Title: Multidimensionality in the thermal niches of dung beetles could limit species' responses to temperature changes

Running Title: Thermal niche multidimensionality

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Abstract

Understanding the consequences of climate change requires understanding how temperature controls species' responses across key biological aspects, as well as the coordination of thermal responses across these aspects. We study the role of temperature in determining the species' diel, seasonal, and geographical occurrence, using dung beetles as a model system. We found that temperature has relatively low –but not negligible– effects in the three spatiotemporal scales, once accounting for alternative factors. More importantly, the estimated thermal responses were largely incongruent across scales. This shows that species have multidimensional thermal niches, entailing that adjustments to fulfil temperature requirements for one biological aspect, such as seasonal ontogenetic cycles, may result in detrimental effects on other aspects, like diel activity. These trade-offs can expose individuals to inadequate temperatures, reducing populations' performance. Paradoxically, the relatively weak effects of temperature we found may have serious consequences for species' responses to warming if temperature regulates essential aspects of species' biology in divergent ways.

35 **Keywords:** biological scale, daily activity, geographic distribution, niche dimensionality,
36 phenology, physiological trade-offs

37

38 **Introduction**

39 Temperature is fundamental for the efficient capture and management of the energy that
40 maintains living organisms (Brown et al. 2004). Temperature variations affect the
41 abundance and distribution of species (Angilletta 2009), the variability of ecological
42 systems (Wang et al. 2009), and even the history of life and biodiversity on Earth itself
43 (Schwartzman 1999, Mayhew et al. 2008). Indeed, temperature plays a critical role in
44 controlling key aspects such as species' spatiotemporal distribution, physiological activity
45 or individual growth rates (Somero 2005, Thackeray et al. 2016, Scranton &
46 Amarasekare 2017, Madrigal-González et al. 2018), among many other things. Here, the
47 effects of temperature on species' geographic distributions and seasonal and diel activities
48 are of particular interest since variation in these aspects can have dramatic consequences
49 for their ecological performance and persistence (Edwards & Richardson 2004,
50 Schweiger et al. 2008, Rader et al. 2013). The ongoing climate changes are drastically
51 modifying the spatial and temporal organization of biodiversity (Chapin III & Diaz
52 2020), which is leading to spatial and seasonal decouples of interacting species (Sheldon
53 et al. 2011) and, thus, to the disruption of food webs and ecosystem services (Román-
54 Palacios & Wiens 2020). Ecologists and climatologists have accumulated a large amount
55 of evidence on these effects during recent decades, which are especially relevant for
56 ectotherms (Paaijmans et al. 2013). Despite this evidence, how temperature responses
57 integrate across different species' aspects is largely unknown. To obtain this knowledge
58 is crucial because incongruous responses can lead to incompatible adjustments to
59 temperature changes along biological aspects, compromising the species' performances
60 under climate change.

61 Delimiting the actual effect of environmental temperature on the distribution and
62 abundance of species may become difficult when other variables that are either spatially
63 or temporally correlated with temperature are considered simultaneously. For instance,
64 the latitudinal distribution of species in the Northern Hemisphere is associated with
65 historical events and dispersal limitations, whose effects generate geographical patterns
66 that can be confounded with those of temperature variations (Araújo et al. 2008, Hortal et
67 al. 2011, Calatayud et al. 2016, 2019). Similarly, the apparent relationships between
68 temperature and either seasonal or diel activities may be indeed conditioned by life-

69 history constraints related with the time required to complete individual development,
70 species' voltinism, the phase in which overwintering occurs, photoperiod limitations,
71 light requirements, and the reliance on solar radiation independently on the
72 environmental temperature (Bradshaw & Holzapfel 2007, 2010, Teder 2020). Hence,
73 assessing the predictive value of temperature in accounting for the spatial and temporal
74 variations in species occurrence and abundance would require considering any alternative
75 variables that could play a significant role in these variations.

76 Experimental setups can help unravel the “true” role of temperature in driving
77 geographical, seasonal and diel patterns for some model organisms while controlling for
78 other variables (Angilletta 2009). However, experiments based on artificial thermal
79 gradients can subject individuals to new and unrealistic stress conditions, thereby
80 providing overestimated projections of species responses (Guo et al. 2020). Alternatively,
81 one could explore the contribution of temperature using observational data where the
82 variations in temperature and other complementary predictors are decoupled. For
83 example, the effects of temperature and solar radiation can be teased apart using diel
84 activity from consecutive days that showed substantial variations in temperature (*i.e.*,
85 while presenting almost equal sunlight incomings). Similarly, the effects of temperature
86 and day length can be teased apart using seasonal data along steep temperature gradients,
87 with nearly equal day lengths (such as *e.g.*, elevational gradients). Finally, the role of
88 temperature in determining the species' distribution can be assessed by comparing
89 geographical areas with different temperature regimens. That is, if temperature is an
90 important variable, we should find similar responses under different background
91 temperatures.

92 The relevance of temperature in accounting for the spatiotemporal variation in
93 species occurrence and abundance may thus be estimated from observational data,
94 comparing the results from including or not alternative predictors to account for
95 complementary causal factors. Temperature will stand out as a relevant factor across
96 different biological scales if its association with several species' responses is high
97 throughout different spatiotemporal dimensions, but also if such responses are congruent
98 across dimensions. The congruence in thermal responses to diel, seasonal and
99 geographical gradients would support the universal and homogeneous role of temperature
100 in delimiting the occurrence and abundance of species. Note here that expectations are
101 that different mechanisms are behind the response to temperature variations associated
102 with geography, seasonality and diel rhythms. For instance, daily temperature variations

should also be related to changes in light or other environmental factors that can generate behavioural, endocrine, and physiological diel rhythms (Levy et al. 2019). In contrast, responses to seasonal temperatures should be associated with the annual rhythms and the need to synchronize life history phases with seasonal variations in climate (Saunders 2020). On the other hand, responses to geographical variations in temperature should relate to local adaptation processes acting at the population level, and likely involving the above-mentioned individual tolerances and ontogenetic timing, as well as other essential species attributes (Sunday et al. 2019).

