

# Reports

*Ecology*, 101(10), 2020, e03138  
© 2020 by the Ecological Society of America

## Assessing the functional relationship between dung beetle traits and dung removal, burial, and seedling emergence

INDRADATTA DECASTRO-ARRAZOLA <sup>1,2,6</sup> JOAQUÍN HORTAL <sup>1,3,4</sup> JORGE ARI NORIEGA <sup>1,5</sup> AND FRANCISCO SÁNCHEZ-PIÑERO <sup>2</sup>

<sup>1</sup>*Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (MNCN-CSIC), CI José Gutiérrez Abascal, 2, Madrid 28006 Spain*

<sup>2</sup>*Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, Campus de Fuentenueva, Granada 18071 Spain*

<sup>3</sup>*Department of Ecology, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia 74001-970 Brazil*

<sup>4</sup>*Faculdade de Ciências, cE3c—Centre for Ecology, Evolution and Environmental Changes, Universidade de Lisboa, Lisboa 1749-016 Portugal*

<sup>5</sup>*Laboratorio de Zoología y Ecología Acuática—LAZOE, Universidad de Los Andes, Bogotá, Colombia*

*Citation:* deCastro-Arrazola, I., J. Hortal, J. Ari Noriega, and F. Sánchez-Piñero. 2020. Assessing the functional relationship between dung beetle traits and dung removal, burial, and seedling emergence. *Ecology* 101(10):e03138. 10.1002/ecy.3138

**Abstract.** The relationship between biodiversity and ecosystem functioning is often assessed through trait diversity. However, the relationship between traits and functions is typically assumed but seldom tested. We analyze the relationship between dung beetle traits and three ecological functions: dung removal, dung burial, and seedling emergence. We set up a laboratory experiment using nine Scarabaeidae species (three endocoprids, four paracoprids, and two telecoprids). We placed a sexual pair of beetles in each experimental unit, together with a mixture of dung and seeds, and measured the amount of dung removed and buried, burial depth, and the number of emerged seedlings. Sixteen morphological traits related to dung removal and burial were measured in each individual. Results indicate that these traits were related to dung beetle performance in dung removal and burial. Most traits were positively related to dung removal, indicating the existence of a general trait syndrome associated with dung manipulation and digging capability. Dung exploitation strategies did not provide further explanatory power. Seedling emergence showed a negative but weak relationship with dung burial amount and depth and species identity. This implies that specific differences in dung–soil interface activity may be important in secondary seed dispersal by dung beetles.

**Key words:** functional traits; laboratory experiment; mesocosms; Scarabaeidae; seed dispersal; trait–function relationship.

### INTRODUCTION

Understanding the role of biological diversity in ecosystem functioning is a major endeavor of ecology in the current scenario of global change and high biodiversity loss (Hooper et al. 2005). In recent decades, functional diversity has been increasingly included in studies on ecology, evolution, and conservation (Petchey and Gaston 2006, Wong et al. 2019). Although in some cases simple functions can be directly measured, avoiding the use of traits (Gollan et al. 2013), species and individual

traits are typically used as proxies for functions (Violle et al. 2007). Indeed, groups of traits have been used to analyze whether functional diversity is related to a given function (Griffiths et al. 2015, 2016), but their relationships with functioning have seldom been evaluated (Noriega et al. 2018). Trait functionality is usually assumed but not explicitly tested (Wong et al. 2019). However, to use traits as proxies of functions safely, it is first necessary to test if these function–trait relationships actually exist (Mlambo 2014, Nervo et al. 2014, Wong et al. 2019).

Decomposition of organic matter is a key ecological process, essential for both carbon and nitrogen cycles (Swift et al. 1979, Bardgett 2005, Nervo et al. 2017). Scarabaeoidea dung beetles are a highly diverse and widely distributed group that exploits feces, mainly from large herbivores (Hanski and Cambefort 1991, Scholtz

Manuscript received 27 January 2020; revised 8 May 2020; accepted 18 June 2020. Corresponding Editor: Kathryn L. Cottingham.

<sup>6</sup>E-mail: indradatta@wanadoo.fr

et al. 2009). They play an essential role in the degradation and relocation of herbivore dung (a nitrogen-rich form of organic matter), as well as in secondary seed dispersal, by relocating viable seeds found in the dung (Shepherd and Chapman 1998, McConkey 2005, Nichols et al. 2008, Beaune et al. 2012). Three main dung beetle “functional groups” have been traditionally established according to their feeding and/or nesting behavior (Doube et al. 1991): endocoprids (dwellers), paracoprids (tunnellers), and telecoprids (rollers). These different dung exploitation strategies determine where dung—and the seeds embedded in it—is relocated.

