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Title: Following the dung or the climate? Species richness pattern of dung beetles (Scarabaeinae) on the Americas

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

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

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Introduction

Latitudinal diversity gradients are a widespread pattern in ecology (Willig et al. 2003; Hillebrand 2004). Since latitude is not an explanation *per se* (Hawkins and Diniz-Filho 2004), many causal explanations, such as productivity, environmental heterogeneity, area, historical factors and biotic interactions were proposed for this geographic pattern (Willig et al. 2003; Field et al. 2009). Among these, climate and productivity are between the most used predictors of latitudinal diversity gradients (Field et al. 2009).

On the other hand, variation on temperature and rainfall may play a role in generating resource bottlenecks that can limit the number of species coexisting (Williams and Middleton 2008). In fact, the climatic stability hypothesis predicts that sites with higher stability possesses higher richness than sites with lesser stability (Pianka 1966) because species can be more specialized on stable environments (Moles and Ollerton 2016). Another factor potentially playing a role in structuring latitudinal richness pattern is resource availability. For example, the number of species of woody plants has been used to explain the richness of arboreal or frugivorous mammals, and figs richness has been demonstrated to determine frugivorous birds richness (Andrews and O'Brien 2000, Kissling et al. 2007; but see Hawkins and Pausas 2004). The rationale behind this hypothesis is that an increase on species richness at basal trophic levels should increase the number of species at higher trophic levels.

Here, I focus on how biotic interactions between fecal detritus producers (mammals) and consumers (dung beetles) (Nichols et al. 2016) can help explain dung beetle diversity pattern along with climatic stability. Dung beetles (Scarabaeinae) is a rich group of detritivores beetles that probably diversified after the transition from saprophagy to coprophagy (Halffter 1991). In this study, two hypothesis will be

evaluated. First, if resources are important for richness patterns of dung beetles, than it is expected that dung beetles diversity should be driven by mammals' diversity, since mammals dungs are the primordial source of food resource for dung beetles (Halffter and Matthews 1966). Thus, a reduction on mammals richness because of hunting should lead to a reduction on dung beetles richness (Nichols et al. 2009). Besides that, a shift on mammals species composition may explain changes on dung beetle composition (Bogoni et al. 2016). Second, if variations on climatic stability should affect dung beetles, than I expect to find that an increase on climatic stability should have positive effects on dung beetle richness. In general, many insects display seasonality patterns of diversity (Wolda 1988), and specifically studies found changes on richness of dung beetle communities as result of temporal rainfall variation (Andresen 2005; Liberal et al. 2011). Climatic stability should also allow dung beetles to be more specialized on feeding resources and present more species because of niche partitioning (Larsen et al. 2006), especially in tropical areas where higher mammal richness are also expected (Davies and Buckley 2011; Safi et al. 2011).

In this study, I test the hypothesis that dung beetle latitudinal richness is explained by 1) an increase feeding resources available because of biotic interactions with mammals, and 2) an increase on climatic stability. For this, I used a spatialized path analysis. I predict that dung beetle richness should increase due increases on mammals' richness and decreases in precipitation seasonality and temperature seasonality. In the latter, I predict increases on dung beetle richness on two ways: directly and indirectly (via increases on mammal richness) (See Figure 1 for more details on proposed path analysis).

Materials and Methods

Dung beetle database

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

Explanatory variables

I used mammal richness as a proxy for resource availability because of biotic interactions between dung beetles and mammals (Nichols et al. 2009, 2013). In order to

measure mammal richness, I downloaded the terrestrial mammals red list range shapefile (IUCN 2016) to estimate the number of mammals richness in the locations where dung beetles were sampled. For each dung beetle locality, I counted the number of mammal species' range shapefiles that overlap their coordinates using package *maptools* (Bivand and Lewin-Koh 2017).

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

Both sampling effort and dung beetle abundance were used to control the effects of different sampling protocols and efforts on dung beetle richness. Furthermore, dung beetle abundance was also included as responding negatively to climatic stability and resource availability.