Despite these differences, a certain level of congruence in the responses would indicate the consistent role of temperature as a holistic and predictable driver of key biological aspects. Such congruence would be evident, for example, if species occurring in colder regions are also active during colder periods of the year and at colder hours of the day in areas of milder climate. Such hypothesized thermal congruence is fundamental to respond adequately to global warming, as decoupling responses across different spatiotemporal gradients may expose local populations to critical temperatures, thus compromising their long-term persistence. For instance, if seasonal and diel responses to temperature are decoupled, species might not be able to adjust seasonal cycles as much as it would be necessary to prevent individuals from facing critical temperatures during diel activities. Following this line of evidence, studying the congruence of thermal responses across evolutionary lineages is also important because a marked phylogenetic signal in thermal niches would also point to the relevance of temperature changes. That is, if thermal adaptations are evolutionarily conserved, species might present limited ability to modify their thermal responses, being unable to cope with climate warming. Should this be true, phylogenetic biases in the potential effects of climate warming would be also expectable. Despite the relevance of studying the consistency of thermal responses across spatiotemporal gradients and evolutionary lineages, integrative studies on this topic are lacking.

Here we study the thermal responses associated with geographical, seasonal, and diel temperature variations using several temperate dung beetle species as a model system. Dung beetles are capable to self-regulate their body temperature and produce heat depending on their body size (Verdú & Lobo 2008, Verdú et al. 2012) a physiological adaptation directly linked to the need of a quick dispersal response to exploit an ephemeral resource. In addition, they feed on cattle from domestic and wild animals, participating in nutrient cycling and seed dispersion (Nervo et al. 2017, Milotić et al

2019), and thus, providing important ecosystem functions. These characteristics make dung beetles an ideal and important group to study thermal responses.

Specifically, we evaluated the responses of dung beetles to changes in temperature associated to: (i) diel rhythms across three consecutive days with contrasted temperatures; (ii) seasonal rhythms across six sites located at different elevations; and (iii) geographical ranges along five river basins in the Iberian Peninsula (Fig. 1). We hypothesized that if temperature is the main factor determining the activity and distribution of dung beetles, its effect should be observed along the three considered spatiotemporal gradients, and its relevance would be higher if the effects of other alternative and/or complementary factors are low. Furthermore, congruence in the different species' thermal responses to diel, seasonal and geographical changes would be expected if the importance of temperature is independent of the spatiotemporal context. On the contrary, a low explanatory capacity of temperature and a lack of congruence in its effects across the three spatiotemporal gradients would support a limited and dissimilar role of temperature depending on the spatiotemporal context. Finally, if species are evolutionarily limited to adapt to new thermal regimens, we expect thermal niches to be phylogenetically conserved.

Material and methods

Data origin

We use data on 16 Iberian dung beetle species of the family Scarabaeidae (ten from Aphodiinae and six from Scarabaeinae subfamilies). These species were selected because they occurred in at least 10% of the samples of the three datasets considered, covering different spatial and temporal extents (see below). All considered species (Table 1) are of small body size, with body weights far smaller than 1.9 g (0.2 g at most), the threshold from which endothermy is thought to appear in this group of beetles (Verdú et al. 2006). Temperature–occurrence associations for all these species were examined along: (i) five geographical areas of similar extent but different temperature regimes within the Iberian Peninsula (geographical dataset or GD); (ii) six sites placed across a steep elevational range in Central Iberia, and sampled during the same dates but differing in their environmental temperatures (seasonal dataset or SD); and (iii) three consecutive days with similar daily variations but different weather conditions in a single locality near the centre of the same elevational range (diel dataset or DD).

170

171 *Geographical Dataset.* The GD is divided in five study areas, corresponding to the major
 172 river basins of the Iberian Peninsula (Ebro, Duero, Tajo, Guadiana and Guadalquivir;
 173 limits extracted from HydroBASINS data available at www.hydrosheds.org, Lehner &
 174 Grill 2013, Fig. 1a). These natural areas were used since their borders correspond with
 175 marked geographical accidents, which are expected to act as dispersal barriers.
 176 Furthermore, they are relatively similar in extent (areas ranging from 5.6×10^4 to $9.7 \times$
 177 10^4 km²) and almost follow a latitudinal gradient, hence showing contrasting
 178 environmental temperatures (Fig. 1b). In each of these basins, we collected all
 179 georeferenced occurrences of the selected species from GBIF (www.gbif.org, accessed
 180 May 2020) and additional published sources (Hortal & Lobo 2011). As this kind of data
 181 is biased due to historically uneven sampling effort (Lobo et al. 2018), the occurrences
 182 were pooled within UTM grid cells of 10 x 10 km spatial resolution. This grain was
 183 selected because it corresponds to the effective resolution of most of the occurrence
 184 information in the dataset, and it is appropriate to avoid the effects of oversampled
 185 localities while retaining a reasonable climatic detail. The frequency of each species'
 186 occurrence data in temperature bins of 1°C (ranging from -3 to 20°C, n=24) was
 187 calculated for each river basin ($24 \times 5 = 120$), and these figures were used as dependent
 188 variables in the subsequent regression analyses.

189

190 *Seasonal dataset.* Six sites along an elevational gradient located in the Sierra de
 191 Guadarrama (Central Spain) (Fig. 1a, Espinoza 2016) were used to explore the effect of
 192 temperature variations in SD. Elevations range from 755 to 1900 m a.s.l., separating sites
 193 approximately 200 m a.s.l.. Each survey site was sampled approximately every three
 194 weeks, totalling fourteen times from May 2012 to June 2013. We choose this elevation
 195 gradient because these sites show considerable variations in temperature during the whole
 196 period of the surveys (Fig. 1b). The sampling protocol in each periodical sample
 197 consisted of five pitfall-traps baited with fresh cattle dung and separated around 30 m
 198 from each other. Traps were placed in open habitats to avoid potential habitat and shadow
 199 effects and were active during 48 h. The individuals of these traps were pooled together,
 200 obtaining an estimation of each species' abundance per elevation site and date ($6 \times 14 =$
 201 84), which were used as response variables in subsequent statistical analyses.

