Spatial and temporal variations of aridity shape dung beetle assemblages towards the Sahara desert

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Background. Assemblage responses to environmental gradients are key to understand the general principles behind the assembly and functioning of communities. The spatial and temporally uneven distribution of water availability in drylands creates strong aridity gradients. While the effects of spatial variations of aridity are relatively well known, the influence of the highly-unpredictable seasonal and interannual precipitations on dryland communities has been seldom addressed.

Aims. Here we study the seasonal and interannual responses of dung beetle (Coleoptera, Scarabaeidae) communities to the variations of water availability along an arid to semiarid region of the Mediterranean.

Methods. We surveyed a 400 km linear transect along a strong aridity gradient from the Mediterranean coast to the Sahara (Eastern Morocco), during four sampling campaigns: two in the wet season and two in the dry season. We measured richness, abundance and evenness. Variations in community composition between sites, seasons and years were assessed through beta diversity partitioning of dissimiliarity metrics based on species occurrences and abundances. The effects of climate, soil, vegetation and dung availability were evaluated using Spearman-Rank Correlations, GLMs and partial least-squares generalized lineal regressions for community structure, and NMDS, PERMANOVA and dbRDA-based variation partitioning for compositional variations.

Results. Dung beetle abundance and richness showed large seasonal variations, but remained relatively similar between years. Increasing aridity resulted in decreasing species richness and an ordered replacement of species, namely the substitution of the trophically diverse Mediterranean fauna by saprophagous and generalist species both in space towards the Sahara and seasonally in the dry season. Indeed, aridity and its interaction with season and year were the strongest correlates of variations in richness and composition.

Discussion. Our study shows that aridity determines composition in dung beetle communities, filtering species both in space and time. Besides the expected decrease in richness, such environmental filtering promotes a functional shift to generalist and saprophagous species in arid conditions, probably related to changes in resource quality along the transect and through the year. Our results highlight the importance of considering the effects of the highly-unpredictable seasonal and interannual variations in precipitation when studying dryland communities.

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16   **ABSTRACT**

17   **Background.** Assemblage responses to environmental gradients are key to understand the general

18   principles behind the assembly and functioning of communities. The spatial and temporally uneven

19   distribution of water availability in drylands creates strong aridity gradients. However, the effects

20   of spatial variations of aridity on diversity remains unclear and the influence of the highly-

21   unpredictable seasonal and interannual precipitations on dryland communities has been seldom

22   addressed.

23   **Aims.** Here we study the seasonal and interannual responses of dung beetle (Coleoptera,

24   Scarabaeidae) communities to the variations of water availability along a semiarid to desert

25   transition of the Mediterranean region.

26   **Methods.** We surveyed a 400 km linear transect along a strong aridity gradient from the

27   Mediterranean coast to the Sahara (Eastern Morocco), during four sampling campaigns: two in the

28   wet season and two in the dry season. We measured richness, abundance and evenness. Variations

29   in community composition between sites, seasons and years were assessed through beta diversity

30   partitioning of dissimiliarity metrics based on species occurrences and abundances. The effects of

31   climate, soil, vegetation and dung availability were evaluated using Spearman-Rank Correlations,

32   GLMs and partial least-squares generalized lineal regressions for community structure, and

33   NMDS, PERMANOVA and dbRDA-based variation partitioning for compositional variations.

34   **Results.** Dung beetle abundance and richness showed large seasonal variations, but remained

35   relatively similar between years. Increasing aridity resulted in decreasing species richness and an

36   ordered replacement of species, namely the substitution of the trophically diverse Mediterranean

37   fauna by saprophagous and generalist species both in space towards the Sahara and seasonally in

38   the dry season. Indeed, aridity and its interaction with season and year were the strongest correlates

39   of variations in richness and composition.

40   **Discussion.** Our study shows that aridity determines composition in dung beetle communities,

41   filtering species both in space and time. Besides the expected decrease in richness, such

42   environmental filtering promotes a functional shift to generalist and saprophagous species in arid

43   conditions, probably related to changes in resource quality along the transect and through the year.

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45   and interannual variations in precipitation when studying dryland communities.

46 **INTRODUCTION**

47 Understanding the processes behind the geographical patterns of diversity is one of the central

48 questions of ecology. Spatial gradients have long served as natural experiments to understand

49 general principles in the ecology of animals, through the study of how changes in environmental

50 factors, such as climate, influence the ecological and evolutionary processes that determine

51 biodiversity variations from local to global scales (e.g. Pianka, 1966; Willig, Kaufman & Stevens,

52 2003; Sanders & Rahbek, 2012). Aridity gradients emphasizing changes in water availability, a

53 key abiotic factor, are especially important to understand geographical variations in biodiversity

54 in warm temperate and tropical systems (Hawkins *et al.*, 2003; Hawkins & Porter, 2003). However,

55 the effects of aridity on diversity remain unclear (Rohde, 1992; Willig *et al.*, 2003) because the

56 response depends on taxa and geographic regions (Polis, 1991; Wiens, Kozak & Silva, 2013). For

57 example, scorpion and bird diversity increase with aridity in North America, but decrease in

58 Australia (Polis 1991). On the contrary, in ants there is a negative relationship of aridity with

59 diversity in North America but the relationship is positive in Australian deserts (Polis 1991) and

60 there is no relationship in Australian Savannas (Andersen, Toro & Parr, 2015). Understanding

61 biodiversity patterns across aridity gradients is also relevant because drylands currently occupy

62 more than 40% of the land on Earth and their extent is expected to increase in the next decades in

63 response to climate change (Huang *et al.*, 2016).

64 Strikingly, temporal variations of diversity patterns along environmental gradients have

65 received scarce attention (Bishop *et al.*, 2014) despite their importance in shaping community

66 assemblages and large-scale diversity patterns (Pianka, 1966; Willis & Whittaker, 2002; White *et*

67 *al.*, 2010; Gouveia *et al.*, 2013). However, both intra-annual (seasonality) and inter-annual

68 environmental variations play a significant role in the origin of diversity patterns and the variations

69   of local species pools (Pianka, 1966; Tonkin *et al.*, 2017). Temporal variations are particularly

70   important in Mediterranean (Agoglitta *et al.*, 2012; Seager *et al.*, 2014) and subtropical (Belda *et*

71   *al.*, 2014) climates, where the spatially uneven distribution of water at fine and broad scales is

72   coupled with large variations in water availability within and between years (i.e. seasonal and

73   interannual variations).

74   Mediterranean areas typically host strong spatial gradients of water availability, often

75   ranging from warm-temperate to desert conditions (Safriel *et al.*, 2018). Mediterranean climate is

76   highly seasonal, with dry hot summers and wet cool winters that result in large differences in water

77   availability throughout the year. Importantly, besides this overall seasonal regime, arid

78   environments show large unpredictable variations in rainfall between seasons and years, that can

79   sometimes be larger than the typical within-year fluctuations (Ward, 2009). These differences may

80   result in differing diversity patterns between seasons, in particular along aridity gradients, where

81   their extremes show distinct seasonal variations – from abundant rains in winter and scarce in

82   summer at the more humid places to scarce rains throughout the year in the desert. Drylands

83   respond differently to extreme precipitations and seasonal rainfall than mesic biomes, with highly

84   variable and temporally-limited increases in plant productivity (Zeppel *et al.*, 2014). Such extreme

85   variations in water and resource availability drive the phenology of desert animals (Polis, 1991),

86   and may produce strong oscillations in their communities (Tonkin *et al.*, 2017). Despite the striking

87   changes in community composition and structure caused by these variations in biologically

88   available water (Seely & Louw, 1980; Polis *et al.*, 1997; Holmgren *et al.*, 2001), the spatial and

89   temporal effects of aridity on the diversity of invertebrates and trophic interactions have been

90   seldom studied (Labidi, Errouissi & Nouira, 2012; Tshikae, Davis & Scholtz, 2013a).

91   Dung beetles of the family Scarabaeidae feed and nest on the faeces of diverse animals,

92   especially mammalian herbivores, showing diverse dung-exploitation strategies (Hanski &

93   Cambefort, 1991). In the Mediterranean, species in the Aphodiinae subfamily are mainly

94   endocoprids that feed and breed within the dung pat (although many species are known to be

95   kleptocoprids, saprophages and root feeders; Christensen & Dobson, 1976; González-Megías &

96   Sánchez-Piñero, 2003; Dellacasa & Dellacasa, 2006). Whereas the Scarabaeinae subfamily

97   includes paracoprid and telecoprid species that feed and breed directly below or away from the

98   dung pat respectively (Hanski *et al.*, 1991). The large abundances, relatively easy-to-identify

99   species, relative stable systematics and wide distribution of dung beetles, makes them ideal to

100   study spatial and temporal changes in community structure (Spector, 2006). Moreover, the

101   diversity of this group is known to respond to large-scale environmental gradients (Hortal-Muñoz,

102   Martin-Piera & Lobo, 2000; Nunes *et al.*, 2016), in particular to variations in water availability

103   (Haloti *et al.*, 2006; Labidi *et al.*, 2012; Tshikae *et al.*, 2013a; Abdel-Dayem *et al.*, 2016). In dry

104   areas dung beetles are thought to be constrained by both their physiological water economy

105   (Sowig, 1996; Chown, Sørensen & Terblanche, 2011) and the decrease in the availability and

106   quality of trophic resources (Lumaret, 1995; Nichols *et al.*, 2009). Further, Palearctic Scarabaeidae

107   are well diversified in mesic and arid Mediterranean areas (Lumaret, 1991; Sánchez-Piñero &

108   Ávila, 2004) and surrounding desert regions (Baraud, 1985), making them a suitable model taxa

109   to investigate biodiversity responses to aridity gradients.