Several morphological features related to size of front and hind tibiae, head, prothorax, body size, and shape (see Appendix S1: Section S1, Supplementary Material and Methods) have been traditionally regarded as adaptations of dung beetles to coprophagy and, especially, dung burial (Halfpiter and Matthews 1966, Edmonds 1972, Halfpiter and Edmonds 1982, Martín-Piera and López-Colón 2000, Raine et al. 2018). These traits have been recently used to analyze the relationship of functional diversity with ecosystem functions (BEF; Griffiths et al. 2015, 2016). However, few studies have experimentally analyzed their relationship with the performance of ecological functions (Nervo et al. 2014, Macagno et al. 2016). Similarly, although the role of dung beetles as secondary seed dispersers is well known (Feer 1999, Laverde et al. 2002, D’hondt et al. 2008, Culot et al. 2011, Iannuzzi et al. 2013, Griffiths et al. 2015), few studies have analyzed the direct effects of dung beetle activities such as dung burial on seedling emergence (Andresen and Levey 2004, D’Hondt et al. 2008, Griffiths et al. 2016).

In this study, we experimentally evaluate the relationships between the outcome of two ecosystem functions delivered by dung beetles (dung removal and dung burial) and morphological traits. Also, we analyze the outcome of a third function, secondary seed dispersal, by looking at the effects of dung removal, dung burial, and depth of buried dung on seedling emergence. Specifically, we assess the following questions:

- 1) Are those morphological traits regarded as adaptations for dung processing and digging actually related to the functional outcomes of dung removal and dung burial?
- 2) Which traits can be used as effective, simple functional proxies for these functions?
- 3) Is dung exploitation strategy also an explanatory variable related to the functional outcome, that is, the amount of dung removed and/or buried?
- 4) Do dung beetles enhance seedling emergence through their activity on dung removal and dung burial?

## MATERIALS AND METHODS

### *Experimental design*

A mesocosm experiment was performed during April–May 2015 in laboratory conditions. We assessed the performance of nine dung beetle species ranging from 3.4 to 29.0 mm in body length, including three endocoprids

(*Acrossus luridus* (Fabricius, 1775), *Aphodius foetidus* (Herbst, 1783), *Euorodalus tersus* (Erichson, 1848)), four paracoprids (*Bubas bubalus* (Olivier, 1811), *Onthophagus vacca* (Linnaeus, 1767), *Onthophagus opacicolis* Reitter, 1892, *Onthophagus ruficapillus* Brullé, 1832) and two telecoprids (*Scarabaeus sacer* Linnaeus, 1758, *Scarabaeus puncticolis* (Latreille, 1819)).

A total of 98 mesocosms (28 cm diameter × 30 cm height pots filled with organic-farming soil up to 25 cm height with 100 g sheep dung on top) were built: 8–10 mesocosms for each dung beetle species and 10 control mesocosms to measure seedling emergence in the absence of beetle activity (see Appendix S1: Section S1, Supplementary Material and Methods). In each mesocosm we placed 100 g of fresh dung containing seeds of three commercially available Mediterranean plants (*Hordeum vulgare* L., *Anthyllis cytisoides* L., and *Cistus albidus* L.), obtained by supplementing the diet of 21 sheep housed indoors. A sexual pair of dung beetles was then placed in each mesocosm, because dung removal and dung burial are largely performed by nesting pairs. After 7 d the dung was dry and dung beetles were retrieved. We discarded mesocosms where dung beetles remained inactive during that period, so our final data (see Data S1) comprise a total of 79 mesocosms (7 *A. luridus*, 5 *A. foetidus*, 6 *E. tersus*, 9 *B. bubalus*, 10 *O. opacicolis*, 9 *O. ruficapillus*, 5 *O. vacca*, 9 *S. sacer*, 9 *S. puncticolis*, and 10 control mesocosms without dung beetles).

In each pot, we measured dung removal, dung burial, and seedling emergence. Dung removal was measured as the difference between the dry weight of a 100-g dung pat and the dry weight of dung remaining on the soil surface. To measure dung burial we used dry weight of dung masses buried in the soil. The number of emerged seedlings was visually counted in each mesocosm. Finally, we measured 16 morphological traits in all individuals used in the experiment, describing the head (length, width, area), prothorax (length, width, height, volume), front tibia (length, area, length of first tooth), hind tibia (curved and straight length, area), total body length, volume, and weight (see Appendix S1: Table S5). Most traits were measured on images taken using a stereomicroscope. To analyze the relationship between morphological traits and dung removal and burial, measurements of traits for each mesocosm corresponded to the average values of the two individuals of each pair (male and female), since the experimental unit was the mesocosm and it was not possible to determine the specific contribution of each individual. This approach also minimized the number of variables in the models. For further details on the experimental design see Appendix S1: Section S1, Supplementary Material and Methods.

