Global distribution patterns provide evidence of niche shift by the introduced African dung beetle *Digitonthophagus gazella*

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Abstract

The establishment of cattle ranches throughout the world has prompted the release of dung beetles as biological control agents that reduce pasture fouling and control dung-breeding flies. One of these beetles, *Digitonthophagus gazella* (Fabricius) (Coleoptera: Scarabaeidae), that is native to southeast Africa, has been introduced into the Americas, Australia, and New Zealand. Distribution records for this species have been used to develop climate models of potential future establishment. Recent studies, however, identify *D. gazella* as a complex of seven species. Taking into account this revision, and the clear identification of the records belonging to the actual *D. gazella*, we developed environmental models to identify factors that have contributed to the establishment of this species across regions and habitats. We compared the environmental conditions of *D. gazella* in its native range against those in the regions where the species has or has not established. Our results indicate that *D. gazella* is still absent in certain parts of Central and South America and parts of Africa where it could potentially establish. We speculate that its distribution in Africa is limited by competitive exclusion. The introduction of *D. gazella* in America is relatively recent, such that the full extent of its distribution has probably yet to be realized. In Australia and North America, *D.*

gazella is present in regions not predicted according to its native environmental conditions. This discrepancy may reflect a lack of competitive exclusion, phenotypic plasticity, and/or genetic adaptation. Our analyses suggest that the species has the ability to adapt to a wide range of environmental conditions that are extremely different from those in their native region. The species represents a useful case study to indicate that an introduced species may expand its realized niche beyond what is expected based on apparent environmental limits in the species native range.

Introduction

What are the mechanisms that allow invasive species to expand their distributions into new geographic regions? This has been a persistent and challenging question in biogeographical studies (Crisp & Cook, 2012; Boucher et al., 2014; Pyron et al., 2015) with important implications for the spread (Broennimann et al., 2007; Petitpierre et al., 2012; Hill et al., 2017) and management (Hugall et al., 2002) of invasive species. Many species expand into new geographic regions when given the opportunity, often as a result of human-aided transport – for example, emerald ash borer, *Agrilus planipennis* Fairmaire; spotted vinegar fly, *Drosophila suzukii* (Matsumura); red fire ant, *Solenopsis invicta* Buren – or, increasingly, climate change (Stachowicz et al., 2002; McGeoch et al., 2010; Turbelin et al., 2016). Such examples do not represent changes in the species' fundamental niches, but rather reflect their establishment into regions for which they are potentially pre-adapted (Simberloff, 1989). Thus, the native range of a species has often been used as a proxy to predict regions of potential future establishment (Broennimann et al., 2007; Boucher et al., 2014). However, the fundamental niche of a species may also allow it to establish in new locations characterized by abiotic or biotic conditions different from those in the native range (Prentis et al., 2008; Wilson et al., 2009; Blackburn et al., 2011; Keller et al., 2011; Sultan et al., 2013). In such cases, predicting distribution based solely on a species' native range can underestimate potential future areas of establishment (Urban et al., 2007; Beaumont et al., 2009; Parker et al., 2013). In addition, the ability of a species to expand into new regions can be aided by genetic change that may alter the boundaries of its fundamental niche to allow it to shift its realized niche (Jezkova & Wiens, 2016; Chapman et al., 2017). Examples of genetic changes include crop cultivars bred to withstand a wider range of drought, temperature, and saline conditions than experienced by wild populations (Matsui & Omasa, 2002; Olesen et al., 2011). Thus, predictions of where species may establish outside their native ranges are confounded by the extent of knowledge of the species' native range, its unanticipated physiological tolerances, phenotypic plasticity, and the potential for genetic changes in established populations due to directional selection.

Digitonthophagus gazella (Fabricius) (Coleoptera: Scarabaeidae, Scarabaeinae, Onthophagini) is an African dung beetle species that is now widely distributed in North America, Central and South America, Australia, and the southwest Pacific, and with a record in Japan (Table 1). Its range expansion has been aided by introduction programs for the biological control of cattle dung on pastures in several regions around the world. These

Table 1. List of introductions and/or first records of *Digitonthophagus gazella* by continent and country around the world outside its native distribution (Génier & Moretto, 2017)

Continent	Country	Year	References
Asia	Japan[1]	1978	Okajima & Araya (2012)
	Madagascar	1885	Génier & Moretto (2017)
Africa	France (Mayotte)	1958	Génier & Moretto (2017)
	Comoros	1958	Génier & Moretto (2017)
	USA (Hawaii)	1957	Legner (1978); Markin & Yoshioka (1998); Génier & Moretto (2017)
North America	USA	1972	Blume & Aga (1978); Anderson & Loomis (1978); Fincher et al. (1983, 1986); Downie (1984); Blume (1985); Hunter & Fincher (1985); Barbero & López-Guerrero (1992); Vulinec & Eudy (1993); MacRae & Penn (2001); Génier & Moretto (2017)
	Mexico	1981	Fincher et al. (1983); Zunino & Halffter (1988); Rivera-Cervantes & García-Real (1991); Barbero & López-Guerrero (1992); Thomas (1993); Kohlmann (1994); Lobo & Montes de Oca (1994, 1997); Montes de Oca & Halffter (1998); Morón et al. (1998); Deloya (2000); Montes de Oca (2001); Morales et al. (2004); Génier & Moretto (2017)
Central America	Guatemala	1987	Kohlmann (1994)
	El Salvador	2016	Pablo-Cea et al. (2017)
	Nicaragua	<1996	A Solís, pers. comm.
(Greater Antilles)	Cuba, Jamaica, Dominican Republic, Puerto Rico (USA)	1990	Ivie & Philips (2008); Génier & Moretto (2017)
(Lesser Antilles)	St Croix (USA), Anguilla (UK), St. Kitts, Antigua, Montserrat (UK), Guadeloupe and Marie-Galante (France), Martinique (France), St. Vincent, Union Island, Grenada	1992	Huchet (1992); Kohlmann (1994); Ivie & Philips (2008); Génier & Moretto (2017)
	Colombia	1995	Noriega (2002, 2016); Noriega et al. (2006, 2011, 2017); Rivera & Wolff (2007); Navarro et al. (2009)
South America	Venezuela	1996	Gámez et al. (1997); Noriega et al. (2017)
	French Guiana	2008	Boilly & Vaz-de-Mello (2013)
	Brazil	~1990	Nascimento et al. (1990); Bianchin et al. (1998); Koller et al. (1999, 2007); Aidar et al. (2000); Miranda et al. (2000); Marchiori et al. (2001, 2003); Schiffler et al. (2003); Scheffler (2005); Matavelli & Louzada (2008); Génier & Moretto (2017)

