.24	0.22	0.27	0.33	0.36	0.26	0.59	0.78	0.88	0.94	0.99	0.92	0.32	0.56	0.78	0.84	0.91	0.99	1.00	-0.33	0.99	0.08	-0.73	-0.70	-0.62	0.57
psaRat	0.30	0.08	0.22	0.41	-0.09	-0.29	-0.23	0.39	0.55	0.68	0.63	-0.38	-0.64	0.01	0.17	0.16	0.12	0.09	0.07	0.01	0.15	0.17	0.19	0.19	0.12	0.52	-0.07	0.13	0.19	0.22	0.15	0.12	0.09	-0.20	0.01	0.10	0.19	0.18	0.16	-0.40	0.40	0.12	-0.03	-0.19	-0.32	-0.21	-0.48	0.33	0.10	-0.06	-0.24	-0.39	-0.33	1.00	-0.35	0.01	0.06	0.15	-0.03	-0.21
PpaM	-0.67	-0.79	-0.75	-0.24	0.46	0.33	0.40	-0.07	0.56	0.42	0.50	0.35	0.30	0.08	-0.62	-0.60	-0.57	-0.57	-0.59	-0.74	-0.72	-0.71	-0.74	-0.75	-0.67	-0.55	0.26	0.22	0.19	0.23	0.31	0.22	-0.17	0.31	0.16	0.14	0.18	0.24	0.28	0.29	0.56	0.74	0.86	0.92	0.98	0.87	0.41	0.57	0.77	0.85	0.92	1.00	0.99	-0.35	1.00	0.07	-0.66	-0.63	-0.55	0.56
PpaRat	-0.14	0.18	-0.01	-0.43	0.35	0.58	0.51	-0.60	0.07	0.07	0.07	0.02	-0.09	1.00	-0.16	-0.09	-0.04	0.01	0.11	0.03	-0.04	-0.06	-0.01	0.09	0.10	-0.17	0.21	0.04	-0.05	-0.04	0.00	0.05	0.00	0.36	0.18	0.07	0.02	-0.03	0.01	0.72	-0.20	-0.11	-0.03	0.02	0.07	0.10	0.17	-0.23	-0.16	-0.05	0.01	0.08	0.08	0.01	0.07	1.00	0.09	0.00	-0.16	-0.26
tmAM	0.87	0.87	0.91	0.47	-0.57	-0.40	-0.49	0.08	-0.62	-0.46	-0.55	-0.41	-0.24	0.09	0.91	0.92	0.93	0.95	0.97	0.94	0.95	0.94	0.95	0.93	0.97	0.22	-0.68	-0.68	-0.68	-0.74	-0.79	-0.64	-0.46	-0.60	-0.60	-0.62	-0.70	-0.80	-0.81	0.06	-0.55	-0.79	-0.80	-0.81	-0.78	-0.87	0.22	-0.37	-0.70	-0.66	-0.68	-0.66	-0.73	0.06	-0.66	0.09	1.00	0.89	0.75	-0.62
TMAM	0.86	0.79	0.87	0.55	-0.44	-0.41	-0.44	0.23	-0.50	-0.37	-0.44	-0.35	-0.27	-0.01	0.87	0.86	0.86	0.89	0.94	0.85	0.88	0.88	0.91	0.96	0.96	0.18	-0.61	-0.51	-0.50	-0.56	-0.67	-0.44	-0.39	-0.59	-0.52	-0.51	-0.58	-0.65	-0.66	0.00	-0.42	-0.67	-0.71	-0.73	-0.76	-0.87	0.25	-0.26	-0.56	-0.57	-0.60	-0.63	-0.70	0.15	-0.63	0.00	0.89	1.00	0.58	-0.76
CDSin	0.79	0.64	0.77	0.60	-0.61	-0.57	-0.62	0.30	-0.59	-0.48	-0.54	-0.29	-0.31	-0.16	0.77	0.79	0.77	0.77	0.73	0.71	0.72	0.71	0.71	0.61	0.70	0.39	-0.51	-0.53	-0.51	-0.55	-0.59	-0.51	-0.36	-0.67	-0.69	-0.66	-0.69	-0.76	-0.73	-0.21	-0.52	-0.69	-0.65	-0.69	-0.66	-0.73	0.05	-0.29	-0.56	-0.48	-0.53	-0.55	-0.62	-0.03	-0.55	-0.16	0.75	0.58	1.00	-0.04
CDCos	-0.46	-0.66	-0.57	-0.02	0.03	-0.10	-0.05	0.19	0.33	0.23	0.28	0.27	0.10	-0.26	-0.50	-0.48	-0.50	-0.55	-0.63	-0.64	-0.65	-0.64	-0.67	-0.79	-0.70	0.02	0.31	0.23	0.24	0.29	0.34	0.15	0.06	0.10	0.02	0.05	0.15	0.20	0.23	-0.28	0.35	0.50	0.58	0.57	0.60	0.64	-0.23	0.37	0.51	0.56	0.55	0.54	0.57	-0.21	0.56	-0.26	-0.62	-0.76	-0.04	1.00

Table 5. Results of 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. Dependant 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%	-

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%	-	-	-	-	-

CHAPTER 3: OPTIMIZATION OF THE METHODOLOGY USED FOR DUNG BEETLES BASED ON THE TIME THAT THE TRAPS MUST BE EXPOSED TO THE ENVIRONMENT (24, 48 OR 72 HOURS)



This chapter is based on the manuscript: Grzechnik, S., & Cabrero-Sañudo, F.J. Time Matters: Optimizing Sampling Time for Comprehensive Dung Beetle Surveys. *Under review*.

Abstract

Dung beetles (Coleoptera, Scarabaeoidea: Aphodiinae, Scarabaeinae, Geotrupinae) are considered one of the most studied taxa among terrestrial arthropods, since they have a key role in ecosystems, as well as they intervene in multitude of ecological processes. One of the most popular methods for sampling dung beetles is the *piftall* trap, an easy and inexpensive method. However, there is no universal methodology, so different aspects of experimental design are highly variable among dung beetle studies. One of these aspects is the length of time a trap must remain active in the field. Thus, the aim of the study is to determine if there would be differences in the diversity indices of the dung beetles after 24, 48 or 72 hours of exposure and whether there are different responses among the subfamilies. Comparing the results obtained from quantitative and qualitative sampling, it can be deduced that exposure time does not seem to have an effect on dung beetle species. In contrast, other variables as sampling day have had an effect on the dung beetles. All of this shows that it is important to adjust the experimental design to the objectives that the study intends to pursue, trying to achieve a balance between obtaining the greatest amount of information and reducing the negative impact on the focus group. So that the studies can be comparable and replicable, it is important that the methodologies are standardized.

Resumen

Los escarabajos coprófagos (Coleoptera, Scarabaeoidea: Aphodiinae, Scarabaeinae, Geotrupinae) son considerados uno de los taxones más estudiados entre los artrópodos terrestres, ya que tienen un papel clave en los ecosistemas, además de intervenir en multitud de procesos ecológicos. Uno de los métodos más populares para tomar muestras de escarabajos coprófagos es la trampa *piftall*, un método fácil y económico. Sin embargo, no existe una metodología universal, por lo que los diferentes aspectos del diseño experimental son muy variables entre los estudios de escarabajos coprófagos. Uno de estos aspectos es el tiempo que una trampa debe permanecer activa en el campo. Así, el objetivo del estudio es determinar si existirían diferencias en los índices de diversidad de los escarabajos coprófagos tras 24, 48 o 72 horas de exposición y si existen diferentes respuestas entre las subfamilias. Comparando los resultados obtenidos del muestreo cuantitativo y cualitativo, se puede deducir que el tiempo de exposición no parece tener efecto sobre las especies de escarabajos coprófagos. Por el contrario, otras variables como el día de muestreo han tenido mayor efecto sobre los escarabajos coprófagos. Todo ello demuestra que es importante ajustar el diseño experimental a los objetivos que se pretende perseguir con el estudio, intentando conseguir un equilibrio entre la obtención de la mayor cantidad de información y la reducción del impacto negativo en el grupo focal. Para que los estudios puedan ser comparables y replicables, es importante que las metodologías estén estandarizadas.

Introduction

Biodiversity can be defined as the sum total of all forms of life on Earth (plants, animals, fungi, and microorganisms), their genetic and phenotypic variation, and the communities and ecosystems of which they are a part (Savard *et al.*, 2000; Dirzo & Raven, 2003). The biodiversity we can see today is the result of billions of years of evolution, shaped by natural processes, and increasingly, by the influence of anthropogenic activities (Rawat & Agarwal, 2015). Over the past decade, biodiversity concerns have spearheaded conservation efforts worldwide (Savard *et al.*, 2000). It has been well-documented that there is a decline in species abundance and richness around the world (Mora-Aguilar *et al.*, 2023). The diversity of plants, vertebrates and invertebrates (such as dung beetles) is declining, with causes ranging from climate change, overhunting, changes of land use, and the introduction of exotic species (Dirzo & Raven, 2003).

Moreover, while significant progress has been made, our understanding of global biodiversity remains incomplete. Knowledge shortfalls exists, regarding the taxonomic data of organisms, as well as their ecological contributions, distribution, abundance, etc. (Hortal *et al.*, 2015). It is a fact that to plan concrete actions to counteract the loss of biodiversity and its knowledge, statistical tools and model organisms are needed to synthesize information on landscape-scale patterns from local biological processes. The development of standardised quantitative methods would allow data-sharing, independent studies to be compared in different biogeographic regions, and changes to be tracked over time (Tocco *et al.*, 2016).

Dung beetles (Insecta: Coleoptera: Scarabaeoidea: Aphodiinae, Geotrupinae, Scarabaeinae) are a diverse and abundant group of insects, considered one of the most studied taxa among terrestrial arthropods (Spector, 2006; Raine & Slade, 2019; Giménez-Gómez *et al.*, 2020). They have been used as bioindicators of habitat disturbance in many ecological research and biodiversity studies around the world (Spector, 2006; Agoglitta *et al.*, 2012; Bourg *et al.*, 2016; Raine & Slade, 2019; Carvalho *et al.*, 2020) due to their sensitivity to environmental changes (Halffter & Favila, 1993; Spector, 2006; Almeida *et al.*, 2011; Bicknell *et al.*, 2014; Gómez-Cifuentes *et al.*, 2017). Because they feed and nest on decomposing matter, mostly vertebrate excrements, they perform several important ecological functions, including soil fertilization and aeration, increased nutrient cycling, secondary seed dispersal and biological control of pest flies and parasites (Andressen, 2002; Nichols *et al.*, 2008; Nichols & Gómez, 2014).

Pitfall traps baited with dung are the most popular used method for capturing dung beetles worldwide (Lobo *et al.*, 1988; Veiga *et al.*, 1989; Halffter & Favila, 1993; Tocco *et al.*, 2016; Mora-Aguilar *et al.*, 2023). *Pitfall* traps are very popular because they are inexpensive and relatively simple to construct, install, collect, and are efficient in capturing large numbers of dung beetles individuals and species, making statistical analyses possible (Siewers *et al.*, 2014; Mora-Aguilar *et al.*, 2023). However, although there are several attempts to standardize the design of *pitfall* traps (Lobo *et al.*, 1988), there is no common agreement, so they remain being contingent on the creativity of researchers, the availability of resources, and the characteristics of the ecosystem where they are deployed (Siewers *et al.*, 2014; Mora-Aguilar *et al.*, 2023). Furthermore, it has been observed that its effectiveness can be influenced by several different factors, such as habitat structure or climatic conditions, as well as by the experimental design used (size of traps, colour of containers, number of traps, bait type, etc.) (Woodcock, 2005; Siewers *et al.*, 2014; Tocco *et al.*, 2016). For example, in tropical forest biomes, traps are often covered to prevent precipitation, accumulation of leaves, or dilution of the preservative solution. In contrast, in Palaearctic and Afrotropical pastures and savannas, where climatic conditions are warmer and drier, there is no need to cover them (Siewers *et al.*, 2014; Tocco *et al.*, 2016).

In terms of experimental design, there have been quite a few studies on the effectiveness of different types of excrements on dung beetles (Hanski & Cambefort, 1991; Wassmer, 1995; Lumaret & Iborra, 1996; Martín-Piera & Lobo, 1996; Barbero *et al.*, 1999; Finn & Giller, 2002; Verdú & Galante, 2002; Frank *et al.*, 2018a, 2018b; Wurmitzer *et al.*, 2017; Tonelli *et al.*, 2021). Other studies have also been carried out to analyse how much separation distance should be left between the traps to avoid overlaps between them (Larsen & Forsyth, 2005; da Silva & Hernández, 2015; Marsh *et al.*, 2018; Moctezuma, 2021). The effectiveness of different types of traps to attract a greater number of dung beetles has even been studied (Lobo *et al.*, 1988; Veiga *et al.*, 1989; Doube & Giller, 1990).