### *Statistical analyses*

To find the combination of morphological traits related to dung removal and dung burial, we used partial

least-squares generalized linear regressions (PLS-GLR, herein called PLSR for simplicity; Bastien et al. 2005) with Gaussian function and identity link; PLSR deals well with collinearity among multiple predictor variables. Cross-validation and Akaike information criterion (AIC) were used to select among PLSR models including different numbers of components. The standardized coefficients and significance of each predictor in the final PLSR model were obtained by bootstrapping (1,000 iterations). We included endocoprids (which do not bury dung) in the analysis of dung burial as a non-burial control for traits. In the analysis, we used individual mesocosms as the sample unit, in order to account for both intraspecific and interspecific variations in traits and performance (Albert et al. 2012, Griffiths et al. 2016). We also analyzed the relationship between functions delivered by dung beetles (dung removal, dung burial, depth of buried dung) and seedling emergence by means of PLSR because of collinearity among predictor variables. Because seedling emergence is a count variable, a PLSR model with Poisson function and log link was performed.

To find whether dung exploitation strategy (i.e., endocoprid, paracoprid, and telecoprid) and species also affected the three functions measured (i.e., added explanatory power to the models), we used generalized linear mixed models (GLMM). We used the selected components of the PLSR analyses above and dung exploitation strategy (=categorical, three levels) as fixed effects. Dung exploitation strategy was included as a fixed effect, because we selected species of each of the three main strategies. Species (=categorical, nine levels) was included as a random effect because different species may not only differ behaviorally, but also be affected in different ways by laboratory conditions. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. We used package lme4 to conduct GLMM analyses. Model selection is shown in Appendix S1: Section S2.

Differences in seedling emergence between the control treatment and the different dung beetle species were analyzed by means of a generalized linear model (GLM) with Poisson function and log link. Significance levels for the comparisons between the control treatment and the different species were determined by sequential Bonferroni correction. Further details of statistical analyses can be found in Appendix S1: Section S1, Supplementary Material and Methods.

## RESULTS

### *Dung removal*

The final GLMM model selected included two PLSR components explaining 57.3% of the variability in dung removal (Appendix S1: Section S2, Model Selection). Neither species identity (as a random factor) nor dung exploitation strategy provided additional explanatory

power to the model (Appendix S1: Section S2, Model Selection). The two PLSR components included in the model indicate that two groups of morphological traits configure different “trait syndromes” (Fig. 1; Appendix S1: Table S1). Most traits showed square weights (i.e., 1/number of explanatory variables) higher than 0.063 in PLSR component 1, and included variables positively related to dung removal. The majority of measured traits were included in this first component, which is mainly related to prothorax traits, head area and width, protibia area and size of the first tooth of the protibia, total volume, weight and total body length. The second component, in contrast, was primarily associated with a group of traits negatively related to dung removal that describe the length of structures used for dung manipulation and burrowing, such as head, protibia, and metatibia (Fig. 1B; Appendix S1: Table S1). This may indicate that the smallest species *E. tersus* (with comparatively shorter legs and head) removed more dung than expected based solely in PLSR component 1, whereas *Scarabaeus* species removed a proportionally smaller amount of dung.

### *Dung burial*

The selected GLMM model included three PLSR components explaining 64.5% of the variability in dung burial (Appendix S1: Section S2, Model Selection). As in the case of dung removal, neither species nor dung exploitation strategy provided additional explanatory power to the model. Only prothorax volume, pronotum length, pronotum width, and protibia area appeared as significant explanatory variables in the PLSR model (Appendix S1: Table S2). However, variable weights in each component indicate the occurrence of trait syndromes related to dung burial. As in the case of dung removal, PLSR component 1 included a set of traits positively related to dung burial (Fig. 2A; Appendix S1: Table S2): in addition to prothorax volume, pronotum length and width, and protibia area (indicated above), body weight, body volume, total length, head area and width, size of first protibia tooth, and metatibia area also appeared as important variables (square weight >0.063) in this component. PLSR component 2 resembles component 1, both in the positively and negatively related traits, and the third component is mainly related to a negative relationship of dung burial with total body length, indicating that beetles with proportionally longer bodies bury smaller amounts of dung (Fig. 2C).