Continent	Country	Year	References
	Peru	1999	Noriega et al. (2010)
	Bolivia	1990	Vidaurre et al. (2008)
	Chile (Easter Island)	1988	Ripa & Rodríguez (1990); Ripa et al. (1995)
	Chile	1988	Ripa & Rodríguez (1990); Ripa et al. (1995)
	Paraguay	1998	Ruiz (2000)
	Argentina	2006	Ocampo & Ruiz-Manzanos (2008); Álvarez et al. (2009)
	Australia	1967	Waterhouse (1974); Génier & Moretto (2017); Reid et al. (2018)
	Papua New Guinea	1973	Génier & Moretto (2017)
Oceania	New Zealand	2013	ERMA (2011); Forgie et al. (2018)
	New Caledonia	1978	Gutiérrez et al. (1988); Génier & Moretto (2017)
	Vanuatu	1978	Gutiérrez et al. (1988); Génier & Moretto (2017)
	Fiji	1978	Génier & Moretto (2017)

[1] No specimen from this locality (Okinawa Island, Japan) has been studied by F. Génier or by any of the co-authors. Further studies are required to verify that this record relates to *D. gazella.*

include Australia (Bornemissza, 1970; Tyndale-Biscoe, 1990; Edwards, 2003, 2007), Brazil (Nascimento et al., 1990), Chile (Ripa et al., 1995), New Caledonia and Vanuatu (Gutiérrez et al., 1988), New Zealand (Forgie et al, 2018), and the USA (Blume & Aga, 1978; Fincher et al., 1983). Adult beetles arrive at fresh dung pats to remove and bury dung in tunnels beneath the pat. This behaviour removes dung that would otherwise act as breeding sites for parasites and arthropods affecting livestock (Blume & Aga, 1978; Fincher et al., 1983; Doube et al., 1991). Additionally, in common with many other dung beetle species, the dung buried by *D. gazella* restores nutrients to the soil and the tunnels increase soil bioturbation, soil aeration, and water percolation (Nichols et al., 2008). *Digitonthophagus gazella* displays a broad tolerance to ecosystems and regions, particularly non-forested cattle pastures in tropical, subtropical, and semi-arid regions (Montes de Oca & Halffter, 1998). It also has a high dispersal rate (Seymour, 1980; Barbero & López-Guerrero, 1992; Kohlmann, 1994; Álvarez et al., 2009; Noriega et al., 2011) and a relatively short generation time (Lee & Peng, 1981, 1982; Floate et al., 2015). Because of these attributes, *D. gazella* has become a dominant member of the dung beetle community in many locations (Doube et al., 1991; Lobo & Montes de Oca, 1997; Aidar et al., 2000; Marchiori et al., 2003; Koller et al., 2007; Matavelli & Louzada, 2008) and also dominates dung beetle literature, appearing in at least 1 120 scientific publications dedicated to its biology, ecology, and taxonomy (Génier & Davis, 2017).

Models that predict regions of potential establishment for *D. gazella* are of interest for two reasons. First, they are useful as a tool to aid future programs of intentional release. Second, they can be used to identify regions where native dung beetle faunas may be at risk by possible competitive interactions with *D. gazella*. However, different models and studies dedicated to the species have frequently produced contrasting predictions. Duncan et al. (2009) used climatic parameters from the species' native range to predict the occurrence of *D. gazella* in Australia at sites where the species is known to occur. However, their model indicated discrepancies between the species' predicted and actual Australian distributions. Medina (2016) compared climatic parameters from *D. gazella*'s native range with that of its global invaded range. The author's results showed a high degree of overlap between the two sets of parameters, suggesting that the climatic niche of the species is stable between native and invaded regions. Floate et al. (2017) used bioclimatic models to predict the potential distribution of *D. gazella* and two other Onthophagini species in North America. Results for *D. gazella* indicated that it has likely already reached the North American limits of its potential distribution. All these distributional predictions have been compromised by new taxonomic insights. In their recent revision of the genus, Génier & Moretto (2017) recognized 16 species belonging to the genus and identified the traditionally defined *D. gazella* as a complex of four cryptic species with an Indo-African distribution. The species now specifically recognized as *D. gazella* has a restricted native range from central to southern Africa, and it is the only member of the species complex that has been widely introduced outside of Africa (Génier & Moretto, 2017). Thus, one of the main results of this revision is that the native range of *D. gazella* is actually more restricted than previously thought. In addition, the name *D. gazella* has been misapplied and is a synonym of a strictly Indomalayan species, *Digitonthophagus catta* (Fabricius). To preserve current usage and stability in nomenclature an application is currently under consideration by the International Commission of Zoological Nomenclature requesting that the name *D. gazella* be retained for the widely distributed African species (Génier & Krell, 2017: case 3722).

In this study, we aim to predict the potential global distribution of *D. gazella* using an updated database of the world occurrence of the species, as well as environmental

information of its native range in Africa (Génier & Moretto, 2017). This potential distribution is compared with the world occurrence of the species (the realized niche), to determine whether novel occupied areas are similar to or divergent from the environmental conditions prevailing in the native range, but also to assess the relevance of a shift in the realized niche to explain this invasion process. If the novel areas are environmentally similar to the native area, it could be assumed that the future distribution of this species may be reasonably anticipated because factors limiting the distribution of the species are universal. In contrast, a shift in the realized niche of *D. gazella* could be hypothesized if much of the novel distribution is defined by environmental conditions that differ from those prevailing in the species' native range. In this case, the future distribution of the species and its possible impact on the dung beetle regional assemblages would be difficult to predict.

Materials and methods

Species data

We compiled a database of 2 582 unique locality records for *D. gazella* in both its native and invaded ranges, which represents the largest data set for this species compared to previous studies (see Appendix S1). Records in this database were obtained from Génier & Moretto (2017) and reviewed by François Génier, who checked male genitalia of at least one specimen from each collecting event from 27 countries around the world (for more details see Génier & Moretto, 2017). This examination determined that the species redistributed outside Africa is *D. gazella* and does not include any other members of the *D. gazella* species complex (Génier & Davis, 2017). Additional records for *D. gazella* were obtained from the scientific literature, unpublished records provided by colleagues, and from specimen labels in private and public collections. Each locality was associated with its longitude and latitude (in decimal degrees) following the WGS 84 coordinates reference system. The database included locality information for specimens collected in 51 countries across four continents (Africa, 19.6%; Asia, 0.3%; North America, 26.8%; Central America and the Caribbean, 3.3%; South America, 21.9%; Oceania, 28.1%).

