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Is *Digitonthophagus gazella* undergoing a naturalization process? A study case in a tropical dry forest of northern Colombia

¿Está *Digitonthophagus gazella* en proceso de naturalización? Estudio de caso en un bosque seco tropical del norte de Colombia

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ABSTRACT

Digitonthophagus gazella was deliberately introduced to several American countries to remove bovine manure and control hematophagous flies and gastrointestinal parasites. This species, typically found in open habitats, has opportunistic strategies for resource utilization, high reproductive and dispersal rates, and processes large quantities of cattle dung. As a result, it rapidly colonized the lowlands of the American continent, achieving a wide distribution; and being currently catalogued as an invasive exotic species in several tropical and subtropical countries. Based on research completed and samples taken during six years in three ecological environments (forest, intensive silvopastoral systems, and treeless pastures) in the Cesar River valley, northern Colombia, an analysis is proposed to evaluate whether *D. gazella* behaves as an invasive or a naturalized species. To assess information about its distribution, food preferences, relationship with native species during temporal succession in resource use, ecological functions related to removing dung and soil perturbation, and risks or benefits this species represents to native dung beetle fauna in the valley were weighed. A classification is presented utilizing conventional criteria. According to our analysis, *D. gazella* could be considered an introduced, naturalized species with minimal impact in the Cesar River valley since it did not enter the forest, did not generate competition through exclusion with native species, prefers bovine dung, completes ecologically important functions for cattle systems, and has economic benefits due to the reduction of agrochemical use. Further research is suggested to corroborate if these results operate nationwide.

Keywords: Competition, Dung beetles, Ecological functions, Ecological interactions, Invasive species

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RESUMEN

Digitonthophagus gazella fue introducida deliberadamente en varios países de América para eliminar el estiércol bovino y controlar moscas hematófagas y parásitos gastrointestinales. Esta especie, normalmente de hábitats abiertos, tiene estrategias oportunistas para la utilización de recursos, altas tasas de reproducción y dispersión, y procesa grandes cantidades de estiércol de ganado. Como resultado, colonizó rápidamente las tierras bajas del continente americano, logrando una amplia distribución. Actualmente es catalogada como una especie exótica invasora. Con base en investigaciones realizadas y muestras tomadas durante seis años en tres ambientes ecológicos (bosque, sistemas silvopastoriles intensivos y pastizales sin árboles) en el valle del río Cesar, norte de Colombia, se propone un análisis para evaluar si *D. gazella* se comporta como invasora o naturalizada. Se estudiaron las funciones ecológicas relacionadas con la remoción de estiércol y perturbación del suelo y los riesgos o beneficios que esta especie representa para la fauna nativa de escarabajos coprófagos en el valle, se evaluó su distribución, preferencias alimentarias y relación con especies nativas durante la sucesión temporal en el uso de recursos. De acuerdo con nuestro análisis, usando criterios convencionales, *D. gazella* podría considerarse una especie introducida, naturalizada y con mínimo impacto en la zona, ya que no ingresa al bosque, no genera competencia por exclusión con especies nativas, tiene preferencia por el estiércol bovino, completa funciones ecológicas en los sistemas ganaderos, con beneficios económicos debido a la reducción del uso de agroquímicos. Se sugiere mayor investigación para corroborar si estos resultados operan a nivel nacional.

Palabras clave: Competencia, Escarabajos estercoleros, Funciones ecológicas, Interacciones ecológicas, Especie invasora

INTRODUCTION

Human activities modify species' geographic distribution. In many cases, the species' movement beyond their geographic ranges of distribution is favored deliberately or is accidental; but under other circumstances, facilitates the colonization of regions in which they did not previously exist (Levine and D'Antonio 1999, Didham *et al.* 2005, Banks *et al.* 2015). It is known that species introduction drives changes in receptor ecosystems (Blackburn *et al.* 2014). Besides, it has been correlated with the extinction of native species (Kohimann 1994, Byers 2002, Gurevitch and Padilla 2004, Clavero and García-Berthou 2005, Matavelli and Louzada 2008) and ecosystem functional disruption, for example, energy flow modifications, changes in nutrient redistribution, and poor pollination, among others (Spencer *et al.* 1991, Lodge 1993, Sanders *et al.* 2003, Torchin *et al.* 2003, Tallamy 2004). Although many studies have been conducted on this topic, determining the invasive potential of a species and its impact on ecosystems continues to be a challenging task (Andersen *et al.* 2004a, 2004b, MacLeod *et al.* 2010).

In recent decades, a debate has arisen regarding the use of imprecise, incorrect, or contradictory terms such as "introduced", "naturalized", "exotic", and "invasive" species (Richardson *et al.* 2000, Blackburn *et al.* 2014, Russell and Blackburn 2017, Crowley *et al.* 2017). A group of individuals of an exotic or introduced species that can establish viable populations in a new locale is considered established or naturalized (Richardson *et al.* 2000, GISD c2005). Instead, if the population of a species is established without human assistance and, consequently, poses a threat to the ecosystem and drives socioeconomic impacts, it is an invasive species (GISD c2005, CDB c2011).

Blackburn *et al.* (2011, 2014) propose a simple standardized system for classifying alien species in terms of the magnitude of their impacts. The classification, in addition to considering environmental impacts, allows us to identify species that have deleterious biotic and abiotic effects and can be applied to different taxa, using unified criteria based on invasive species evaluation mechanisms of the International Union for Conservation of Nature (IUCN) Global Invasive Species Database ([GISD], http://www.

issg.org/database). This classification considers the consequences of the impacts of biological invasions based on the best available evidence and applied at different spatial scales, from regions, countries, or globally. In this system, Blackburn *et al.* (2014) identified a set of six impacts (herbivory, competition, predation, disease transmission, hybridization, and ecosystem) as a set of mechanical impacts. Following the unified framework proposed by these authors, there are different barriers for species (geographic, survival, reproduction, dispersal, and environmental). These determine the failure or success of the biological invasion and allow us to distinguish between Causal / Introduced, Naturalized / Established, or Invasive species. In this context, there is an urgent need for a multi-criteria method to facilitate the evaluation, comparison, and prediction of the effects of invasive species on ecosystems, such as those that occur in species that are deliberately introduced in cattle systems in different Latin American countries (e.g., the Indo-African dung beetle *Digitonthophagus gazella* (Fabricius, 1787).

In this study, we investigated whether *D. gazella* behaves as an invasive species based on the classification system proposed by Blackburn *et al.* (2014). In many countries, *D. gazella* was deliberately introduced as a solution for the excrement accumulation problem (see Blume and Aga, 1978, Fincher *et al.* 1983, Ripa and Rodríguez 1990, Zunino and Barbero 1993, Kohimann 1994, Noriega *et al.* 2006, Vidaurre *et al.* 2008, Álvarez-Bohle *et al.* 2009, Noriega *et al.* 2010, Isaza-López *et al.* 2015, Noriega *et al.* 2017, Pablo-Cea *et al.* 2017, Gámez *et al.* 2021).

