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2 **Title:** Climatic stability and resource availability explains dung beetles (Scarabaeinae)
3 richness pattern on the Americas

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7 **Abstract:** Climatic conditions are the main driver of species richness. Specifically, the
8 increase in climatic instability may reduce species richness directly and indirectly by
9 reducing resources available. This hypothesis is evaluated here using a producer-
10 consumer interaction to explain dung beetle richness on a continental scale (America)
11 using mammal richness as resource proxy and temperature and precipitation seasonality
12 as a proxy for climatic instability. A spatial path analysis was built in order to evaluate
13 this hypothesis while controlling for spatial autocorrelation and differences in the
14 sampling effort and abundance of each study (n=115) gathered from the literature. Dung
15 beetle richness was directly explained by temperature seasonality, precipitation
16 seasonality, and mammal richness, whereas only precipitation seasonality had an effect
17 modulated by mammal richness. This result reinforces the notion that species richness
18 can be explained by climatic conditions, but also reveals the importance of biotic
19 interactions in order to understand the mechanisms behind such patterns.

20 **Keywords:** climatic instability, resource diversity, dung beetle diversity, mammal
21 richness, Scarabaeidae

22 **Declarations of interest:** none.

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26 beetle communities used as source data for this study.

27 **Introduction**

28 Latitudinal diversity gradients are a widespread pattern in ecology (Gaston 2000;
29 Willig et al. 2003; Hillebrand 2004). To understand latitudinal gradient one must go
30 beyond the pattern and therefore evaluate causal hypotheses, which encompass three
31 types of explanations: ecological, historical and evolutionary (Gaston 2000; Hawkins
32 and Diniz-Filho 2004; Mittelbach et al. 2007). Examples of hypotheses proposed for
33 this geographic pattern are productivity, environmental heterogeneity, area, historical
34 factors and biotic interactions (Willig et al. 2003; Field et al. 2009). Among the above
35 mentioned, climatic hypotheses are between the most used explanations behind the
36 pattern of latitudinal diversity gradients (Field et al. 2009). However, climatic stability
37 can have different weights in determining the latitudinal gradient. One rationale is
38 climatic stability is more important to determine the latitudinal gradient in temperate
39 regions (e.g.: temperate species have higher climatic tolerance than their tropical
40 counterparts (Stevens 1989)), whereas biotic interactions play a major role in tropical
41 regions (Dobzhansky 1950). Albeit this is not a new idea, our understanding of how
42 species richness changes along latitudinal gradients can be improved by weighting the
43 relative contributions of climatic stability and biotic interactions.

44 The aggregate effects of climatic stability and biotic interactions can be noticed,
45 for example, when variations on temperature and rainfall can reduce the time window
46 when resources are available for species which may generate resource bottlenecks that
47 can limit the number of species coexisting (Williams and Middleton 2008). In fact, the
48 climatic stability hypothesis predicts that sites with higher stability possesses higher
49 richness than sites with lesser stability (Pianka 1966), and one of the explanations for
50 such phenomena invokes the role of biotic interactions because climatic stability would
51 allow species to be more specialized on stable environments (Moles and Ollerton 2016;

52 but see Schleuning et al. 2012). Direct effects of resource availability on species can
53 also play a role in explaining the causes of the latitudinal richness pattern. For example,
54 the number of species of woody plants has been used to explain the richness of arboreal
55 or frugivorous mammals, and figs richness has been demonstrated to determine
56 frugivorous birds richness (Andrews and O'Brien 2000, Kissling et al. 2007; but see
57 Hawkins and Pausas 2004). The rationale behind this hypothesis is that an increase in
58 species richness at basal trophic levels should increase the number of species at higher
59 trophic levels.