Environmental predictors

A total of 27 environmental variables at a resolution of 2.5 min (approximately 25 km^2) were used as predictors. These included five topographic (elevation, elevation diversity, slope, slope diversity, and aspect diversity), one edaphic (soil or edaphic diversity), and 21 climatic predictors (see Appendix S2). Elevation was calculated from a digital elevation model (DEM) downloaded from the USGS EROS Data Center (www.eros.usgs.gov). This DEM was used to calculate both a slope and an aspect map, and to estimate the diversity of slopes and aspects in a 7 × 7 pixel window using the classic Shannon diversity index. In the same manner as for topographic variables, we used the world map of soil orders from the U.S. Natural Resource Conservation Service (www.nrcs.usda.gov) to calculate the diversity of soils. Finally, the 19 bioclimatic variables of WorldClim were also used (www.worldclim.org; Hijmans et al., 2005), adding aridity and continentality as calculated by Valencia-Barrera et al. (2002).

Modelling procedure

Georeferenced localities in the native range of *D. gazella* were used at a resolution of 2.5 min to identify regions of the globe with abiotic conditions similar to those in the native range or potential distribution (i.e., a provisional image of the inhabited localities when the set of contingent factors preventing the colonization of suitable regions have not affected the distribution; see Lobo, 2016). To identify regions of potential *D. gazella* establishment outside the native range, we accounted for three main disadvantages of the procedures frequently used to estimate these distributions: (1) the lack of reliable absence data, (2) the use of complex modelling techniques, and (3) the arbitrary selection of a geographical extent (García-Roselló et al., 2019). We excluded the use of pseudo-absences selected at random from the studied area that are generally used when reliable absence data are lacking (Hastie & Fithian, 2013; Iturbide et al., 2018). We also established an appropriate geographic area of analysis, which is fundamental for correctly selecting the appropriate predictors of distribution (VanDerWal et al., 2009; Barve et al., 2011; Acevedo et al., 2012), in order to generate reliable models and assess their accuracy (Lobo et al., 2008; Hijmans, 2012; Somodi et al., 2017).

Thus, assuming that populations in the native range maintain a certain degree of genetic connectivity (i.e., geographic barriers do not isolate populations), we firstly delimited the continuous distributional extent or geographical background (GB) of *D. gazella* in its native range (i.e., the area colonized by the species in which the populations are probably interconnected). The delimitation of this GB minimized the effects of contingent events and factors able to limit the dispersal of the species (Acevedo et al., 2012) because the area used to estimate the most explanatory environmental conditions is assumed to be only the one that is accessible to the species. Given that drainage basins constitute natural landform units, the GB area was delimited as the one composed by the river basins with presence observations in the native area that, in turn, enables the connection of all the available occurrences (all the selected basins must be connected). The watershed information provided by the WaterBase project (www.waterbase.org) was used for this purpose, which includes a hierarchical coding system to recognize river basins of different levels. This information is managed by the ModestR software (García-Roselló et al., 2013, 2014, 2019) in order to select the minimum level of river basins with occurrences that generate a contiguous and connected area. Subsequently, the most relevant predictor variables were selected within this GB area to enhance the detection of preferred environmental conditions within the inhabited basins.

To identify variables with the highest predictive value, we firstly excluded those with a variance inflation factor (VIF) lower than five. In statistics, VIF quantifies the multicollinearity of predictors. This step eliminated 12 variables from further consideration because they were correlated with the other variables (see Appendix S2). The remaining 15 variables were then screened to identify those with the highest capacity to discriminate between the environmental conditions in the 'presence' cells against those prevailing in the GB area. For this purpose, an instability index, included within the ModestR software, was estimated by dividing each continuous predictor into bins and comparing the relative frequency of the cells with presence data against those of GB for each bin (Guisande et al., 2017). The explanatory variables showing greatest percentage of contribution to the instability index (80% of total variability) were assumed to be those that have the highest capacity to discriminate the cells of occurrence in the selected region (Guisande et al., 2006, 2017). As a result of this screening, six additional variables were eliminated from consideration (see Appendix S2). The remaining nine variables were retained: (1)

precipitation during the wettest month, (2) precipitation during the warmest quarter, (3) precipitation during the driest month, (4) precipitation seasonality, (5) continentality (i.e., the degree to which the climate of a region exemplifies that of the interior of a landmass), (6) mean diurnal range of temperature, (7) isothermality (i.e., the range of temperatures throughout a day in comparison to annual variations), (8) mean temperature during the wettest quarter, and (9) edaphic diversity. The so selected explanatory variables are not intended to be those that are causally and micro-environmentally linked to the occurrence and abundance of the studied species. These true causal variables can change spatially, may be difficult to detect in the absence of ecophysiological knowledge, and should reflect the environmental requirements of all development stages of an insect species. Given the frequent correlation between environmental variables, the process of selection that was followed only aimed to diminish the number of correlated variables and reject those with a reduced capacity of being explanatory for the target species at the examined resolution. Thus, it is assumed that at least some of the selected predictors directly influence demographic processes that are important for the species (Austin, 1980).

The values of the nine selected environmental predictors were used to generate a map of potential distribution according to a simple multidimensional envelope or generalized intersection procedure (Jiménez-Valverde et al., 2011; Booth et al., 2014). This binary suitability map was generated by estimating the maximum and minimum environmental values in cells of species presence for each selected environmental variable. For each variable, we assume that the species may colonize areas showing conditions within and up to these extremes at which native occurrences are observed. Therefore, the map should show the potential world distribution based on similar environmental conditions to those existing in the observed area of occurrence. To assess continuous suitability representation of this potential distribution, the formerly selected environmental variables were used to calculate the scale-invariant Mahalanobis distance (MD; Farber & Kadmon, 2003), thus measuring the environmental distance between the observations of *D. gazella* in its native range and all the remaining world cells. The upper quartile MD value in the native range has been considered as the cut-off value to discriminate the most suitable localities within the potential distribution.