Digitonthophagus gazella is well adapted to the utilization of the dung of large herbivores, including cattle (Rougon and Rougon 1980, Cambefort 1984, Brito *et al.* 2007, Rivera and Wolff 2007, Álvarez-Bohle *et al.* 2009, Pokhrel *et al.* 2020). It shows opportunistic strategies for the utilization of the resources (Barbero and López-Guerrero 1992, Álvarez-Bohle *et al.* 2009). Also, it displays a high reproductive rate (Blume and Aga 1978, Barbero and López-Guerrero 1992), high dispersion capacity (Hanski and Cambefort 1991), and a high potential for processing large quantities of cattle dung (Behling-Miranda *et al.* 2000, Álvarez-Bohle *et al.* 2009). Additionally, it is easily established in areas sparsely vegetated, with high temperatures and rainy periods throughout the year (Rivera and Wolff 2007). These attributes have contributed to the perception that *D. gazella* is an invasive species (Noriega 2002, Amat-García *et al.* 2011, Noriega *et al.* 2017) which threatens native dung beetle populations (Noriega *et al.* 2011, Filho *et al.* 2018).

Based on the facts that *D. gazella* is a species of great importance in cattle systems, that rapidly colonize the American continent, it is essential to have diagnostic elements that allow us to adequately assess its invasive potential of ecosystems and its real impacts on the associated scarab native populations. Information about spatial distribution, food preferences, relationship to native species, and temporal succession associated with *D. gazella,* over six years in remnants of Tropical Dry Forest at the Cesar River valley, was gathered and analysed. The use of the resource, ecological functions related to dung removal and soil perturbation, and the risks or benefits this species represents to native dung beetle fauna inhabiting were also included. Based on this information, a solid and arguable assessment is made for the first time on *D. gazella*. Further, the implications of its distribution in cattle ranches in the Cesar River valley are also discussed.

MATERIALS AND METHODS

This study took place between August 2012 and December 2018 on eight cattle ranches located in the Cesar River valley in northern Colombia (Supplement fig. 1, Supplement table 1) covering four land uses, Treeless Pastures (TP), Intensive Silvopastoral Systems (ISPS), Scattered Trees in pastures (ST), and Forest Fragments (F). The region is classified as a Tropical Dry Forest (bs-T) (Holdridge 1978) and has clayey/sandy soil formations with low permeability. Average annual rainfall and temperature are 1100 mm and 25 °C, respectively. Rainfall presents a bimodal pattern with the highest precipitations in April-June and August-November. The driest periods are December-March and July-August (Medina-Rangel 2011, Arcila *et al.* 2012, Delgado-Gómez *et al.* 2012).

Dung beetle diversity in cattle ranches

To determine the distribution of *D. gazella* in the livestock landscape and establish its habitat preferences, dung beetles were sampled between August 2012 and December 2018 under three land uses, Forest (as reference habitat), ISPS or ST (sustainable cattle ranching system) and TP. In each ranch, 15 pitfall traps were installed. Details of the procedure are described in Montoya-Molina *et al.* (2016).

A total of eight repetitions were done. Diversity sampling was only completed once in each ranch.

Species determination was done using taxonomic keys (Vaz-de-Mello *et al.* 2011) and corroborated by experts from the Instituto Alexander von Humboldt (IAvH), Villa de Leyva, Colombia. The specimens were deposited in the Entomological collections of the Universidad del Valle (MUSENUV) (Cali) and at IAvH (Villa de Leyva) in Colombia.

Diversity analyses

To visualize the changes in the dung beetle community composition under different land uses and the *D. gazella* distribution, a triangular Q–mode matrix of similarity using the Bray-Curtis index was constructed. The index ranged from 0 (no species in common between samples) to 1 (identical species composition and abundance). Non-metric multidimensional scaling (NMDS) was used to define the overall differences in species composition between land uses. NMDS was chosen because neither normality nor linearity of data is assumed (Kruskal and Wish 1978). To evaluate how many dimensions are needed to reproduce similarity between sites, a stress value was calculated. The smaller the stress value, the better the fit of the reproduced similarity matrix observed. In this analysis, the distance between environmental variables was calculated using the use of a matrix of locations and species, utilizing the metaMDS and envfit functions in the vegan package of the R statistical program (R Development Core Team c2008).

Digitonthophagus gazella distribution, interactions, and ecological functions

Two temporal successional experiments were carried out during rainy periods (October 2013) aimed to determine any interaction of *D. gazella* with native dung beetle species. The experiment was designed to establish whether there is competition for exclusion during the first 96 h of cattle dung on the soil surface. Both experiments took place under three land uses, Forest, ISPS, and TP on a ranch (Salsipuedes) (Supplement Table 1). Fresh cattle dung was collected during milking and carefully examined to guarantee that it did not contain beetles. Later, it was placed in a 50 L vessel and homogenized to produce lots of 100 dung piles of 432 cm^3 each. These were distributed in each land use within a 2500 m^2 rectangle in which they were evenly separated by 5 m. Every six hours, for four consecutive days, three dung piles were randomly selected. In each case, all beetles encountered within the dung pile or in recently constructed tunnels immediately below the dung piles were collected and identified.

In each round of dung pile revision, the following variables, related to the dung beetle ecological functions were quantified: *Species interaction*: The temporal interaction between *D. gazella* and native species was evaluated and recorded during the manure exposure time. *Soil removed*: Soil from the upper and outer parts of the dung was carefully removed and weighed with a precision scale (Ozeri™, 0.1-500 g) to the quantity of soil that dung beetles removed during the process of incorporation of excrement into the soil. *Number of tunnels*: as the dung was lifted, the number of visible tunnels attributable to the dung beetles was quantified. *Tunnel depth*: visible tunnels were carefully followed with the help of a spatula to the places where nest balls were found. The distances of the balls at an angle of 90° to the surface of the soil were then recorded. *Number of nest balls*: the number of nest balls buried below each dung pile was registered. *Mass of nest balls*: the fresh individual mass (g) of each nest ball was measured using a precision scale.

Digitonthophagus gazella interaction and ecological function analyses

Interaction diagrams were developed to determine relationships between *D. gazella* and native species during the 96 hours that the bovine manure was exposed. Data were analyzed using the bipartite package in the R statistical program (R Development Core Team c2008). Later, a C-score was obtained, representing the average number of units; checkerboard equivalents for each species with singular interactions were determined. The higher the C-score, the less co-occurrence, on average, between all the species' pairs in the matrix. A relatively large C-score indicates a more segregated matrix and a relatively small C-score indicates a more aggregated matrix (Gotelli and Ulrich 2010).

A frequency histogram graph was constructed based on the occurrence of beetles and the abundance of dung piles found in the land uses. The purpose of this was to determine whether cattle dung is a limited resource for beetle fauna and if this situation represents the possibility of competition within the beetle community. Density corresponded to the percentage of the total population captured in each interval in which the histogram was divided.