However, other aspects have received little attention, and there is no consensus on the matter. For example, the amount of bait required to sample dung beetles effectively is an issue with great inconsistencies across studies. There is a great disparity in their results, there are even studies in which this information is omitted (Mora-Aguilar *et al.*, 2023). Regarding the time that a trap should remain active in the field, there is a certain consensus towards 48 hours of exposure (Lobo *et al.*, 1988; Veiga *et al.*, 1989; Martín-Piera & Lobo, 1996; Jay-Robert *et al.*, 2003; Bogoni & Hernández, 2014; Correa *et al.*, 2016; Wassmer, 2020; Mora-Aguilar *et al.*, 2023). However, in dry-forest ecosystem studies, traps usually have a 24-hour active period (Rangel-Acosta *et al.*, 2012; Salomão *et al.*, 2018). As extreme microclimatic conditions cause rapid dehydration of dung, the temporal sequence of colonization is greatly accelerated, and the maximum number of dung beetles is reached during the first day. In other studies, they saw that dung beetles occurred in greater numbers in 72 hours old dungs (Barbero *et al.*, 1999; Kessler & Balsbaugh, 1972). In Sabu *et al.* (2006) and Vinod & Sabu (2007) they even left the traps for a week to attract a subset of species, which they know are not attracted to fresh dung. In Iberian Peninsula, Lobo *et al.* (1988) and Veiga *et al.* (1989) suggested that traps had to remain active for a maximum of 48 hours in the field. However, since their contributions this aspect has not been studied again and given the existing discrepancies it would be interesting to check if 48 hours are still the optimal time to collect the traps. Thus, the purpose of this study was to determine: 1) how long traps should be left in the field to obtain the greatest diversity of dung beetles; 2) if there would be differences when studying the subfamilies separately. According to the null hypothesis: 1) it is expected that after 48 hours of exposure the greatest diversity of dung beetles will be collected; 2) there would be no difference in responses among the subfamilies.

Material and methods

Study area

The study was carried out in the village of Mataelpino, located in the northwest of the Madrid Autonomous Community (Spain). More specifically, a semi-open plot for livestock uses located on the outskirts of the village on its western side was used as a sampling area (**Figure 1**). Its area is 1.16 hectares, located at an altitude of 1,140 metres above sea level and at the coordinates 40.73ºN, 3.96ºW. 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.

The study area is characterized by having a continental Mediterranean climate, typical of the interior of the peninsula. Winters are particularly cold and wet, with possible frosts from November to April. In contrast, summers are hot and dry with drought for some months (Rivas-Martínez, 1983). The average annual temperature is between 8ºC and 15ºC, although values of up to -7ºC have been recorded during the coldest months and 38ºC in the warmest. In terms of rainfall, the pluviometric regime is characterized by being seasonal. The periods of greatest precipitation are associated with the autumn and spring months, while the summer months are characterized by being the driest. Average annual rainfall records are usually around 700 millimetres (Meteoclimatic, 2020).

The landscape of the study area has a purely forest character, with tree masses predominating over shrublands and herbaceous grasslands. Holm oaks (*Quercus ilex* spp. *ballota* (Desf.) Samp.) and Pyrenean oaks (*Quercus pyrenaica* Willd.) forests, frequently mixed with a landscape of pastures and bushes are the most common vegetation formations. In addition, pine forests of European red pine, accompanied by eagle fern (*Pteridium aquilinum* (L.) Kuhn) and Iberian silver-leaved broom (*Genista florida* L.) can be found. Among the bushes, the most representative are brooms, junipers, and rock roses. In the herbaceous stratum, grazing meadows for livestock use predominate (Rivas-Martínez & Cantó, 1987). These climatic and vegetation characteristics place the study area in the lower Supramediterranean bioclimatic floor (Rivas-Martínez, 1983).

The study area is characterized by having a faunal community composed of both domestic and wild species. Cattle (*Bos taurus* Linnaeus, 1758) and horses (*Equus ferus caballus* Linnaeus, 1758) predominate due to the high level of livestock activity. As for wild species, the vast majority are species adapted to living in forest areas. For example, herbivores such as roe deer (*Capreolus capreolus* (Linnaeus, 1758)), Iberian ibex (*Capra pyrenaica* Schinz, 1838) or European rabbit (*Oryctolagus cuniculus* (Linnaeus, 1758)) can be found. In addition, omnivores such as wild boar (*Sus scrofa* Linnaeus, 1758) or fox (*Vulpes vulpes* (Linnaeus, 1758)), and carnivores, such as those of the Iberian wolf (*Canis lupus signatus* Cabrera, 1907) can be found (Viejo, 2013). It is important to highlight the faunal community of the study area since the excrements of these animals are the main source of food for the local dung beetle community.

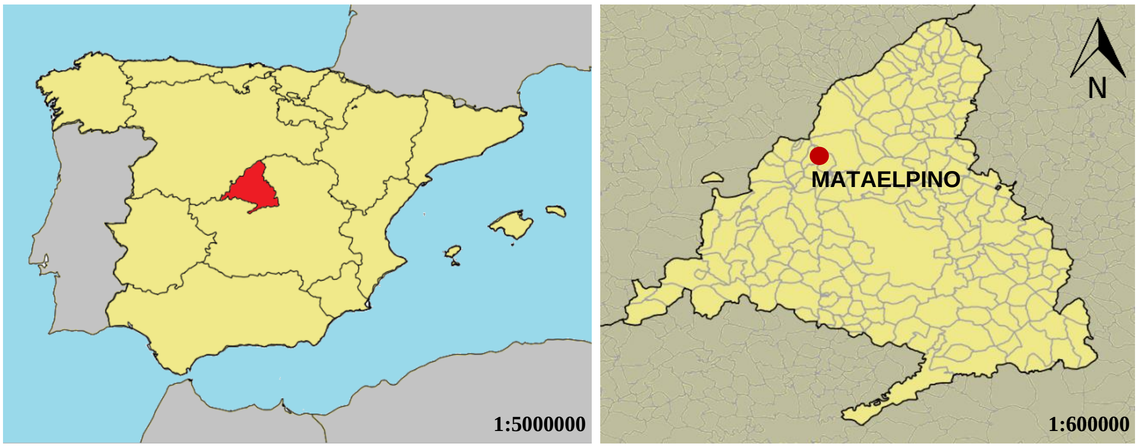


Figure 1. Location maps of the sampling area. The study was carried out in the city of Mataelpino, in the northwest of the Madrid Autonomous Community, Central Spain. The coordinates are 40.73ºN, 3.96ºW. Black and grey lines represent administrative boundaries.

Sampling design

Samplings were carried out over a period of almost two years, with one visit per month from May 2018 to February 2020. Although a 24-month study was intended, the situation of sanitary confinement interrupted it for the last two months. Permits for sampling and collecting dung beetles were obtained from the Department of the Environment, Territorial Planning and Sustainability of the Madrid Autonomous Community (References 10/065982.9/18 and 10/135977.9/20) for the entire sampling period.

The experimental design consisted of setting 36 *pitfall* traps in the study area, following the method recommended by Lobo *et al.* (1988) and Veiga *et al.* (1989). The traps were organized in six hexagons, randomly placed throughout the sampling area, with a minimum separation of 50m between each one. Within each hexagon, the traps were separated with a minimum distance of 10m (Lobo *et al.*, 1988; Lobo, 1992a, 1992b; Martín-Piera & Lobo, 1996). Although in some studies the distance between traps was less than 3m to simulate a real situation in nature (Filgueiras *et al.*, 2009; Martínez *et al.*, 2012; Rangel-Acosta *et al.*, 2012), for this sampling the distances among the traps were big enough to avoid overlaps among dungs of the same hexagon or between adjacent hexagons (Larsen & Forsyth, 2005). *Pitfall* traps were baited with 250 grams of untreated fresh dungs coming from different animals (Grzechnik & Cabrero-Sañudo, *in press*). This hexagon design, which does not affect the objectives of the present study, is related to the development of another parallel study (Grzechnik & Cabrero-Sañudo, *in press*), for which it was necessary to take into account the origin of the six different excrements. In addition, two dung-free traps were placed in the meadow as control traps.

To determine how long the traps should remain active in the field to obtain the greatest diversity of dung beetles, traps were collected within three days of being placed in the sampling area. For each exposure time (24, 48 and 72 hours), two hexagons were randomly selected, and the twelve corresponding traps were collected. Each batch of 12 traps from each exposure time (24, 48 and 72 hours) was homogeneous in that it contained the same types of excrements, so that they could be compared with each other.

Sample processing

The collected dung beetles (coprophagous Scarabaeoidea) were kept separated according to individualized traps and preserved in 70% alcohol until identification. The individuals were subsequently identified using a binocular magnifier and the use of dichotomous keys (Veiga, 1998; Martín-Piera & López-Colón, 2000). Once dry-prepared, all the specimens found in the samplings were incorporated into the UCME collection (Entomology Museum at the Complutense University, Madrid).

Analytical procedures

Several statistical analyses were carried out to determine how long traps should be left in the field to achieve the greatest information on dung beetle diversity with the shortest exposure time. The analyses were conducted for all dung beetles as a whole (coprophagous Scarabaeoidea) and for each subfamily separately (Aphodiinae, Geotrupinae and Scarabaeinae).

At first, an estimate of biological diversity was carried out for each exposure time using the estimation method proposed in Chao & Jost (2015). Based on the Hill series of numbers (Hill, 1973; Chao *et al.*, 2021, 2023), this method allows to quantify the species diversity of an assemblage by calculating continuous diversity profiles estimated as a function of q. The calculated diversity profiles are, 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 & Jost, 2015; Chao *et al.*, 2014, 2020, 2021, 2023). With the data of the potential and observed richness, it has been possible to establish a relationship to validate the sampling effort, considering above 70% 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 version 0.1.1 with the Diversity function to compute diversity estimates (Chao *et al.*, 2016). So, the diversity profiles, the observed abundance of individuals and the species richness obtained from the field data, all quantitative variables, were considered as the study variables.

As the study variables were not normally distributed, non-parametric tests were used to compare the diversity parameters obtained for each exposure time. Since the data were dependent samples according to dates, a Friedman Anova test was performed (Friedman, 1937, 1940), as it allows three or more repeated measurements of ordinal data to be analysed. Then, a Wilcoxon signed rank test was performed to detect differences between pairs of ordinal-level data (Wilcoxon, 1945), with a Bonferroni correction. In this way, it was possible to determine if the time a trap remains in the ecosystem could be affecting the diversity of dung beetles. All the statistical analyses were carried out with STATISTICA package version 10 (StatSoft Inc., 2011).

To quantify the effect that the independent variable (exposure time) has on the dependent variables (q_0, q_1, q_2, Ab, and R_0), General Linear Models (GLMs) were carried out (McCullagh & Nelder, 1989; Crawley, 1993). As the experiment was carried out at different times of the year, the sampling day was included as an additional independent variable. As it is considered cyclical, it was transformed into both sine and cosine (each day represents a portion of the complete 360º circular range) (Cuesta *et al.*, 2021; Lobo & Cuesta, 2021), considering them two different time-related variables. 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 of each selected variable increased the explanatory capacity of the model (Dobson, 1999). In cases in which both sine and cosine were significant, a backward removal procedure was used to find the best global predictive model for the time-related variable (Hsieh & Lu, 2006). When there was an effect of any of the time-related variables, the residuals were used to discern the effect that was due solely to the exposure time variable (Pierce & Schafer, 1986). The goodness of fit of the obtained models was measured using the deviance statistic and the change in deviance was tested using the F-ratio test (McCullagh & Nelder, 1989; Dobson, 1999) with a 5% significance level. The percentage of explained deviance was calculated for each model (Dobson, 1999). All the statistical analyses were carried out with R version 4.2.1 (R Core Team, 2022) and the STATISTICA package version 10 (StatSoft Inc., 2011).

On the other hand, several qualitative analyses were carried out to support the results obtained from the quantitative analyses. First, a comparison of the richness obtained values for each exposure time was carried out. For each sampling period, the total richness obtained was calculated, which was used to determine the proportion of species found at each exposure time. The comparison was also made on a temporal scale, to check how the results of each exposure time varied over time. Secondly, the resulting communities for each exposure time were studied and compared, in order to find similarities, as well as recognize species that may show a preference for a specific exposure time.