Data Analysis

A path analysis was built using the piecewise structural equation modelling approach that allows incorporation of different models by building each model separately (Shipley 2009; Lefcheck 2016). Additionally, path analysis helps to disentangles direct and indirect effects of climatic and resources on the richness patterns (Kissling et al. 2007; Moura et al. 2016). First, I built three generalized least squares models (GLS) in order to account spatial autocorrelation using the package *nlme*

(Pinheiro et al. 2014). Spatial correlation structure present on the three models was reduced by selecting the best among four spatial correlations: Spheric, Exponential, Gaussian and Rational quadratic. The first model was built using mammal richness as response variable, precipitation seasonality and temperature seasonality as explanatory variables, and using a rational quadratic spatial correlation structure. The Second model was built using dung beetle abundance as response variable, precipitation seasonality, temperature seasonality, mammal richness and sampling effort as explanatory variables, and using an exponential spatial correlation structure. The third model was built using dung beetle richness as response variable and precipitation seasonality, temperature seasonality, mammal richness and dung beetle abundance as explanatory variables. These three models were assembled in a path analysis using the package *piecewiseSEM* (Lefcheck 2016). Significance of the piecewise SEM was evaluated using Fisher's C statistic in which a p-value above 0.05 is an indication that the model fits well to the data.

In all models dung beetle abundance and dung beetle richness were log10 transformed in order to achieve residuals with normal distribution. All analyses were carried out on R environment (R Core Team 2017).

Results

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

I found that the proposed path analysis had a good fit to the observed data (Fisher's C = 5.05; d.f. =4; P=0.282; Figure 3). Mammal richness was negatively affected both by temperature seasonality and precipitation seasonality (R^2=71.31%)

whereas dung beetle abundance variation was explained only by sampling effort (R^2=9.03%).

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

Discussion

Here I have corroborated my hypothesis that dung beetle richness was higher on areas with higher climatic stability and higher resource availability. Despite this, dung beetle abundance was poorly explained on the model and that could be a consequence of lack of standardization between sampling protocols of studies (Larsen and Forsyth 2005; da Silva and Hernández 2015). As far as I known, this is among the firsts empirical assessments of dung beetle richness pattern (see: Frank et al. 2018), since only anecdotal evidence and local scale assessments were previously made (Halffter and Matthews 1966; Hernández and Vaz-de-Mello 2009; Liberal et al. 2011).

Two non-exclusive explanations help to understand why there are more dung beetle species on areas with more resources available (i.e. higher mammals' richness). First, an increase on resource availability should allow dung beetles to specialize on certain types of dung (e.g.: Larsen et al. 2006, Jacobs et al. 2008) and reduce interspecific competition between dung beetles. However, a recent study have shown an

opposite trend – dung beetles have low specificity on resource use even on communities with high richness (Frank et al. 2018). Second, an increase on mammal richness could result on an increase of different traits and lineages of mammals (Safi et al. 2011). That in turn can increase the number of mammals with different activity times (e.g.: diurnal or nocturnal) and with different feeding and digestive systems (e.g.: herbivores or carnivores). Indeed, dung beetle community structure changes between night and day (Lopes et al. 2011) or depending on dung type used as bait (Filgueiras et al. 2009).

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

Here I had shown the importance of incorporating biotic interactions in order to decouple direct and indirect effects of climatic on species richness patterns. Furthermore, I present analytical evidence that dung beetle richness is largely affected by mammals' richness and that mammal's richness can mediate climatic instability effects on dung beetles.

Conflict of Interest: The author declares that he have no conflict of interest.