The potential global distribution derived from native occurrences was considered to represent a global geographical projection of the realized niche of the species, given the used predictors and the available recorded observations. Derived in such a way, the potential distribution cannot be subjected to classic validation procedures because reliable absences are lacking, and also because occurrence data cannot be used to validate potential distributions (Lobo, 2016). The geographic area currently occupied by *D. gazella* (realized distribution) can only be estimated using known observations (Figure 1). Thus, an α-shape procedure was applied (Pateiro-López & Rodríguez-Casal, 2011) to generate non-convex polygons by incorporating discontinuities in species distributions. The overlap of the so obtained potential and realized distributions allowed us to identify three types of areas outside the GB area: (1) environmentally suitable areas that have been successfully invaded (suitable invaded areas, SIAs), (2) environmentally suitable areas not yet invaded (SNIAs), and (3) environmentally unsuitable areas that have been successfully invaded (UIAs). All analyses were conducted using the packages ModestR (García-Roselló et al., 2013, 2014; www.ipez.es/ModestR) and STATISTICA v.12.0 (StatSoft, Tulsa, OK, USA).
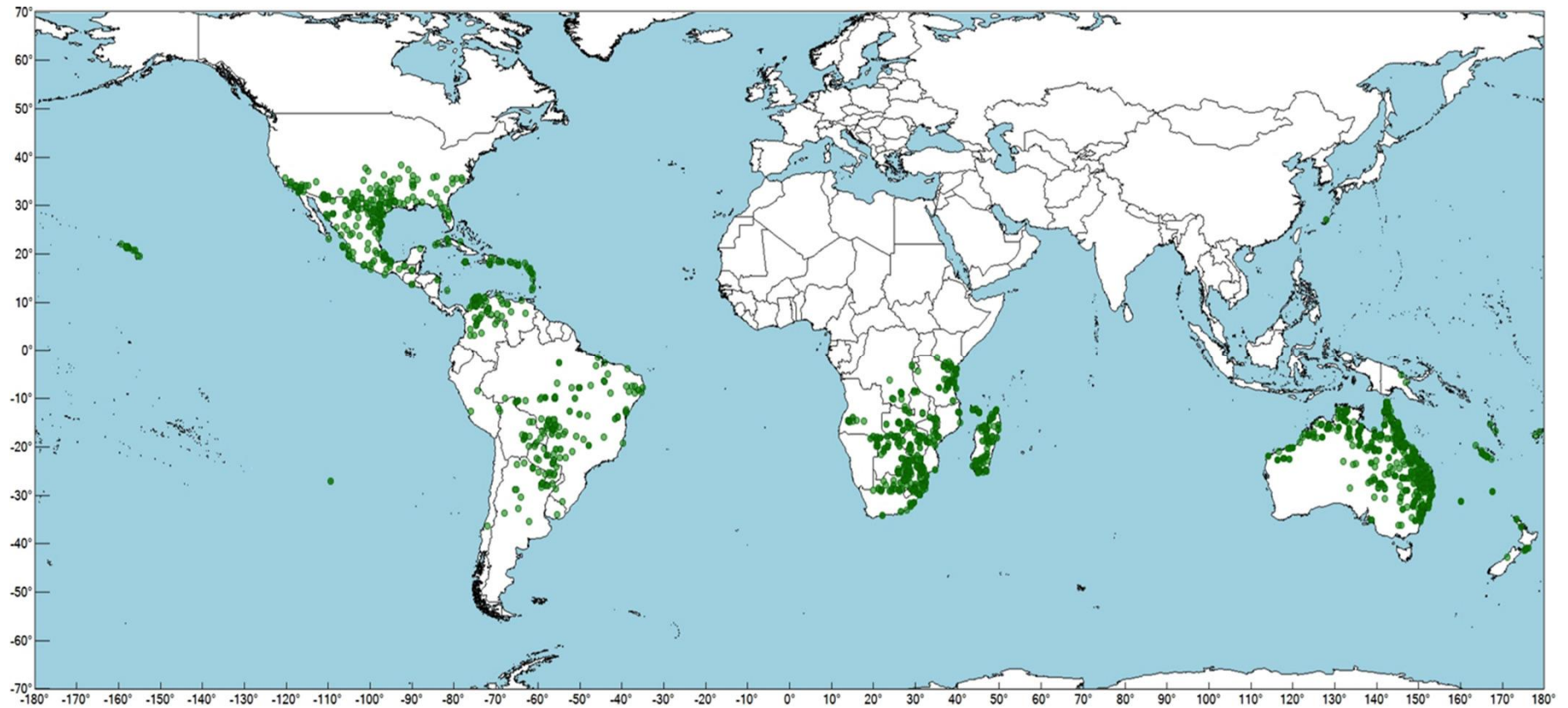
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Figure 1. World occurrences of *Digitonthophagus gazella* used in this study (2.5-min cells). Native occurrences are the records in mainland Africa with the exception of those from Madagascar and the Comoro islands.
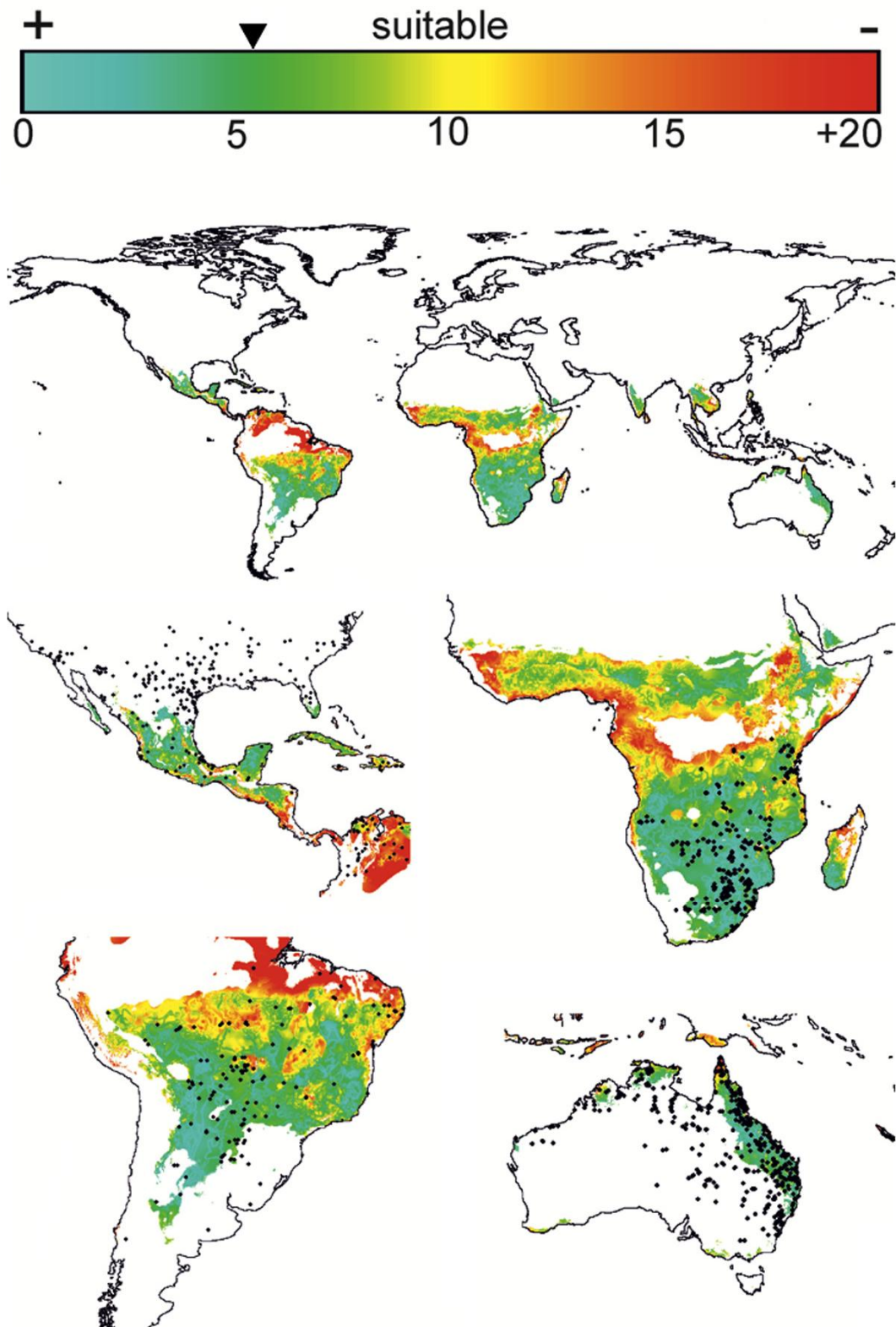
Figure 2. Worldwide potential distribution of *Digitonthophagus gazella* using selected climatic variables from its native occurrences and a multidimensional enveloping procedure. The four regional maps, displayed in greater detail, show the potential distribution of *D. gazella* and the observed occurrences (black points). The colour gradient reflects the Mahalanobis distance (MD) from the conditions existing in the native range. The upper MD quartile value of the native range represents the most suitable localities within the potential distribution (▼ = 5.27). Uncoloured areas lie outside the potential distribution of the species.