Results

In total, 121,825 dung beetles belonging to 50 species were collected (**Appendix 1. Table 1**). According to the values of the abundance of individuals (Ab) and the species richness obtained (R_0) from the field data, differences have been observed among the different exposure times (**Table 1**). At 24 hours of exposure, 41 different dung beetle species were found with a total of 16,810 specimens, 46 species and 45,751 individuals at 48 hours, and at 72 hours, 46 species and 59,264 specimens were collected. If the subfamilies are studied separately, it has been observed that Aphodiinae was the most diverse and abundant subfamily, while Geotrupinae subfamily was the least represented taxon in both indices. For R_0, Aphodiinae represents 54% of the dung beetle species found, followed by the Scarabaeinae subfamily with 38%, and finally the Geotrupinae subfamily (8%). Regarding the abundance, 84% of the collected individuals belonged to the Aphodiinae subfamily, 38% to the Scarabaeinae subfamily and less than 1% to the Geotrupinae subfamily. In addition, the diversity profiles (q_0, q_1 and q_2) are shown in **Table 1**.

As all the values of the ratios were greater than 70.00%, it can be assumed that the representation of the data is good (**Table 1**). As a whole (coprophagous Scarabaeoidea), the dung beetle community is well represented, finding the best representation at 48 hours of exposure (98.08%). If the subfamilies are studied separately, it has been observed that Geotrupinae was the best represented, having found all possible species for the study area at any exposure time. Then, Scarabaeinae with a minimum representation of 78.63% at 72 hours of exposure. In comparison, the worst represented was the Aphodiinae family at 72 hours, finding only 75% of dung beetle species.

	Exposure time (hours)	**q_0**	**q_1**	**q_2**	**Richness Obtained (R_0)**	**Abundance (Ab)**	**R_0/ q_0 Ratio**
Scarabaeoidea	24	42.13	4.69	3.10	41	16,810	97.33%
	48	46.90	5.70	3.90	46	45,751	98.08%
	72	58.50	4.54	3.19	46	59,264	78.63%
Aphodiinae	24	23.25	2.64	2.25	21	14,154	90.32%
	48	25.67	3.09	2.47	25	34,777	97.40%
	72	32.00	3.00	2.57	24	52,959	75%
Geotrupinae	24	4.00	3.36	2.99	4	37	100%
	48	4.00	2.58	2.11	4	85	100%
	72	4.00	2.84	2.30	4	89	100%
Scarabaeinae	24	16.00	5.97	3.61	16	2,619	100%
	48	17.25	3.82	2.57	17	10,889	98.55%
	72	19.00	5.60	3.89	18	6,216	94.74%

Table 1. **Results of the estimation method**. At different taxonomic levels of dung beetles, the results of the three exposure times studied are shown. 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 significance of the sampling effort is assumed when the values of the ratios are equal to or higher than 70.00% (marked in red).

Figure 2 shows the results of the non-parametric analyses that were carried out to compare the different exposure times and examine whether there were differences among them. The results of the Ab and R_0 are shown at the different taxonomic levels at which the dung beetles can be represented (as a whole or separated by subfamilies). Regarding R_0, the general pattern that can be observed is that the results obtained at 48 and 72 hours do not differ significantly from each other, but they do differ significantly with those after 24 hours of exposure. Also, significant differences between the results of 24 hours with those of 48 and 72 hours can be observed for Ab. However, for Aphodiinae subfamily it seems that better values have been obtained at 72 hours of exposure, while in Scarabaeinae it has been at 48 hours. Regardless of the exposure time studied, the results obtained for the diversity profiles are similar to those obtained for the R_0.

The results of the GLMs analysis have allowed to check if the independent variables have had an effect on the dependent variables studied. All the statistically significant relationships between them are shown in **Appendix 1. Table 2**. For the time-related variable, the global predictive models are shown (**Table 2**). When there is only an effect of one variable, the global model coincides with its results. In contrast, if both variables (sine and cosine) are capable of explaining part of the deviance, the global model is a combination of them, increasing their explanatory power. The data of the F statistic with a significant p-value ($p<0.05$) and its explained variance (R^2) are provided.

When dung beetles are studied as a whole (coprophagous Scarabaeoidea), sine explain 11.04%, 26.85%, 18.51% and 16.92% of the deviance of q_0, q_1, q_2 and R_0, respectively. In contrast, exposure time only affects R_0 and explains 10.41% of the deviance. The same pattern is observed in the subfamilies Scarabaeinae and Aphodiinae. In Scarabaeinae subfamily, the deviance explained by the sine is greater in all cases, unlike exposure time which only explains 6.63% of the deviance. In Aphodiinae, cosine explain 11.57% of q_0 and 18.78% of R_0, while sine explain 15.14% and 14.00% of q_1 and q_2, respectively. Exposure time only explain 6.29% of the deviance. In the Geotrupinae subfamily, both time-related variables and exposure time affect all the dependent variables studied. For q_0, q_1, q_2, R_0 and Ab, the joint effect of sine and cosine explains 47.48%, 47.21%, 45.65%, 47.50% and 32.23% of the deviance, respectively. In contrast, the exposure time explain 9.30%, 9.59%, 7.16%, 9.83% and 8.43% of the deviance, respectively.

The results of the qualitative analysis show how R_0 varies over time for each exposure time (**Appendix 2. Figure 1**). In general, the pattern that can be observed is that the R_0 values at 24 hours of exposure are lower than those at 48 and 72 hours. In contrast, there are no major differences between the results of 48 and 72 hours. This same pattern can be observed either studying the dung beetle community as a whole (coprophagous Scarabaeoidea) or each subfamily separately (Aphodiinae, Geotrupinae and Scarabaeinae). However, no significant differences are observed in the composition of the dung beetle communities among the exposure times (**Figure 3**). Some species have been exclusive to 48 and/or 72 hours of exposure. However, they are considered accidental since for the vast majority of the species no more than 5 records have been obtained. *Bodiloides ictericus* (Laicharting, 1781) was the only species for which more specimens have been obtained as the exposure time increases beyond 24 hours (19 individuals collected).

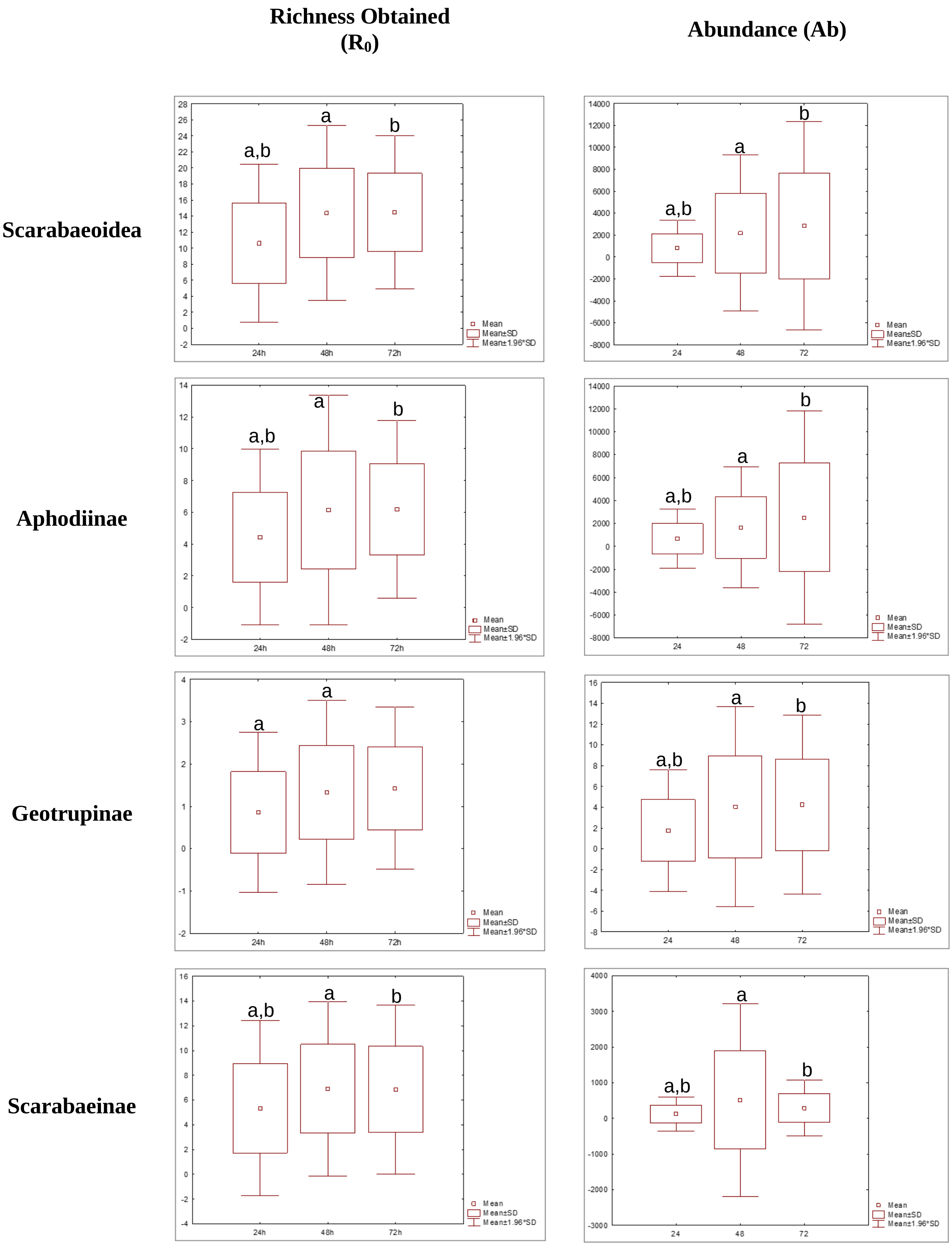


Figure 2. Graphical representation of non-parametric analyses. The results of the abundance (Ab) and richness observed (R_0) in the field for each exposure time (24, 28 and 72 hours) are shown. The analyses were performed at the different taxonomic level in which the dung beetles can been represented (as a whole or separated by subfamilies). Significant differences have been found between some exposure times, which are shown with a lowercase letter. The lowercase letter identifies the pair of exposure times where these differences had been observed.

	SCARABAEOIDEA				
	q_0	**q_1**	**q_2**	**Richness Obtained (R_0)**	**Abundance (Ab)**
Time-related model	$F=7.57^A$ 11.04%	$F=22.39^A$ 26.85%	$F=13.86^A$ 18.51%	$F=12.22^A$ 16.92%	-
Exposure time	-	-	-	F=7.08 10.41%	-
	APHODIINAE				
	q_0	**q_1**	**q_2**	**Richness Obtained (R_0)**	**Abundance (Ab)**
Time-related model	$F=7.98^B$ 11.57%	$F=10.88^A$ 15.14%	$F=9.93^A$ 14.00%	$F=14.11^B$ 18.78%	-
Exposure time	-	-	-	F=5.00 6.29%	-
	GEOTRUPINAE				
	q_0	**q_1**	**q_2**	**Richness Obtained (R_0)**	**Abundance (Ab)**
Time-related model	$F=54.24^C$ 47.48%	$F=53.66^C$ 47.21%	$F=50.39^C$ 45.65%	$F=54.29^C$ 47.50%	$F=28.53^C$ 32.23%
Exposure time	F=6.26 9.30%	F=6.47 9.59%	F=4.70 7.16%	F=6.65 9.83%	F=5.61 8.43%
	SCARABAEINAE				
	q_0	**q_1**	**q_2**	**Richness Obtained (R_0)**	**Abundance (Ab)**
Time-related model	$F=50.72^A$ 45.40%	$F=46.00^A$ 42.99%	$F=31.56^A$ 34.10%	$F=70.00^A$ 53.85%	-
Exposure time	-	-	-	F=4.33 6.63%	-

Table 2. Results of GLMs analysis. Data of F (1,62) statistic with a significant p-value ($p<0.05$) and explained variance (R^2) for each independent variable are shown. Dependant 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). Independent variables are sine, cosine and exposure time. For the time-related variable, the global predictive models are shown. The superscript refers to the independent variable or variables that have been selected in the global models of the time-related variable: A) Sine; B) Cosine; C) Sine + Cosine.