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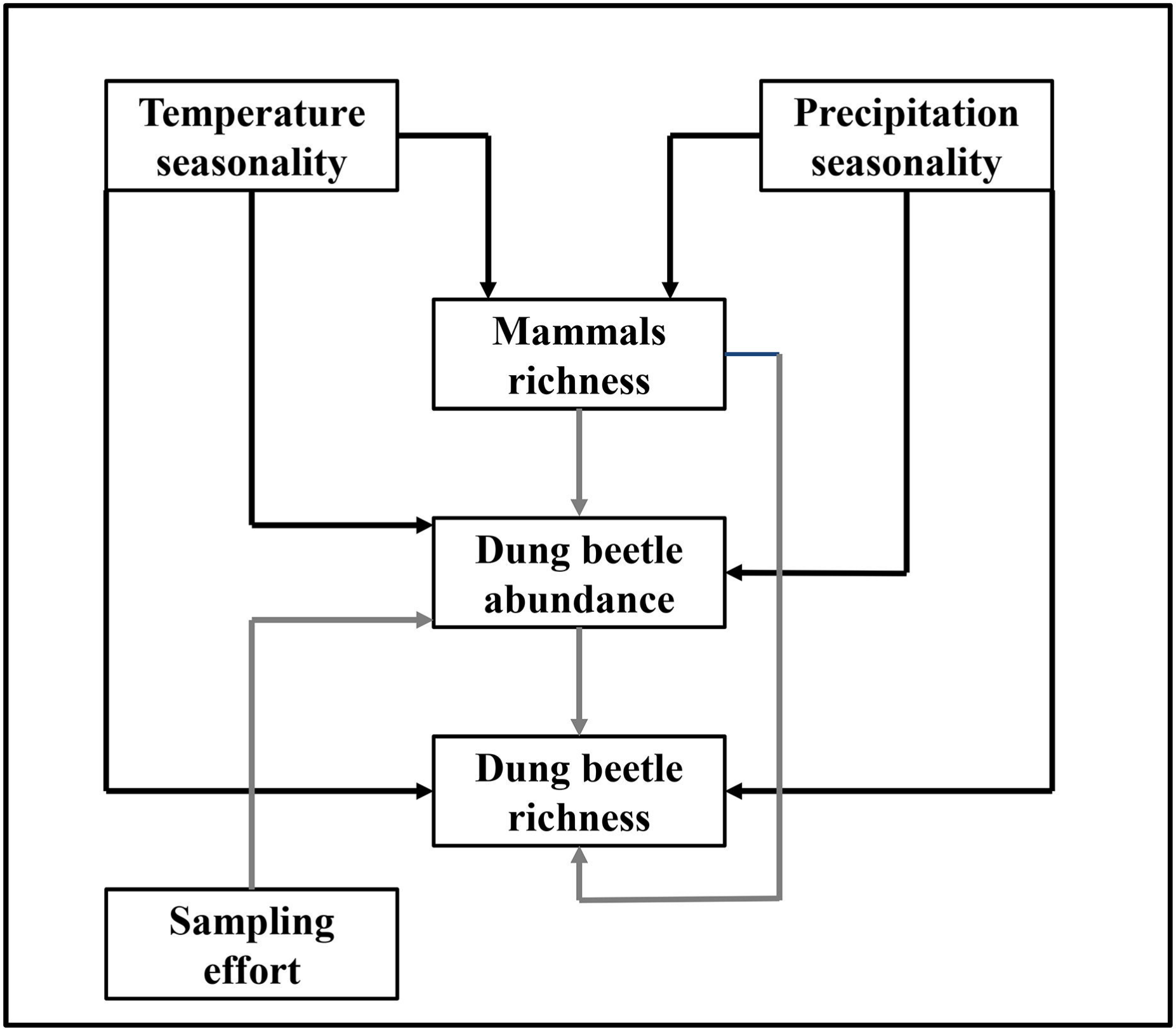