60 Here, I focus on how dung beetle diversity pattern can be shaped by biotic
61 interactions between fecal detritus producers (mammals) and consumers (dung beetles)
62 (Nichols et al. 2016) along with climatic stability. Dung beetles (Scarabaeinae) is a rich
63 group of detritivores beetles that probably diversified after the transition from
64 saprophagy to coprophagy (Halffter 1991). In this study, two hypotheses will be
65 evaluated. First, if resource availability is important for richness patterns of dung
66 beetles then it is expected that dung beetles diversity should be driven by mammals'
67 diversity since mammals dungs are the primordial source of food resource for dung
68 beetles (Halffter and Matthews 1966; Nichols et al. 2009). Examples of how dung
69 beetle diversity is related to mammal diversity are that hunting-related reductions on
70 mammals richness lead to a reduction in dung beetles richness (Nichols et al. 2009;
71 Culot et al. 2013) and that changes on mammals species composition may explain
72 changes on dung beetle composition (Bogoni et al. 2016). Second, if variations on
73 climatic stability should affect dung beetles then I expect to find that an increase in
74 climatic stability should have positive effects on dung beetle richness. In general, many
75 insects display seasonality patterns of diversity (Wolda 1988), and dung beetle
76 communities, in particular, have increased richness with increased temperature and

reduction of rainfall seasonality (Andresen 2005; Hernández and Vaz-de-Mello 2009; Liberal et al. 2011). Climatic stability should also allow dung beetle species to be more specialized in feeding resources, therefore an increase in niche partitioning between co-occurring dung beetle species caused by trophic specialization could increase dung beetle species richness (Larsen et al. 2006), especially in tropical areas where higher mammal richness are also expected (Davies and Buckley 2011; Safi et al. 2011). Even though most dung beetles are generalists and only a few species can be sorted in guilds that use different dung types (Filgueiras et al. 2009; Bogoni and Hernandez 2014).

In this study, I test the hypothesis that dung beetle latitudinal richness is explained by 1) increase in feeding resources availability because of biotic interactions with mammals that produce dung beetle feeding resources, and 2) an increase on climatic stability and 3) both resource availability and climatic stability. To evaluate these hypotheses, I used a spatialized path analysis which allows dissociating the direct and indirect effects of the climatic stability. First, I predict that dung beetle richness should increase due increases in climatic stability, in other words, decreases in precipitation seasonality and temperature seasonality. Second, increases on mammals' richness, here used as a proxy for resource availability, should result in increases of dung beetle richness. Since mammals richness can also respond to precipitation seasonality and temperature seasonality, therefore climatic stability indirect effects can change dung beetle richness through mediated effects in mammals richness (See Figure 1 for more details on proposed path analysis).

98

99

100 **Materials and Methods**

101

102 *Dung beetle database*

103 I performed a search on the Scopus database for dung beetles inventories using
 104 the following keywords: “*dung beetle*” or “*Scarabaeinae*”. I only included the period
 105 between 1980 and 2016. This search retrieved a total of 1443 articles and after applying
 106 the following criteria, the database comprised 115 studies and 213 sites (Figure 2): 1)
 107 sampled dung beetles should belong to the subfamily Scarabaeinae (in other words,
 108 studies with only Aphodinae, Geotrupinae and Troginae were excluded); 2) the study
 109 employed a standardized sampling protocol and clearly stated the number of pitfalls,
 110 sites and temporal replication used while sampling the dung beetles. Sampling protocol
 111 information was used to the measure sampling effort using in each study. The sampling
 112 effort was the total number of pitfalls measured as pitfalls multiplied per area multiplied
 113 per temporal replications. Differences on use of different baits (types of dung,
 114 decomposing meat or rotten fruits) were ignored 3) provided a list of sampled species
 115 and their respective abundances 4) sampled in the American continent and presented
 116 geographic coordinates or specified the municipality where the sampled occurred. If one
 117 study sampled more than one site and provided a geographic coordinate for each site
 118 thus each site was included on the database. However, species lists were combined in
 119 cases where there was only one geographic coordinate for multiples sites. Studies
 120 included in the analysis are available on the Supplementary File 1.

121

122 *Explanatory variables*

123 I used mammal richness as a proxy for resource availability because of biotic
 124 interactions between dung beetles and mammals (Nichols et al. 2009, 2013). In order to
 125 measure mammal richness, I downloaded the terrestrial mammals' red list range
 126 shapefile (IUCN 2016) to estimate the number of mammals richness in the locations

127 where dung beetles were sampled. For each dung beetle locality, I counted the number
128 of mammal species' range shapefiles that overlap their coordinates using package
129 *maptools* (Bivand and Lewin-Koh 2017).