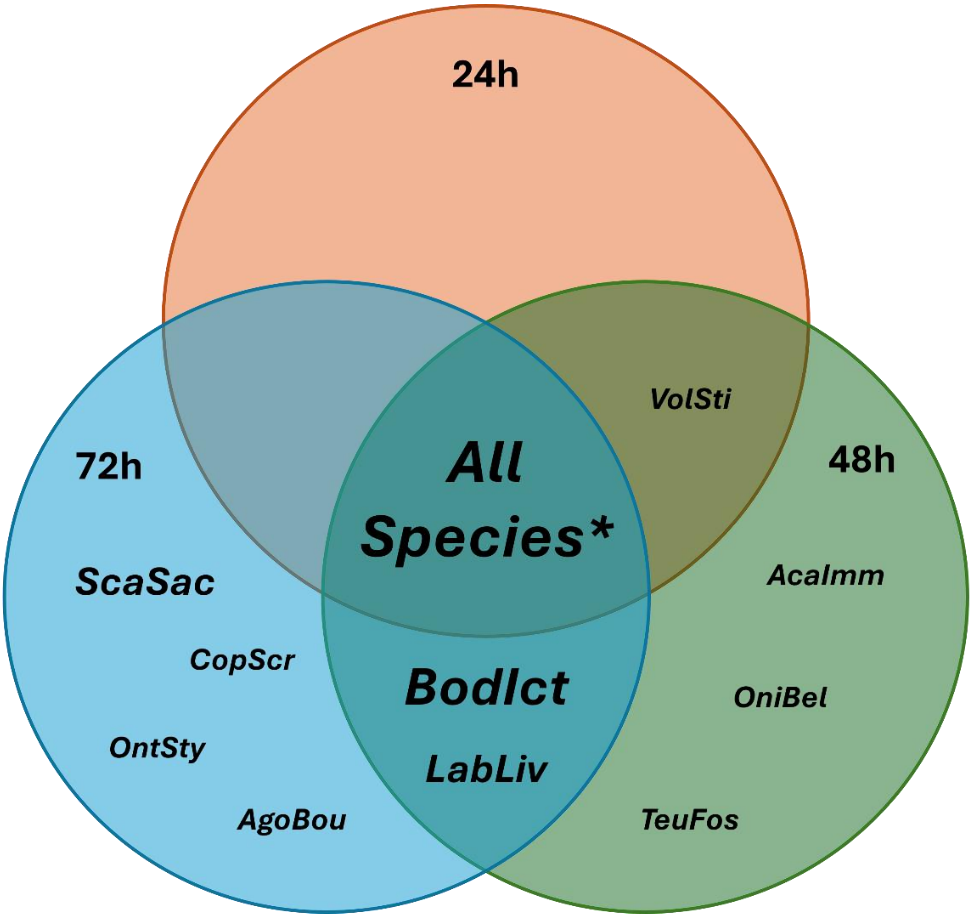


Figure 3. Graphical representation of the dung beetle community found in the study area. The figure shows the distribution of the species according to the exposure times in which they were collected. If a species has been recorded at all the exposure times studied, it has been located in the centre of the graph. As a species becomes more restrictive it moves away from the centre. At the extremes are the species that have been found only at one exposure time. The font size is proportional to the recorded abundance of each species. The (*) refers to all species of dung beetles found, excluding: *Acanthobodilus immundus* (AcaImm); *Agolius bonvouloiri* (AgoBou); *Bodiloides ictericus* (BodIct); *Coprimorphus scrutator* (CopScr); *Labarrus lividus* (LabLiv); *Onitis belial* (OniBel); *Onthophagus stylocerus* (OntSty); *Scarabaeus sacer* (ScaSac); *Teuchestes fossor* (TeuFos) and *Volinus sticticus* (VolSti).

Discussion

The results of the study showed that the exposure time, although significant, does not extremely affect the diversity indices of dung beetles sampled. The vast majority of species have been collected indifferently at the three exposure times. In the case of abundance, more disparate results have been observed but it does not seem to be due to the exposure time either. Furthermore, similar patterns have been observed when the subfamilies have been studied separately.

Firstly, if the results of the quantitative and qualitative analyses are compared, certain discrepancies can be observed. In the case of R_0, quantitative analyses show significant differences between traps that have been active for 24 hours and those that were collected at 48 and 72 hours. In contrast, there seems to be no difference between leaving the traps for 48 or 72 hours. However, if a descriptive analysis of the results is carried out, it can be observed that for R_0 there are no major differences among the exposure times. The communities observed at 24, 48 and 72 hours of exposure are composed of practically the same species, with slight variations. Of the total, only ten species were observed exclusively at a specific exposure time. However, their records were very low and appeared completely randomly throughout the duration of the study. Therefore, one must be skeptical when defining them as specialists for a specific exposure time.

In both quantitative and qualitative analyses, abundance appears to be affected by exposure time. In the quantitative analyses, the abundances at 24 hours differ significantly from those obtained at 48 and 72 hours, while there do not seem to be significant differences between the latter two. In contrast, in the qualitative analyses it can be observed that the abundances increased according to the days of exposure, except in the Scarabaeinae subfamily, where the peak of greatest abundance of dung beetle individuals occurred at 48 hours.

It is possible that some of these results are related to the faunal succession that is manifested in the excrements when they appear in the field (Lobo, 1992a). Different taxa of insects participate in this succession, with dung beetles being the first groups to colonize the excrement along with flies (Doube *et al.*, 1988, Barth *et al.*, 1994, Tixier *et al.*, 2015). To avoid interspecific competition, dung beetles have developed different strategies, from having different diel activity periods (diurnal, crepuscular, and nocturnal), preferences for dung of different types and ages (Hanski & Cambefort, 1991; Wassmer, 1995; Lumaret & Iborra, 1996; Martín-Piera & Lobo, 1996; Barbero *et al.*, 1999; Finn & Giller, 2002; Verdú & Galante, 2002; Frank *et al.*, 2018a, 2018b; Wurmitzer *et al.*, 2017; Tonelli *et al.*, 2021), having different nesting behaviours (Halffter & Edmonds, 1982), among others. In general, the first to appear are species of the Scarabaeinae and Geotrupinae subfamilies, while the members of the Aphodiinae subfamily arrive later in the excrement (Montes de Oca & Halffter, 1995, Krell *et al.*, 2003, Krell-Westerwalbesloh *et al.*, 2004). In some studies, they suggest that aphodians, generally prefer older dungs because the moisture conditions are more suitable and there is less competitive interference from bigger dung beetles (Lumaret, 1995; Sullivan *et al.*, 2017). This could explain why the *B. ictericus* species has not been recorded in the 24-hour traps and that the diversity indices for the Aphodiinae increased as more days passed since the trap appeared in the field. Furthermore, other studies affirm that Aphodiinae are the majority elements in high mountain areas (Sullivan *et al.*, 2017), where the cold and humid climate is much more favourable for them, which would be in accordance with the results of this study (Cabrero-Sañudo & Lobo, 2009). In the case of the Scarabaeinae subfamily, such a high peak of abundance at 48 hours could be due to the fact that they usually appear during the first hours after the appearance of excrement in the environment, and after that time their number is drastically reduced, leaving of excrement (Sullivan *et al.*, 2017).

If these strategies were the only ones that explained the diversity indices of dung beetles, a segregation of the results at different exposure times should have been observed. However, since this has not been the case, there must be other factors that are influencing the dung beetles simultaneously. For example, the sampling day seems to have a considerable effect on dung beetles, unlike the exposure time whose results have been very low. This could be related to the climatic conditions that occur at a certain time and place. There are many studies in which it has been observed that dung beetles are influenced by temperature and precipitation (Halffter & Edmonds, 1982; Lumaret & Kirk, 1991; Lobo *et al.*, 2002; Labidi *et al.*, 2012; Numa *et al.*, 2012; Dortel *et al.*, 2013; Ferreira *et al.*, 2018; Calatayud *et al.*, 2021; Ambrozova *et al.*, 2022), developing distribution patterns according to their preferences. For example, members of the Aphodiinae and Geotrupinae subfamilies have a preference for colder and wetter climates, while the Scarabaeinae subfamily is well adapted to warm and dry conditions (Lumaret & Kirk, 1991; Lobo & Halffter, 2000; Errouissi *et al.*, 2004; Jay-Roberts *et al.*, 2008a, 2008b; Cabrero-Sañudo & Lobo, 2009; Errouissi *et al.*, 2009). However, there are other factors beyond climatic ones that can also affect the diversity indices of dung beetles. The type of dung used as bait can also have an effect on the dung beetle community, having more or less attractive power depending on the preferences of the dung beetles (Sánchez-Piñero & Ávila, 1991; Wassmer, 1995; Lumaret & Iborra, 1996; Gittings & Giller, 1998; Verdú, 1998; Barbero *et al.*, 1999; Galante & Cartagena, 1999; Finn & Giller, 2002; Verdú & Galante, 2002; Tonelli *et al.*, 2021). This could also explain part of the results, especially in abundance, where neither time-related variables nor exposure time have had an effect. It is worth highlighting the results of the Geotrupinae subfamily, which do not support the rest of the results. Precisely this subfamily, being the only one that has recorded all its species at all three exposure times, should not have any effect of exposure time.

The results of this study determine that although there are some differences among the three exposure times, there does not seem to be enough justification to extend the exposure time for more than 24 hours, since with this exposure time representative diversity index values can be obtained, with a smaller number of individuals sacrificed and with the representation of the most species. Therefore, if someone wanted to develop a study on dung beetle communities in a similar place and with a similar experimental design, it would be enough to leave the traps for 24 hours. The difference with Lobo *et al.* (1988), Veiga *et al.* (1989) and the other studies (Wassmer, 2020; Kessler & Balsbaugh, 1972), where a different optimal time was stipulated, is mainly that there is no universal methodology (Tocco *et al.*, 2016; Mora-Aguilar *et al.*, 2023). Each study has been carried out under specific conditions, with specific excrements, a type of traps, a specific number of traps, etc. that influence on a greater or lesser extent the dung beetle species. In addition, sampling effort also influences the results, so it is important to take it into account (Tocco *et al.*, 2016). When studies differ in one or more aspects of the experimental design, the results are incomparable (Tocco *et al.*, 2016; Mora-Aguilar *et al.*, 2023). Therefore, if one of the critical aspects of scientific studies is the possibility of replicating the results, efforts should be directed to finding an effective standardised quantitative sampling method (Tocco *et al.*, 2016; Mora-Aguilar *et al.*, 2023).

Finally, do not forget that researchers should always look for the methodology that best suits their hypothesis or place of study. They should always prioritize obtaining as much information as possible, but also try to ensure that the negative effect on the study group is minimal. In some situations, researchers will need to weigh whether to use a method commonly used in other studies or one that is less used but might be more appropriate for their study (Hohbein & Conway, 2018). For example, for ground beetles and spiders, the passive traps often employed in their survey required a long period of activity (Woodcock, 2005) during which non-target organisms may be killed unnecessarily. Therefore, before carrying out the sample design, researchers should check whether studies have already been carried out in the study area and what type of methodologies they have used.

In recent years, other non-lethal methodologies have been developed for the study and monitoring of dung beetles. This procedure is based on metabarcoding (Camila *et al.*, 2021; Drinkwater *et al.*, 2021; Sigsgaard *et al.*, 2021; Pedersen *et al.*, 2024), which analyses the DNA found in the gut contents of dung beetles to determine what excrements they have fed on. Thanks to this, it is also possible to know the population dynamics of the mammals with which dung beetles are associated (Pedersen *et al.*, 2024). Even animals that are in danger of extinction have been detected (Drinkwater *et al.*, 2021). Although this technique is offering quite promising results, there is still a long way to go in this direction (Drinkwater *et al.*, 2021; Sigsgaard *et al.*, 2021; Pedersen *et al.*, 2024). So, for the moment, we will have to continue resorting to *pitfall* traps if there is no other option.

Conclusion

Dung beetles are an excellent focal taxon for ecological research and biological studies as they respond quickly to environmental changes. One of the advantages of using dung beetles is that the usual way to capture them is using *pitfall* traps, a simple and economical methodology. However, since there is no standardization of the methodology, the results of the studies are incomparable. In the case of the time that traps should remain active in the field, there was a consensus for 48 hours. However, in this study it has been seen that proper and similar results are achieved after 24 hours. Therefore, a balance must always be struck between obtaining as much information as possible and reducing the negative effect that may be caused by sacrificing individuals for the focal group.

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Appendix 1

Table 1. List of the 50 dung beetle species registered in Mataelpino, indicating the abundance for each exposure time studied (24, 48 and 72 hours). The species were ordered and grouped by subfamilies.