### *Seedling emergence*

There were differences in seedling emergence between the control treatment and the different species (Fig. 3A; Appendix S1: Table S3). *Aphodius foetidus*, *B. bubalus*, *O. vacca*, *S. puncticollis*, and *S. sacer* experiments showed no differences in seedling emergence with respect to the control treatment, whereas *E. tersus*, *A. luridus*, *O.*

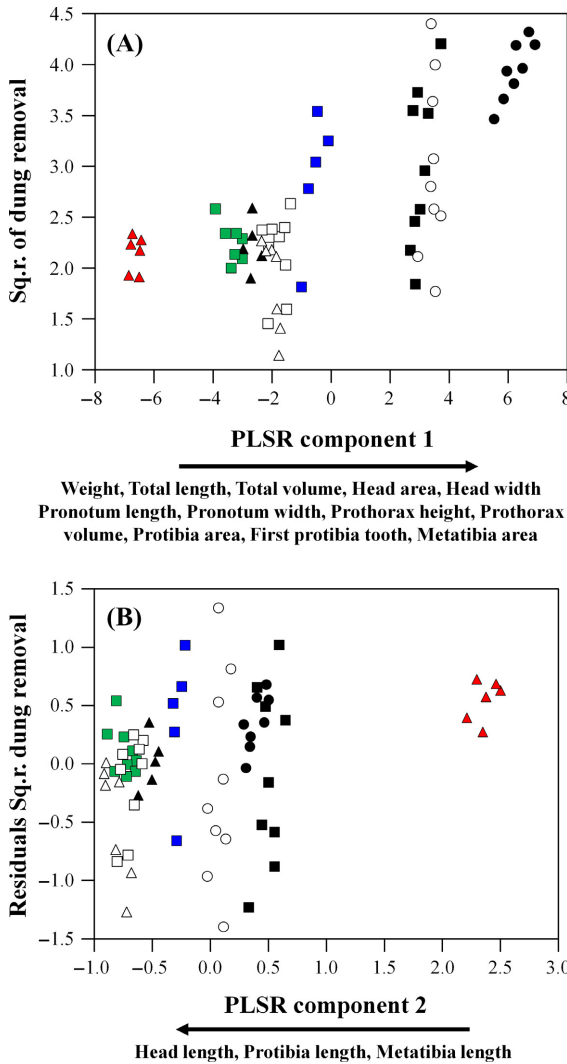


FIG. 1. Associations between partial least-squares generalized linear regressions (PLSR) components and dung removal by pairs of dung beetles of nine different species. Arrows below the PLSR components indicate the morphological traits related to the component and whether they are positively or negatively related to the response variable (Sq. r. = square root). Traits with significant ( $P < 0.05$ ) standardized coefficients are shown in bold type. Triangles: white = *Acrossus luridus*; black: *Aphodius foetidus*; red: *Euorodalus tersus*. Squares: green: *Onthophagus ruficapillus*; white: *Onthophagus opacicollis*; blue: *Onthophagus vacca*; black: *Bubas bubalus*. Circles: white: *Scarabaeus puncticollis*; black: *Scarabaeus sacer*. [Color figure can be viewed at wileyonlinelibrary.com]

*ruficapillus*, and *O. vacca* significantly increased seedling emergence (Fig. 3A; Appendix S1: Table S3).

The final GLMM indicated that species identity had a significant effect on seedling emergence (Appendix S1: Section S2, Model Selection). The species differ in the intercept with respect to the single component resulting from the PLSR analysis. Depth of buried dung and dung burial were the most important variables in the single