110   Here we study the temporal and spatial variations of dung beetle communities along a water

111   availability gradient in Eastern Morocco, spanning 400 km from coastal Mediterranean to desert

112   Saharan conditions. We aim to answer three specific questions: (Q1) Are dung beetle communities

113   of desert areas reduced subsets of communities living in less arid areas? (Q2) Are community

114   variations along the aridity gradient stable within and between years? (Q3) Do climatic factors,

115   soil features and resource availability contribute to shape the diversity and composition of

116   communities along the aridity gradient? According to the water–energy hypothesis (Hawkins *et*

117   *al.*, 2003), we expect a decrease in dung beetle diversity with increasing aridity. Progressively

118   dryer conditions will filter out the most sensitive species while selecting for highly adapted species

119   able to cope with a harsher climate and limited resource availability, thus promoting high spatial

120   species turnover and locally distinct species assemblages (Arakaki *et al.*, 2011; Sánchez-Piñero *et*

121   *al.*, 2011). In addition, we expect temporal shifts in the relationship between dung beetle diversity

122   and aridity, due to the strong variations in precipitation patterns. While in Mediterranean areas the

123   higher water availability during the wet season will cause a stronger diversity–aridity relationship

124   than in the dry season, desert environments will show lower seasonal species turnover but higher

125   inter-annual shifts in assemblage composition because the temporally stochastic nature of their

126   precipitations limits the adaptation to cope with seasonal environmental shifts (Tonkin *et al.*,

127   2017).

128   Question Q1 was investigated by analysing species richness, abundance, evenness and

129   community composition along the aridity gradient. To answer question Q2 we analysed variations

130   in community composition at seasonal (between wet and dry seasons) and annual (between years)

131   temporal scales. Finally, we assessed question Q3 by analysing the effects of climate, soil,

132   vegetation and dung availability on dung beetle assemblages.

133

134   **MATERIALS & METHODS**

135   **Study area**

136   We surveyed a linear transect spanning approximately 400 km in east Morocco, parallel to the

137   Algerian border (Figure 1). The transect was placed along a strong aridity gradient, from a semiarid

138   region at the Mediterranean coast (near Saïdia, 35°5'59" N, 2°17'15" W) towards the hyperarid

139   Sahara desert (near Figuig, 32°6'33" N, 1°13'47" W) (Supplementary file S1, table 2), with a

140   threefold annual rainfall gradient (from ca. 350 mm at the coastal semiarid area to 100 mm at the

141   nearly hyperarid Saharan end of the gradient) and a Mediterranean precipitation regime

142   characterized by summer drought and rainy season in November-March (Belda *et al.*, 2014). The

143   difference in rainfall between the wet and dry seasons (as exemplified by the precipitation in April,

144   the wettest month, and September, the driest month) ranged from 45 to 19 mm at the semiarid end,

145   and showed no difference at the desert end (i.e. 13 mm in both months). However, during the dry

146   season, the greatest rainfall (22 mm) was not registered in the coast, but in the middle of the

147   gradient.

148   Livestock breeding is the main economic activity along the whole gradient. Sheep occur

149   along the entire transect, while cattle appears mainly in the semiarid end of the gradient toward

150   the Mediterranean coast. Donkeys also occur along the whole transect and dromedary herds appear

151   in the Saharan areas, but both are scarce. The transect is dominated by a single soil type (Petric

152   Calcisols) except the coastal area near Saïdia. This area shows coastal Gleyic Solonchak soil that

153   differ from the dominant Petric Calcisol because of a thicker silt layer ($\geq$ 50 cm depth) and higher

154   salt concentration (Jones *et al.*, 2013). The northern part of the transect mainly corresponds to

155   agricultural land, with forest areas restricted to mountain ranges, while the middle and the southern

156   parts are dominated by grazing rangelands with shrub vegetation (20-30% cover, 25 $\pm$ 13 cm

157   height; mean $\pm$ SD).

158

159   **Sampling design**

160   Dung beetles were sampled during four campaigns held in two consecutive years: two in the wet

161 season (April 2013 and 2014) and two in the dry season (September 2013 and 2014). These months

162 were chosen to include the two peaks of dung beetle richness and abundance in the Mediterranean

163 region (as recommended by Hortal & Lobo, 2005). In each campaign we surveyed 10 sampling

164 sites along the Moroccan road N17 from the Sahara towards the Mediterranean, separated by an

165 interval of around 40 km (Figure 1). Sampling and beetle collection were carried out under research

166 permits Reference Numbers 01/2013 HCEFLCD/DLCDPN/DPRN/CFF and 01/2014

167 HCEFLCD/DLCDPN/DPRN/CFF issued by the Haut Commisariat aux Eaux et Forêts et à Lutte

168 Contre la Désertification (Morocco). All sampling sites were placed at least 100 m away from the

169 road margin. Annual precipitation was similar in both years at the three places with available

170 meteorological stations (Saïdia and Oujda in the north and Figuig in the south;

171 www.worldweatheronline.com), although it was about 20% higher in 2012–2013 than in 2013–

172 2014 in all three stations.

173   Each sampling site was replicated twice. Replicates were placed 1 km apart, and consisted

174 of five baited pitfall traps (thus, 100 traps per sampling campaign) separated 20 m one from another

175 following a straight line (thus, 80m from trap 1 to trap 5). Each pitfall trap consisted of a 1 l plastic

176 cup (11.5 cm diameter, 14 cm depth) covered by a 2 cm x 2 cm mesh on top of which 300 g fresh

177 cow dung was laid as bait (see Lobo, 1988). To avoid any spurious effects due to differences in

178 dung composition, fresh organic-farming cow dung was harvested from a single farm (Colmenar

179 Viejo, central Spain) and well-mixed to obtain a homogeneous dung mass, adding water and

180 mixing right before placing the traps to ensure adequate dung moisture levels. All traps were filled

181 with 300 ml of a soapy preservative water solution with chloral hydrate (10 g/l) to prevent quick

182 insect degradation due to high temperatures and fungi proliferation. Traps were active for a

183 standard period of 72 h (Labidi *et al.*, 2012; Amraoui *et al.*, 2016). All captures were immediately

184   transferred to 96% ethanol in the field and transported to the lab where individuals were sorted

185   and identified to species level.

186   During the sampling campaigns we gathered data on resource availability, vegetation and

187   soil characteristics (Supplementary file S1, table 1). GIS data on annual aridity (AI = mean annual

188   precipitation / mean annual evapotranspiration) and solar radiation were obtained from Trabucco

189   & Zomer (2009), and mean monthly temperature, annual and monthly precipitation and altitude

190   from Hijmans *et al.* (2005). Resource availability was estimated using the amount of five types of

191   dung (sheep/goat, cow, horse/donkey, dromedary and carnivore droppings) present in the locality

192   as a general proxy for the actual amount of fresh dung that is available for dung beetles. To do

193   this, in each replicate in the four campaigns we conducted two perpendicular 250 m long and 2 m

194   wide linear transects, each surveyed by one researcher following a standardized sampling protocol,

195   covering a total of 1000 m² per replicate (similar to Lobo, Hortal & Cabrero-Sañudo, 2006). In

196   each transect the total mass of the five types of dung mentioned above was estimated based on

197   dung volume, according to previous measurements of dung pats of different volume in the field

198   (González-Megías & Sánchez-Piñero, 2004). Dung availability included "cow dung" and "sheep

199   + other dung" (all expressed in g/100 m²). Vegetation height (cm) and vegetation percentage cover

200   were estimated using the point-quarter method every 5 m along a 250 m x 2 m transect at each

201   replicate and campaign to account for seasonal and yearly variations. Finally, we extracted three

202   arbitrarily located soil cores (4 cm diameter and 30 cm depth) from each replicate. Soil samples

203   were split into three depths (0-10 cm, 10-20 cm and 20-30 cm) and kept in separate air-tight plastic

204   bags for further laboratory analyses. From these samples, seven soil variables were measured

205   (Supplementary file S1, table 1) accounting for structure (hardness, bulk density), water content

206   (water field capacity) and particle size (percentage of gravel, sand, silt, and clay) (see Tovar, 2015).