List of species	24 hours	48 hours	72 hours
Subfamily Aphodiinae			
Acanthobodilus immundus (Creutzer, 1799)	0	1	0
Agolius bonvouloiri (Harold, 1860)	0	0	2
Agrilinus constans (Duftschmid, 1805)	41	67	85
Ammoecius elevatus (Olivier, 1789)	2	6	47
Anomius castaneus (Illiger, 1803)	6,241	10,439	22,754
Aphodius conjugatus (Panzer, 1795)	1	3	1
Aphodius fimetarius (Linnaeus, 1758)	7	30	39
Aphodius foetidus (Herbst, 1783)	126	441	433
Biralus mahunkaorum Adam, 1983	7	31	48
Bodiloides ictericus (Laicharting, 1781)	0	8	11
Bodilus longispina (Küster, 1854)	4	3	7
Calamosternus granarius (Linnaeus, 1767)	25	265	66
Chilothorax distinctus (Müller, 1776)	47	148	119
Chilothorax lineolatus (Illiger, 1803)	2	7	3
Colobopterus erraticus (Linnaeus, 1758)	26	82	141
Coprimorphus scrutator (Herbst, 1789)	0	0	1
Esymus merdarius (Fabricius, 1775)	13	17	16
Eudolus quadriguttatus (Herbst, 1783)	5	2	12
Heptaulacus testudinarius (Fabricius, 1775)	9	26	30
Labarrus lividus (Olivier, 1789)	0	4	1
Melinopterus sphacelatus (Panzer, 1798)	7,073	19,109	23,231
Nimbus contaminatus (Herbst, 1783)	492	4,008	5,807
Otophorus haemorrhoidalis (Linnaeus, 1758)	16	20	46
Sigorus porcus (Fabricius, 1792)	1	2	5
Teuchester fossor (Linnaeus, 1758)	0	2	0
Trichonotulus scrofa (Fabricius, 1787)	15	55	54
Volinus sticticus (Panzer, 1798)	1	1	0
Subfamily Scarabaeinae			
Bubas bison (Linnaeus, 1767)	15	30	32
Bubas bubalus (Olivier, 1811)	22	39	61
Caccobius schreberi (Linnaeus, 1767)	33	45	36
Cheironitis ungaricus (Herbst, 1789)	15	34	38
Copris lunaris (Linnaeus, 1758)	111	240	173
Euoniticellus fulvus (Goeze,1777)	329	741	837
Onitis belial Fabricius, 1798	0	1	0
Onthophagus coenobita (Herbst, 1783)	2	2	7
Onthophagus fracticornis (Preyssler, 1790)	29	51	51
Onthophagus furcatus (Fabricius, 1781)	75	91	75

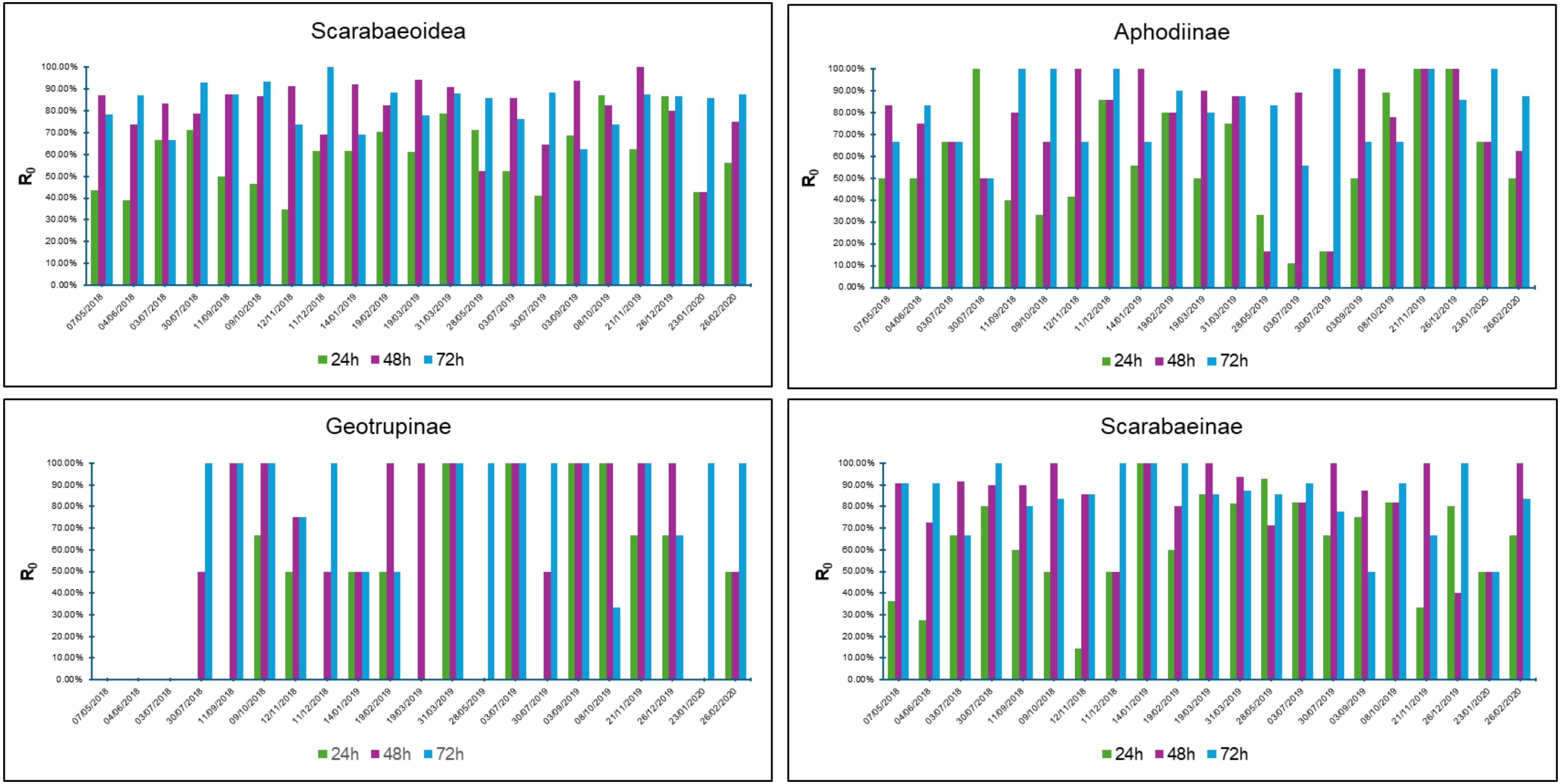
Onthophagus illyricus (Scopoli, 1763)	23	26	27
Onthophagus lemur (Fabricius, 1781)	108	159	138
Onthophagus opacicollis Reitter, 1892	326	2,691	1,613
Onthophagus punctatus (Illiger, 1803)	2	2	1
Onthophagus similis (Scriba, 1790)	1,273	6,175	2,251
Onthophagus stylocerus Graëlls, 1851	0	0	1
Onthophagus taurus (Schreber, 1759)	171	399	407
Onthophagus vacca (Linnaeus, 1767)	85	163	194
Scarabaeus sacer Linnaeus, 1758	0	0	4
Subfamily Geotrupinae			
Anoplotrupes stercorosus (Scriba, 1791)	4	4	8
Ceratophyus hoffmannseggi Fairmaire, 1856	3	4	5
Geotrupes ibericus Baraud, 1958	17	54	54
Geotrupes mutator (Marsham, 1802)	13	23	22

Table 2. Results of GLMs. Data of $F_{(1,62)}$ statistic and explained variance (R^2) are shown, but only the results where the F statistic offers values with a significant p-value ($p<0.05$). Dependant 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). Independent variables are exposure time, sine and cosine. In addition, the global predictive models of the time-related variable are shown.

	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
Sine	F=7.57 11.04%	F=22.39 26.85%	F=13.86 18.51%	F=12.22 16.92%	-	-	F=10.88 15.14%	F=9.93 14.00%	-	-	F=23.72 27.99%	F=25.80 29.72%	F=26.85 30.56%	F=24.12 28.34%	F=10.72 14.95%	F=50.72 45.40%	F=46.00 42.99%	F=31.56 34.10%	F=70.00 53.85%	-
Cosine	-	-	F=7.98 11.57%	F=7.57 11.04%	-	F=7.98 11.57%	-	-	F=7.57 11.04%	-	F=12.05 16.49%	F=10.42 14.59%	F=8.61 12.37%	F=11.78 16.19%	F=10.92 15.19%	-	-	-	-	-
Global model time-related variable	F=7.57 11.04%	F=22.39 26.85%	F=13.86 18.51%	F=12.22 16.92%	-	F=7.98 11.57%	F=10.88 15.14%	F=9.93 14.00%	F=7.57 11.04%	-	F=54.24 47.48%	F=53.66 47.21%	F=50.39 45.65%	F=54.29 47.50%	F=28.53 32.23%	F=50.72 45.40%	F=46.00 42.99%	F=31.56 34.10%	F=70.00 53.85%	-
Exposure time	-	-	-	F=7.08 10.41%	-	-	-	-	F=4.10 6.29%	-	F=6.26 9.30%	F=6.47 9.59%	F=4.70 7.16%	F=6.65 9.83%	F=5.61 8.43%	-	-	-	F=4.33 6.63%	-

Appendix 2

Figure 1. Graphical representation of the qualitative analysis. For each exposure time, the R_0 values obtained for each sampling period are shown. The results have been represented both for when the dung beetle community is studied as a whole (coprophagous Scarabaeoidea) and for each subfamily separately (Aphodiinae, Geotrupinae and Scarabaeinae).



DISCUSIÓN GENERAL

A lo largo de esta tesis se ha querido profundizar en diferentes aspectos relacionados con la ecología de una comunidad de escarabajos coprófagos de la Sierra de Guadarrama (Madrid, España). Uno de los principales objetivos de esta tesis ha sido determinar si las especies de escarabajos coprófagos mostraban preferencias por ciertos tipos de excremento, incluso si éstos procedían de animales exóticos para la zona de estudio. Este interés se debe a que los escarabajos coprófagos siempre han dependido de los mamíferos para su supervivencia, al alimentarse de sus excrementos. De ahí, que sus historias evolutivas estén muy ligadas a las historias evolutivas de los mamíferos. Por otro lado, los patrones de distribución de los escarabajos coprófagos no solo se rigen por la disponibilidad del alimento, sino tambien por las condiciones climáticas que se dan en una localización concreta. Diferentes factores ecológicos, ya sean climáticos o relacionados con el tiempo, pueden influir en mayor o menor medida sobre los valores de riqueza y abundancia de los escarabajos coprófagos. Por último, se ha querido testear el diseño experimental para ver si era efectivo a la hora de obtener resultados representativos en diferentes tiempos de exposición de las trampas. Aunque la metodología empleada para los escarabajos coprófagos esté muy extendida, no hay ninguna estandarización al respecto, por lo que es muy complicado desarrollar medidas o promover iniciativas que tengan como objetivo realizar seguimientos estandarizados de las poblaciones de escarabajos coprófagos y así, por tanto, facilitar su conservación.

En todos los capítulos de la tesis, los análisis se han abordado teniendo en cuenta a los escarabajos coprófagos en su conjunto (Scarabaeoidea coprófagos) y de forma separada (Aphodiinae, Geotrupinae y Scarabaeinae), para examinar si las respuestas observadas podían diferir entre las distintas subfamilias. En esta discusión general se van a abordar los objetivos de cada uno de los capítulos, ofreciendo explicación a todos los resultados obtenidos. No obstante, aunque los resultados nos han permitido responder a todas las preguntas planteadas, se nos abren otras muchas preguntas, por lo cual sería conveniente seguir investigando para profundizar en la ecología de los escarabajos coprófagos.

Según los resultados del primer capítulo, la tendencia general de los escarabajos coprófagos es tener una alimentación variada, pudiendo alimentarse de diferentes excrementos de mamífero, incluso de excrementos procedentes de animales foráneos a la zona de estudio. El carácter generalista viene condicionado a que los excrementos son un recurso efímero y limitado en la naturaleza (Halffter & Matthews, 1966; Hanski & Cambefort, 1991; Lobo, 1992a), restringiendo que los escarabajos coprófagos puedan desarrollar algún tipo de especificidad hacia un excremento en concreto. De hecho, en los bosques tropicales, como la competencia por el alimento es tan intensa, los escarabajos coprófagos han tenido que diversificar sus hábitos alimenticios para poder subsistir, alimentándose tanto de excrementos como de hongos, cadáveres o fruta en descomposición, entre otros (Halffter & Matthews, 1966; Gill, 1991; Hanski & Cambefort, 1991; Hill, 1996; Verdú *et al.*, 2007; Scholtz *et al.*, 2009; da Silva *et al.*, 2012; Salomão *et al.*, 2014, 2018; Stavert *et al.*, 2014; Ebert *et al.*, 2019; Giménez-Gómez *et al.*, 2020; Weithmann *et al.*, 2020).