202

203 *Diel Dataset.* Temperature effects on diel activity were assessed using dung beetle data
 204 from a grassland located next to El Ventorrillo MNCN field station, placed in the Sierra
 205 de Guadarrama at an approximate elevation of 1500 m a.s.l. (Fig. 1a). This locality was
 206 chosen as it shows a high diversity of dung beetles (between 30 and 40 species belonging
 207 to the considered subfamilies; Cuesta & Lobo 2019). We sampled three consecutive days
 208 (April 28th–30th 2015) that showed contrasting temperatures, with around 8 °C of
 209 difference between the mean temperatures of the coldest and the hottest days (Fig. 1b).
 210 Each day, ten pitfall traps baited with fresh cattle dung were distributed around a
 211 circumference of approximately 50 m. of radius (*i.e.*, traps were at least 30 m apart from
 212 each other). Since we intended to measure the flight activity during short periods, the bait
 213 was introduced into a nylon stocking piece to avoid the stagnancy of beetle individuals
 214 within the dung bait along different sampling events. We checked all traps every 30 min.
 215 from dawn to dusk (approximately from 7:30 am to 7:00 pm, n=23), collecting all
 216 individuals to subsequently identify them in the laboratory. Traps were also checked
 217 during the night to discard nocturnal activity. Individuals from the ten traps were pooled
 218 together, obtaining an estimation of the abundance of active individuals from each
 219 species each 30 min (23 x 3 = 69), which were further used as dependent variables.

220

221 *Temperature measures and alternative correlates*

222 Temperature measures were obtained from different standardized methods for each one
 223 of the different spatio-temporal scales considered, but trying to maintain a considerable
 224 degree of congruence among them. For the *Geographical Dataset*, we obtained mean
 225 annual temperatures at a 30 sec resolution from the WorldClim database (see
 226 www.worldclim.org, Hijmans et al. 2005). We preferred mean annual temperatures over
 227 monthly average figures since the precise seasonal activity over the complete study area
 228 was unknown for most of the species. Nevertheless, spring and autumn temperatures (the
 229 seasons when phenological peaks occur for most species) were positively correlated with
 230 mean annual temperatures (Pearson's $r = 0.99$ and 0.97 , respectively), so we assume that
 231 mean annual temperature is a reasonable proxy for both of them.

232 For the *Seasonal Dataset*, we set up a temperature data logger in each of the
 233 elevational points during the whole period of the study. This device was placed in the
 234 shadow at one meter from the ground to escape from extreme temperatures due to
 235 insolation, mimicking the meteorological stations on which WorldClim data are based on.

236 Temperature was recorded each 10 min. and we used the mean daily temperature when
237 pitfall-traps were active.

238 In the case of the *Diel Dataset*, temperature measurements were taken using five
239 data loggers placed in the study site just in the centre of the circumference formed by the
240 traps. Data loggers were placed to recover temperature measurements from the different
241 microclimatic conditions available for dung beetles: two at one meter over the ground, in
242 the sun and shadow; another two directly on the ground, also both in the sun and shadow;
243 and one buried at 10 cm depth. Preliminary results showed that the mean temperatures
244 from the data logger placed on the ground in the sun were those that best correlated with
245 the species' diel activity, so we used these measurements in subsequent analyses.
246 Temperature was recorded each minute, and average temperatures during the 30 min
247 before traps were checked were used as predictors.

248 As previously stated, the effects of temperature measurements might be
249 overestimated due to its collinearity with other factors with which it shares spatial (in the
250 case of GD) or temporal structure (in the case of SD and DD). We quantified this
251 potential overestimation effect by using different “contrast variables”, alternative
252 predictors which are often partly correlated with temperature but are either measures or
253 proxies of other potential causal factors for dung beetle spatial and temporal responses.
254 These alternative predictors were temperature availability and survey effort in the case of
255 GD, day of the year for SD, and hour of the day in the case of DD. The effect of
256 temperature on the frequency of occurrence (GD) or abundance (SD and DD) that is
257 independent of these contrast variables was assessed as the “pure” effect of temperature
258 variations that is independent of the range of temperatures available (GD), the period of
259 the year (SD), and the hour of the day (DD) (see analytical methods below).

260 Temperature availability for each basin is the relative frequency of 10 x 10 km
261 UTM cells in each 1°C temperature bin. This variable aims to represent the thermal
262 spectrum available in each basin. Hence, a high explanatory capacity of this variable on
263 the frequency of occurrence of a species would imply that the apparent thermal
264 preference of this species can be simply because its spatial pattern of occurrence mimics
265 the distribution of temperatures in the analyzed basin. Further, the typical correlation
266 between the observed pattern of occurrence of a species and the spatial distribution of
267 survey effort can also generate spurious correlations between species' frequency and
268 temperature in each basin. This potential source of error was considered here by
269 calculating the relative frequency for each 1°C temperature bin of all dung beetle records

270 included in the formerly mentioned databases and pooled within the 10 x 10 km UTM
271 cells. Nevertheless, we found that this estimation of survey effort and temperature
272 availability were highly and positively correlated in all basins (Pearson's r ranging from
273 0.97 to 0.99), since the most frequent temperatures have been also surveyed more often,
274 which implies that the surveys are randomly allocated within the available temperatures.
275 Consequently, we discarded using survey bias as contrast variable, considering that the
276 effect of temperature availability also includes differences in survey effort. In the case of
277 SD data, the day of the year was obtained by first ordering the available dates from the
278 day corresponding to the summer solstice (June 21th = 0 or 360), to subsequently convert
279 these figures into radians and obtaining two circular variables by calculating their cosine
280 and sine values. Thus, the summer-winter oscillation is represented by the cosine of the
281 date and oscillates from 1 to -1, whereas the spring-autumn transition is represented by
282 the sine of the date scale 1 to -1. Finally, the hour of the day (DD data) is simply codified
283 as the number of minutes from dawn.