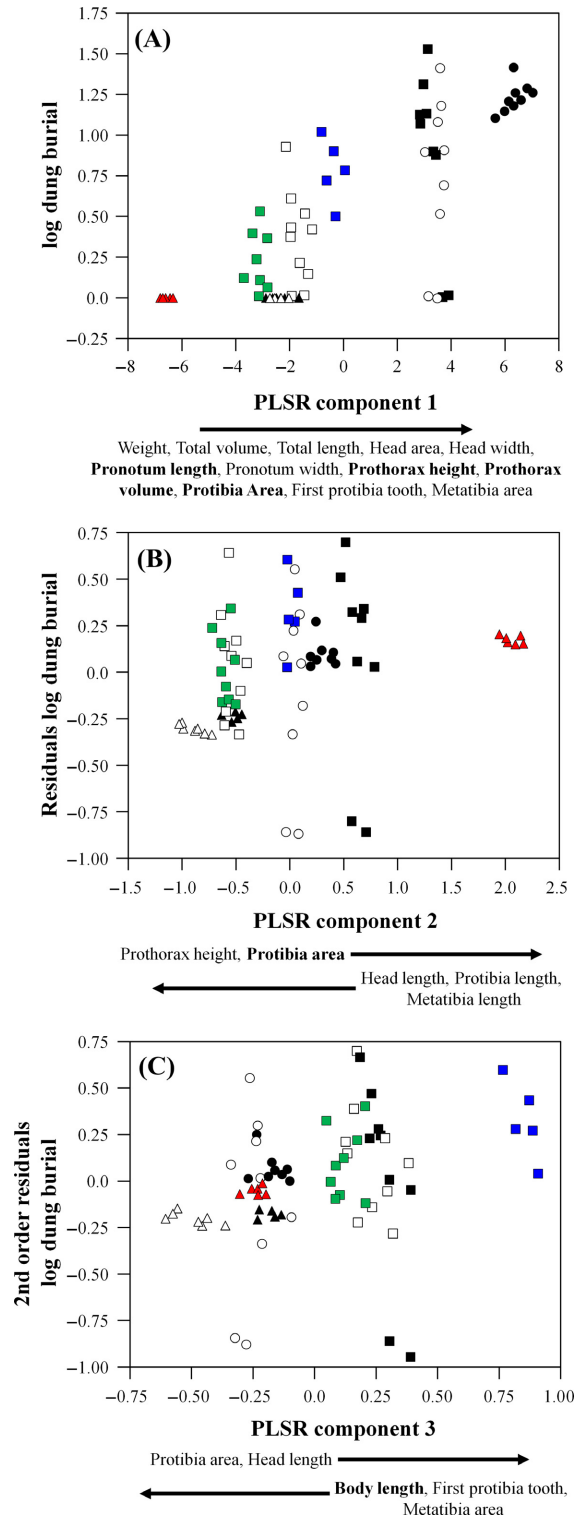


FIG. 2. Associations between partial least-squares generalized linear regressions components and dung burial by pairs of dung beetles of nine different species. Arrows and symbols as in Fig. 1. [Color figure can be viewed at wileyonlinelibrary.com]

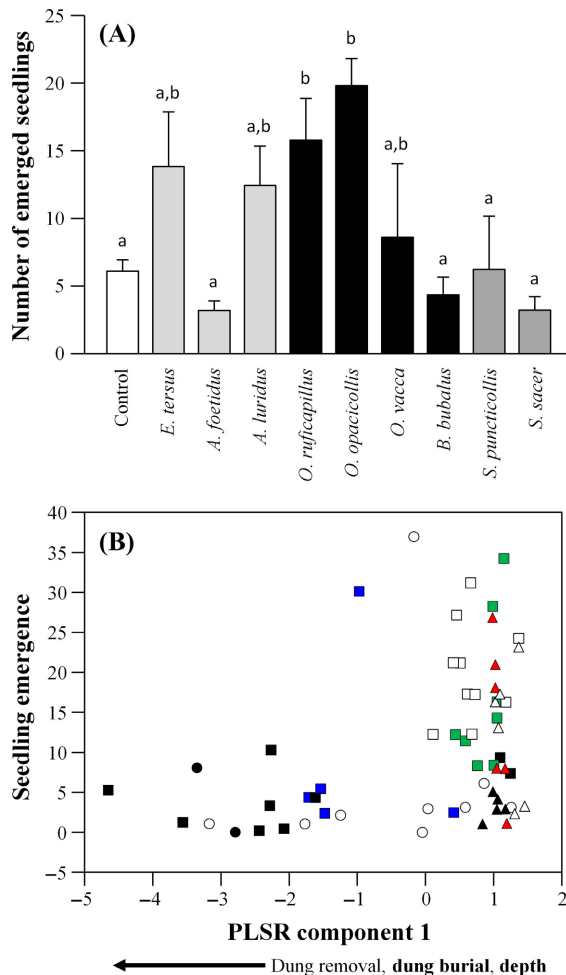


FIG. 3. (A) Mean number of emerged seedlings in control pots and in pots with different dung beetle species. Colors of bars group dung exploitation strategies of species (light gray = endocoprids, black = paracoprids, dark gray = telecoprids). Letters (a, b) indicate significance of comparisons between the control treatment and each species by means of a GLM (Poisson function, log link; see Appendix S1: Table S3) after sequential Bonferroni correction. same letter = no significant difference; different letters = significant difference at  $P < 0.0001$ . (B) Associations between partial least-squares generalized linear regressions components and seedling emergence. Arrows as in Fig. 1, but for functions (dung removal, dung burial, depth of buried dung). Symbols as in Fig. 1. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

significant component of the PLSR analysis (Fig. 3B; Appendix S1: Table S4).