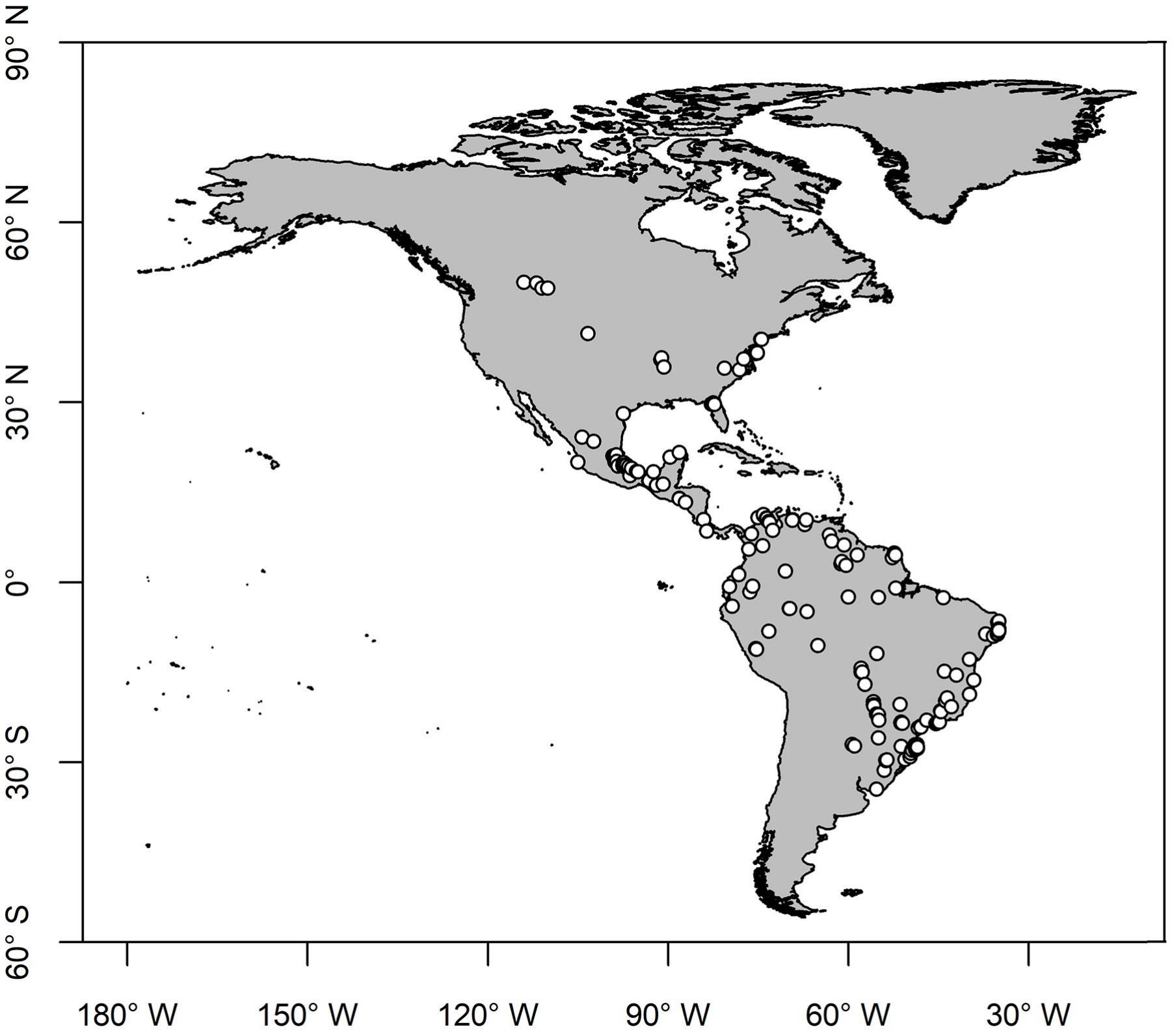
Figures legends