130 Climatic stability was measured as precipitation seasonality and temperature
131 seasonality obtained from the worldclim with 5 arc-minutes resolution (approximately
132 10 km at equator line) (Hijmans et al. 2005). I opted for a coarser resolution because
133 many localities had their geographic coordinates manually assigned. These variables are
134 important drivers of mammals distribution and are commonly used on studies with
135 species distribution of mammals (e.g.: Moura et al. 2016, Ribeiro et al. 2016). Values of
136 precipitation seasonality and temperature seasonality were extracted for each locality
137 using package raster (Hijmans 2016).

138 Both sampling effort and dung beetle abundance were used to control the effects
139 of different sampling protocols and sampling efforts on dung beetle richness because
140 measures of species richness disregarding differences in sampling effort may lead to
141 biases estimations (Gotelli and Colwell 2001). Additionally, dung beetle abundance
142 may change positively to increased climatic stability and resource stability because of
143 other hypotheses (e.g.: more individuals hypothesis), therefore these confounding
144 effects are minimized by incorporating this path in the structural model equations.
145 Furthermore, there are cases in which dung beetle abundance may increase with a
146 decrease in mammals' richness (Culot et al. 2013). However, this is an effect of
147 selective defaunation of large mammals and if this effect is noticeable it should be
148 accounted in the path analysis.

149

150 *Data Analysis*

151 A path analysis was built using the piecewise structural equation modeling
152 approach that allows the incorporation of different models by building each model
153 separately (Shipley 2009; Lefcheck 2016). Additionally, path analysis helps to
154 disentangle direct and indirect effects of climatic and resources on the richness patterns
155 (Kissling et al. 2007; Moura et al. 2016). First, I built three generalized least squares
156 models (GLS) in order to account spatial autocorrelation using the package *nlme*
157 (Pinheiro et al. 2014). Spatial correlation structure present on the three models was
158 reduced by selecting the best among four spatial correlations: Spheric, Exponential,
159 Gaussian and Rational quadratic. The first model was built using mammal richness as
160 the response variable, precipitation seasonality and temperature seasonality as
161 explanatory variables, and using a rational quadratic spatial correlation structure. The
162 second model was built using dung beetle abundance as the response variable,
163 precipitation seasonality, temperature seasonality, mammal richness and sampling effort
164 as explanatory variables, and using an exponential spatial correlation structure. The
165 third model was built using dung beetle richness as the response variable and
166 precipitation seasonality, temperature seasonality, mammal richness and dung beetle
167 abundance as explanatory variables. These three models were assembled in a path
168 analysis using the package *piecewiseSEM* (Lefcheck 2016). The significance of the
169 piecewise SEM was evaluated using Fisher's C statistic in which a p-value above 0.05
170 is an indication that the model fits well to the data.

171 In all models, dung beetle abundance and dung beetle richness were log10
172 transformed in order to achieve residuals with a normal distribution. All analyses were
173 carried out on the R environment (R Core Team 2017). More details in model selection
174 and models assumptions are found in the Supplementary file 2.

175

176 **Results**

177 Dung beetle richness ranged from one to 101 species (mean $\pm$ SD = 21.5 ± 17.2),
178 whereas mammals richness ranged from three to 193 species (113.9 ± 39.5). Dung
179 beetle abundance ranged from seven to 93,274 individuals ($5,226.8 \pm 11,606.66$).

180 I found that the proposed path analysis had a good fit to the observed data
181 (Fisher's $C = 5.05$; d.f. =4; $P=0.282$; Figure 3). Mammal richness was negatively
182 affected both by temperature seasonality and precipitation seasonality ($R^2=71.31\%$)
183 whereas dung beetle abundance variation was explained only by sampling effort
184 ($R^2=9.03\%$).

185 In the model, 56.32% of the variation on dung beetle richness was explained. An
186 increase on four units of dung beetle abundance resulted on an increase of one unit on
187 dung beetle richness ($b = 0.2472$), and an increase of mammal richness resulted on an
188 increase of dung beetle richness ($b_{\log10}=0.0023$; $b_{\text{antilog}}= 1.01$). As expected, negative
189 effects on dung beetle richness included a direct and an indirect effect, modulated
190 through mammal richness, of temperature seasonality ($b_{\text{direct}}=-0.0001$ and $b_{\text{indirect}}= -$
191 0.00003), but only indirect effects of precipitation seasonality dung beetle richness
192 ($b_{\text{indirect}}= -0.0005$).