## DISCUSSION

The results of our experiment reveal that there is an actual relationship between morphological traits generally regarded as involved in dung removal and dung burial, and the delivery of these ecological functions by dung beetles. Further, these morphological traits indirectly affected seedling emergence through burial depth, dung removal and dung burial. Importantly, there were

large variations in performance among individual pairs of the same species in our experiment. Dung beetles in the field usually colonize a dung pat only for feeding, without nesting (e.g., Verdú et al. 2018). In dry Mediterranean environments, this results in lower rates of dung removal and very low or no dung burial for nesting in many colonized faeces (Gonzalez-Megías 1999). In addition, nests in the field show a large variation in the number and size of brood masses (Gonzalez-Megías 1999, González-Megías and Sánchez-Piñero 2003). We thus believe that dung beetle performance in our experiment represents the actual range of dung use by individuals and nesting pairs of the studied species in nature.

Our results confirm that the morphological traits measured in this experiment are related to dung beetle performance in dung removal and burial, as proposed by Halffter and Matthews (1966) (see also Halffter and Edmonds 1982). Among the most important traits positively related to dung removal in the first PLSR component were body mass and body size, generally identified as relevant traits in previous studies (Nervo et al. 2014, Piccini et al. 2018). However, traits related to prothorax characteristics (prothorax height, volume, pronotum length, and pronotum width) and protibial area are indicated as equally important and significant traits (in line with Griffiths et al. 2015, 2016, Macagno et al. 2016). Interestingly, the second PLSR component indicated that length of digging structures (mainly head and protibia, but also metatibia) were negatively related to dung removal. This component could be interpreted as a potential effect of species-specific behavior (Nervo et al. 2014, Griffiths et al. 2016) expressed by lower performance in telecoprids (as pointed out by Halffter and Matthews 1966, Halffter and Edmonds 1982, Martín-Piera and López-Colón 2000) and higher performance in *E. tersus*, the species with shorter and stouter head and legs (Fig. 1B).

In contrast to dung removal, only a few traits were significantly related to dung burial. Features of the prothorax (prothorax volume, pronotum length, and width) and protibial area were the only traits significantly and positively related to the amount of buried dung. The prothorax accommodates the large extrinsic muscles responsible for leg movement (Edmonds 1972), whereas the area and shape of the protibia are related to burrow depth in *Onthophagus* (Macagno et al. 2016). Interestingly, body length was negatively related to dung burial in the third PLSR component, indicating that proportionally longer beetles actually bury a smaller amount of dung (see Halffter and Edmonds 1982, Cambefort et al. 1991). The second PLSR component also indicated that length of head, protibia, and metatibia (also related to telecoprid dung beetles) were negatively related to dung burial, which corroborates the statement that telecoprids have a lower burrowing ability than paracoprids (Halffter and Matthews 1966, Halffter and Edmonds 1982, Martín-Piera and López-Colón 2000). All in all, our results indicate that a combination of traits related to

prothorax size (especially volume of prothorax), area of protibia, length of head and pro- and metatibia, and total body length are better predictors of dung burial than dung exploitation strategy. Therefore, although body mass has usually been considered as a proxy related to dung burial, the use of additional traits could provide better estimates of dung utilization (see also Nervo et al. 2014).

Strikingly, we were unable to detect any significant effect of behavioral traits related to dung exploitation strategies on performance in either dung removal or dung burial. However, these behavioral traits consider the main dung exploitation strategies (Halffter and Matthews 1966), and are usually included in studies of dung beetle functional diversity. Three main factors could explain this contrasting and relatively unexpected result:

1) We included an array of morphological traits that, altogether, were able to account for the differences in body design of the species performing each one of the three major dung exploitation strategies (as in Inward et al. 2011, Raine et al. 2018).

2) This result could also be due to the small number of species included in the experiment.

3) The lack of species showing certain “body size–dung exploitation strategy” combinations (e.g., small telecoprids or large endocoprids) could cause a bias in the analyses (Huston 1997). Nonetheless, our species selection adequately resembles the size-exploitation strategy structure of assemblages in the region we sampled (Sánchez-Piñero and Ávila 2004). Disentangling the effect of morphology from the effect of behavior (i.e., dung exploitation strategy) on dung burial requires that future studies include species with different behaviors but similar body size.

Seedling emergence was negatively affected by dung burial and burial depth in our experiment, in agreement with previous studies (Feer 1999, Andresen and Levey 2004, D’hondt et al. 2008, Beaune et al. 2012, Griffiths et al. 2016). Despite the similarity with previous findings, our results emphasize the differential effect of species regarding seedling emergence. This result strongly suggests that behavioral differences among species are also involved in the final outcome of dung beetle activity on seedling emergence. Differences in species activity in the soil–dung interface influencing soil surface properties have been proposed as a potential factor to explain the positive effect of endocoprids and shallow nesting species in seedling emergence (Griffiths et al. 2016).