207

Statistical analyses

209   We assessed inventory completeness for each sampling site at each campaign using Sample

210   Coverage (Chao & Jost, 2012) as implemented in iNEXT R package (Hsieh, Ma & Chao, 2016).

211   Average sample coverage was 99.18%, with a minimum of 91.50% for the site located at the

212   semiarid end of the gradient in the wet season of 2014. For this reason, species richness (S) was

213   measured as the total number of species recorded in each sampling site at each sampling campaign.

214   Evenness (J') was measured using Pielou's index, i.e. Shannon $H' / \ln(S)$ (Magurran, 2004).

215

Variations of species richness, abundance, and evenness along the aridity gradient

217   We analysed the relationship between aridity and species richness, abundance (mean number of

218   individuals/trap) and evenness (question Q1) through a multivariate general linear regression

219   (GLM) with restricted sigma parameterization. We considered aridity and its interactions with both

220   season and year as factors, to assess their eventual influence on the relationship between

221   community descriptors and aridity. The '*aridity * season * year*' interaction was also included to

222   assess whether these relationships show different seasonal patterns in the two study years.

223   Significance levels were Bonferroni-corrected, since the same analysis was carried out for three

224   different response variables (richness, abundance and evenness).

225

Variations in community composition

227   To assess variations in community composition (questions Q1 and Q2) we used non-metric

228   multidimensional scaling (NMDS; Quinn & Keough, 2002), based on the Bray-Curtis similarity

229   index. Abundance was Hellinger standardized prior to the similarity analyses, to balance relative

230 abundances of species and minimize the double-zero problem typical of community samples

231 (Legendre & Gallagher, 2001). Pairwise differences in Bray-Curtis similarity at each site between

232 years, seasons and their interaction (independent of aridity) were analyzed by means of a

233 PERMANOVA (9999 iterations) using PAST 3.15 statistical package (Hammer, Harper & Ryan,

234 2001).

235

236 In addition, we used a beta diversity partitioning framework based on both presence-absence data

237 using Sørensen's dissimilarity index and abundance data using Bray-Curtis dissimilarity index.

238 First, Sørensen dissimilarity was partitioned into its "true species turnover" (i.e. species

239 replacement) and "nestedness" (i.e. species loss) components (Baselga & Orme, 2012). This

240 partitioning of dissimilarity only accounts for presence-absence variations in the data (Baselga *et*

241 *al.*, 2013), so to consider also species abundances we followed a similar procedure. We calculated

242 abundance-based Bray-Curtis dissimilarity index (herein B-C dissimilarities for short),

243 partitioning it into "balanced" (i.e. substitution of individuals of one species in one site by the same

244 number of individuals of different species in another site) and "gradient" (i.e. loss of individuals

245 from one site to another) components (Baselga, 2013). Multiple site dissimilarity was used to

246 calculate overall beta diversity partitioning in the turnover/nestedness and balanced/gradient

247 components of Sørensen and B-C dissimilarities, respectively, for each season in each year (i.e.,

248 for each one of the four campaigns). To analyze whether turnover/nestedness and

249 balanced/gradient components of Sørensen and B-C dissimilarities varied along the aridity

250 gradient, we carried out non-parametric Spearman-rank correlations between pairwise

251 dissimilarities and the differences in aridity between each pair of sites. We used Sperman-rank

252 correlations because residuals from GLM models did not fit a normal distribution and were

253   heteroscedastic. All Sørensen and B-C dissimilarities calculations were done using the R package

254   Betapart 1.5.0 (Baselga *et al.*, 2013). In addition, we identified the most representative species of

255   three sections of the transect representing the semiarid end, the intermediate zone and the arid end

256   for each year and season using the Indicator Value Index (IndVal), calculated with the R package

257   indicspecies (DeCaceres & Legendre, 2009). Due to small sample size, a Wilcoxon signed rank

258   test was carried out to test whether the Scarabaeinae/Aphodiinae abundance ratios were lower in

259   the dry than in the wet season, using the R package stats.

260   We also used Sørensen's and B-C dissimilarities to analyse variations in community

261   composition between seasons (wet vs dry) and between years (2013 vs 2014) for each one of the

262   ten points along the transect. Then, to analyse whether these site similarities between seasons and

263   between years were related to (continuous) variations in aridity we carried out a multivariate GLM

264   with restricted sigma parameterization considering aridity and its interactions with both season

265   and year.

266

267   **Relationship of environmental variables with diversity and composition of communities**

268   We evaluated the relationships of richness, abundance and evenness with climate, soil, vegetation

269   and dung availability (question Q3) through partial least squares generalized lineal regressions

270   (PLS-GLR; Bastien, Vinzi & Tenenhaus, 2005). This method allows analysing data characterized

271   by a large number of multicollinear predictor variables by extracting a set of orthogonal

272   components (or latent vectors) considering not only the structure of predictor variables (as

273   provided by a PCA) but also their relationship with the response variable. Once the components

274   were computed, a GLM with Gaussian function and identity link of the response variable on the

275   PLS components was carried out in order to test for the significance of the components and the

276   whole model. Abundance data were log10-transformed to meet assumptions of homoscedasticity

277   and normality of model residuals. Because communities differed mainly between seasons (see

278   Results below), four PLS-GLR analyses were conducted (2 descriptor variables x 2 seasons) and

279   the critical significance level of the models was set by Bonferroni correction ($p < 0.0125$). Cross-

280   validation and corrected Akaike Information Criterion (AICc), due to low sample size were used

281   to select among models including different number of components. When a model component

282   coefficient was not significant ($p > 0.0125$), the next optimal model indicated by cross-validation

283   and AICc was chosen. To identify the importance of each predictor in the model, the standardized

284   coefficients of the final PLS-GLR model were obtained by bootstrapping (1000 iterations).

285   We assessed the best combination of environmental variables explaining variations in

286   species composition (question Q3) through multivariate RDA-based variation partitioning

287   (Borcard, Gillet & Legendre, 2011) (Supplementary file S3, Figure 1). Further, we used distance-

288   based RDA (dbRDA) to assess the best predictors of Sørensen's and Bray-Curtis dissimilarities

289   between all sites in each campaign. In both cases (RDA and dbRDA) we previously forward

290   selected environmental and spatial predictors applying the two-step procedure proposed by

291   Blanchet, Legendre & Borcard (2008) to select significant predictor variables. We calculated the

292   amount of variation of the different biodiversity metrics explained by the different groups of

293   predictors (climate, space, soil and dung, as found in Supplementary file S1, table 1) and evaluated

294   the significance of the pure fractions (for each group of variables accounting for the variance

295   explained by all other factors) using partial RDA for species composition and partial dbRDA for

296   Sørensen and B-C dissimilarities.

297   We performed a spatial autocorrelation analysis to account for any spatially-structured

298   unexplained variability. We did this by including the vectors obtained from a Moran's Eigenvector

299   Map (Borcard *et al.*, 2004; Borcard *et al.*, 2011) into the analyses. These vectors were calculated

300   using R packages spdep (Bivand & Piras, 2015) and spacemakeR (Dray, 2013). PLS-GLR analyses

301   were conducted using the R package plsRglm (Bertrand, Meyer & Maumy-Bertrand, 2014), and

302   the multivariate variation partitioning analyses with the function varpart of R package vegan

303   (Oksanen *et al.*, 2016).

304

305   **RESULTS**

306   We captured 70,326 individuals of 61 dung beetle species in the four sampling campaigns (9,627

307   individuals of 29 Scarabaeinae species and 60,699 individuals of 32 Aphodiinae species; see

308   Supplementary file S2). Overall, dung beetle abundance and richness were slightly higher in 2014

309   compared to 2013 for both seasons (Figure 2).

310

311   **Variations in species richness, abundance and evenness**

312   There was a significant pattern of decreasing species richness along the gradient, but neither

313   abundance nor evenness showed a significant relationship with aridity (Figure 2, Table 1). The

314   relationship between species richness and aridity strongly varied seasonally, with a higher slope

315   of the *Season*Aridity* interaction in the wet than in the dry season. The significant *Year*Aridity*

316   interaction indicates that the relationship between species richness and aridity varied between

317   years, 2014 showing a steeper slope than 2013 due to the higher number of species in the semiarid

318   end of the transect, but not in the desert areas (Table 1, Figure 2). In fact, species richness showed

319   a clear change only during the wet season, from low values (5–10 species) in the desert to the

320   highest richness (15–20 species) in the semiarid zone (Figure 2). During the dry season, species

321   richness hardly increased from the desert to semiarid areas in 2013, although a slight increase

322   appeared near the semiarid end of the gradient, particularly in 2014.