284

285 *Statistical analyses*

286 *Explanatory capacity of temperature*

287 We first explored the independent capacity of temperature to explain variations in dung
288 beetle data in GD, SD, and DD. For each dataset, we conducted Generalized Linear
289 Regression Models of the relative frequency or the abundance of each species as a
290 function of temperature values. All data coming from the five basins (in GD), the six
291 elevational sites (SD), and the three days (in DD) were considered at the same time in
292 each one of the three models. A curvilinear quadratic function of temperature was
293 included in all the cases to account for the typical unimodal performance curves of
294 ectotherms (Huey & Kingsolver 1989). A negative binomial error distribution for the
295 dependent variable was assumed to avoid overdispersion issues associated with the
296 Poisson error distribution (Blasco-Moreno et al. 2019), and it was related to the set of
297 predictors via a logarithmic link function. It is important to note that we did not include a
298 term in the models to account for the different spatial (*i.e.*, basins and elevations) and
299 temporal (*i.e.*, days) units. By doing so, we were ignoring other factors that may affect
300 the distribution and activity of dung beetles, besides temperature and the contrast
301 variables analyzed. However, this allows us to tease apart the effects of temperature and
302 the formerly mentioned contrast variables with a spatial and temporal structure while
303 avoiding model overparameterization. Hence, we fitted three supplementary GLMs

representing different hypotheses regarding the importance of temperature: (i) a full model where both temperature and contrast variables are included altogether, (ii) a model including only these contrast variables, and (iii) a null model where only the intercept was included. We assumed a linear relationship between the density of occurrence and temperature availability (GD); whereas in SD and DD, we assumed curvilinear relationships between abundance and contrast variables by including a quadratic term of both the number of minutes from dawn, and date sine and cosine. We used a deviance partition approach (Legendre 1993, see also Calatayud et al. 2019 for the same approach) to calculate the deviance explained by each set of variables alone (*i.e.*, temperature *vs.* contrast variables; herein, total pseudo R^2) and once accounting for the collinearity with other variables (herein, partial pseudo R^2). Model performance was assessed using the Akaike Information Criterion corrected for small sample size (AICc).

Thermal niche attributes

Deriving thermal niches from occurrence data typically provides a partial description of the whole potential response of the species (Sánchez-Fernández et al. 2012, Saupe et al. 2018). However, occurrence-based thermal niches may nevertheless be characterized by different attributes such as the optimum temperature and niche breadth (Gouveia et al. 2014, Löffler & Pape 2020, Fig. 2). The temperature optimum of each species was assessed by fitting quadratic curves in a GLM and calculating the maxima as their inflection point (see Villén-Pérez & Carrascal 2015 for a similar procedure). Thermal niche breadth was also obtained as the area under the curve of these fitted curves. Fitted values were normalized to reach a maximum value of one to make calculations comparable among datasets and species.

We evaluated the intraspecific dissimilarity in the thermal niches across different spatial and temporal scales, herein called “thermal lability”, using data from the different study units used in each dataset; that is, between river basins, elevation sites, and days (Fig. 2). Thermal lability between pairs of units was measured using the Simpson index as follows:

$$S = \frac{\min(b,c)}{a + \min(b,c)},$$

where a represents the area under the curves where both curves overlap, and b and c represent the independent areas under the curves in study units (see Fig. 2). The larger the overlap between the curves obtained at different scales, the smaller the thermal lability

will be. We computed this index for all pairs of units in each dataset (*i.e.*, for each pair of basins, each pair of elevations, and each pair of days) and then considered the maximum dissimilarity among all pairs from the same dataset, as this measure will provide a more realistic estimate of the potential thermal lability of each species.

341

342 *Congruencies in thermal niches*

343 The congruence in the thermal niches of the different species derived from the three
344 datasets (*i.e.*, GD, SD, and DD) was assessed using Spearman rank correlations between
345 the deviance explained by temperature (*i.e.*, both for the total and partial pseudo R^2 s), as
346 well as the obtained temperature optima, thermal niche breadths and thermal labilities for
347 each pair of datasets. In addition to these descriptors, we explored the congruence in the
348 overlap of thermal niches estimated from different datasets. To do this, we examined
349 whether interspecific thermal niche dissimilarities were correlated between the different
350 datasets. We computed dissimilarities between the models' normalized fitted values
351 where the temperature was the only explanatory variable using the Simpson index as
352 previously explained, but in this case between pairs of species (see also Fig. 2). By doing
353 so, we created a thermal niche pairwise dissimilarity matrix for each dataset. Then, we
354 conducted Mantel tests based on Spearman's ρ correlation coefficient to assess the
355 relationship between dissimilarity matrices obtained from the different datasets.
356 Significance was evaluated by comparing observed ρ coefficients with 999 null values
357 obtained by permuting the dissimilarity matrices.

358

359 *Phylogenetic signal*

360 The potential lability of thermal niches shall be also assessed from an evolutionary point
361 of view. In this sense, a marked phylogenetic signal would indicate both potential
362 evolutionary constraints for temperature variation responses, and phylogenetically-
363 structured effects of global warming. We reconstructed a Bayesian phylogenetic
364 hypothesis for 18 species present in our datasets based on two mitochondrial (COI and
365 COII) and one nuclear markers (28S RNA, see Appendix S1 for details on phylogenetic
366 reconstruction). DNA markers were sequenced for this study and retrieved from Genbank
367 (Table S1, accessed in June 2016). Pagel's λ test (Pagel, 1999) and Blomberg's K
368 statistics (Blomberg et al. 2003) were used to explore the phylogenetic signal in the five
369 variables considered (total and partial deviance explained by temperature, temperature
370 optimum, thermal niche breadth, and thermal lability). , Significance for Pagel's λ was

assessed with a likelihood ratio test comparing the negative log likelihood obtained from the original tree topology with the negative log likelihood from a topology transformed to remove the signal (*i.e.*, $\lambda = 0$). In the case of Blomberg's K, we tested for significance by randomizing the labels of the phylogenetic tips and comparing observed and random K values. Finally, we also investigated for phylogenetic signal in the thermal niche dissimilarities for each dataset. To do so, Spearman correlations between thermal dissimilarities and phylogenetic distances were used, assessing significance by comparing observed correlations with null values where the labels of the tips of the phylogeny were randomized. In all cases where tip labels were randomized, p-values were calculated as the proportion of null values being equal or higher than observed values.