Tanto si se estudian los escarabajos coprófagos en su conjunto como por subfamilias se puede advertir que las comunidades de cada excremento utilizado están compuestas por prácticamente las mismas especies. En cada una de las redes tróficas resultantes, se puede distinguir con claridad la elevada cantidad de interacciones entre los diferentes elementos de las redes, lo que indica que las comunidades están formadas por especies de carácter generalista. En Scarabaeoidea y Aphodiinae, se podría pensar que existen dos comunidades diferentes, una compuesta por las especies recogidas en los excrementos de elefante, búfalo, jabalí y gamo y, otra formada por las especies de los excrementos de cabra y oso pardo. No obstante, si se hace un análisis más en profundidad se puede ver que las comunidades están anidadas, es decir, que la comunidad resultante de los excrementos de cabra y oso pardo está incluida dentro de la comunidad constituida por los excrementos de búfalo, elefante, jabalí y gamo, no habiendo diferencias aparentes entre las comunidades. Es posible que esto se deba a la baja representatividad de los datos obtenidos para cabra y oso pardo.

Aunque la tendencia general sea tener una dieta generalista (Hanski & Cambefort, 1991; Martín-Piera & Lobo, 1996; Simmons & Ridsdill-Smith, 2011; Frank *et al.*, 2017, 2018a, 2018b; Wurmitzer *et al.*, 2017; Raine & Slade, 2019), se ha podido advertir que cuando los escarabajos coprófagos son expuestos a diferentes tipos de excremento, pueden mostrar preferencias por alguno de ellos (Dormont *et al.*, 2004, 2007; Frank *et al.*, 2018a; Urrutia *et al.*, 2022). En conjunto, la mayor diversidad y abundancia de escarabajos coprófagos fue encontrada en los excrementos de mamíferos herbívoros (Hanski & Cambefort, 1991; Martín-Piera & Lobo, 1996; Scholtz *et al.*, 2009; Simmons & Ridsdill-

Smith, 2011; Frank *et al.*, 2017, 2018a, 2018b; Wurmitzer *et al.*, 2017; Raine & Slade, 2019), aunque los excrementos de los animales omnívoros no quedaron en muy mala posición, sobre todo gracias al excremento de jabalí. Dentro de los excrementos de los herbívoros, el excremento de elefante ha sido con diferencia el que ha albergado la mayor diversidad de especies y abundancia de individuos de escarabajos coprófagos (Vinod & Sabu, 2007; Hewavithana *et al.* 2016). El excremento de búfalo, aunque no ha alcanzado unos valores tan altos como los del excremento de elefante, sobre todo en términos de abundancia de individuos, ha demostrado ser muy parecido a éste en riqueza de especies. Si se tiene en cuenta que uno de los análogos al excremento de elefante es el de caballo y el de búfalo es el de vaca, se entendería que estos excrementos fuesen los más exitosos al estar los escarabajos coprófagos más que acostumbrados a ellos por las prácticas ganaderas tradicionales (Martín-Piera & Lobo, 1996; Barbero *et al.*, 1999; Galante & Cartagena, 1999; Errouissi *et al.*, 2004; Dormont *et al.*, 2007; Frank *et al.*, 2018a, 2018b). En el caso del excremento de gamo, los resultados demuestran que es un excremento que tiene cierto poder de atracción, pero no resulta ser tan atrayente como los demás excrementos de los mamíferos herbívoros (Martín-Piera & Lobo, 1996; Dormont *et al.*, 2007). No obstante, el que ha resultado ser una sorpresa ha sido el excremento de cabra. En comparación con otros estudios (Finn & Giller, 2002; Dormont *et al.*, 2007, 2010; Frank *et al.*, 2018a, 2018b), donde se utilizó el excremento de un análogo de la cabra (oveja), se obtuvieron unos resultados muy altos, siendo incluso considerado de los mejores excrementos del estudio (Finn & Giller, 2002; Dormont *et al.*, 2007, 2010). En cambio, en base a los resultados de la tesis, ha resultado ser de los que menor diversidad y abundancia han albergado.

Por otro lado, los excrementos de los animales omnívoros han obtenido unos resultados dispares. Por un lado, el excremento de jabalí ha despuntado del excremento de oso pardo, tanto en riqueza de especies como en abundancia de individuos de escarabajos coprófagos. De hecho, ha sido el segundo excremento, por detrás del excremento de elefante, en albergar la mayor abundancia de individuos. En comparación a otros estudios, existe una dualidad con este excremento, desde los que afirman que los escarabajos coprófagos aparecen esporádicamente en excrementos de jabalí (Carpaneto & Fabbri, 1983; Martín-Piera & Lobo, 1996; Barbero *et al.*, 1999; Frank *et al.*, 2018b) hasta los que apuntan que es de los excrementos más atrayentes (Frank *et al.*, 2018a; Sathiandran *et al.*, 2021). En este caso, los resultados de la tesis apuntan a que el excremento de jabalí produce un efecto considerable sobre la comunidad de escarabajos coprófagos de la zona de estudio. A diferencia del jabalí, la comunidad del excremento de oso pardo ha sido bastante pobre, tanto en riqueza de especies como en abundancia de individuos. Es muy probable que su poder de atracción sea muy bajo en comparación a los otros excrementos utilizados, como apuntan algunos estudios previos (Hewavithana *et al.*, 2016; Frank *et al.*, 2018b). No obstante, resulta curioso que, en otras regiones del planeta, los excrementos de omnívoros sean de los más utilizados en este tipo de estudios, ya que resultan ser de los más efectivos (Estrada *et al.*, 1993, Filgueiras *et al.*, 2009, Amézquita & Favila, 2010; Carpaneto *et al.*, 2010; Whipple & Hoback, 2012; Marsh *et al.*, 2013; Bogoni & Hernández, 2014; Bourg *et al.*, 2016*;* Correa *et al.*, 2016; Giménez-Gómez *et al.*, 2020; Sathiandran *et al.*, 2021).

Aunque existen estudios en donde se ha documentado la existencia de preferencias tróficas en los escarabajos coprófagos (Sánchez-Piñero & Ávila, 1991; Wassmer, 1995; Lumaret & Iborra, 1996; Gittings & Giller, 1998; Verdú, 1998; Barbero *et al.*, 1999; Galante & Cartagena, 1999; Finn & Giller, 2002; Verdú & Galante, 2002, 2004; Carpaneto *et al.*, 2011; Tonelli *et al.*, 2021), en muy pocos se ha visto una clara especificidad hacia un excremento en concreto (Sánchez-Piñero & Ávila, 1991; Verdú, 1998; Galante & Cartagena, 1999; Verdú & Galante, 2002, 2004; Tonelli *et al.*, 2021). Como en la península iberica existen algunas especies endémicas específicas de ciertos excrementos, se hizo una caracterización de las comunidades para ver si entre las especies registradas hubiese alguna que pudiera tener una relación directa con alguno de los excrementos utilizados. Entre las especies que el análisis determinó que podrían tener especificidad hacia algún excremento, cabe destacar la presencia de tres especies endémicas de la península ibérica, *Onthophagus stylocerus* Graëlls, 1851, *Onthophagus punctatus* (Illiger, 1803) y *Ceratophyus hoffmannseggi* Fairmaire, 1856. No obstante, está bien documentado que estas especies tienen un espectro trófico relativamente polífago, pudiendo colonizar excrementos de diversos tipos de animales (Martín-Piera & López-Colón, 2000). Además, solo se tiene un registro de cada una de ellas, por lo que sería muy precipitado calificarlas de específicas de alguno de los excrementos. Para el resto de especies calificadas como específicas, ocurre algo parecido: hay muy pocos registros como para poder pensar que son específicas de un excremento en concreto. Solo una especie ha sido calificada como fiel, *Onthophagus similis* (Scriba, 1790), la cual parece tener fidelidad hacia los excrementos de búfalo y oso pardo. No obstante, es una de las especies más características de la comunidad coprófaga en pastos abiertos, pudiendo alimentarse de una gran variedad de excrementos (Martín-Piera & López-Colón, 2000), con lo cual tambien habría que actuar con precaución.

En la península iberica, el interés por las preferencias tróficas de los escarabajos coprófagos ha sido ampliamente estudiado (Sánchez-Piñero & Ávila, 1991; Martín-Piera & Lobo, 1996; Verdú, 1998; Galante & Cartagena, 1999; Verdú & Galante, 2002). Sin embargo, nunca antes se habían utilizado excrementos de animales no autóctonos. De acuerdo con otros estudios, donde también se utilizaron excrementos tanto de animales exóticos como nativos, el origen de los excrementos no pareció afectar a los escarabajos coprófagos (Gittings & Giller, 1998; Whipple & Hoback, 2012). De hecho, el estudio comparativo que se ha realizado demuestra que el excremento de elefante alberga la mayor diversidad de especies de escarabajos coprófagos, encontrando en él todas las especies registradas de la subfamilia Geotrupinae, casi todas las especies de Aphodiinae y más del 85% de las especies de Scarabaeinae. Sin embargo, se esperaba una mayor abundancia y riqueza de especies de escarabajos coprófagos en los excrementos de los mamíferos rumiantes (búfalo, gamo y cabra), ya que digieren mejor los alimentos que los no rumiantes (elefante) (Holter, 2016). Además, se ha visto que la calidad nutritiva de los excrementos de los no rumiantes suele ser menor en proporción a la de los excrementos de rumiantes (Finn & Giller, 2002). Por ejemplo, el índice C/N, que se utiliza para describir la calidad de un compuesto orgánico (Holter & Scholtz, 2007), suele ser más alto en los excrementos de los herbívoros no rumiantes, lo que indica unos niveles bajos de aminoácidos. Estos elementos son cruciales para el desarrollo de los insectos, al intervenir en los procesos de eclosión de la pupa, son precursores de pigmentos y promueven el crecimiento en larvas y adultos (Frank *et al.*, 2017). Por ello, la cantidad y composición de los compuestos orgánicos volátiles y otras propiedades organolépticas deben jugar un papel clave en la selección del excremento de elefante (Frank *et al.*, 2017). Finn & Giller (2002) observaron que el excremento de caballo desprendía un olor muy fuerte y característico, lo que podría asemejarse al elefante y, de ahí, su éxito entre los escarabajos coprófagos.

En cuanto a los trabajos previos, no se esperaba que los excrementos procedentes de animales omnívoros resultasen ser muy significativos (Carpaneto & Fabbri, 1983; Martín-Piera & Lobo, 1996; Barbero *et al.*, 1999; Frank *et al.*, 2018b). A diferencia del excremento de oso pardo, el excremento de jabalí ha resultado ser toda una revelación. A pesar, de que ambos sean animales omnívoros y que su dieta varie de forma estacional, el oso pardo suele consumir más alimentos de origen animal que el jabalí. Por ello, sus excrementos tendrían más parecido con los de un carnívoro, mientras que los excrementos de jabalí se parecerían más a los de los herbívoros. Frank *et al.* (2017) observaron que, aunque los excrementos de los carnívoros son los más ricos en nutrientes (alta relación C/N), podrían contener bacterias patógenas, que son percibidas por los escarabajos coprófagos a través de señales olfativas, lo que explicaría los bajos resultados obtenidos con el excremento de oso pardo (Martín-Piera & Lobo, 1996; Frank *et al.*, 2018b). Sin embargo, resulta curioso que dos especies de escarabajos, conocidos por sus hábitos polífagos, se encontraran exclusivamente en este tipo de excremento. De ahí, que los resultados del estudio comparativo lo seleccionaran como el segundo excremento que mayor diversidad de especies de Scarabaeinae albergaba. En cuanto al excremento de jabalí, es posible que le ocurra algo similar que al excremento de elefante. Frank *et al.* (2018a) observaron que algunos de los compuestos orgánicos volátiles que emanan del excremento de jabalí eran de los más atractivos para los escarabajos coprófagos, lo que podría explicar los resultados de este estudio.

El creciente abandono del pastoreo extensivo en muchos pastizales de Europa puede suponer una gran amenaza para la supervivencia de las comunidades de escarabajos coprófagos. Se han investigado ampliamente las respuestas de la comunidad de escarabajos coprófagos a los cambios ambientales (Menéndez & Gutiérrez, 2004; Dortel *et al.*, 2013; Menéndez *et al.*, 2014), pero poco se sabe sobre las consecuencias que causaría la modificación de una red trófica. Probablemente, la desaparición de los grandes mamíferos herbívoros en los pastizales provocaría un desequilibrio importante en las redes tróficas del ecosistema. A medida que disminuyera la disponibilidad de alimento, habría una mayor competencia entre las especies de escarabajos coprófagos, llegando incluso a provocar extinciones locales de algunas especies de escarabajos coprófagos. A pesar de sus preferencias alimentarias generalistas, la desaparición de los grandes mamíferos herbívoros tendría un impacto negativo en las comunidades de escarabajos coprófagos y, por tanto, en las funciones ecosistémicas que desempeñan (Raine & Slade, 2018). Si se llegara a dar el caso, conocer los hábitos alimenticios de los escarabajos coprófagos y su plasticidad trófica, podría ser de gran ayuda para establecer medidas preventivas y/o programas de conservación frente a su extinción.