323   Total abundance did not show a significant relationship with aridity and was very similar

324   along the gradient in both sampling seasons (Table 1, Figure 2). The wet season showed relatively

325   small variations of abundances throughout the gradient, with a decrease at both ends, while there

326   was a striking increase in abundance in the semiarid end of the gradient in the dry season (Figure

327   2). Although evenness was not directly related to aridity, there was a significant *Season*Aridity*

328   interaction (Table 1), indicating that evenness patterns change throughout the year along the

329   gradient, especially because of the contrasting evenness values between the wet and the dry

330   seasons at the semiarid end of the transect (Figure 2).

331

332   **Variations in community composition**

333   Although there were no significant relationships of total abundance with aridity, there were large

334   seasonal differences in the relative abundance at the subfamily level. Communities in the wet

335   season were dominated by Scarabaeinae, which accounted for 60-90% of total abundance in most

336   sites. This contrasts with the dry season, when the communities were almost dominated by

337   Aphodiinae, which accounted for more than 97% of abundance in most sites. Thus, the ratio of

338   Scarabaeinae/Aphodiinae abundances significantly differed between seasons (2013: $\chi^2 =$

339   10632.53, p < 0.001; 2014: $\chi^2 = 22483.74$, p < 0.001). However, these differences did not hold for

340   richness, which showed approximately a 1:1 ratio in the number of species in both seasons.

341   Community composition along the aridity gradient showed a strong seasonal structure. The

342   communities during the wet and dry seasons were clearly different, except in the most arid extreme

343   of the gradient (specially sites 2 and 3), as shown by NMDS ordination (Figure 3). While NMDS

344   shows a clear spatial structure in community composition along the gradient in the wet season, in

345   the dry season only the semiarid end of the transect (sites 8-10) shows a marked difference with

346   all the other sites (Figure 3). PERMANOVA results corroborate that community composition

347   significantly differed seasonally (pseudoF = 8.255, p < 0.0001, d.f. = 1,36) while showing similar

348   patterns in both sampling years (pseudoF = 1.341, p = 0.1968, d.f. = 1,36), with no significant

349   interaction between both factors (pseudoF = 0.604, p = 0.805, d.f. = 1,36). Changes in community

350   composition between years were indeed small, with total Sørensen values of 0.2 and 0.3 for the

351   wet and dry season respectively (Figure 4a), and total B-C of 0.3 in the wet season and 0.2 in the

352   dry season (Figure 4b). Indeed, the indicator species of communities (IndVal analyses) sampled

353   were the same in 2013 and 2014 (see Appendix S3, Table 1). In contrast, three Aphodiinae species

354   were indicators of communities sampled during the dry season (IndVal > 0.95), while seven

355   Scarabaeinae and seven Aphodiinae species were indicators of wet season communities (see

356   Supplementary file S3, table 4).

357

358   **Variations in community dissimilarities in space and time**

359   Dissimilarity between wet and dry season communities (both Sørensen and B-C) significantly

360   decreased with aridity (Figure 4), and there was no interaction with year (Table 2). In contrast,

361   Sørensen dissimilarity between 2013 and 2014 communities was not affected by aridity (Figure

362   4), although B-C dissimilarity significantly increased with aridity with an interaction with season

363   due to the stronger pattern occurring in the dry season (Table 2, Figure 4). Hence, total B-C

364   dissimilarity was low between seasons in the most arid sites, but very high towards the semiarid

365   end of the gradient (Figure 4b).

366   Multisite Beta diversity-partitioning showed that Sørensen dissimilarity among sites was

367   mainly due to species turnover along the gradient in both seasons, although nestedness increases

368   in importance in the dry season (Figure 5a). In contrast, according to B-C dissimilarity analyses

369   balanced changes in abundance were prevalent in both seasons, with some gradient in the wet

370   season (Figure 5b). This pattern was similar in both years. Interestingly, both pairwise Sørensen

371   and B-C dissimilarities showed similar relationships with pairwise differences in aridity. The

372   turnover and balanced components increased in relation to differences in aridity between sites,

373   while nestedness and gradient components did not change significantly with differences in aridity

374   (Table 3).

375

376   **Relationships of environmental variables with the diversity and composition of communities**

377   The PLS-GLR analysis shows that the relationship between environmental variables and

378   species richness and abundance along the gradient largely differed between seasons. Results for

379   evenness are not shown as data did not meet the premises of neither normality nor homocedasticity

380   for the wet season and were not significant for the dry season. PLS components were only

381   significantly related to species richness variations in the wet season and to abundance variations

382   in the dry season (Supplementary file S3, table 5). PLS standardized coefficients indicate that

383   variations of species richness in the wet season were positively related to precipitation (both

384   monthly and annual rainfall) and negatively related to radiation (Figure 6a). Differences of

385   abundance in the dry season appeared positively related to cow dung availability (Figure 6b).

386   Variation partitioning of multivariate data identified significant relationships of Sørensen

387   and B-C dissimilarities and raw community composition with climate, space, soil and dung

388   availability (Supplementary file S3, figure 1). As expected, space and climate explained a large

389   proportion of the variance in all cases, although in a few cases this latter factor only rendered

390   significant results in partial dbRDAs. Dung availability and soil variables explained a relatively

391 small proportion of the variance in B-C dissimilarities and community composition, mainly in both

392 seasons of 2013. Variation of Sørensen dissimilarity in all campaigns was irregularly explained

393 (and rarely significantly, see Supplementary file S3, figure 1) solely by climate and space (from

394 71% to only 23%), with the only exception of the dry season of 2013, where dung availability also

395 explained a marginal 4%.

396

397 **DISCUSSION**

398 Although our results support the general expectation that water availability is a major factor

399 structuring the diversity of communities in semiarid environments, they provide novel insights on

400 how such relationship affects community structure through time. Even though dung beetle species

401 richness shows a clear decrease with increasing aridity, contrary to our expectations abundance

402 and evenness did not change along the gradient. And importantly, aridity fosters a gradual

403 replacement of species, so the most arid areas are inhabited by distinct assemblages of dung beetle

404 species adapted to the dry and resource-poor desert conditions, rather than poor subsets of the less

405 arid areas (our question Q1). But perhaps the most striking of our results is that diversity–aridity

406 relationships show marked seasonal differences (our question Q2). And further, these changes may

407 be consistent between years, rather than stochastic. This, together with the somehow unexpected

408 lack of predictive power of resource (dung) availability (our question Q3) points to a strong

409 environmental filtering as the major process behind not only of the distribution of dung beetles

410 along the studied gradient, but also of their phenology.

411 Low water availability and/or precipitation is known to limit the diversity of many

412 organisms (e.g., Sommer *et al.*, 2010; Maestre *et al.*, 2015), including dung beetles (e.g. Hortal,

413 Lobo & Martin-Piera, 2001; Tshikae, Davis & Scholtz, 2013b, c). Such negative relationship is

414   however inexistent or even reversed in other organisms and/or systems (Polis, 1991; Polis *et al.*,

415   1997; Delsinne *et al.*, 2010; Andersen *et al.* 2015). Water availability may determine species

416   richness through two main mechanisms: physiological constraints (Chown *et al.*, 2011) – thus

417   following the water–energy hypothesis (Hawkins *et al.*, 2003a); and resource availability (Nichols

418   *et al.*, 2009; Tshikae *et al.*, 2013c) –following the species–energy hypothesis (Wright, 1983).

419   While precipitation was directly related to species richness in our analysis, supporting the

420   prediction of the water–energy hypothesis, dung availability did not correlate with species richness

421   in our study. This is consistent with the claims that many other factors not directly related to

422   resource availability may determine large-scale diversity gradients (e.g. Currie *et al.*, 2004;

423   Hurlbert & Jetz, 2010). In the case of our gradient, the higher dung beetle richness at the semiarid

424   end near the coast may be sustained by the increase in diversity of dung types provided by the

425   appearance of cow herds (Lobo *et al.*, 2006; Tshikae *et al.*, 2013b). Further, some Aphodiinae

426   species are generalist saprophages (Christensen *et al.*, 1976; Dellacasa *et al.*, 2006; Holter, Scholtz

427   & Stenseng, 2009), so the higher availability of detritus resources (not quantified in this study)

428   such as leaf litter in this area of higher plant production may be also promoting a higher richness.

429   Further, neither dung beetle abundance nor evenness showed any significant relationship

430   with increasing aridity towards the Sahara. This result is also in contradiction with the species–

431   energy hypothesis, and the general argument that greater productivity can maintain more

432   individuals and therefore viable populations of a larger number of species (Hutchinson, 1959;

433   Brown, 1981; Wright, 1983). Instead, we found an unexpected decline in abundance at the

434   semiarid end of the gradient in the wet season. This area was, by far, the one with higher

435   availability of cattle dung (Supplementary file S1, table 2), the richest resource present in the whole

436   gradient, so it is unlikely that such low numbers are due to limited resource availability. Rather,

437   the lower abundance of dung beetles in the coastal site may be partly explained by both land use

438   intensification caused by cropland and urban spread (Davis, Scholtz & Swemmer, 2012; Nichols

439   *et al.*, 2013) and/or the higher salinity of the deep and superficial layers of the soil –that may deter

440   burying dung beetle species to nest. Further, the large increase of beetle abundance at this area

441   during the dry season was due to a single species, the aphodiid *Anomius baeticus*. This

442   saprophagous beetle feeds on plant detritus (Sánchez-Piñero *et al.*, 2004; Verdú & Galante, 2004),

443   which enables it to have massive population outbreaks in the dry season.