All analyses were conducted in R environment (R Core Team 2020), using the *AICcmodavg* package (Mazerolle 2019) to calculate AICc values, the function "sintegral" as implemented in the *Bolstad2* package (Curran 2013) to assess areas under the curves, the *vegan* package (Oksanen et al. 2019) for the Mantel tests, and the *phytools* package (Revell 2012) to calculate Pagel's λ and Blomberg's K.

Results

There is an evident gradient in the explanatory relevance of temperature towards higher relevance at progressively larger scales (*i.e.*, geographical > seasonal > diel). Model selection revealed that the full model, including temperature and contrast variables, was the most parsimonious for most species in most datasets (Table 1). As exceptions to this general pattern, in the geographical dataset, the model only including temperature was equivalent to the full model (according to AICc) for one species, and it was also the best supported for another species. In the seasonal dataset, the model only including temperature was the best supported for four species, whereas the model only including contrast variables was equivalent to the full model for just one species. Finally, the model including minute from dawn in DD data was equivalent to the full model for only two species and even better for one species (Table 1). In general, the total deviance explained by the models including temperature and contrast variables was considerably high (mean pseudo- R^2 s = 0.62, 0.63, and 0.77; ranges = 0.51-0.75, 0.38-0.86, and 0.64-0.86, respectively for GD, SD, and DD; see Fig. 3). Partial regressions revealed that the effects of temperature and contrast variables largely overlap, being the deviance independently explained by temperature considerably low (see Fig. 3). Interestingly, the percentage of

deviance explained by temperature decreased from the geographical (mean pseudo- R^2 s = 0.33; range 0.13–0.48), to the seasonal (0.19; 0.05–0.36) and diel datasets (0.08; 0.01–0.20) (see Fig. 3).

Thermal niche attributes derived from the different datasets showed little congruence. Neither the pseudo R^2 explained by temperature alone nor the total pseudo R^2 were positively and significantly correlated between any pair of datasets, and none of the thermal niche attributes were significantly correlated between the three considered datasets (Table 2). Moreover, Mantel tests showed that interspecific niche dissimilarities were not correlated among the three studied spatiotemporal scales (Table 2). Finally, we did not find phylogenetic signal for any of these variables in any of the datasets, except in the case of niche breadth for the diel dataset (Table 3).

Discussion

Our results show that the spatial and temporal responses of the studied species show large associations to contrast variables besides temperature, but also that temperature controls to dung beetle occurrence may increase towards larger temporal and spatial scales. This contrasts with our preliminary expectations of a high importance of temperature for dung beetle occurrence and activity based on the known basal ectothermic physiology of the considered species. Further, thermal niches were incongruent across scales for the studied species and lacked phylogenetic signal, indicating that thermal adaptations are highly variable both between and within species.

The generally low partial effects of temperature found in our study lead to two important conclusions: (i) the abundance, distribution, and activity of dung beetles are controlled by other factors different from temperature, which are at least partially represented by the *ad hoc* contrast variables used here; and (ii) dung beetle species must have biological mechanisms that provide them with the plasticity required to cope with the temperature variations associated to each spatiotemporal context. Thermoregulation and body heat gain are intimately linked to solar radiation in ectotherms (Angilletta 2009). Indeed, empirical evidence suggest that solar radiation is associated with dung beetles' body temperatures (Bartholomew & Heinrich 1978) and temporal variations in their abundance and species richness (Lobo et al. 1998). Hence, it is likely that this factor is a key environmental control of the diel activity of dung beetles. Regarding annual rhythms, photoperiod seems to be a crucial environmental cue regulating insects' seasonality (Nijhout 1994, Bradshaw & Holzapfel 2007). This is likely the case for dung

438 beetles, given the relatively weak effects of temperature on their phenology found in our
 439 study. Also, the different life-history phases of an insect need to be synchronized
 440 seasonally, and these require a minimum amount of time to complete. The development
 441 of a dung beetle individual requires from 30 to 80 days depending on the species
 442 (Christensen & Dobson 1977, Romero-Samper & Martín-Piera 1995, 2007, Arellano et
 443 al. 2017), a time that determines key life-history characteristics such as the number of
 444 generations per year or the overwintering phase. These developmental constraints are
 445 therefore hard to modify without major evolutionary changes (Teder 2020), thereby
 446 limiting the effects of environmental temperature on the seasonal abundance and
 447 occurrence of dung beetle species. Finally, many factors contribute to shaping the
 448 geographical distribution of dung beetle species, including dispersal limitations (Lobo et
 449 al. 2006), historical events (Hortal et al. 2011), or the response to other environmental
 450 variables such as precipitation, soil, habitat, or trophic preferences (Hanski et al. 1991,
 451 Hortal et al. 2001, Lobo & Martín-Piera 2002). It is important to note that we have not
 452 quantified the effects of these variables explicitly, so their inclusion could further weaken
 453 the pure effect of temperature.