193

194 **Discussion**

195 Here I have corroborated my hypothesis that dung beetle richness was higher in
196 areas with higher climatic stability and higher resource availability. Despite this, dung
197 beetle abundance was poorly explained on the model and that could be a consequence of
198 lack of standardization between sampling protocols of studies (Larsen and Forsyth
199 2005; da Silva and Hernández 2015). As far as I have know, this is among the firsts
200 empirical assessments of dung beetle richness pattern (see: Frank et al. 2018), since

201 only anecdotal evidence and local scale assessments were previously made (Halffter and
202 Matthews 1966; Hernández and Vaz-de-Mello 2009; Liberal et al. 2011).

203 Two non-exclusive explanations help to understand why there are more dung
204 beetle species on areas with more resources available (i.e. higher mammals' richness).
205 First, an increase on resource availability should allow dung beetles to specialize on
206 certain types of dung (e.g.: Larsen et al. 2006, Jacobs et al. 2008) and reduce
207 interspecific competition between dung beetles. However, a recent study has shown an
208 opposite trend – dung beetles have low specificity on resource use even on communities
209 with high richness (Frank et al. 2018). Second, an increase in mammal richness could
210 result in an increase of different traits and lineages of mammals (Safi et al. 2011). That,
211 in turn, can increase the number of mammals with different activity times (e.g.: diurnal
212 or nocturnal) and with different feeding and digestive systems (e.g.: herbivores or
213 carnivores). Indeed, dung beetle community structure changes between night and day
214 (Lopes et al. 2011) or depending on dung type used as bait (Filgueiras et al. 2009).

215 Climatic instability affects directly the time of activity when dung beetles can be
216 active due to physiological constraints, mostly of small dung beetles (<2g) that are
217 thermoconformers (Verdú et al. 2006). Considering that areas with more climatic
218 instability should have a higher variation on temperature during the day and during the
219 year, this could in turn limit the number of dung beetles species active. Additionally,
220 climatic instability should also increase the number of generalist dung beetle species in
221 order to deal with a decrease on resource availability, climatic instability also reduces
222 the number of mammals' species, which reduces dung beetle species due to interspecific
223 competition (Finke and Snyder 2008). Surprisingly, dung beetle richness was not
224 directly affected by precipitation seasonality. This once again points towards climatic
225 instability having an indirect effect through resource availability.

226 Here I had shown the importance of incorporating biotic interactions, here as
 227 trophic relationships between dung beetles and mammals, in order to decouple direct
 228 and indirect effects of climatic on species richness patterns, particularly because
 229 patterns of trophic groups can arise from random effects (Gaston 2000). For example, a
 230 study revealed that congruent pattern of richness found with ants and trees are mostly
 231 explained by similar responses to environmental gradients (Vasconcelos et al. 2019).
 232 Furthermore, I show analytical evidence that dung beetle richness is largely affected by
 233 mammals' richness and that mammal's richness can mediate climatic instability effects
 234 on dung beetles. My finding increases the understanding of the intrinsic relationship
 235 between detritivore (dung beetle) and producers (mammals) which have an important
 236 role in ecosystem services (e.g.: nutrient cycling and seed dispersal) (Nichols et al.
 237 2009) and since dung beetle are widely dependent of mammals conservation actions
 238 must take in consideration the need to preserve the actors involved in the detritus food
 239 web in order to conserve these ecosystem services.

240

241

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380

381 Figure 1. Path analysis representing the theoretical relationships between predictors of
382 dung beetle richness. Black arrows are negative effects while gray arrows are
383 positive relationships.

384 Figure 2. Localities of the 115 dung beetle inventories performed on the America
385 continent and used on the analysis.

386 Figure 3. Observed path analysis used to predict dung beetle richness. Dashed arrows
387 are non-significant relationships between variables ($p>0.05$) while continuous arrows
388 are significant relationships ($p<0.05$). Black arrows are negative effects while dark gray
389 arrows are positive effects. Double arrow represents correlations between exogenous
390 variables. Note that both dung beetle richness and dung beetle abundance was log
391 transformed.