444   Strikingly, changes in community composition along the gradient follow an ordered

445   replacement with aridity rather than a mere loss of species, although the rate of such replacement

446   is progressively lower towards the Sahara. Most variation in composition was due to a balanced

447   turnover in all surveys, with both Sørensen and B-C dissimilarities increasing towards the

448   Mediterranean coast. Despite the decrease in species richness with increasing aridity, nestedness

449   and gradient compositional changes were much smaller, remaining constant throughout the whole

450   gradient. Such pre-eminence of species replacement indicates that the strong filtering imposed by

451   aridity is not limited to the progressive inability of the species adapted to Mediterranean conditions

452   to inhabit desert areas. Rather, there is a distinct pool of dung beetle species adapted to arid Saharan

453   conditions (e.g. *Onthophagus transcaspicus*, *Scarabaeus aegyptiacus, Mendidius palmenticola* or

454   *Calasmosternus lucidus*; Baraud, 1985), that progressively substitutes the semiarid elements of the

455   communities. These species are seemingly adapted to the low –and stochastic– availability of

456   resources, and form distinct communities compared to neighbouring areas with more mesic

457   environments (Sánchez-Piñero *et al.*, 2011). Extreme arid conditions determine the occurrence of

458   a highly adapted biota in desert ecosystems (Arakaki *et al.*, 2011), usually including a high

459   proportion of endemics (Le Houérou, 2001). Whether this pattern of pre-eminence of species

460   replacement with increasing aridity is common in desert communities needs further investigation

461   since no other studies partitioned beta diversity along aridity gradients before.

462   Importantly, although the general pattern of decrease in richness and balanced turnover along the

463   gradient holds on for all surveys, our results also show important temporal variations. Indeed, the

464   significance of the interactions of season and year with aridity evidence that the effect of water

465   availability on species richness changes in time. Dung beetle faunas showed strong seasonal

466   changes, with a steeper decline of richness with aridity in the wet season. In arid and semiarid

467   environments this season is not only characterized by milder climate, but also by the higher

468   abundance and quality of trophic resources (Hanski, 1987). Further, the richness–precipitation

469   relationship was weaker in 2013 than in 2014 –with no significant changes in species richness

470   across the gradient in the dry season of the former year. These differences may be related to

471   temporal changes in precipitation, as this factor was an important predictor of richness in spring

472   but not in the dry season. The marked precipitation gradient along the transect in spring contrasts

473   with the scarce difference in the amount of rain along the gradient at the end of the summer-early

474   fall (from 46 to 13 and 22 to 13 mm of monthly precipitation, respectively). Spring precipitations

475   allow a higher plant productivity that in turn results in more hydrated dung of better quality for

476   nesting (Lumaret, 1995), and ultimately higher reproductive success and the emergence of larger

477   populations in the next generation. Indeed, annual precipitation was higher in 2013 than in 2012,

478   allowing a higher abundance of dung beetles emerging the year after because of the higher

479   reproductive success in 2013. Long-term data would be strongly needed to analyse these temporal

480   changes in species richness and precipitation.

481   The spatial structure of dung beetle assemblages along the transect also varied in time.

482   During the favourable conditions of the wet season species composition followed a structured

483   sequence of replacement from the semiarid sites to the desert. This structure was disassembled in

484   the harsher dry season, when assemblages were largely homogeneous, particularly in the arid and

485   nearly hyperarid areas, and only the three sites in the semiarid end of the gradient showed

486   compositional differences. Importantly, the temporal changes in composition at each site also

487   varied in relation to aridity. Seasonal variations in species dissimilarity were lower as aridity

488   increased, regardless of the relative effects of abundance. Similar findings have been reported for

489   ant assemblages along an elevational gradient (Bishop *et al.*, 2014), and corroborate the prediction

490   that seasonal variations in assemblage composition are lower in more unpredictable habitats

491   (Hawkins *et al.*, 2003a). Hence, our results may indicate that desert communities inhabiting highly

492   unpredictable systems show a higher seasonal similarity than more mesic sites. This is likely due

493   to the ability of some species to cope with the harsh desert conditions regardless of the season

494   (Pierre, 1958; Noy-Meir, 1974; Heatwole, 1996; Ghabbour & Mikhail, 1997).

495   In contrast, the most unpredictable arid habitats showed higher inter-annual compositional

496   variations. However, these inter-annual differences were only significant when accounting for

497   species abundances through the use of Bray-Curtis dissimilarities. This indicates that species

498   composition at each season remains relatively constant from one year to another, and community

499   structure only changes according to the variations in abundance. This is particularly true in the dry

500   season, as revealed by the importance of the *season*aridity* interaction when analysing inter-

501   annual variations in B-C dissimilarity. Differences in assemblage composition between two

502   consecutive years in arid areas of SE Spain were mainly due to the differences in abundance of a

503   single species, *Anomius baeticus*, which abundance differed one order of magnitude between the

504   two years (Sánchez-Piñero *et al.*, 2011). Large differences between consecutive years in the

505   abundance of particular species are characteristic of Mediterranean arid systems (Noy-Meir, 1974;

506   Sánchez-Piñero *et al.*, 2011). Our results are consistent with the predictions that inter-annual

507   variations in assemblage composition will be higher in more unpredictable habitats (Tonkin *et al.*,

508   2017), although studies considering a greater number of years will be necessary, especially in the

509   more unpredictable desert sites (Polis, 1991).

510   Interestingly, changes in aridity through space and time also promote a spatio-temporal

511   shift in the dominance of the two dung beetle subfamilies, Scarabaeinae and Aphodiinae.

512   Aphodiinae are more abundant in the desert communities during the wet season (see also Abdel-

513   Dayem *et al.,* 2016), a change that may be related to a spatial shift in dung use strategies forced by

514   environmental conditions. While all Mediterranean Scarabaeinae species are either paracoprids or

515   telecoprids, the Aphodiinae include endocoprid, saprophagous and kleptocoprid species (Sánchez-

516   Piñero, 1994; González-Megías *et al.*, 2003). Hence, the observed changes in relative abundance

517   of Aphodiinae in the desert communities in the wet season, also reported in previous studies

518   (Labidi *et al.*, 2012; Abdel-Dayem *et al.*, 2016), result in a functional shift from para- and

519   telecoprid beetles to endocoprids and more generalist saprophagous species. Such shift also occurs

520   in time, for Aphodiinae dominate in abundance during the dry season throughout the whole

521   gradient (totalling > 95% of individuals in all local communities), a pattern also found in other

522   Mediterranean dung beetle assemblages (e.g. Sánchez-Piñero *et al.*, 2004; Sullivan *et al.*, 2016).

523   In fact, our results suggest that the ability of many Aphodiinae species to use different resources

524   for feeding and nesting may allow them to maintain populations in more limiting dry conditions

525   (both in more arid areas as well as in drier seasons), and their relative abundance will diminish

526   when and where milder conditions allow Scarabaeinae to thrive and hold large populations and

527   species-rich communities. Whether this is merely an effect of differences in environmental

528   filtering between the two groups or by the eventual displacement of Scarabaeinae species by the

529   superior competitive ability in dry conditions of the copro-saprophagous Aphodiinae remains an

530   open question.

531

532   **CONCLUSIONS**

533   To summarize, climate-driven environmental filtering is the main process shaping the structure of

534   dung beetle communities along the aridity gradient studied here. However, such filtering may be

535   partly related with the availability of high-quality resources for feeding and nesting. In fact, the

536   diversity–aridity relationship changes through time, determined by the highly variable seasonal

537   and inter-annual patterns of precipitation, that in turn affect the quality and quantity of mammal

538   dung. This results in a ordered replacement of functionally-different species in space and time, as

539   generalist and saprophagous dung beetles become dominant in desert conditions and dryer seasons

540   and years. That is, desert communities are not impoverished subsets of species from species-rich

541   communities from milder climatic conditions, but unique combinations of species adapted to such

542   conditions. Whether this pattern of pre-eminence of species replacement with increasing aridity is

543   common in desert communities needs further investigation since no other studies partitioned beta

544   diversity along aridity gradients before. The limited temporal extent of our study does not allow

545   assessing the effects of large inter-annual changes in precipitation either, but it can however be

546   expected that semiarid dung beetle faunas respond to the climate change-driven progressive

547   aridification of East Mediterranean with large functional changes in community structure (see

548   Tonkin *et al.*, 2017). The loss of spatial structure of the dung beetle communities in the dry season

549   for most of the gradient points to a reduction of richness and a higher homogeneity of assemblages

550   if drought becomes a pervasive factor. Indeed, the expected lower seasonal changes in precipitation

551   in progressively more arid conditions is likely to result in a generalized loss of diversity with

552 climate change. But beyond these general patterns of change, the exact nature behind dung beetle

553 responses to aridity remains elusive. Data on functional traits, physiological responses to aridity

554 and long-term community variations are needed to understand the complex mechanisms behind it.