Con base en los resultados del segundo capítulo, se pudo interpretar que las condiciones climáticas, así como los factores relacionados con el tiempo, tenían un efecto sobre los patrones de diversidad de los escarabajos coprófagos. De entre todas las variables estudiadas, las variables relacionadas con el día han resultado ser las más explicativas, lo que demuestra que las condiciones climáticas ligadas a una zona concreta ejercen un efecto sobre las especies de escarabajos coprófagos. En general, la diversidad de escarabajos coprófagos era mucho mayor durante los meses de primavera y otoño, mientras que en los meses de verano e invierno, la diversidad se veía reducida (Lobo, 1982; Lumaret & Kirk, 1987, 1991; Jay-Roberts *et al.*, 2008a; Agoglitta *et al.*, 2012; Senyüz *et al.*, 2019). Esto concuerda con el clásico patrón bimodal de la subfamilia Aphodiinae (Lumaret & Kirk, 1991; Senyüz *et al.*, 2019), la cual presenta dos picos de máxima diversidad y abundancia durante los meses de primavera y otoño. De hecho, los resultados sugieren que la mayor diversidad de especies de Aphodiinae se suele encontrar durante los meses otoñales. Al ser especies endocópridas y vivir dentro del excremento, les hace ser muy vulnerables a las sequías y heladas propias de los meses de verano e invierno, respectivamente (Lumaret, 1995; Jay-Roberts *et al.*, 2008a). Por ello, es complicado ver adultos durante estos meses del año. Sin embargo, los representantes de las subfamilias Scarabaeinae y Geotrupinae suelen presentar un patrón unimodal. En Scarabaeinae, los resultados muestran que la mayor riqueza de especies se encuentra principalmente en los meses de verano. Esto coincide con otros estudios, en los que se vio que los miembros de esta subfamilia eran más activos en el periodo estival, ya que están bien adaptados a las condiciones cálidas, estando prácticamente ausentes durante el invierno (Jay-Roberts *et al.*, 2008a; Errouissi *et al.*, 2009; Hortal *et al.*, 2011). La gran mayoría de Scarabaeinae son paracópridos, por lo que entierran las bolas de excremento dentro del suelo, en galerías profundas para evitar que se desequen durante las sequías (Jay-Roberts *et al.*, 2008a; Labidi *et al.*, 2012). En cambio, en la subfamilia Geotrupinae, el pico de mayor actividad se produce a finales de año, concretamente en los meses de otoño (Lumaret & Kirk, 1987; Errouissi *et al.*, 2004, 2009; Jay-Roberts *et al.*, 2008a). Después de las primeras lluvias otoñales, los adultos emergen y se reproducen para así pasar las épocas desfavorables en forma de huevo, larva o pupa (Lumaret, 1995). Sin embargo, los resultados de la tesis no se ven apoyados por esta idea. Es posible que la presencia de las especies *C. hoffmannseggi* y *Anoplotrupes stercorosus* (Scriba, 1791), las cuales necesitan ambientes más secos para que sus larvas se desarrollen correctamente

(Galante & Rodríguez, 1988; Marczak & Mroczynski, 2018), estén interfiriendo en los resultados globales.

En cuanto a las variables climáticas, los efectos de la temperatura y humedad han sido ampliamente estudiados, además de ser considerados los factores climáticos más influyentes sobre la diversidad de escarabajos coprófagos (Lumaret & Kirk, 1987, 1991; Lobo *et al.*, 2002; Errouissi *et al.*, 2004, 2009; Numa *et al.*, 2012; Dortel *et al.*, 2013; Ferreira *et al.*, 2018; Ambrozova *et al.*, 2022). Sin embargo, en este estudio han resultado ser las menos relevantes, ya que sólo han influido en las subfamilias Geotrupinae y Scarabaeinae. Ninguno de estos dos factores parece influir en Aphodiinae, aunque se esperaba una respuesta similar a la de la subfamilia Geotrupinae, al tener ambas las mismas preferencias climáticas (Lumaret & Kirk, 1991; Lobo & Halffter, 2000; Errouissi *et al.*, 2004; Jay-Roberts *et al.*, 2008b; Cabrero-Sañudo & Lobo, 2009).

Los resultados muestran que los índices de diversidad de la subfamilia Scarabaeinae están influenciados positivamente por las variables relacionadas con la temperatura. De hecho, la temperatura parece tener un efecto casi exclusivo sobre la subfamilia Scarabaeinae, sobre todo las variables relacionadas con la temperatura máxima alcanzada durante el día. Esto coincidiría con el hecho de que la mayoría de las especies registradas son diurnas, mostrando un pico de actividad en las horas centrales del día. Por ejemplo, *O. similis*, *Onthophagus opacicollis* Reitter, 1893 y *Euoniticellus fulvus* Goeze, 1777, las cuales resultaron ser las especies más abundantes del estudio, mostraron este patrón (Lumaret & Kirk, 1987; Ávila & Pascual, 1988; Mena *et al.*, 1989; Martín-Piera & López-Colón, 2000). Incluso, otras especies no tan representativas, como *Onthophagus lemur* (Fabricius, 1781), *Onthophagus taurus* (Schreber, 1759) u *Onthophagus vacca* (Linnaeus, 1767) también muestran este mismo carácter termófilo (Lumaret & Kirk, 1987; Ávila & Pascual, 1988; Baz, 1988; Mena *et al.*, 1989; Wassmer, 1995; Martín-Piera & López-Colón, 2000).

En Geotrupinae, el factor climático que parece ser más importante es la humedad. No obstante, estos resultados no coinciden con otros estudios previos en los que sí se vio una relacion positiva entre los patrones de diversidad de Geotrupinae y la humedad (Lumaret & Kirk, 1991; Lobo & Halffter, 2000; Martín-Piera & López-Colón, 2000; Errouissi *et al.*, 2004; Mena, 2001). Como se mencionó anteriormente, es posible que la presencia de dos especies con requerimientos ecológicos diferentes al resto de Geotrupinae esté interfiriendo en los resultados globales.

Una novedad de este estudio fue la incorporación de la presión atmosférica como una variable climática más, un factor que nunca antes se había estudiado en los escarabajos coprófagos. Los pocos estudios que existen utilizaron como grupo de estudio a moscas o avispas parasitoides y, la mayoría de los estudios, se llevaron a cabo en condiciones de laboratorio (Ankney, 1984; Marchand & McNeil, 2000; Fournier *et al.*, 2005; Rousse *et al.*, 2009; Pellegrino *et al.*, 2013; Austin *et al.*, 2014; Dagaeff *et al.*, 2016; Adonyeva *et al.*, 2021). Según Wellington (1946) un clima tranquilo, seco y soleado está asociado con niveles altos de presión atmosférica, mientras que niveles bajos suelen ir acompañados de precipitaciones y vientos de alta velocidad. Por tanto, detectar fluctuaciones de la presión atmosférica permitiría a los insectos identificar cambios inminentes en las condiciones climáticas, las cuales podrían suponer una amenaza para su supervivencia (Pellegrino *et al.*, 2013).

Sorprendentemente, la presión atmosférica no solo parecía tener un efecto sobre los escarabajos coprófagos, sino que además tenía un efecto inverso, es decir, que a medida que la presión atmosférica aumentaba, la diversidad de escarabajos coprófagos disminuía. Los resultados para la subfamilia Aphodiinae se ven negativamente afectados por niveles altos de presión atmosférica, algo que tendría sentido al tener estos picos de mayor actividad durante los meses lluviosos (primavera y otoño) (Lumaret & Kirk, 1991; Senyüz *et al.*, 2019). De hecho, parece afectar sobre todo a las especies más abundantes, que han sido *Anomius castaneus* (Illiger, 1803), *Melinopterus sphacelatus* (Panzer, 1798) y *Nimbus contaminatus* (Herbst, 1783), las cuales tiene una marcada fenología otoñal (Veiga, 1998; Agoiz-Bustamante, 2008; Errouissi *et al.*, 2009). Se esperaba obtener una respuesta similar para la subfamilia Geotrupinae, al tener ambos las mismas preferencias climatológicas y éstos una marcada fenología otoñal (Lumaret & Kirk, 1991; Lobo & Halffter, 2000; Martín-Piera & López-Colón, 2000; Mena, 2001; Errouissi *et al.*, 2004). No obstante, la presión atmosférica no parece ejercer ningún efecto sobre la comunidad de especies de la subfamilia Geotrupinae.

Por otro lado, se esperaba un mayor efecto de la presión atmosférica sobre las especies de la subfamilia Scarabaeinae, al estar muy ligadas a condiciones de calor y estar concentrada su actividad durante las horas más calurosas del día (Lumaret & Kirk, 1991; Martín-Piera & López-Colón, 2000; Errouissi *et al.*, 2004, 2009; Jay-Roberts *et al.*, 2008a). Es posible que haya un efecto que no se esté advirtiendo, al quedar enmascarado, o que esté interactuando con otra variable de mayor peso, como las variables relacionadas con el tiempo o la temperatura.

A diferencia de lo que ocurría con las preferencias tróficas, cuando se estudió el efecto de las variables climáticas y las relacionadas con el tiempo sobre el conjunto de escarabajos coprófagos (Scarabaeoidea coprófagos), los resultados aportaron información contradictoria. Es posible que la representación conjunta de grupos taxonómicos con diferentes adaptaciones y respuestas ecológicas, de lugar a malinterpretaciones de los resultados. Por ello, es mejor estudiar los efectos de estas variables, analizando los escarabajos coprófagos de forma separada en subfamilias.

Teniendo en cuenta estos dos primeros capítulos, los resultados permiten tener una visión más completa de los factores que pueden influir sobre las comunidades de los escarabajos coprófagos. Por ejemplo, prácticamente ninguna variable climática o relacionada con el tiempo se vio que tuviese un efecto sobre la abundancia. En cambio, en el primer capítulo se pudo ver cierta relación de la abundancia con algunos tipos de excremento, por lo que la variabilidad observada de la abundancia podría deberse en parte a las características fisicoquímicas de los excrementos (Treitler *et al.*, 2017) o bien por otros factores que ni se tuvieron en cuenta, como las características del microhábitat, la cantidad de cebo colocado en la trampa o la disponibilidad de la comida (Bogoni *et al.*, 2016). Hay que tener en cuenta, que esta tesis se ha centrado en una comunidad concreta de escarabajos coprófagos y en estudiar algunos aspectos que podrían tener un efecto sobre los índices de diversidad de los escarabajos coprófagos. No obstante, existen otros factores, ya sean ecológicos, geográficos e históricos, que no se han tenido en cuenta en este estudio y que tambien podrían ejercer un efecto sobre las especies de escarabajos coprófagos (Barbero *et al.*, 1999). Por ejemplo, algunos estudios han visto un efecto de la altitud (Martín-Piera *et al.*, 1992; Jay-Robert *et al.*, 1997, 2008a; Errouissi *et al.*, 2004; Labidi *et al.*, 2012) o del tipo de hábitat (Halffter & Edmonds, 1982; Lumaret & Kirk, 1987; Martín-Piera *et al.*, 1992; Jay-Roberts *et al.*, 2008b) en los patrones de distribución de los escarabajos coprófagos, por lo que sería conveniente tenerlos en cuenta para futuros trabajos. Por tanto, este estudio considera que tiene sus limitaciones y que una parte de la variabilidad observada dependerá de factores que no se han tenido en cuenta.

Por último, el tercer capítulo de la tesis se ha centrado en analizar si la metodología empleada permite obtener resultados representativos. Más concretamente, en saber si existen diferencias entre los tiempos que debe permanecer activa una trampa en el campo.

Tanto al estudiar a los escarabajos coprófagos como el total (Scarabaeoidea coprófagos) o como por subfamilias, los resultados obtenidos fueron muy similares.

Del análisis comparativo entre los métodos cuantitativos y cualitativos, se pudo determinar dónde se hallaban las semejanzas y diferencias entre los diferentes tiempos de exposición. En un primer momento, podría parecer que hubiese diferencias entre las trampas de 24 horas con las de 48 y 72 horas. No obstante, esta idea se tuvo que rechazar al ver que el tiempo de exposición no explicaba casi nada de la variabilidad observada (en muchos casos no llegaba ni al 10%) y que las comunidades resultantes de cada trampa compartían la mayoría de las especies registradas en el estudio. Solo diez especies fueron encontradas de forma exclusiva en un tiempo de exposición u otro, pero sus registros eran tan bajos que ni se tuvieron en cuenta a la hora de hablar de especificidad. En cuanto a la abundancia, aunque se vieron resultados más dispares, se comprobó que el tiempo de exposición tampoco tuvo ningún efecto sobre la abundancia, ni siquiera las variables relacionadas con el tiempo. Como se ha visto en capítulos anteriores, la abundancia parece depender de otros factores, como el tipo de excremento empleado como cebo.