Results

The potential distribution derived from the multidimensional enveloping procedure (Figure 2) suggests that several regions of the Americas, Africa, and Australia have environmental conditions similar to those existing in the native range of *D. gazella*. Suitable conditions also occur in Madagascar and north of the current species distribution reported in Africa, excluding most arid and tropical areas. Environmentally favourable conditions are predicted to occur in a sizeable part of South and Central America, northern and eastern Australia, and even in southern India and Indochina. In total, the potential distribution of *D. gazella* could encompass around 27.8 million km^2. Of this area, approximately 20.2 million km^2 (73%) still remains un-colonized, but this percentage corresponds mainly to a priori suitable areas located in Africa and South America.

About half (48%) of the presence cells (Table 2) appear under a priori environmentally favourable conditions but a slightly higher number of cells (52%) occur in unfavourable areas (n = 567). *Digitonthophagus gazella* seems to have invaded favourable areas (i.e., SIAs) with conditions falling within extremes similar to those experienced in the native area (see maximum and minimum values in Table 2), but with different average values. Suitable invaded localities have slightly higher edaphic diversity and isothermality values than native ones (Table 2), but also higher values of the mean temperature during the wettest quarter and greater general precipitation figures (precipitation during the driest month, the wettest month, and the warmest quarter). Suitable invaded localities have, however, lower values of precipitation seasonality and mean diurnal temperature range than native localities (Table 2).

The overlap of realized and potential distributions (Figure 3) indicates that large regions of North America and central Australia have been intentionally occupied (as a combination of introduction programs and natural dispersal events) without harbouring the a priori suitable environmental conditions of the native range (southeast Africa, around 6 million km^2). The worldwide invaded localities where environmental characteristics are outside the favourable values of the native observations (UIAs) seem to show significantly higher average values of continentality and precipitation during the driest month (Table 2). In addition, these invaded localities indicate that the extreme conditions reached by some occurrences greatly exceed those existing in the native area. This occurs for all of the selected variables, but especially for precipitation-related variables. Invasive *D. gazella* populations seem to inhabit wetter, warmer, and more continental areas than populations in their native range (Table 2). When mapping the particular environmental conditions of the invaded localities that are not shared with those present in the native area, there is no suitable 2.5-min cell in Africa (e.g., only in some equatorial and Malagasy areas it is possible to observe rain values higher than 60 mm m^{-2} during the driest month, and mean temperatures over 30 °C during the wettest quarter can only be experienced in the Sahel and the Horn of Africa).

Table 2. Mean values of the selected climatic variables (± 95% confidence intervals) for the 2.5-min cells with occurrence observations of *Digitonthophagus gazella* in native and invaded areas. Within the invaded area, SIAs are climatically suitable and UIAs are climatically unsuitable according to conditions prevailing in the native distribution areas. The numbers in parentheses indicate ranges of climatic values. Temperatures are in decimal degrees and precipitation in mm