Digitonthophagus gazella environmental impact classification

To evaluate whether *D. gazella* behaves as an invasive species, data on species composition, the geographical distribution in the livestock landscape, food preferences, interactions with other dung beetle species, and ecological function of *D. gazella* and native dung beetle species were collected for six years and analysed based on the standardized classification proposed by Blackburn *et al.* (2014). The scheme also categorizes species that are data deficient or have data that are assumed according to the scientific literature. The classification scheme proposes six impact scenarios that are scored from 0-5. These scores correspond to, (0) No discernible impact; (1) Impact discernible, but with no effect on the aptitude of individuals; (2) Effect on the aptitude of individuals, but not on populations; (3) Changes in populations, but not in the composition of the community; (4) Reversible changes in the community; (5) Irreversible changes in the community, extinction of species (Blackburn *et al.* 2014).

Environmental variables

To determine the environmental factors that influence *D. gazella* distribution patterns, the following variables were measured: temperature (°C) and relative humidity (%) with a digital thermohygrometer (Fisher Scientific™ Traceable™ Jumbo Thermo-Humidity Meter (Accuracy ±2 to ±4 %); canopy cover (%) with a spherical densitometer (Forestry Suppliers); and the percentage of soil cover (bare soil, leaf litter, and vegetation) was estimated within a 50 m linear transect, sampling stations every 0.5 m.

RESULTS AND DISCUSSION

Our results provided strong evidence to consider *D. gazella* as an introduced but naturalized species with minimal impact on the Cesar River valley, which is one of the most important livestock regions in Colombia. The data show that the distribution of *D. gazella* is exclusively within cattle systems and that this species prefers cattle dung, which is not a limited resource in the Cesar Valley region. Furthermore, it can coexist with native dung beetle species for more than 96 hours in the same dung pile, thus par-

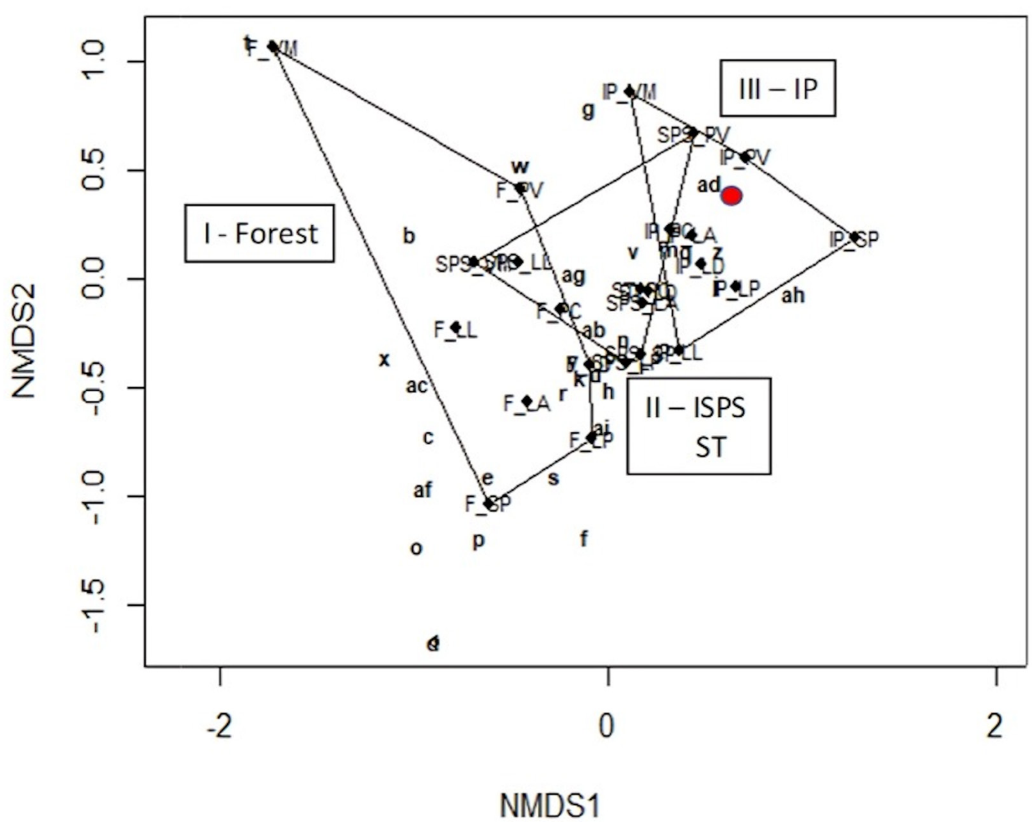

Figure 1. NMDS ordination diagram. Letters represent the species as coded in the Table 3. Red circle: Digitonthophagus gazella. Triangles identify land uses: I (Forest), II (Intensive silvopastoral systems - ISPS and Scattered Trees in Pastures - ST) and III (Treeless Pastures - TP). Stress value: 0.034.

ticipating in the ecological function of soil removal under cattle land use. This assessment is backed by the following results which are discussed in the light of the scientific literature available.

Digitonthophagus gazella and dung beetle diversity in cattle systems

In the dung beetle diversity survey, 6,239 individuals were collected belonging to 32 species and 18 genera. *D. gazella* was absent in forested areas and was only found within the evaluated cattle systems (ISPS, PSA, ST; Supplement table 2). After six years of research on the distribution of dung beetles in the Cesar River Valley, it was found that *D. gazella* prefers cattle grazing areas. Thus, the forest that lacks cattle dung is an unattractive habitat for this species.

Non-metric multidimensional scaling (NMDS) showed that species are distributed in three groups according to land use (Fig. 1). In this ordination, *D. gazella* was located between ISPS and TP in a different ordination group than forest species. This result confirms that *D. gazella* does not use native forests. Moreover, we corroborated that