#### CONCLUSIONS

The results of our experiment demonstrate that there is a relationship between a set of morphological traits and two important functions provided by dung beetles. They also point to a negative effect of the elongation of certain structures and a relatively longer body shape. These structures should therefore be used as effect traits in studies on functional performance and diversity. Our

experiment shows how explicitly testing trait–function relationships can provide solid grounds to understand how the diversity of functional traits may be related to ecological functioning. We encourage researchers to test potential relationships between traits and functions experimentally to convert assumptions on their functionality into actual knowledge.

#### ACKNOWLEDGMENT

We thank Ana Belén Robles for invaluable help with seed selection, and Ángel Revelles and workers of Finca los Morales (Rodríguez-Peñalva Foundation, Granada, Spain). We are also grateful to Teresa Soriano for allowing us to conduct the experiment at IFAPA Centro del Camino de Purchil, and to Javier Seoane and Ignasi Bartomeus for advice with mixed models. This work was supported by the Spanish Ministry of Science and Innovation project SCARPO (grant CGL2011-29317). IdCA was funded by a FPI grant from the Spanish Ministry of Science and Innovation (BES-2012-054353) and JAN was supported by a Colombian COLCIENCIAS Ph.D. scholarship. Author contributions: IdCA, FSP, and JH conceived the ideas; IdCA and FSP designed the methodology; FSP and IdCA collected the beetles for the experiment; IdCA and JAN performed the experiments and collected the data with FSP; IdCA and FSP analyzed the data; IdCA, FSP, and JH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### LITERATURE CITED

- Albert, C., F. de Bello, I. Boulangeat, G. Pellet, S. Lavorel, and W. Thuiller. 2012. On the importance of intraspecific variability for the quantification of functional diversity. *Oikos* 121:116–126.
- Andresen, E., and D. Levey. 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia* 139:45–54.
- Bardgett, R. 2005. *The biology of soil. A community and ecosystem approach.* Oxford University Press, Oxford, UK.
- Bastien, P., V. E. Vinzi, and M. Tenenhaus. 2005. PLS generalised linear regression. *Computational Statistics & Data Analysis* 48:17–46.
- Beaune, D., L. Bollache, F. Bretagnolle, and B. Fruth. 2012. Dung beetles are critical in preventing post-dispersal seed removal by rodents in Congo rain forest. *Journal of Tropical Ecology* 28:507–510.
- Cambefort, Y. 1991. Biogeography and evolution. Pages 51–67 in I. Hanski, and Y. Cambefort, editors. *Dung beetle ecology.* Princeton University Press, Princeton, New Jersey, USA.
- Culot, L., D. J. Mann, F. J. Mucoz Lazo, M.-C. Huynen, and E. W. Heymann. 2011. Tamarins and dung beetles: An efficient diplochorous dispersal system in the Peruvian Amazonia. *Biotropica* 43:84–92.
- D’hondt, B., B. Bossuyt, M. Hoffmann, and D. Bonte. 2008. Dung beetles as secondary seed dispersers in a temperate grassland. *Basic and Applied Ecology* 9:542–549.
- Doube, B., I. Hanski, and Y. Cambefort, editors. 1991. *Dung beetle ecology.* Pages 133–155 in *Dung beetles of Southern Africa.* Princeton University Press, Princeton, New Jersey, USA.
- Edmonds, W. 1972. Comparative skeletal morphology, systematics and evolution of the Phanaeinae dung beetles (Coleoptera: Scarabaeidae). *University of Kansas Science Bulletin* 49:731–874.
- Feer, F. 1999. Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the