| Climatic variables	Native	Invaded	
		SIAs (suitable)	UIAs (unsuitable)
No. cells	292	516 (47.6%)	567 (52.4%)
Continentality	9.05 ± 0.65 (0–28)	9.23 ± 0.62 (0–28)	22.93 ± 1.32 (0–66)
Edaphic diversity	0.57 ± 0.05 (0–1.73)	0.74 ± 0.04 (0–1.73)	0.62 ± 0.04 (0–1.97)
Isothermality	58.55 ± 0.65 (49–85)	61.72 ± 0.79 (50–84)	51.83 ± 0.92 (26–92)
Mean diurnal temperature range	134.78 ± 2.79 (62–172)	118.74 ± 1.87 (63–172)	125.16 ± 2.20 (61–190)
Mean temperature during the wettest quarter	234.16 ± 2.90 (96–286)	254.79 ± 2.04 (96–284)	248.15 ± 4.25 (33–327)
Precipitation during the driest month	7.39 ± 1.11 (0–59)	17.42 ± 1.28 (0–59)	29.75 ± 2.71 (0–244)
Precipitation seasonality	83.59 ± 2.33 (16–129)	73.91 ± 2.30 (27–126)	62.64 ± 2.75 (8–136)
Precipitation during the warmest quarter	292.47 ± 12.38 (25–884)	407.03 ± 13.79 (71–807)	359.23 ± 24.04 (3–1403)
Precipitation during the wettest month	158.64 ± 7.70 (39–465)	218.74 ± 8.61 (47–458)	182.23 ± 10.96 (17–648)
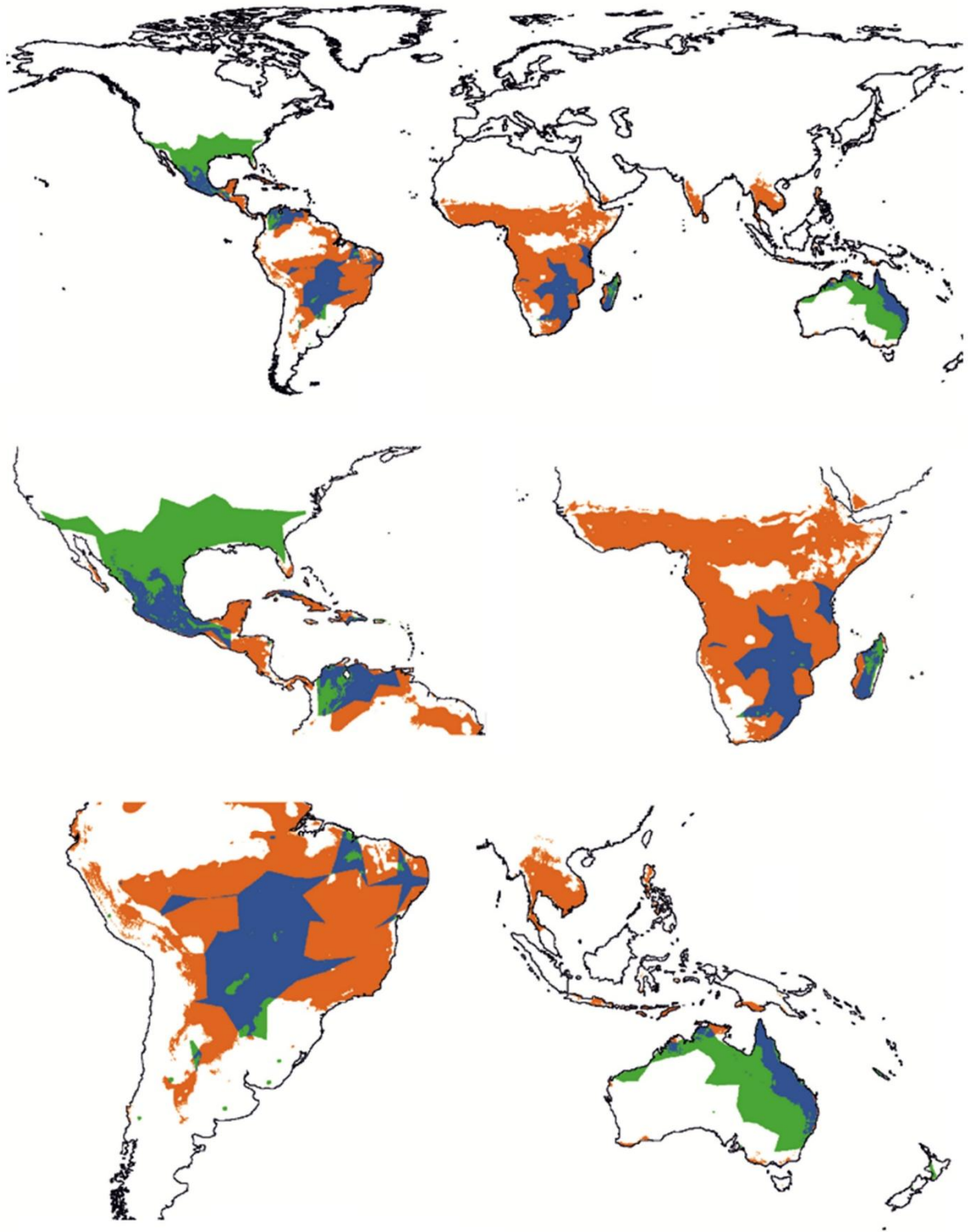
Figure 3. Mapping of the current and potential distribution of *Digitonthophagus gazella* showing the extent and location of the environmentally suitable invaded areas (SIAs, in blue; equivalent to the native range in mainland Africa), the suitable not yet invaded areas (SNIAs, in orange), unsuitable invaded areas (UIAs, in green), and unsuitable not invaded areas (UNIAs, without colour).

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Discussion

In this study we analysed the distribution and the associated probable niche shift of *D. gazella*, an invasive species deliberately introduced into several regions around the world. We based our analysis on recent clarification of the species' native distribution and used all currently available information to evaluate the magnitude and tendency of the environmental niche shift exhibited by this species. In this study, we modelled the global distribution of *D. gazella* to assess whether its ability to establish outside of its native range has been facilitated by a change in its environmental niche. Our model incorporated new knowledge of the species' native range, environmental parameters associated with its native range, and an exhaustive database of its current global distribution. Our results show that *D. gazella* has established in extensive regions where establishment was not predicted by our model. This discrepancy may reflect a weakness of the model, indicate that *D. gazella* has a broader environmental niche than is predicted by its native range, and/or that *D. gazella* has expanded its environmental niche tolerance. This latter process potentially occurs via microevolutionary processes, hybridization, and/or biotic interactions (Sherpa et al., 2019; Manzoor et al., 2020). Thus, about half of the distribution records for *D. gazella* are centred on regions with differing environmental conditions to those in its African native range. As a result, *D. gazella* is now the most widespread dung beetle in tropical and subtropical pastures around the globe. This result casts doubts on the possibility of predicting the future geographical expansion of this species without a deeper understanding of its physiological plasticity, ecological requirements, genetic and evolutionary variability, and the potential relevance of anthropic disturbance and relaxation of competition in new areas.