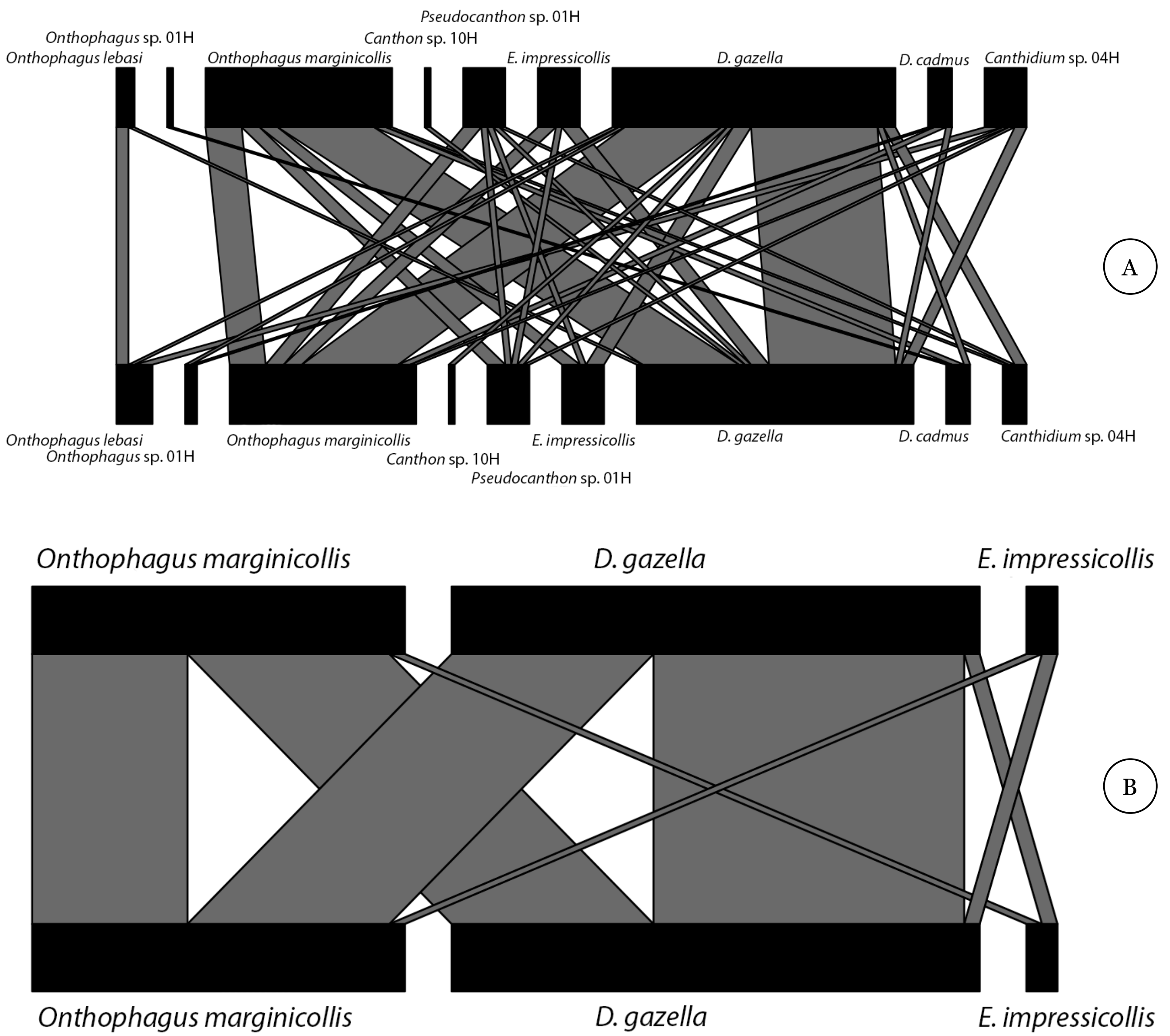

Figure 2. Interaction webs of coprophagous dung beetles. A. Intensive Silvopastoral Systems (ISPS), C- Score: 0.24. B. Treeless Pastures, C. Score: 0.0. Black horizontal bars represent the total abundance of each species in the system, while grey longitudinal bars represent the abundance of individuals that coexist between two related species.

D. gazella does not directly contend with native species dependent on the small patches of endemic forest and mammals' dung for food and nidification resources (Favila 2012).

Several studies refer that *D. gazella* is restricted to open areas in the Neotropics (Noriega *et al.* 2006, Rivera and Wolff 2007, Noriega *et al.* 2010, 2011) but none of them have reliably shown its presence in areas of native vegetation. Its occurrence in open spaces is not surprising given the habitat origin of *D. gazella*, a stenotopic species predominantly linked to the savannas with large herbivores of the Indo-African region (Blume and Aga 1978). In Veracruz, Mexico, Lobo and Montes de Oca (1994) documented that *D. gazella* did not penetrate shaded zones. Still, it was detected in transects lacking vegetal coverage with high temperature and low relative humidity. These authors concluded that *D. gazella* is a species adapted to open environments without arboreal vegetation. Some vegetation coverage represents a barrier to its dispersion (Lobo and Montes de Oca 1994, Montes de Oca and Halffter 1998). According to these authors, *D. gazella* has penetrated Mexico along cattle ranching areas avoiding forested areas. Therefore, the most accurate classification of the dung beetle *D. gazella* at the Cesar River valley should be as an "introduced and naturalized species" *vis a vis* Richardson *et al.* (2000). By not crossing the barrier imposed by natural ecosystems, the species cannot be considered invasive.

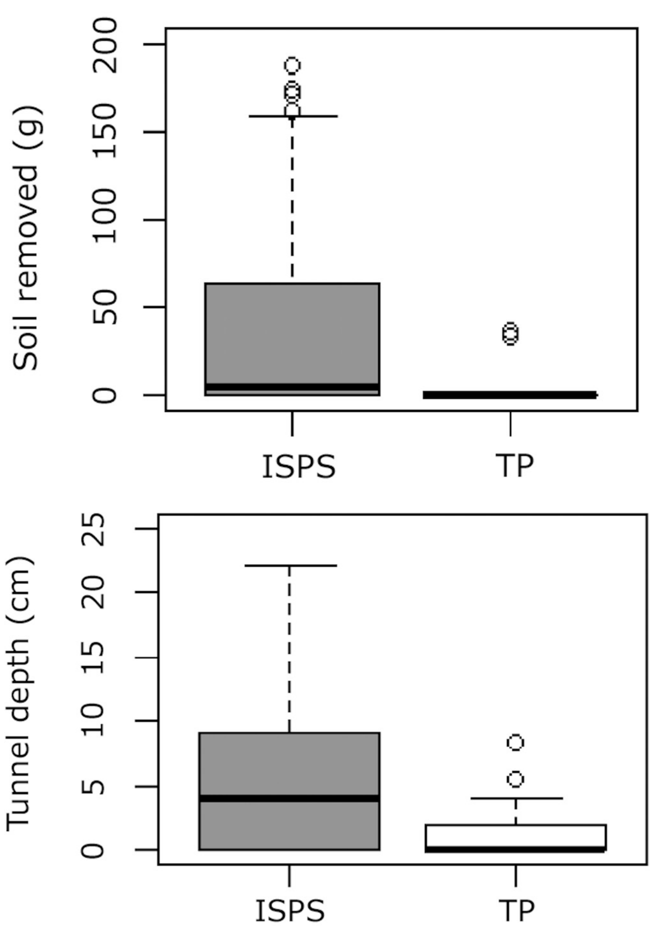

Figure 3. Box-whisker plots comparing two ecological functions: A. Removed soil parameters (g) and B. Maximum depth of tunnels (cm) in ISPS and TP. In plots median (bold line), 25% quartiles (boxes), extremes (whiskers), and outliers (peripheral dots).

Digitonthophagus gazella distribution, interactions, and ecological functions

During the temporal succession sampling, 141 individuals belonging to 16 species and 12 genera were associated with cattle dung (Supplement Table 3). This means that only half of the total species of the Cesar River valley can process cattle dung, even if the resource is introduced experimentally into the forest in a controlled manner. These results abide with the notion that *D. gazella* is a species well adapted to exploit bovine manure and corroborate that the forest represents an unsuitable habitat to be used by this species. In this way, spatial segregation that limits competition with native species may have occurred.

Digitonthophagus gazella interactions with local fauna

The interaction webs (Fig. 2) show the species that colonize the same dung patties in cattle ranches of the Cesar River valley. At the ISPS can be observed that *D. gazella* shares the resource and coexists with several native species such as *Onthophagus marginicollis* Harold, 1880, *O. lebasi* Boucomont, 1932, *Onthophagus* sp.01H, *Canthon* sp.10H, *Pseudocanthon* sp.01H, *Eurysternus impressicollis* Laporte, 1840, *Diabroctis cadmus* (Harold, 1868), and *Canthidium* sp.04H (Fig. 2a). Meanwhile, in TP, the abundance of *D. gazella* and *O. marginicollis* was similar, and both species shared the resource (Fig. 2b). Only one individual of *E. impressicollis* was caught sharing the manure with the mentioned two species in this cattle system.