454 Regardless of the effects of alternative factors, it seems accurate that dung
 455 beetles have mechanisms to withstand marked temperature variations, especially those
 456 associated with diel and seasonal rhythms. Given the nature of our data and analyses,
 457 these mechanisms can be operating either at the population level, at the individual level,
 458 or both. At the population level, a high genetic diversity linked to large phenotypic
 459 variability can produce the apparently labile thermal responses. That is, as individuals are
 460 sorted in time and/or space according to their environmental adaptations, population(s)
 461 formed by individuals with different thermal preferences would show a certain level of
 462 thermal independency. This mechanism seems more plausible to explain results in the
 463 geographical datasets, where river basins can act as dispersal barriers, limiting gene flow
 464 and enhancing local adaptation to different temperature regimens (Lenormand 2002).
 465 However, it seems less likely that this phenotypic variability alone is responsible for the
 466 responses to diel and seasonal temperature variations, where a high gene flow is expected
 467 between the individuals and populations that are active at different elevations or days.
 468 Physiologically plastic responses allowing individuals to be active at different
 469 temperatures seem a more plausible mechanism in this case (Crispo 2008). In any case,
 470 these two potential mechanisms (phenotypic variability and individual plasticity) are in
 471 agreement with the observed lack of phylogenetic signal on species responses to

472 temperature across scales, which indeed suggests a lack of thermal niche conservatism
473 (Gilbert & Miles 2019). The relative contribution of population phenotypic variability
474 and individual plasticity remains elusive, calling for further studies directed to unravel the
475 detailed mechanisms behind the diverse responses to temperature found in our study.

476 Be that as it may, the effects of temperature were significant and not negligible,
477 being larger for species distribution than for seasonal activity, and even smaller for diel
478 activity. The increasing importance towards larger scales may be related to the fact that
479 the effects of temperature on the studied biological aspects are nested. That is, the
480 occurrence in a given location would entail that a species holds the adaptations required
481 to maintain a stable population there, which include physiological and/or behavioural
482 adaptations to cope with the seasonal temperature variations that occur in that locality. In
483 the same way, a population with adults active during a given period of the year should
484 present adaptations to handle the daily temperature variations happening during the days
485 when adults are active. Hence, the hierarchically cumulative effects of temperature across
486 these biological scales may explain why temperature becomes more important for
487 geographic distributions than for temporal activities. Ascertaining the plausibility of this
488 idea requires further investigation of intraspecific responses to daily temperature
489 variations across seasons and seasonal temperature responses throughout different
490 populations placed across the species' geographic distribution.

491 Perhaps the most interesting of our results is the lack of congruence in the
492 realized thermal niches across the studied species and spatiotemporal contexts. This
493 means that, for instance, species occurring in colder regions do not appear in colder
494 months nor at colder hours of the day in other regions. This somehow counterintuitive
495 result could be related to the uneven relevance of the alternative variables for the
496 different species and spatiotemporal contexts, which facilitates the decoupling of the
497 thermal responses associated with the distribution and activity of dung beetles. It is likely
498 that the processes involved in adult movements, life-history cycles, and population
499 maintenance are differently regulated by temperature, despite of their nested nature. In
500 other words, our results suggest that species have multidimensional thermal niches, where
501 each critical biological aspect responds to temperature along a different dimension.
502 Therefore, rather than exerting a universal effect, temperature plays multiple roles in a
503 species' biology and metapopulation dynamics. This lack of congruence, together with
504 the low independent effects of temperature found in our deviance partition analyses,
505 indicates that estimates of thermal niches will be, in general, inaccurate and context-

506 dependent. This calls from being particularly cautious when using responses measured at
507 different scales as proxies for future responses to climate change. Overall, our results
508 show the difficulties in estimating general thermal niches of species, challenging
509 forecasts of species future dynamics under climate warming based on unidimensional
510 thermal niches (Gvoždik, 2018).

511 The partial control of temperature on the activity and distribution of dung beetles
512 may be both a blessing and a curse regarding the effects of climate warming. On the one
513 hand, the apparent thermal lability suggests that temperature increases should not
514 strongly modify neither diel and seasonal activities nor the geographic distribution of
515 dung beetles, likely preventing mismatches with interacting species and the subsequent
516 food chain perturbations. This assumption would contradict the results of studies
517 suggesting moderate or even large effects of climate change on dung beetle distributions
518 (Dortel et al. 2013, Menéndez et al. 2013, Holley & Andrew 2019). On the other hand,
519 the diel, seasonal, or geographical adjustments are among the fastest responses to climate
520 warming (Levy et al. 2019, Duchenne et al. 2020). However, our results suggest that the
521 response towards temperature variations is relatively independent at each spatiotemporal
522 scale. This entails that adjustments to temperature requirements may not be coordinated
523 across key biological aspects. Hence, adjustments to fulfil the temperature requirements
524 for one biological aspect may result in detrimental effects on other aspects, thereby
525 reducing individual and population performance as, *e.g.*, seasonal adjustments may
526 expose individuals to inadequate temperatures during diel activity. In the worst-case
527 scenario, the incapacity of species to adjust their temperature requirements by modifying
528 diel, seasonal, and geographical patterns at convenience will increase the likelihood of
529 local extinctions when the individuals are exposed to critical temperatures in their daily
530 or yearly periods of activity. Paradoxically, the partially weak effects of temperature we
531 found may have serious consequences for climate warming if temperature regulates
532 important aspects of species' biology in divergent ways (Tsai et al. 2020).

533 Overall, our results show that temperature may be less important than other
534 factors in determining dung beetle activity and distribution. Further, the incongruences in
535 thermal niches estimated from the geographic distribution and seasonal and diel activities
536 show the complex effects of temperature on key species aspects, pointing to a truly
537 multidimensional nature of thermal niches. Together with the partially weak control of
538 temperature on species activity and distribution, these incongruences may difficult fast

539 responses to climate warming, potentially exposing individuals to critical, or at least
540 inadequate, temperatures and reducing individual and population's fitness.

541

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Table 1. AICc values for the models of each species in each dataset. In all cases, we conducted a complete model (Full) including temperature and the corresponding contrast variables, a model only including temperature (Temp), a model only including contrast variables (Cont), and a null model where no predictor variable was included (Null). Contrast variables were minutes from dawn and its quadratic term for the diel data set; date sine and cosine and their quadratic terms for the seasonal dataset; and temperature availability for the geographic data set. The best models in terms of AICc and the equivalent ones ($\Delta AICc < 2$) are highlighted in bold.