- French Guianan rain forest. *Journal of Tropical Ecology* 15:129–142.
- Gollan, J. R., L. L. de Bruyn, N. Reid, and L. Wilkie. 2013. Monitoring the ecosystem service provided by dung beetles offers benefits over commonly used biodiversity metrics and a traditional trapping method. *Journal for Nature Conservation* 21:183–188.
- Gonzalez-Megías, A. 1999. *Ecología reproductiva de escarabajos coprófagos en zonas áridas del sureste ibérico*. Master's thesis. Universidad de Granada, Granada, Spain.
- González-Megías, A., and F. Sánchez-Piñero. 2003. Effects of brood parasitism on host reproductive success: evidence from larval interactions among dung beetles. *Oecologia* 134:195–202.
- Griffiths, H. M., R. D. Bardgett, J. Louzada, and J. Barlow. 2016. The value of trophic interactions for ecosystem function: dung beetle communities influence seed burial and seedling recruitment in tropical forests. *Proceedings of the Royal Society B* 283:20161634.
- Griffiths, H. M., J. Louzada, R. D. Bardgett, W. Beiroz, F. França, D. Tregidgo, and J. Barlow. 2015. Biodiversity and environmental context predict dung beetle-mediated seed dispersal in a tropical forest field experiment. *Ecology* 96:1607–1619.
- Halffter, G., and W. D. Edmonds. 1982. *The nesting behavior of dung beetles (Scarabaeinae). An ecological and evolutive approach*. Instituto de Ecología, Mexico City, Mexico.
- Halffter, G., and E. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomologica Mexicana* 12–14:1–312.
- Hanski, I., and Y. Cambefort. 1991. *Dung beetle ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Hooper, D., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Huston, M. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–460.
- Iannuzzi, L., L. Leal, M. Meiado, S. Ribeiro, and R. Salomão. 2013. First record of myrmecochorous diaspores removal by dung beetles in the Caatinga vegetation, a Brazilian semiarid ecosystem. *Journal of Arid Environments* 88:1–3.
- Inward, D. J. G., R. G. Davies, C. Pergande, A. J. Denham, and A. P. Vogler. 2011. Local and regional ecological morphology of dung beetle assemblages across four biogeographic regions. *Journal of Biogeography* 38:1668–1682.
- Laverde, L., M. Castellanos, and P. Stevenson. 2002. Dispersión secundaria de semillas por escarabajos coprófagos (Scarabaeidae) a partir de heces de churuco (*Lagothrix lagothricha*) en el Parque Nacional Tinigua, Colombia. *Universitas Scientiarum* 1:17–24.
- Macagno, A. L. M., A. P. Moczek, and A. Pizzo. 2016. Rapid divergence of nesting depth and digging appendages among tunneling dung beetle populations and species. *The American Naturalist* 187:E143–E151.
- Martín-Piera, F., and J. López-Colón. 2000. *Fauna Ibérica Coleoptera Scarabaeoidea I*. Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain.
- McConkey, K. R. 2005. Influence of faeces on seed removal from gibbon droppings in a dipterocarp forest in Central Borneo. *Journal of Tropical Ecology* 21:117–120.
- Mlambo, M. 2014. Not all traits are functional?: Insights from taxonomy and biodiversity–ecosystem functioning research. *Biodiversity and Conservation* 23:781–790.
- Nervo, B., E. Caprio, L. Celi, M. Lonati, G. Lombardi, G. Falson, G. Iussig, C. Palestini, D. Said-Pullicino, and A. Rolando. 2017. Ecological functions provided by dung beetles are interlinked across space and time: evidence from 15N isotope tracing. *Ecology* 98:433–446.
- Nervo, B., C. Tocco, E. Caprio, C. Palestini, and A. Rolando. 2014. The effects of body mass on dung removal efficiency in dung beetles. *PLoS One* 9:e107699.
- Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amezcuita, and M. Favila. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* 141:1461–1474.
- Noriega, J., et al. 2018. Research trends in ecosystem services provided by insects. *Basic and Applied Ecology* 26:8–23.
- Petchey, O., and K. Gaston. 2006. Functional diversity: Back to basics and looking forward. *Ecology Letters* 9:741–758.
- Piccini, I., B. Nervo, M. Forshage, L. Celi, C. Palestini, A. Rolando, and T. Roslin. 2018. Dung beetles as drivers of ecosystem multifunctionality: Are response and effect traits interwoven? *Science of the Total Environment* 616:1440–1448.
- Raine, E. H., C. L. Gray, D. J. Mann, and E. M. Slade. 2018. Tropical dung beetle morphological traits predict functional traits and show intraspecific differences across land uses. *Ecology and Evolution* 8:8686–8696.
- Sánchez-Piñero, F., and J. M. Ávila. 2004. Dung–insect community composition in arid zones of south-eastern Spain. *Journal of Arid Environments* 56:303–327.
- Scholtz, C., A. Davis, and U. Kryger. 2009. *Evolutionary biology and conservation of dung beetles*. Pensoft Publishers, Sofia, Bulgaria.
- Shepherd, V., and C. Chapman. 1998. Dung beetles as secondary seed dispersers: Impact on seed predation and germination. *Journal of Tropical Ecology* 14:199–215.
- Swift, M., O. Heal, and J. Anderson. 1979. *Decomposition in terrestrial ecosystems*. Blackwell, Oxford, UK.
- Verdú, J. R., et al. 2018. Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: An interdisciplinary field study. *Science of the Total Environment* 618:219–228.
- Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional!. *Oikos* 116:882–892.
- Wong, M. K. L., B. Guénard, and O. Lewis. 2019. Trait-based ecology of terrestrial arthropods. *Biological Reviews* 94:999–1022.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3138/supinfo>