Onthophagus marginicollis was found both in the interior of forest remnants and in TP (Fig. 2), exhibiting behavior like *D. gazella*: a high preference for cattle dung patties and high plasticity in habitat usage. This is the only native species in the Cesar River valley that uses bovine manure in TP. Lozano (2010) documented that this species outnumbered *D. gazella* under secondary forest conditions and an abundance of bovine dung.

Table 1. Criteria for assigning categories of classification of impacts for the introduced scarab *Digitonthophagus gazella* in the Cesar river valley. Classification and values were assigned according to Blackburn *et al.* (2014) and justification was based on the results obtained during six years of observations.

Impact Type	Classification	Value	Justification
Competition	Minimal	1	Does not generate competition with native species. Reduction of native species cannot be attributed to *D. gazella.*
Depredation	Minimal	1	*D. gazella* is not a predator; thus, native species are not in risk for this factor.
Hybridization	Deficient data	0	Hybridization and crossing processes have not been registered between *D. gazella* and native scarabs.
Transmission of diseases to native species	Deficient data	0	Information for determining if *D. gazella* is a carrier of transmissible diseases to native species does not exist.
Parasitism	Minimal	1	*D. gazella* is not a parasite; thus, it does not affect native species through parasitism.
Poisoning/toxicity	Minimal	1	*D. gazella* is not poisonous, toxic, allergenic, or allelopathic; thus, it does not reduce the aptitude of native species by these means. Nor does it seem to be toxic to its predators.
Biocontamination	Minimal	1	*D. gazella* is not a biocontaminant for native species.
Pasturage, herbivory	Minimal	1	The species is not an herbivore, nor does it affect native plants.
Physical, chemical, or structural impact on the ecosystem	Minimal	1	There are no chemical, physical, and/or structural changes to the ecosystem due to *D. gazella*. Changes in the nutrient cycle (removal of manure and soil) are beneficial for cattle systems. There are no detectable changes in succession and the aptitude of natives is not reduced.
Interaction with other introduced species	Minimal	1	*D. gazella* interacts indirectly with other species including *Bos taurus*, *Bos indicus* and their crosses. However, these interactions are positive because they favour the relocation of manure. None of the species, *per se*, nor their interactions, generate reduction in the aptitude of natives. Other effects related to cattle system management may be responsible for reduction the reduction of native species.
Total Score		8	***D. gazella* can be considered an introduced scarab with minimal environmental impact in the study area.**

Based on these results we propose two types of competitive interactions between *D. gazella* and native species: Firstly, an interspecific competition (*sensu* Begon *et al.* 1996, cited by Zhou *et al.* 2010, Shurin and Greenfest-Allen 2001, Lang and Benbow 2013) might occur to native species due to the *D. gazella* capacity to rapidly colonize bovine manure. This represents an adaptive advantage that allows it to monopolize the resource rapidly and generate competitive exclusion. However, as the data show, *D. gazella* coexists without interspecific competition. Therefore, this introduced species does not seem to represent a risk to local populations in the Cesar River valley.

The second type of competition that might occur is exploitation (Gause 1932). This occurs when individuals interact indirectly by competing for communal resources such as territory, prey, or food (Lang and Benbow 2013). According to this type of competition, the use of the resource by one species diminishes the quantity available for other organisms that utilize the same resource. Depending on the competitor's degree of competition and adaptive advantages, this may exclude the less adapted species in this area or region (Gause1932, Lang and Benbow 2013).

The interaction of *D. gazella* with native species can favor ecological functions. As depicted in (Fig. 3), assemblies shaped by native species and *D. gazella* favor the completion of soil removal and tunneling. Both latter are important ecological functions for the dynamics of ISPS.

Despite the presence of *D. gazella* in TP, the ecological function of soil removal and tunnel construction is not performed adequately in this cattle system, possibly because this species is unable to penetrate the compacted soil on its own. *D. gazella* deposits nest balls inside the patty 0-2 cm from the surface of the soil, behaving like *D. cadmus* as a resident species. On the contrary, in the ISPS, the presence of *D. gazella*, together with large native species, favours the removal of soil and the construction of tunnels, which improves the ecological function of the dung beetles in these grazing systems. *D. gazella* builds numerous tunnels below the patties that reach up to 20 cm in depth. We hypothesize that the activity of *D. gazella* could be potentiated by the improved soil conditions and the interaction with native species in cattle systems, and their combined action could favour the reestablishment of ecological processes in systems undergoing restoration.

In that direction, the conversion of conventional livestock systems to systems that generate more favourable environmental conditions, such as ISPS, for native scarab fauna not only guarantees the functional integrity of the ecological processes in which the scarabs participate (e.g., excrement removal) but also contributes to increased connectivity on the landscape scale that supports the native species dispersal (Giraldo *et al.* 2011, Montoya-Molina *et al.* 2016).

In the cattle systems of the Cesar River valley, each cow produces, on average, twelve patties per day exceeding the removal capacity of native species and even that of *D. gazella*. Hence, dung beetles associated with bovine patties, depending on the species abundance that initially colonizes the resource, may eventually show exploitative competition on the part of the dominant species. Cattle manure was permanently found in the lots designated as animal pastures. Indeed, in ISPS and TP more than 60 % of the patties did not have dung beetles associated with them during the first 96 hours after deposition. This suggests that bovine manure is an abundant, rather than a limiting food resource, which, by definition, contributes to a reduction of interspecific competitive exclusion.

Some researchers have hypothesized that the colonization of new territories by *D. gazella* has contributed to a decline in populations of native dung beetles (Filho *et al.* 2018). However, to date, few studies have evaluated populations of native dung beetles before and after the arrival of *D. gazella* in a territory (Mesquita-Filho *et al.* 2018, Filho *et al.* 2018). This type of study is challenging and requires the inclusion of multifactorial ecological variables to discard other external such as deforestation, temperature increase, and use of agrochemicals or veterinary drugs, which might also explain the decline in native beetle populations. Matavelli and Louzada (2008) did not find a relationship between the introduction of *D. gazella* and the population size of *Canthon* sp.1, a scarab native to the Brazilian savanna, which by the contrary kept its importance as the most abundant species. Their results suggest that *D. gazella* in these areas was negatively influenced by the abundance of the native species, indicating a certain natural resistance of the native Scarabaeinae community to *D. gazella* presence.