Subfamily	Species	Diel				Seasonal				Geographic			
		Full	Temp	Cont	Null	Full	Temp	Cont	Null	Full	Temp	Cont	Null
Aphodiinae	<i>Acrossus depressus</i> (Kugelann, 1792)	176.53	245.53	187.59	264.43	120.25	126.26	120.67	149.35	172.98	173.17	209.50	209.95
Aphodiinae	<i>Agriolus constans</i> (Duftschmid, 1805)	140.21	197.94	145.50	214.29	200.92	210.56	206.92	216.62	211.85	218.76	269.52	289.54
Aphodiinae	<i>Aphodius fimetarius</i> (Linnaeus, 1758)	116.91	162.51	121.10	177.61	201.68	199.58	217.13	214.00	380.68	404.55	419.41	455.12
Aphodiinae	<i>Aphodius foetidus</i> (Herbst, 1783)	42.72	56.56	44.51	64.09	138.39	133.18	146.06	144.19	634.53	679.39	753.81	861.04
Aphodiinae	<i>Colobopterus erraticus</i> (Linnaeus, 1758)	128.81	150.10	136.82	164.96	208.49	251.21	217.59	272.82	343.34	366.05	372.06	410.67
Aphodiinae	<i>Esymus pusillus</i> (Herbst, 1789)	175.62	227.70	171.67	241.45	151.68	163.52	217.18	191.76	147.93	153.05	177.47	180.48
Aphodiinae	<i>Melinopterus sphaelatus</i> (Panzer, 1798)	471.34	534.10	493.63	577.91	307.12	322.42	321.94	343.35	289.63	304.26	354.89	390.33
Aphodiinae	<i>Teuchestes fossor</i> (Linnaeus, 1758)	194.71	256.95	208.75	280.58	89.06	98.58	96.18	116.19	258.00	268.42	304.76	318.01
Aphodiinae	<i>Trichonotulus scrofa</i> (Fabricius, 1787)	144.87	185.24	160.35	207.64	204.82	226.12	216.37	261.94	182.51	186.38	221.98	242.86
Aphodiinae	<i>Volinus sticticus</i> (Panzer, 1798)	305.09	342.35	310.59	371.12	116.05	407.35	121.57	122.05	133.88	132.11	167.53	169.92
Scarabaeinae	<i>Euronitellus fulvus</i> (Goeze, 1777)	39.24	59.86	49.17	67.31	446.74	473.23	454.04	519.71	285.43	306.31	306.07	352.08
Scarabaeinae	<i>Onthophagus fracticornis</i> (Preyssler, 1790)	255.26	325.6	266.11	350.04	188.32	184.52	200.87	201.75	274.14	279.86	317.51	329.60
Scarabaeinae	<i>Onthophagus lemuri</i> (Fabricius, 1781)	117.11	153.81	124.15	170.30	200.57	158.52	205.75	174.36	231.64	238.74	290.70	313.01
Scarabaeinae	<i>Onthophagus opacicollis</i> Reitter, 1892	71.03	80.84	76.13	90.69	343.31	355.11	350.70	356.49	207.58	215.60	218.29	251.59
Scarabaeinae	<i>Onthophagus similis</i> (Scriba, 1790)	256.91	342.23	260.48	359.42	612.48	617.79	646.30	658.81	312.48	328.99	363.43	400.08
Scarabaeinae	<i>Onthophagus vacca</i> (Linnaeus, 1767)	248.03	300.37	248.30	318.63	285.06	296.59	299.48	318.99	315.14	337.44	352.21	409.05

Table 2. Spearman's ρ correlation coefficients and P-values between the considered thermal niche attributes measured by the three studied datasets are detailed.. DD: Diel dataset. SD: Seasonal dataset. GD: Geographical dataset. * Results based on Mantel test.

	DD vs SD		DD vs GD		SD vs GD	
	ρ	P	ρ	P	ρ	P
Breadth	-0.074	0.788	-0.385	0.141	0.100	0.713
Optimum	-0.262	0.326	-0.179	0.505	0.394	0.132
Thermal lability	-0.261	0.347	-0.339	0.216	0.132	0.625
Total pseudo R²	0.029	0.914	-0.016	0.953	-0.200	0.456
Partial pseudo R²	-0.561	0.024	-0.440	0.088	0.053	0.848
Niche dissimilarity *	0.260	0.056	0.242	0.051	0.120	0.153

Table 3. Phylogenetic signal in thermal niches attributes for the three studied datasets (*i.e.*, geographical, seasonal and diel). Significant variables are highlighted in bold. * Results based on Mantel test.

Variable	Dataset	K	P	λ	P	ρ	P
Breadth	Geographical	0.480	0.150	0	1	-	-
	Seasonal	0.285	0.798	0	1	-	-
	Diel	0.998	0.001	1.096	0.002	-	-
Optimum	Geographical	0.292	0.811	0.002	0.990	-	-
	Seasonal	0.477	0.188	0.361	0.160	-	-
	Diel	0.292	0.710	0	1	-	-
Thermal lability	Geographical	0.475	0.171	0	1	-	-
	Seasonal	0.295	0.900	0	1	-	-
	Diel	0.467	0.228	0.007	0.970	-	-
Total pseudo R²	Geographical	0.287	0.857	0	1	-	-
	Seasonal	0.324	0.710	0	1	-	-
	Diel	0.313	0.726	0	1	-	-
Partial pseudo R²	Geographical	0.367	0.476	0	1	-	-
	Seasonal	0.388	0.398	0	1	-	-
	Diel	0.425	0.350	0	1	-	-
Niche dissimilarity *	Geographical	-	-	-	-	-0.100	0.089
	Seasonal	-	-	-	-	0.200	0.980
	Diel	-	-	-	-	-0.080	0.139

Figure 1. a) The areas of study for the geographical, seasonal and diel datasets (from left to right). Red squares show the position of the following down-scaled study site. b) Temperature variations in study sites. Lines correspond with predictions of general additive models (GAM) of: (i) temperature availability (measured as the number of 10 km² grid cells whose temperature fell within predefined temperature bins) as function of temperature for the geographic dataset (left); (ii) temperature as a function of days from New Year and minutes from dawn for the seasonal and diel datasets respectively. Analyses were computed independently for each basin, for each elevational site and for each day. GAMs explained an average of 0.90 of deviance across all analyses (median = 0.92, ranging from 0.79 to 0.97).

a) Study site

b) Temperature variations

Figure 2. Thermal niche attributes and overlap measure. x and y represent thermal response curves of two species or of a single species in two different study units (*i.e.*, days, elevation or river basins). From this curve we obtained the optimum temperature and the niche amplitude. Further, we used the overlap between them (a) and the two independent areas (b and c) to calculate the Simpson's dissimilarity index, as a measure of the congruence between the responses to temperature of the same species at different scales, and of different species within the same scale.