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

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

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


Temperature seasonality
Precipitation seasonality
Mammals richness
Dung beetle abundance
Dung beetle richness
Sampling effort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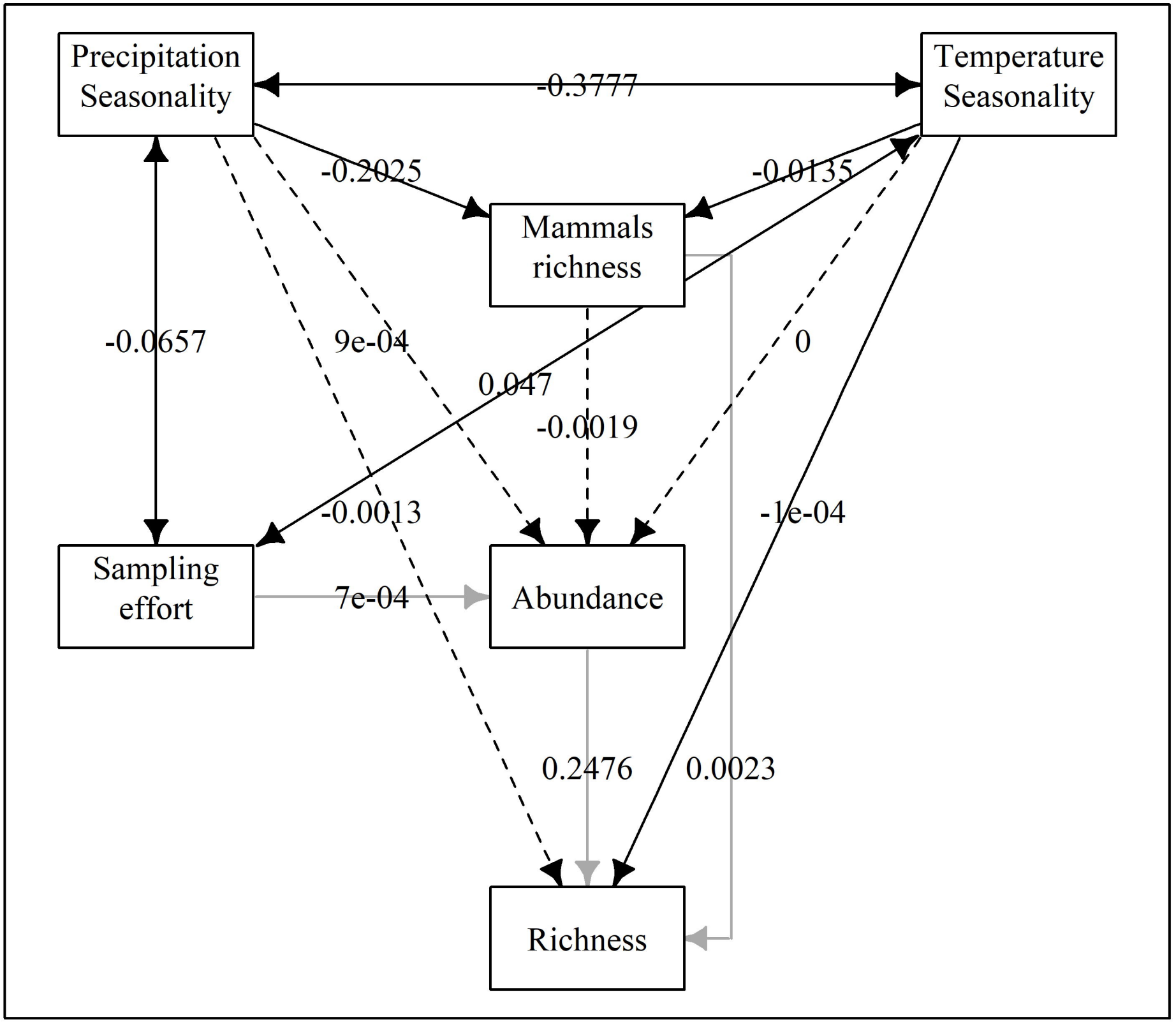
Precipitation Seasonality
Temperature Seasonality
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-0.2025
-0.0135
Mammals richness
-0.0657
9e-04
0
0.047
-0.0019
-0.0013
-1e-04
Sampling effort
7e-04
Abundance
0.2476
0.0023
Richness