Noteworthy, a study in the tropical lowlands of Veracruz, Mexico, before and after the arrival of *D. gazella*, showed a significant reduction in the abundance of the native species *Onthophagus batesi* Howden & Cartwright, 1963 (Montes de Oca and Halffter 1998). Despite the results, the authors did not attribute this reduction to the introduced species, since the study site had suffered a large anthropic transformation during the previous 20 years, which may have affected the native species. Additionally, they found that both species showed spatial segregation: *D. gazella* occupied open areas and was able to colonize patties completely exposed to sunlight, while *O. batesi* was found in sites partially covered with vegetation. Hence, although the accelerated transformation of natural ecosystems into pastures may have favored the rapid distribution of *D. gazella* across the American continent (Montes de Oca and Halffter 1998, Noriega *et al.* 2017, 2020), there is no strong evidence confirming it as the main cause of the decline of the scarab native populations.

It should be important to identify the factors that benefit the rapid expansion of *D. gazella* in non-native areas. After a study of niche modulation, Matos Medina (2016) suggested that the rapid expansion of *D. gazella* in non-native areas is due in part to the accidental transport of individuals present during livestock transport, as cattle dung presents a virtually exclusive and unlimited food resource. In the cattle areas of the Cesar River valley as well as in other Colombian areas, the expansion of *D. gazella* may be attributable to the loss of vegetation cover related to the accelerated deforestation of the Tropical Dry Forest, the most threatened ecosystem in Latin America (Castellanos-Castro and Newton 2015, DRYFLOR *et al.* 2016).

Digitonthophagus gazella environmental impact classification

(Table 1) shows the revised, classified, and scored impacts of *D. gazella* using the new system of Generic Impact Scoring (GISS) proposed by the Commission for the Survival of Species (CSE), an IUCN group of Specialists on Invasive Species (Blackburn *et al.* 2014).

As far as we know, no information for *D. gazella* is reported in the GISD database (GISD c2015). Therefore, this is the first effort to understand the behaviour of this species in new distribution areas, as well as its potential impact on native species. In a niche modelling study, Matos Medina (2016), found that *D. gazella* has similar climate niche occupancy in native and invasive ranges (98.5 %) with a small number of niche expansions into invasive ranges (1.5 %) and a small number of unfilled niches (2.1 %).

Final remarks and recommendations

The dominance of *D. gazella* in conventional cattle systems is consistent with its high specificity for bovine resources and the impossibility of the establishment of most native species in these systems. The conversion of pastures without trees to ISPS might favor the coexistence of native species and *D. gazella* as well as potentiate the ecological functions of the assemblies of species for the benefit of producers and the tranquillity of conservationists. From the conservation point of view, the greatest threat to the diversity of native scarabs may not be the presence of *D. gazella* (Noriega *et al.* 2011), but rather the destruction and transformation of natural habitats that restrict their distribution and access to resources.

Overall, the results of this study suggest that *D. gaz*ella could be considered an introduced species that has been naturalized in cattle systems of the Cesar River valley in Colombia, rather than an invasive species that puts the stability of populations of native scarabs at risk. According to the classification scheme proposed by Blackburn *et al.* (2014), this species can be considered to have minimal impact (MI), considering that its presence is not related to a decrease in the density of native scarab populations. However, a cautionary principle is mandatory in this case given the relatively early introduction of the species to Colombia and the limited scale of our study.

Finally, it is important to emphasize that the authors of the present investigation are not suggesting or promoting the introduction of foreign species to new territories. The data utilized in this study were gleaned from the analysis of a species that was already dispersed throughout much of the Colombian territory at the time of the study.

AUTHOR'S CONTRIBUTION

CG and SMM concept design of the project; data collecting as part of their, respectively, doctoral and undergraduate research projects at the Universidad del Valle. JDCh, JML, and FE statistical analyses, writing and revision of the text.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interests.

LITERATURE CITED

Álvarez-Bohle MC, Damborsky MP, Bar ME, Ocampo FC. 2009. Registros y distribución de *Digitonthophagus gazella* (Coleoptera: Scarabaeidae: Scarabaeinae) en Argentina. Rev. Soc. Entomol. Arg. 68: 373–376.

Amat-García G, Amat-García E, Ariza-Marín E. 2011. Insectos invasores en los tiempos del cambio climático. Innovación y Ciencia. 18: 44–53.

Andersen MC, Adams H, Hope B, Powell M. 2004a. Risk analysis for invasive species: general framework and research needs. Risk Analysis. 24(4): 893-900. doi: https://doi.org/10.1111/j.0272-4332.2004.00487.x

Andersen MC, Adams H, Hope B, Powell, M. 2004b. Risk assessment for invasive species. Risk Analysis. 24(4): 787–793. doi: https://doi.org/10.1111/j.0272-4332.2004.00478.x

Arcila AM, Valderrama C, Chacón de Ulloa P. 2012. Estado de fragmentación del bosque seco de la cuenta alta del río Cauca, Colombia. Biota Colombiana. 13(2): 86–101.

Banks NC, Paini DR, Bayliss KL, Hodda M. 2015. The role of global trade and transport network topology in the human-mediated dispersal of alien species. Ecol. Letters. 18: 188–199. doi: https://doi.org/10.1111/ele.12397

Barbero E, López-Guerrero Y. 1992. Some considerations on the dispersal power of *Digitonthophagus gazella* (Fabricius 1787) in the New World (Coleoptera Scarabaeidae Scarabaeinae). Trop. Zool. 5(1): 115. doi: https://doi.org/10.1080/03946975.1992.10539184

Behling-Miranda CH, Dos Santos JC, Bianchin I. 2000. The role of *Digitonthophagus gazella* on pasture clearing and production as a result of burial of cattle dung. Pasturas Tropicales. 22: 14–18.

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugala A, Nentwig W, Pergl P, Pysek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S. 2014. A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biology. 12: p.e. doi: https://doi.org/10.1371/journal.pbio.1001850

Blackburn TM, Pysek P, Bacher S, Carlton JT, Duncan RP, Jarosik V, Wilson JRU, Richardson DM. 2011. A proposed unified framework for biological invasions. Trends Ecol. Evol. 26(7): 333–339. doi: https://doi.org/10.1016/j.tree.2011.03.023

Blume RR, Aga A. 1978. *Onthophagus gazella* F.: progress of experimental release in south Texas. Folia Entomol. Mex. 29-40: 190-191.

Brito LG, da Silva Netto FG da, Barros RB. 2007. Controle integrado da mosca-do-chifre para a microrregião de Ji-Paraná Rondônia. Comunicado Técnico: 327.

Byers JE. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos. 97(3): 449. doi: https://doi.org/10.1034/j.1600-0706.2002.970316.x

Cambefort Y. 1984. Étude écologique des coléoptères. Scarabaeidae de Côté d` Ivoire. Travail Chercher Lamto. 3: 1–320.