Figure 3. Partial regression results. The deviance explained by temperature alone, the contrast variables alone, and the overlap between them is shown. The contrast variables were minutes from dawn and its quadratic term for the diel data set (a); date sine and cosine and their quadratic terms for the seasonal data set (b), and temperature availability for the geographic data set (c).

Supporting information

Appendix S1

Genomic DNA was extracted from each individual using the BIOSPRINT 15 DNA Kit (Qiagen), following standard manufacturer's protocols for blood, and resuspended in 100 µl of buffer AE. We used COI Sca F, COI Sca R, COII am Sca and COII B 605 Sea (Villalba et al. 2002) and the universal 28S a y 28S 5b primers to amplify fragments of the mitochondrial cytochrome oxidase I (COI), the cytochrome oxidase II (COII) and the 28S genes. Amplifications for all gene fragments were performed in a 50 µl reaction containing 39.7 µl of H₂O, 5 µl of 10x PCR buffer, 1 µl of dNTP mix (10 mM), 0.5 µl of each primer (10 µM), 0.3 µl of AmpliTaq® DNA polymerase (Applied Biosystems) and 3 µl of DNA template. Thermocycling conditions consisted of an initial denaturing step at 94 °C for 4 min, followed by two cycles: (i) a precycle of 5 amplification cycles of 94 °C for 45 sec, 40 °C for 1 min and 72 °C for 1 min, and (ii) a cycle of 35 amplification cycles of 94 °C for 45 sec, 44 °C for 1 min and 72 °C for 1 min, followed by a final elongation step at 72 °C for 10 min and a rapid thermal ramp down to 4 °C. For all reactions, the presence of amplicons of the expected sizes was checked by electrophoresis on a 0.8 % agarose gel. PCR products were purified with the ethanol-precipitation method (Sambrook et al., 1989). Sequencing was performed by Secugen S.L. (Madrid, Spain), using BigDye® and the automated ABI PRISM 3730xl DNA Analyzer. Sequence chromatograms were read and contigs assembled using Sequencher version 4.7 (Gene Codes Corporation, Ann Arbor, MI). All new sequences were deposited in GenBank (see accession numbers in Table S1).

Sequences were aligned in CLUSTALW and MUSCLE, followed by visual inspection using BioEdit (Hall, 1999). Prior to phylogenetic analysis, jModeltest 2.1.1 (Darriba et al., 2012) was used to choose the best-fit model of nucleotide substitution for each of the four genes, and for combined matrices under the corrected Akaike information criterion (AICc). For the COI and COII, HKY was obtained, while Jukes Cantor for 28S. Phylogenetic analyses were performed in a Bayesian framework using BEAST v 2.4 (Drummond and Rambaut, 2007). We established 3 calibrations points based on Ahrens et. al (2014), setting uniform priors with lower and upper boundaries. The calibrations represent the basal split of the following taxa: Aphodiinae (58.7 – 55.8 Million years ago), *Aphodius* (37.2 – 33.9 Mya) and Scarabaeinae (92 – 83.5 Mya). For the age of the rest of the nodes, we set a LogNormal relaxed molecular clock for each

gene and let the software estimate the rate from the priors. The MCMC chain ran for 100.000.000 steps, sampled every 10.000 steps. Posterior distribution of all the parameters were checked using Tracer, as well as all ESS values being above 200. We built the tree using Tree Annotator, using the Maximum Clade Credibility implemented method after discarding the first 25% samples as a burn-in.

References

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Fig. S1. Bayesian phylogenetic hypothesis for the studied species. Posterior probabilities are provided. Blue bars represent the 95% credible interval around node ages.

Species	28	COI	COII
<i>Aphodius constans</i>	-	AY039372	AY039372
<i>Aphodius depressus</i>	ABXXXX	ABXXXX	ABXXXX
<i>Aphodius erraticus</i>	ABXXXX	ABXXXX	ABXXXX
<i>Aphodius fimetarius</i>	ABXXXX	ABXXXX	ABXXXX
<i>Aphodius foetidus</i>	-	ABXXXX	ABXXXX
<i>Aphodius fossor</i>	ABXXXX	ABXXXX	ABXXXX
<i>Aphodius pusillus</i>	ABXXXX	ABXXXX	ABXXXX
<i>Aphodius scrofa</i>	ABXXXX	ABXXXX	ABXXXX
<i>Aphodius sphacelatus</i>	ABXXXX	ABXXXX	ABXXXX
<i>Aphodius sticticus</i>	-	ABXXXX	-
<i>Euoniticellus fulvus</i>	ABXXXX	ABXXXX	ABXXXX
<i>Geotrupes stercorarius (OUT)</i>	KP419463	AY039377	AY039377
<i>Onthophagus fracticornis</i>	ABXXXX	-	-
<i>Onthophagus grossepunctatus</i>	ABXXXX	AY039347	AY039347
<i>Onthophagus lemur</i>	ABXXXX	AY039353	AY039353
<i>Onthophagus opacicollis</i>	-	ABXXXX	ABXXXX
<i>Onthophagus ovatus</i>	ABXXXX	AY039351	AY039351
<i>Onthophagus similis</i>	ABXXXX	ABXXXX	ABXXXX
<i>Onthophagus vacca</i>	ABXXXX	AY039359	AY039359
<i>Taurocerastes patagonicus (OUT)</i>	KP419662	GU984611	GU984611

Table S1. GenBank accession numbers of the used sequences. Outgroup species are indicated.