555

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569

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Multivariate GLM on the effects of temporal (seasonal and interanual) variations of aridity over species richness, abundance and evenness.

Significance levels after Bonferroni correction: **** $p < 0.0001$; *** $p < 0.0003$; ** $p < 0.003$; * $p < 0.016$.

Effect	Richness	log10 Abundance	log10 Evenness
	F (1, 35)	F (1, 35)	F (1,35)
Aridity	15.17 ***	6.39	1.43
Season*Aridity	67.07 ***	2.72	38.75 ***
Year*Aridity	7.57 *	2.48	5.16
Year*Season*Aridity	1.11	0.02	4.27

Variation of seasonal (wet-dry) and interannual (2013-2014) dissimilarity for species occurence (Sørensen) and abundances (Bray-Curtis) in relation to aridity and its interaction with year and season.

Sørensen dissimilarity for interannual comparison and Bray-Curtis dissimilarity for both seasonal and interannual comparisons were arcsin transformed. Statistical significance levels after Bonferroni correction: *p < 0.0125; **p < 0.0025; ***p < 0.00025.

	Sørensen		Bray-Curtiss	
Effect	Coefficient ± S.E.	F (1,17)	Coefficient ± S.E.	F (1,17)
Seasonal				
Aridity	-1.974 ± 0.406	23.63***	-3.473 ± 0.458	57.58***
Year*Aridity	0.019 ± 0.032	0.33	0.064 ± 0.036	3.14
Interannual				
Aridity	0.184 ± 0.529	0.12	1.468 ± 0.424	12.00**
Season*Aridity	0.008 ± 0.042	0.04	0.109 ± 0.034	10.49**

Spearman rank correlation coefficients for the relationship between pairwise difference in aridity between sites and the components of the partitioning of Beta and Bray-Curtis dissimilarities.

We used beta diversity (turnover and nestedness components of Sørensen index) and abundance-based dissimilarity (balanced and gradient components of Bray-Curtis index) for the different surveys. Significance values after Bonferroni correction: ms = marginally significant; * $p < 0.003$; ** $p < 0.0006$; *** $p < 0.00006$.

Year	Season	Sørensen		Bray-Curtis	
		Turnover	Nestedness	Balanced	Gradient
2013	Wet	0.429	-0.022	0.593***	-0.135
	Dry	0.493**	-0.210	0.487*	-0.331
2014	Wet	0.536**	-0.208	0.683***	-0.402
	Dry	0.590***	0.116	0.479*	-0.308

Figure 1

Map of the ca. 400 Km transect from a semiarid zone (mor.10, Mediterranean coast) to the desert area (mor.1, Sahara desert).

The map is constructed by overlapping an aridity layer (Trabucco *et al.*, 2009) depicted in green-yellow-brown shading and an altitude layer (Hijmans *et al.*, 2005) converted into elevation isolines (spaced 200 altitudinal meters).

mor.10

mor.9

mor.8

mor.7

mor.6

mor.5

mor.4

mor.3

mor.2

mor.1

**Aridity
(no units)**

5000

4000

3000

2000

1000

200
400
1000
600
1400
1200
800
1000
1200
1000
1000
1200
1400
1600
1400
1200
1400
1400
1600
1600
1400
1000
1600
1400
1200
1400
1000

35.0

34.5

34.0

33.5

33.0

32.5

32.0

-2.2   -2.0   -1.8   -1.6   -1.4   -1.2

N

0km 20km 40km
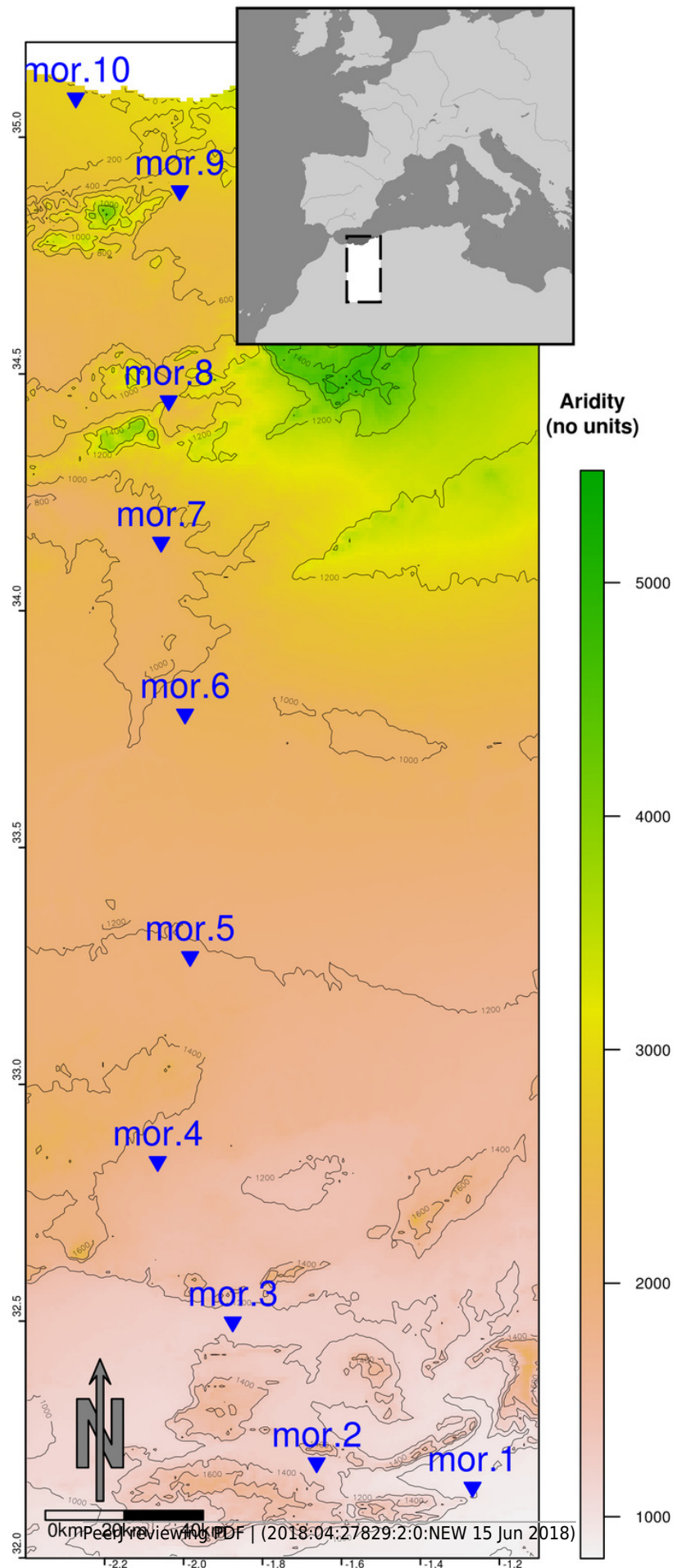
Figure 2

Variations in dung beetle community descriptors along an aridity gradient from a semiarid zone to the Sahara desert during the wet and dry seasons in 2013 and 2014.