Castellanos-Castro C, Newton AC. 2015. Environmental heterogeneity influences successional trajectories in Colombian seasonally dry tropical forests. Biotropica. 47(6): 660-671. doi: https://doi.org/10.1111/btp.12245

CDB. (c2011). Plan estratégico para la diversidad biológica 2011-2020. Convenio sobre la diversidad. Canadá. https://www.cbd.int/undb/media/factsheets/undb-factsheet-sp-es.pdf

Clavero M, García-Berthou E. 2005. Invasive species are a leading cause of animal extinctions. Trends Ecol. Evol. 20(3): 110. doi: https://doi.org/10.1016/j.tree.2005.01.003

Crowley SL, Hinchliffe S, Redpath SM, McDonald RA. 2017. Disagreement about invasive species does not equate to denialism: A response to Russell and Blackburn. Trends Ecol. Evol. 32(4): 228-229. doi: https://doi.org/10.1016/j.tree.2017.02.004

Delgado-Gómez P, Lopera A, Rangel-Ch JO. 2012. Variación espacial del ensamblaje de escarabajos coprófagos (Scarabaeidae: Scarabaeinae) en remanentes de bosque seco en Chimichagua (Cesar, Colombia). pp. 833-849. In: Colombia Diversidad Biótica XII: La región Caribe de Colombia. (eds. J.O. Rangel-Ch.). Instituto de Ciencias Naturales, Bogotá 1046 pp.

Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmell NJ. 2005. Are invasive species the drivers of ecological change? Trends Ecol. Evol. 20(9): 470-474. doi: https://doi.org/10.1016/j.tree.2005.07.006

DRYFLOR, Banda-R K, Delgado-Salinas A, Dexter KG, Linares-Palomino R, Oliveira-Filho A, Prado D, Pullan M, Quintana C, Riina R, Rodríguez M GM, Weintritt J, Acevedo-Rodríguez P, Adarve J, Álvarez E, Aranguren B A, Arteaga JC, Aymard G, Castaño A, Ceballos-Mago N, Cogollo Á, Cuadros H, Delgado F, Devia W, Dueñas H, Fajardo L, Fernández Á, Fernández MÁ, Franklin J, Freid EH, Galetti LA, Gonto R, González-M R, Graveson R, Helmer EH, Idárraga Á, López R, Marcano-Vega H, Martínez OG, Maturo HM, McDonald M, McLaren K, Melo O, Mijares F, Mogni V, Molina D, Moreno ND, Nassar JM, Neves DM, Oakley LJ, Oatham M, Olvera-Luna AR, Pezzini FF, Domínguez OJ, Ríos ME, Rivera O, Rodríguez N, Rojas A, Särkinen T, Sánchez R, Smith M, Vargas C, Villanueva B, Pennington RT. 2016. Plant diversity patterns in neotropical dry forests and their conservation implications. Science. 353(6306): 1383–1387. doi: https://doi.org/10.1126/science.aaf5080

Favila ME. 2012. Historical, biogeographical and ecological factors explain the success of some native dung beetles after the introduction of cattle in Mexico. Pastos. 42: 161-181.

Fincher GT, Stewart TB, Hunter JS. 1983. The 1981 distribution of *Onthophagus gazella* Fabricius from releases in Texas and *Onthophagus taurus* Schreber from an unknown release in Florida (Coleoptera: Scarabaeidae). Coleopt. Bull. 37: 159–163.

Filho WM, Flechtmann CAH, Godoy WAC, Bjornstad ON. 2018. The impact of the introduced *Digitonthophagus gazella* on a native dung beetle community in Brazil during 26 years. Biol. Invasions. 20: 963–979. doi: https://doi.org/10.1007/s10530-017-1603-1

Gámez, J., Accocia, R., Noriega, J.A. 2021. Nuevos registros de distribución de *Digitonthophagus gazella* (Fabricius, 1787) (Coleoptera: Scarabaeidae: Scarabaeinae) en Venezuela. Entomotropica. 36: 46-50.

Gause GF. 1932. *Experimental studies on the struggle for existence I. Mixed population of two species of yeast*. Zoological Museum, University of Moscow. pp. 389–402. doi: https://doi.org/10.1242/jeb.9.4.389

Giraldo C, Escobar F, Chará JD, Calle Z. 2011. The adoption of silvopastoral systems promotes the recovery of ecological processes regulated by dung beetles in the Colombian Andes. Insect Conserv. Divers. 4(2): 115–122. doi: https://doi.org/10.1111/j.1752-4598.2010.00112.x

GISD. c2015. Global invasive species database. Available at: https://www.iucngisd.org/gisd/ /

Gotelli N, Ulrich W. 2010. Null model analysis of species associations using abundance data. Ecology. 91(11): 3384-3397. doi: https://doi.org/10.1890/09-2157.1

Gurevitch J, Padilla DK. 2004. Are invasive species a major cause of extinctions? Trends Ecol. Evol. 19(9): 470–474. doi: https://doi.org/10.1016/j.tree.2004.07.005

Hanski I, Cambefort Y. 1991. Resource partitioning. In: Hansky I and Cambefort Y, editors. 1991. Dung Beetle Ecology. Princeton, New Jersey. P. 330–349. doi: https://doi.org/10.1515/9781400862092.330

Holdridge LR. 1978. Ecología basada en zonas de vida. Instituto Interamericano de Cooperación de la Agricultura (IICA): Serie de Libros y Materiales Educativos, pp. 34.

Isaza-López LM, Montoya-Molina S, Giraldo-Echeverri C, León-González G, González-Alvarado F, Montoya-Lerma J. 2015. Nuevos registros de distribución de *Digitonthophagus gazella* (Fabricius, 1787) (Coleoptera: Scarabaeinae) en Colombia. Biota Col. 16(1): 45-53.

Kohimann B. 1994. A preliminary study of the invasion and dispersal of *Digitonthophagus gazella* (Fabricius, 1787) in Mexico (Coleoptera: Scarabaeidae: Scarabaeinae). Acta Zool. Mex. 61: 35–42. doi: https://doi.org/10.21829/azm.1994.61611666

Kruskal JB, Wish M. 1978. Multidimensional scaling. Newbury Park, CA: Sage. doi: https://doi.org/10.4135/9781412985130

Lang JM, Benbow E. 2013. Species interactions and competition. Nat. Ed. Knowl. 4: 1–8.

Levine JM, D'Antonio CM. 1999. Elton revisited: a review of evidence linking diversity and invisibility. Oikos. 87(1): 15–26. doi: https://doi.org/10.2307/3546992

Lobo J, Montes de Oca E. 1994. Distribución local y coexistencia de *Digitonthophagus gazella* (Fabricius, 1787) y *Onthophagus batesi* Howden & Cartwright, 1963 (Coleoptera: Scarabaeidae). Elytron. 8: 17–127.

Lodge DM. 1993. Biological invasions: Lessons for ecology. Trends Ecol. Evol. 8(4): 133-137. doi: https://doi.org/10.1016/0169-5347(93)90025-K

Lozano C. 2010. Nuevos registros de escarabajos coprófagos para la Orchila, Sierra de Perijá, Venezuela. Bol. Ctr. Inv. Biol. 44: 83-89.

MacLeod CJ, Paterson A. Tompkins DM, Duncan RP. 2010. Parasites lost - do invaders miss the boat or drown on arrival? Ecol. Lett. 13(4): 516-527. doi: https://doi.org/10.1111/j.1461-0248.2010.01446.x

Matavelli RA, Louzada JNC. 2008. Invasion of intra-Amazonian savannas by the dung beetle *Digintonthophagus gazella* (Fabricius, 1787) (Insecta: Coleoptera: Scarabaeidae). Acta Amaz. 38(1): 148–153. doi: https://doi.org/10.1590/S0044-59672008000100017

Matos Medina A. 2016. What can an invasive dung beetle tell us about niche conservatism? Environ. Entomol. 45(5): 1141-1145. doi: https://doi.org/10.1093/ee/nvw092

Medina-Rangel GF. 2011. Diversidad alfa y beta de la comunidad de reptiles en el complejo cenagoso de Zapatosa, Colombia. Rev. Biol. Trop. 59: 935-968.