Estos resultados demuestran que no hay grandes diferencias entre los tres tiempos de exposición, por lo que se si se quisiese hacer un estudio con la misma metodología y en una zona con las mismas características climáticas, se recomendaría dejar las trampas un máximo de 24 horas. La diferencia con otros estudios en los que las trampas se dejaban 48 horas (Lobo *et al.*, 1988, Veiga *et al.*, 1989; Wassmer, 2020) o durante más tiempo (Kessler & Balsbaugh, 1972), se debe a que no existe una metodología universal para muestrear escarabajos coprófagos (Tocco *et al.*, 2016; Mora-Aguilar *et al.*, 2023). Cada uno de estos estudios se ha llevado a cabo en unas condiciones determinadas, con unos excrementos determinados, un tipo de trampas concretas, un número definido de trampas, etc., lo que parece influir en mayor o menor medida en las especies de escarabajos coprófagos. Otro factor importante a tener en cuenta es el esfuerzo de muestreo (Tocco *et al.*, 2016). De esta manera, si los estudios difieren en el diseño experimental, no son comparables entre sí (Tocco *et al.*, 2016; Mora-Aguilar *et al.*, 2023) y no se puede llegar a ninguna conclusión razonable. Por ello, todos los esfuerzos deberían estar destinados en encontrar una forma de estandarizar la metodología y que sea lo más homogénea posible para todas las regiones del planeta (Tocco *et al.*, 2016; Mora-Aguilar *et al.*, 2023).

Además, los investigadores deberían tener presente que, para llevar a cabo su estudio, la metodología debe adaptarse lo mejor posible a su hipótesis o lugar de estudio. Siempre deben priorizar la obtención de la mayor cantidad de información posible, pero también tratar de minimizar el efecto negativo sobre el grupo de estudio. En algunas situaciones, tendrán que sopesar si utilizar un método comúnmente utilizado en otros estudios o uno que se emplea menos pero que podría ser más apropiado para su estudio (Hohbein & Conway, 2018). Por lo tanto, antes de realizar cualquier diseño experimental, los investigadores deberían verificar si ya existen estudios en la zona de estudio y/o qué tipo de metodologías se han utilizado.

En los últimos años, se han desarrollado otras metodologías no letales para el estudio y seguimiento de los escarabajos coprófagos. Este procedimiento se basa en el *metabarcoding* (Camila *et al.*, 2021; Drinkwater *et al.*, 2021; Sigsgaard *et al.*, 2021; Pedersen *et al.*, 2024), que analiza el ADN que se encuentra en el contenido intestinal de los escarabajos coprófagos para determinar de qué excrementos se han alimentado. Gracias a ello, también es posible conocer la dinámica poblacional de los mamíferos con los que están asociados (Pedersen *et al.*, 2024). Incluso se han podido detectar animales que se encuentran en peligro de extinción (Drinkwater *et al.*, 2021). Aunque este procedimiento está ofreciendo resultados bastante prometedores, todavía le queda un largo camino por recorrer en esta dirección (Drinkwater *et al.*, 2021; Sigsgaard *et al.*, 2021; Pedersen *et al.*, 2024). Por lo que, de momento, si no queda otra opción se tendrá que seguir recurriendo a los métodos tradicionales.

Como resumen, esta tesis ha querido profundizar en el conocimiento de los escarabajos coprófagos, en algunos aspectos como puede ser el tipo de alimentación que tienen o cuales son los factores que en mayor medida moldean sus patrones de distribución. Además, se ha evaluado el grado de optimización de la metodología empleada para la captura de los escarabajos coprófagos. No es casualidad que los escarabajos coprófagos sean de los taxones más estudiados dentro de los insectos (Spector, 2006; Raine & Slade, 2019; Giménez-Gómez *et al.*, 2020). Todos los servicios ecosistémicos que ofrecen al ecosistema (Andressen, 2002; Nichols *et al.*, 2008; Nichols & Gómez, 2014), unidos al hecho de que puedan ser utilizados como bioindicadores (Spector, 2006), explican que hayan sido utilizados en multitud de investigaciones ecológicas y estudios de biodiversidad en todo el mundo (Spector, 2006; Agoglitta *et al.*, 2012; Bourg *et al.*, 2016; Raine & Slade, 2019; Carvalho *et al.*, 2020). Hacer estudios globales de un ecosistema es muy complejo y, a menudo, da lugar a interpretaciones erróneas de los patrones subyacentes, por lo que el papel de los grupos bioindicadores entra en juego (Davis *et al.*, 2001). De ahí, que cuanto más conocimiento se tenga sobre los escarabajos coprófagos y del medio que les rodea, más fácil será comprender el funcionamiento de los ecosistemas. Aunque exista mucha literatura sobre los escarabajos coprófagos, esta tesis ha aportado nuevos enfoques que anteriormente no se habían tenido en cuenta, quedando todavía muchas preguntas sin respuestas. El único factor limitante es el tiempo, por lo que estudios como éste son cruciales para aprender a realizar la monitorización y la conservación de las especies y sus respectivos ecosistemas.

FUTURAS INVESTIGACIONES

El objetivo general de esta tesis ha sido profundizar en algunos aspectos ecológicos de los escarabajos coprófagos de los cuales ya se tenía constancia, pero añadiendo nuevas aportaciones. Por ejemplo, se utilizaron por primera vez excrementos de animales exóticos a la zona de estudio para determinar la existencia de preferencias tróficas; o, se analizó el efecto que tiene la presión atmosférica sobre los patrones de distribución de los escarabajos coprófagos, algo que tampoco antes se había estudiado. Esto demuestra que, aunque los escarabajos coprófagos sean un grupo muy conocido y ampliamente estudiado en todas las regiones del planeta por su papel como grupo bioindicador, aún queda mucho por descubrir sobre ellos. Esta tesis ha conseguido responder satisfactoriamente a todas las hipótesis planteadas, pero ha tenido sus limitaciones. Por ejemplo, cuando se estudiaron los efectos de las diferentes variables climáticas, se pudo ver que ninguna de las variables ecológicas era capaz de explicar el 100% de la variabilidad observada. Esto indica que existen otras variables no contempladas en este estudio que están ejerciendo un efecto sobre los patrones de diversidad de los escarabajos coprófagos. Algunos estudios han podido constatar que existen otros factores ecológicos, como la cobertura vegetal, el tipo de hábitat o la altitud, entre otros, que tambien parecen ejercer un efecto sobre los escarabajos coprófagos. Por tanto, sería interesante hacer un estudio que englobara los diferentes factores que se conoce que surten un efecto sobre los escarabajos coprófagos, para así, discernir cuanto explica cada uno de ellos.

Por otro lado, aunque se haya demostrado que las especies de los escarabajos coprófagos muestran preferencias por algunos tipos de excremento, no se sabe con certeza qué es lo que desencadena esta respuesta. Algunos estudios afirman que los compuestos orgánicos volátiles que emanan de los excrementos son los principales responsables de que los escarabajos coprófagos desarrollen preferencias por uno u otro excremento. No obstante, aún se desconoce bastante sobre este tema, por lo que sería interesante para futuros trabajos tener en cuenta este componente. Un aspecto que mejorar para futuros estudios, sería incluir excrementos de carnívoros, algo que fue imposible de conseguir para la tesis. Aun sabiendo que no suelen tener mucho éxito este tipo de excrementos, sería conveniente ver la respuesta que tendrían los escarabajos coprófagos de la zona de estudio a un régimen alimenticio diferente al que se ha estudiado. Otro aspecto por mejorar y que podría ser muy interesante sería el uso de otros recursos tróficos diferentes al excremento. Aunque en la región Paleártica parece ser una respuesta minoritaria, no es algo que se haya estudiado con demasiado detalle. Por tanto, estudios que quieran seguir profundizando en el tema de las preferencias tróficas, podrían incluir otros recursos tróficos y examinar si los escarabajos coprófagos se sentirían atraídos por ellos.

De entre todos los aspectos estudiados en esta tesis, en el que habría que invertir un mayor esfuerzo sería en la optimización de la metodología empleada. Si bien es cierto que las trampas *pitfall* gozan de mucha popularidad al ser sencillas y fáciles de usar, además de ser muy eficaces a la hora de capturar escarabajos coprófagos; esto ha resultado ser una desventaja a la hora de encontrar un consenso en el diseño experimental. La cantidad de variantes existentes imposibilita que se puedan llegar a encontrar soluciones conjuntas. Por ello, todos los esfuerzos deberían estar puestos en buscar una alternativa que permita resolver este problema.

Por último, con el creciente abandono de las prácticas ganaderas en gran parte de los pastizales europeos, sería conveniente establecer un programa de monitorización a medio y largo plazo de las comunidades de escarabajos coprófagos para ver cómo varían sus dinámicas poblaciones a lo largo del tiempo, que también sirviera de sistema de vigilancia para que si fuera necesario intervenir, las respuestas en pro de su conservación llegasen lo antes posible.

CONCLUSIONES

Las conclusiones que se pueden extraer de esta tesis son las siguientes:

I. Los escarabajos coprófagos de las zonas supramediterráneas ibéricas son generalistas y oportunistas con respecto a la fuente de alimento, siendo capaces de alimentarse de excrementos procedentes de diferentes animales. No obstante, cuando fueron expuestos a excrementos con cualidades fisicoquímicas diferentes mostraron tener ciertas preferencias tróficas.

II. El origen del excremento no parece influir sobre las especies de escarabajos coprófagos. Por ejemplo, la mayor diversidad de especies y abundancia de individuos de escarabajos coprófagos se encontró en las trampas cebadas con excremento de elefante.

III. Las diferentes variables climáticas y aquellas relacionadas con el tiempo ejercen un efecto sobre las comunidades de escarabajos coprófagos. Las variables relacionadas con el tiempo parecen ser las más explicativas, lo que demuestra que los patrones de diversidad de los escarabajos coprófagos varían a lo largo del año.

IV. Es la primera vez que se estudia el efecto de la presión atmosférica sobre los escarabajos coprófagos. Aunque no se han observado resultados determinantes, sería interesante continuar con el estudio de esta variable y sus posibles efectos.

V. Hay que tener en cuenta que existen otros factores, ya sea ecológicos, geográficos o históricos, que no se han considerado en este estudio y que tambien son responsables de los patrones de diversidad actuales de los escarabajos coprófagos.

VI. No existen diferencias considerables entre los tres tiempos de exposición estudiados, siendo las comunidades prácticamente idénticas. Por ello, se aconseja mantener las trampas un máximo de 24 horas, ya que mantenerlas más tiempo no aportaría mucha más información sobre la biodiversidad. Además, de esta forma, se beneficia a las comunidades de escarabajos coprófagos.

VII. Sería conveniente hallar la forma de estandarizar la metodología y evitar que haya tanta heterogeneidad en los diseños experimentales. Solo así se podrá avanzar en la misma dirección para la conservación de los escarabajos coprófagos y sus ambientes.

CONCLUSIONS

The conclusions that can be drawn from this thesis are the following:

I. Dung beetles from Supramediterranean floor are generalists and opportunists regarding their food source and can feed on excrement from different animals. However, when they were exposed to excrement with different physicochemical qualities, they showed certain trophic preferences.

II. The origin of dung does not seem to influence dung beetle species. For example, it turned out that the highest species diversity and abundance of dung beetle individuals was found in traps baited with elephant dung.

III. Different climatic and time-related variables influence dung beetle communities. Time-related variables appear to be the most explanatory, demonstrating that dung beetle diversity patterns vary throughout the year.

IV. This is the first time the effect of atmospheric pressure on dung beetles has been studied. Although not all the results have been as expected, it would be interesting to continue the study of this variable and its possible effects.

V. It must be considered that there are other factors, whether ecological, geographical or historical, that have not been considered for this study and that are also responsible for the current diversity patterns of dung beetles.

VI. There are no considerable differences between the three exposure times studied, the communities being practically identical. Therefore, it is advisable to keep the traps for a maximum of 24 hours, since keeping them longer would not provide much difference. In addition, dung beetle communities benefit in this way.

VII. It would be convenient to find a way to standardize the methodology and avoid so much heterogeneity in experimental designs. Only in this way can progress be made in the same direction for the conservation of dung beetles and their environments.

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