Variations in species (A, D) richness, (B, E) log abundance and (C, F) evenness along an aridity gradient from a semiarid zone (300 mm mean annual rainfall) to the Sahara desert (100 mm) during the wet (April, blue lines) and dry (September, red lines) seasons in 2013 (A-C) and 2014 (D-F). The straight lines in the figures for species richness show the regression lines for the wet and dry season each year. Abundance and evenness did not show either linear nor unimodal fits to aridity. The range of Y axis was standardized to allow easier comparison between years.
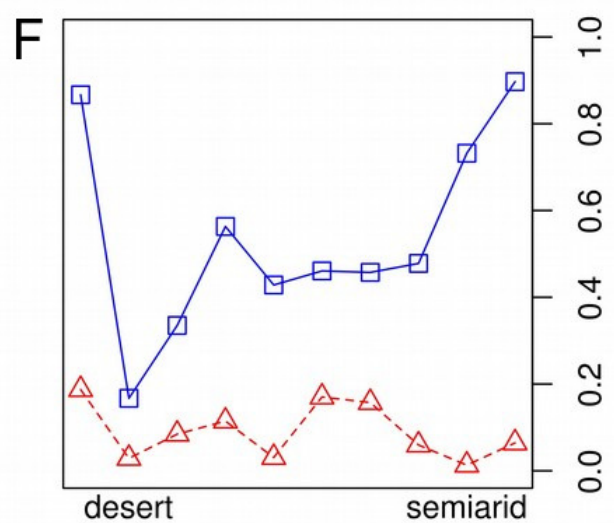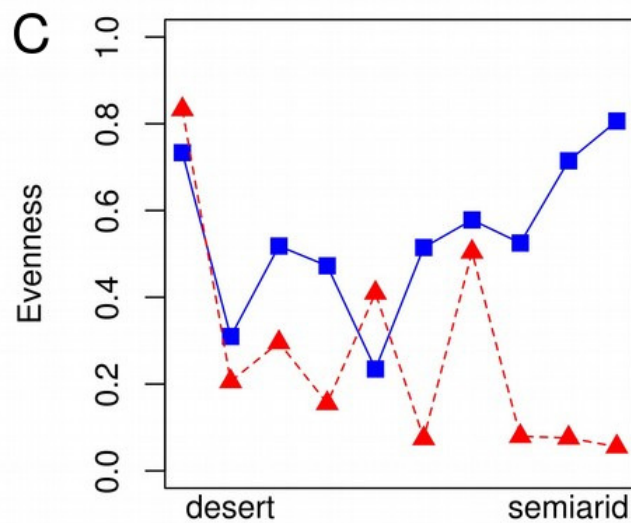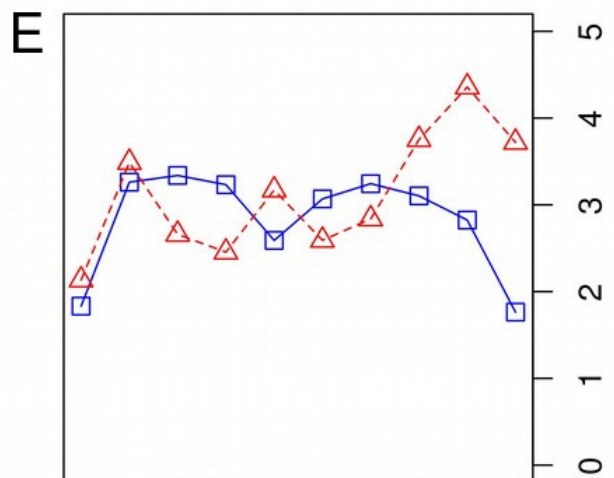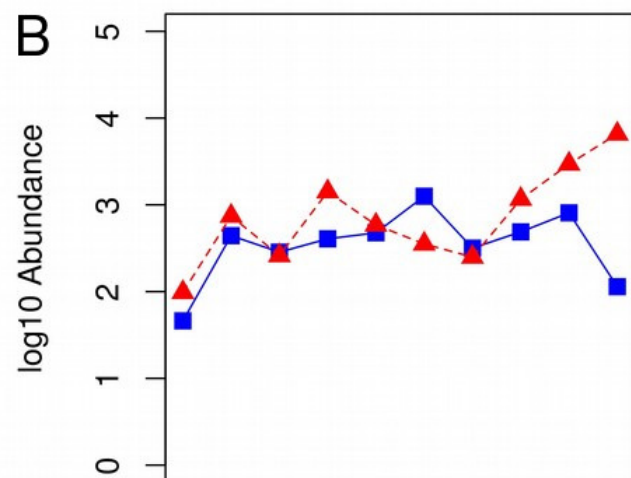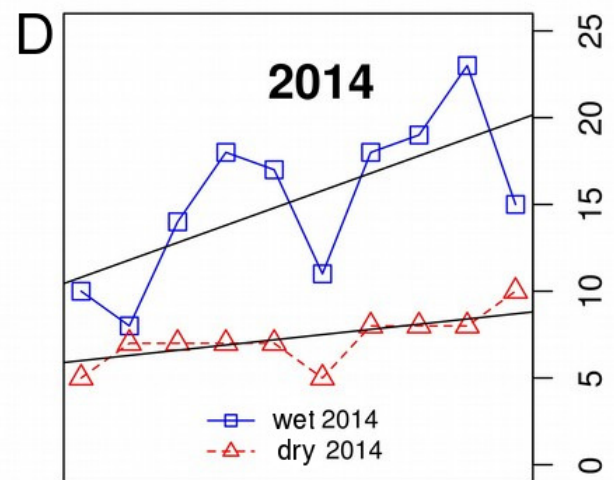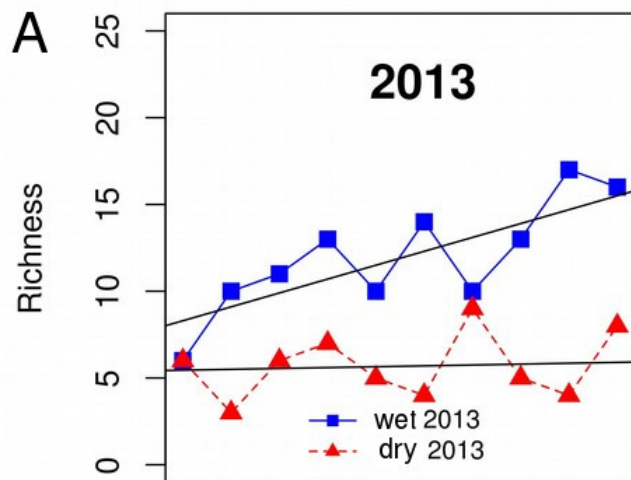
Figure 3

Non-metric multi-dimensional scaling (NMDS) ordination (stress = 0.12) of community composition for the different sites in the wet and the dry season of the two sampled years (2013 and 2014).
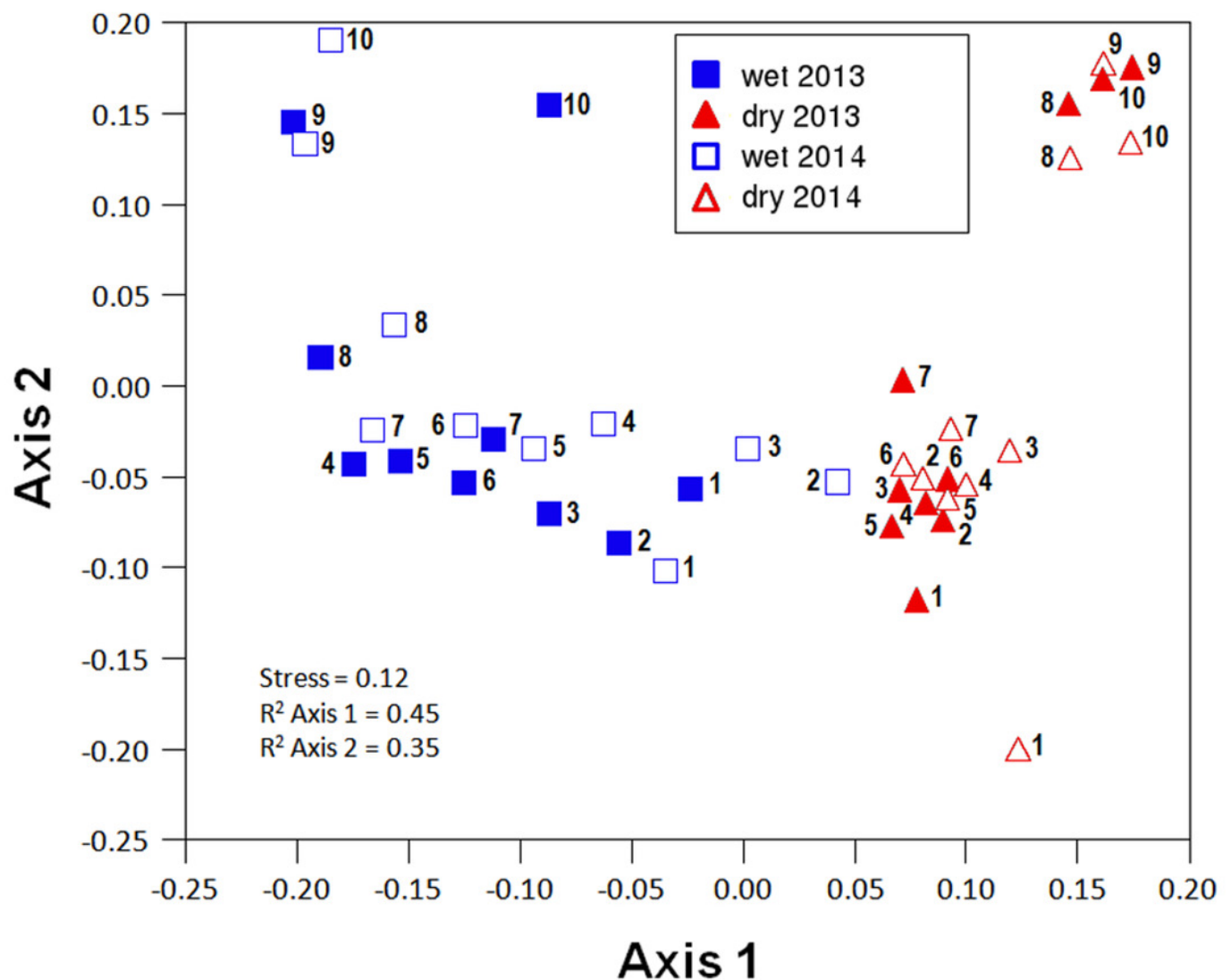
Figure 4

Temporal beta diversity (Sørensen coefficient) and Bray-Curtis dissimilarities of dung beetle communities along the aridity gradient.