Competitive interactions, habitat characteristics, and environmental barriers

In its native range, *D. gazella* populations co-occur with seven closely related species that occupy the same functional guild (Génier & Moretto, 2017). These latter species are absent in all of the regions into which *D. gazella* has been introduced (i.e., Australia, North America, Central America, and South America). Evaluation of potential negative interactions between *D. gazella* and other native dung beetles (i.e., competition, spatial displacements, or local extinctions) has been generally inconclusive, especially in saturated dung beetle assemblages (Noriega et al., 2017). Although reports from the USA, Mexico, the West Indies, and Brazil suggest that introduced *D. gazella* have caused a decline in native species (Howden & Scholtz, 1986; Montes de Oca & Halffter, 1995; Young, 2007; Ivie & Philips, 2008; Filho et al., 2017), this is disputed by other findings from the USA, Mexico, and Nicaragua (Lobo & Montes de Oca, 1994; Howden & Howden, 2001; Horgan, 2008; Tiberg & Floate, 2011). Nevertheless, studies from the USA and Brazil indicate clear changes in the abundance structure of assemblages (Fincher et al., 1986; Filho et al., 2017), and studies from the USA and Australia indicate changes in the dominance of *D. gazella* in terms of assemblage abundance (Edwards, 2003; Kaufman & Wood, 2012).

The speed with which *D. gazella* has established in areas with environmental conditions similar to those in the native range has been variable (Barbero & López-Guerrero, 1992; Kohlmann, 1994; Noriega et al., 2011). This may partially reflect different levels of competition with native species. Establishment success may be hindered in regions where the functional guild of *D. gazella* (i.e., crepuscular-nocturnal fast tunnelers in grassland environments) in cattle dung is already occupied by native species. Conversely, the absence of native species in this functional guild may explain the dominance of *D. gazella* in Central America (and possibly South America) (Horgan, 2008). Although there are no studies that

evaluate the importance of biotic interactions as potential barriers (e.g., competitors, predators, parasitoids) to the invasion of *D. gazella*, we suggest that the main reason for the species' absence in some potential areas of Africa is due to biotic interactions (i.e., resource competition) with other very similar species that act as an ecological barrier to its expansion. The existence of several neighbouring species could prevent the expansion of the species, particularly as they occur within the northern and southern limits of the distribution of *D. gazella* (Génier & Moretto, 2017). Another possible element that could affect the distribution pattern of *D. gazella* outside its native range is reduced predation pressure. Doube (1991) suggested that the low numbers of individuals of *D. gazella* in African populations in comparison to those recorded in Australia (North Queensland) might be related to the frequent predation on pats by termites that are common in African grasslands but lack functional equivalents in Australia.

One of the most evident barriers to the distribution of the species in many regions is vegetation cover. *Digitonthophagus gazella* possesses a broad distribution range occupying many ecosystems: savannas, pastures, and various altered and open landscapes, especially associated with livestock (Noriega et al., 2017). In its native range, *D. gazella* strongly favour grassland (75%) over woodland (18%) and shaded thickets (7%) with a bias to finer-grained rather than coarser-grained soils (77% sandy clay loam: 23% deep sand; Davis, 1996). It appears unable to invade and colonize forested areas (Lobo & Montes de Oca, 1994; Noriega et al., 2010; Davis et al., 2014; Noriega et al., 2017). However, Matavelli & Louzada (2008) report that in Brazil *D. gazella* has been able to invade inter-Amazonian grasslands that are geographically isolated from cattle pastures by an extensive barrier of rainforest. Although some of these introductions could result from individuals hitchhiking rides within cattle dung during cattle transportation from one pasture to another. In the case of inland zones of Australia, Floate et al. (2017) suggested that irrigation programs in dry regions could allow *D. gazella* to colonize and expand into these new areas that were previously not suitable for the species. However, some of the new localities outside its predicted range are almost entirely non-irrigated (SOE, 2017), so that other unknown factors may have facilitated this expansion. Vidaurre et al. (2008) mention that it could be difficult for the species to invade dry inter-Andean valleys and regions below the Puna because of climatic conditions. However, in Colombia the species has been recovered in an inter-Andean valley (Noriega, 2016) with a very dry environment (Tatacoa desert, 30 °C, 60% relative humidity, and <1 000 mm precipitation annually), which further exemplifies the high plasticity of this species to adapt to extreme conditions.

It is almost certain that the success of *D. gazella* in many regions is due to the conversion of forests into grasslands on which cattle have been introduced. It is to be expected that within a future scenario of an increase in anthropogenic disturbance (e.g., deforestation, conversion of forestland to agricultural systems, and the spread of grassland areas for cattle production), the establishment and invasion of *D. gazella* will be favoured. These new open areas create suitable habitat conditions, having available food resources that the species needs. Most of the new records of this species in Central and South America are attributed to livestock intensification and cattle movement between countries (Noriega, 2002; Vidaurre et al., 2008; Noriega et al., 2010, 2017; Pablo-Cea et al., 2017). Besides, the native range of *D. gazella* in Africa matches to the more diverse areas of the native distribution of bovids (Deshler, 1963; Heywood, 2010). In some regions of Australia the presence of *D. gazella* is used as a clear indicator of disturbance of native woodlands (Gollan et al., 2010). In addition, Wallace & Richardson (2005) and Cave (2005) found that *D. gazella* is able to adapt to city environments and can use the dung of domestic animals (dogs), favouring the potential

expansion of the species from rural to urban areas. If we place together all the biotic and abiotic elements that we know might restrict the spread and invasion of *D. gazella*, the main environmental barriers could be: (1) vegetation cover (i.e., secondary and primary forests, such as in the Amazon region), (2) elevation (most of the records are below 2 000 m a.s.l.), (3) extremes in average annual temperatures (i.e., >30 or <6 °C), (4) extremes in average annual precipitation (i.e., >4 400 or <90 mm), (5) latitude (i.e., between 40–45°N and 40–45°S), and (6) saturated assemblages with similar functional species.

Microevolutionary processes and ecological plasticity

Given the prevalence of invasive species, and their potential economic impacts, it is useful to identify cases where native and introduced populations differ ecologically and, consequently, where they may have diverged genetically. *Digitonthophagus gazella* offers an interesting case study, where potential differences between native and invasive populations of *D. gazella* that are living outside the limits of predicted ranges might be used to uncover genetic shifts in physiological tolerances. Under a global climate change scenario, it is highly probable that *D. gazella* will be favoured (in some specific areas) and will be able to colonize higher elevations, northern and southern latitude areas that could be warmer in the future, taking into consideration regional precipitation changes. However, additional studies of the interactions between a changing climate and biological restrictions are needed (Simberloff, 2000). Studies of other taxa suggest that the potential adaptation of invasive species to novel and extreme conditions is strongly connected to genetic plasticity (Sexton et al., 2002; Geng et al., 2007). Distribution programs for *D. gazella* began in the 1960s (Bornemissza, 1970; Edwards, 2007), providing a 50-year period of culturing the species. A short generation time combined with multiple generations per year (Tyndale-Biscoe, 1990; Floate et al., 2015) could facilitate genetic changes between native and introduced populations. Molecular analyses seem warranted to assess the potential genetic differences between local ecotypes, regional, and intercontinental populations (the various climate strains referred to by Edwards, 2007). Further molecular studies (i.e., epigenetic analyses of recognized heat/cold tolerance genes) are needed to compare genetic differences between native and worldwide-introduced populations and identify probable genetic changes experienced by invaders. This suggestion receives some support from Whipple et al. (2012) who report high genetic diversity between South African and Puerto Rican populations of *D. gazella* with genetic differentiation best explained by geographic isolation in the absence of evidence for inbreeding depression.