Montes de Oca E., Halffter G. 1998. Invasion of Mexico by two dung beetles previously introduced into the United States. Stud. Neotrop. Fauna Environ. 33(1): 37–45. doi: https://doi.org/10.1076/snfe.33.1.37.2174

Montoya-Molina S, Giraldo-Echeverri C, Montoya-Lerma J, Chará J, Escobar F, Calle Z. 2016. Land sharing vs. Land sparing in the dry Caribbean lowlands: A dung beetle´s perspective. Appl. Soil Ecol. 98: 204-212. doi: https://doi.org/10.1016/j.apsoil.2015.10.017

Noriega JA. 2002. First report of the presence of the genus *Digitonthophagus* (Coleoptera: Scarabaeidae) in Colombia. Caldasia. 24: 213–215.

Noriega JA, Delgado O, Blanco JI, Gámez J, Clavijo J. 2017. Introduction, establishment, and invasion of *Digitonthophagus gazella* (Fabricius, 1787) (Coleoptera: Scarabaeinae) in the Savannas of Venezuela and Colombia. Nat. Res. 8(5): 370-381. doi: https://doi.org/10.4236/nr.2017.85023

Noriega JA, Delgado O, Blanco JI, Gámez J, Clavijo J. 2006. Registro continental de *Digitonthophagus gazella* (Coleoptera: Scarabaeidae) en Colombia. Caldasia. 28: 379–381.

Noriega JA, Folate K.D, Génier F, Reid CAM, Kohlmann B, Horgan FB, Davis LV, Forgie SA, Aguilar C, Ibarra MG, Vaz-de-Mello FZ, Ziani S, Lobo JM. 2020. Global distribution patterns provide evidence of niche shift by the introduced African dung beetle *Digitonthophagus gazella*. Entomol. Exp. Appl. 168(10): 766-782. doi: https://doi.org/10.1111/eea.12961

Noriega JA, Horgan F, Larsen T, Valencia G. 2010. Records of an invasive dung beetle species, *Digitonthophagus gazell*a (Fabricius, 1787) (Coleoptera: Scarabaeidae), in Peru. Acta Zool. Mex. (n.s.) 26: 451–456.

Noriega JA, Moreno, J, Otavo S. 2011. Quince años del arribo del escarabajo coprófago *Digitonthophagus gazella* (Fabricius, 1787) (Coleoptera: Scarabaeidae) a Colombia: proceso de invasión y posibles efectos de su establecimiento. Biota Col. 12: 35-44.

Pablo-Cea JD, Velado-Cano MA, Fuentes R, Cruz M, Noriega JA. 2017. First report of *Digitonthophagus gazella* (Fabricius, 1787) and new records for *Euoniticellus intermedius* (Reiche, 1849) (Coleoptera: Scarabaeidae Latreille, 1802) in El Salvador. Acta Zool. Mex. (n.s.) 33(3): 527-531. doi: https://doi.org/10.21829/azm.2017.3331154

Pokhrel MR, Cairns SC, Andrew NR. 2020. Dung beetle species introductions: when an ecosystem service provider transforms into an invasive species. PeerJ 8: e9872 doi: https://doi.org/10.7717/peerj.9872

R Development Core Team. c2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3–900051–07–0, URL http://www.R–project.org

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Dane Panetta F, West CJ. 2000. Naturalization and invasion of alien plants: concepts and definitions. Divers. Dist. 6(2): 93–107. doi: https://doi.org/10.1046/j.1472-4642.2000.00083.x

Rivera C, Wolff M. 2007. *Digitonthophagus gazella* (Coleoptera: Scarabaeidae): Distribution in America and two new records for Colombia. Rev. Col. Entomol. 33(2): 190-192. doi: https://doi.org/10.25100/socolen.v33i2.9343

Ripa R., Rodríguez F. 1990. Introducción de escarabajos coprófagos a Chile. *Resúmenes XII Congreso Nacional de Entomologia*, Valparaíso, pp. 51.

Rougon C., Rougon D. 1980. Contribution á la biologie des coléoptères coprophages en région sahélienne. Étude du developpement d' *Onthophagus gazella* (Coleoptera: Scarabaeidae). Rev. Écol. Biol. Sol 17 (3): 379-392.

Russell JC., Blackburn TM. 2017. The rise of invasive species denialism. Trends Ecol. Evol. 32(1): 3-6. doi: https://doi.org/10.1016/j.tree.2016.10.012

Sanders NJ, Gotelli NJ, Heller NE, Gordon DM. 2003. Community disassembly by an invasive species. Proc. Natl. Acad. Sci. USA. 100(5): 2474-2477. doi: https://doi.org/10.1073/pnas.0437913100

Shorthouse DP. 2010. SimpleMappr, an online tool to produce publication-quality point maps. [Retrieved from https://www.simplemappr.net. Accessed April 18, 2020].

Shurin JB, Greenfest-Allen E. 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. Am. Nat. 158(6): 624-37. doi: https://doi.org/10.1086/323589

Spencer CN, Riley McClelland B, Stanford JA. 1991. Shrimp stocking, salmon collapse, and eagle displacement. BioScience. 41(1): 14-21. doi: https://doi.org/10.2307/1311536

Tallamy DW. 2004. Do alien plants reduce insect biomass? Conserv. Biol. 18: 1689-1692. doi.org/10.1111/j.1523-1739.2004.00512.x

Torchin ME, Lafferty KD, Dobson AP, MacKenzie VJ, Kuris AM. 2003. Introduced species and their missing parasites. Nature. 421: 628-630. doi: https://doi.org/10.1038/nature01346

Vaz-de-Mello FZ, Edmonds WD, Ocampo FC, Schoolmeesters P. 2011. A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the new world (Coleoptera: Scarabaeidae). Zootaxa. 2854(1): 1-73. doi: https://doi.org/10.11646/zootaxa.2854.1.1

Vidaurre T, Noriega JA, Ledezma MJ. 2008. First report on the distribution of *Digitonthophagus gazella* (Fabricius, 1787) (Coleoptera: Scarabaeidae) in Bolivia. Acta Zool. Mex. (n.s.) 24(3): 217–220. doi: https://doi.org/10.21829/azm.2008.243917

Zhou ZS, Chen ZP, Xu ZF. 2010. Niches and interspecific competitive relationships of the parasitoids, *Microplitis prodeniae* and *Campoletis chlorldeae,* of the Oriental leafworm moth, *Spodoptera litura*, in tobacco. J. Ins. Sci. 10(1). doi: https://doi.org/10.1673/031.010.1001

Zunino M, Barbero E. 1993. Escarabajos, ganado, pastizales: algunas consideraciones deontológicas. Folia Entomol. Mex. 87: 95-101.