(A-B) Seasonal beta diversity and Bray-Curtis dissimilarities respectively; each bar compares communities for the same site in the wet and the dry seasons. (C-D) Interannual beta diversity and Bray-Curtis dissimilarities respectively; each bar compares communities for the same site in the two years included in this study. Beta diversity is partitioned in two components: beta turnover (dark colours) and beta nestedness (light colours). Bray-Curtis dissimilarities are also partitioned in two components: BC gradient (dark colours) and BC balanced (light colours). The range of Y axis (showing all possible variation of beta diversity or BC, 0-1) was standardized in all plots to allow easier comparison.
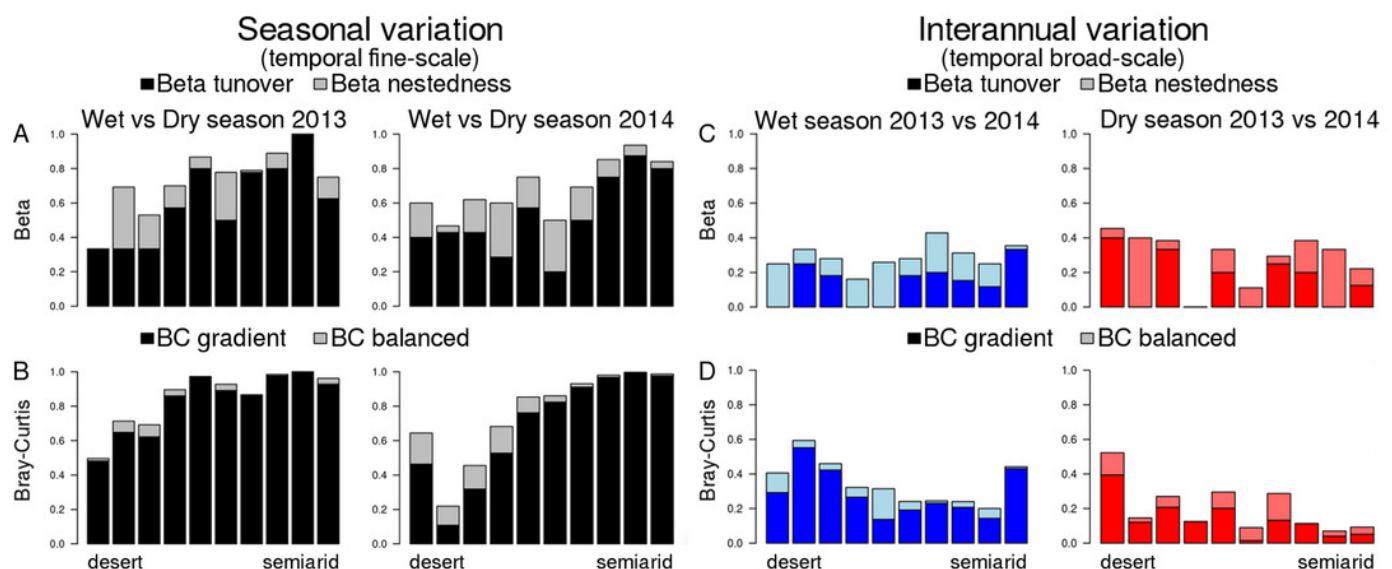
Figure 5

Multiple site dissimilarity of dung beetle communities along the aridity gradient based on species occurrence (Sørensen) and considering species abundances (Bray-Curtis).

Multiple site dissimilarity partitioning into turnover/nestedness or balanced/gradient components of dung beetle communities along the aridity gradient for the different seasons and years sampled based on (A) species occurrence (Sørensen) and (B) considering species abundances (Bray-Curtis).
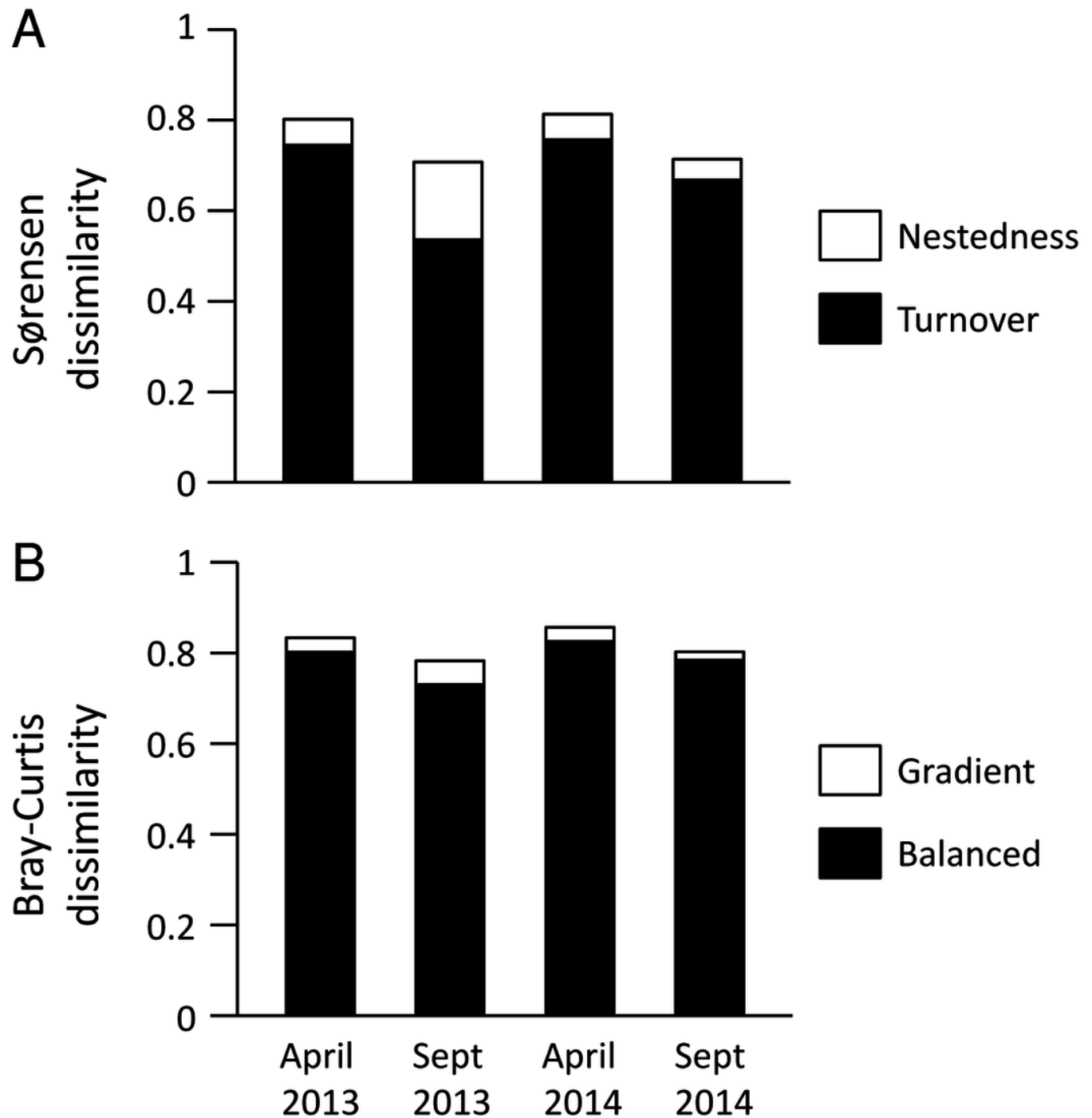
Figure 6

Distribution of standardized coefficients of PLS-GLR models for richness and abundance using all available environmental variables.

Boxplots show standardized coefficients of PLS-GLR models for species richness in the wet season (A) and abundance in the dry season (B) of dung beetle communities along an aridity gradient from a semiarid zone (300 mm mean annual rainfall) to the Sahara desert (100 mm). Standardized coefficients were obtained by bootstrap (1000 iterations) to identify the importance of predictor variables in the models. Significant predictor variables differ from 0.

A

B

Gravel
Sand
Silt
Clay
Bulk density
Consistency
Field capacity
Vegetatioin height
Vegetation cover
Cow dung
Sheep + other dung
Radiation
Annual precipitation
Monthly precipitation
Monthly Temperature
Altitude