Potential areas of colonization by Digitonthophagus gazella around the world

Based on conditions occurring in its native range, our results suggest that vast areas of the Americas, Africa, Australia, India, and Indochina have environmentally favourable conditions for *D. gazella*, making the invasion of new areas highly probable. More than 27.8 million km^2 (almost 3× the size of the USA) could be part of the potential distribution range of the species, following a very conservative estimation. These new areas to be invaded (especially those that are different from the native conditions and were not predicted to be suitable) expand the potential range conditions (showing a higher continentality, a higher edaphic diversity, a higher isothermality, a highest diurnal range and wettest quarter temperature, a highest precipitation during the warmest quarter, of the driest, and wettest month, and a lower precipitation seasonality). This potential invaded range could be much higher if the environmental conditions in the invaded areas now detected as unsuitable are considered as favourable, thus increasing the capacity of the species to invade new regions with more extreme climatic conditions.

The study of the colonization limits of *D. gazella* is important, particularly in terms of latitude, elevation, and physiological restrictions. The highest elevational records are around 1 500 m a.s.l. in the native range (Génier & Moretto, 2017) vs. 1 920 m a.s.l. in the Americas (Anduaga, 2004), although high elevation sites typically range from 1 200 to 1 500 m a.s.l. (Vidaurre et al., 2008; Noriega et al., 2010). The northern latitudinal limit in North America corresponds to Missouri, USA (38°N; Floate et al., 2017). The southern latitude limit in South America is in Chillan, Chile (36°S). Its establishment in Victoria, Australia at 36°S (Edwards, 2003) and parts of New Zealand (34–47°S; Forgie et al., 2018) demonstrate the ability of *D. gazella* to survive in more southerly latitudes. Floate et al. (2015) report that *D. gazella* does not have an obligatory diapause and that the minimum temperature for egg development is 18 °C (with an average egg-to-adult development time of 52.2 days at 22 °C, a development threshold of 18 °C equates to 209 degree days). Tyndale-Biscoe (1990) suggests that the species overwinters in Australia in both adult and larval stages. This combination of factors could limit the northernmost extent of its range. Some authors think that the species has reached the maximum extent of its potential distribution in North America (Floate et al., 2017). However, it is possible that the species could expand its actual distribution even further to colonize new areas, including regions that are outside of the actual potential distribution zone that we have established here.

Caveats and future prospects

The predicted potential distribution of a species is dependent on the environmental variables used during the modelling method. A large number of environmental variables were used here and the frequent correlations between variables suggest that the predicted geographical representations from our model would not change significantly with the addition of new predictors. With regard to the modelling method, we chose a multidimensional envelope procedure able to generate a map representing the localities with similar environmental conditions to those existing in the observed area of occurrence. This simple procedure prevents the use of background absences, favours a cautious selection of the predictors, and generates reliable potential distributions given the predictors used and the available recorded observations (García-Roselló et al., 2019).

Given its membership of a 'complex of morphological indistinguishable species' (Génier & Moretto, 2017), careful morphological or molecular examination of all specimens recovered outside of Africa is encouraged to establish species identity. Examination of male genitalia support the contention that the species recovered outside of Africa (e.g., American and Australian specimens) is *D. gazella*, but we do not exclude the possibility that other species in this complex may have been relocated outside the African continent due to many introduction programs. For example, Maes et al. (1997) reported the presence of the species in the Natural Reserve of Bosawas (north-eastern Nicaragua). However, in that paper they mention the small size of the specimens (0.5 cm; the average size of *D. gazella* is around 1 cm) and also the collection of just one specimen in an area without human and cattle activity (primary rain forest), which is very unusual for this species. For these reasons, we suggest that this initial report represented a probable confusion with *Onthophagus gazellinus* Bates, a native species that has a similar overall shape and colour pattern but that it is smaller than *D. gazella* and inhabits rainforest. However, we now have the confirmation of the presence of *D. gazella* in Nicaragua (A Solís, pers. comm.). A correct taxonomical identification is crucial to determine the extant and future distribution of this species, as well as its environmental limitations. Using incomplete or erroneous data that do not correspond to the native range, incorrect localities, or mistaken data because of a poor taxonomic

classification could generate incorrect estimations of distribution ranges. For example, using the data of other species that were included erroneously in the 'D. gazella' complex (Génier & Moretto, 2017) could generate a lot of noise, as it happens in the study of Medina (2016).

It is also crucial to study the genetic differences between invaded and native populations, as well as to learn more about the natural history, physiology, and ecology of this species in order to assess differences in thermal preferences, reproductive rates, and fitness between populations in its native and expanded ranges. Given that the main reason for their introduction to several regions is the 'assumed' capacity of D. gazella to work as an excellent dung removal recycler and to also act as an efficient biological control agent for flies and gastrointestinal helminths (Doube et al., 1991; Miranda et al., 2000), we know very little about the ecosystem services that this species performs in invaded communities. It would be useful to validate and quantify the functional role of this species in the introduced regions.

Conclusions

In Central and South America and in Africa, *D. gazella* seems to be absent in potentially habitable regions. Competitive exclusion may be the limiting factor in Africa, whereas the recent introduction of *D. gazella* in Central and South America may be the reason that the species has not yet spread to all habitable areas and that the distribution has not yet reached an equilibrium with the environmental conditions. In Australia and North America, *D. gazella* is present in regions not predicted based on native environmental conditions. Furthermore, and importantly, the environmental conditions in these invaded regions have no equivalent in the native range of *D. gazella*. Thus, our analyses suggest that the species has the ability to maintain viable populations under environmental conditions that are extremely different from those that exist in the original African native region. Several climatic, habitat, and biotic factors may have restricted or facilitated the spread and invasion of *D. gazella*, including competitive exclusion, phenotypic plasticity, or genetic adaptation. Finally, our results are consistent with a substantial shift in the realized environmental niche of the species, casting doubt over our capacity to anticipate the future distribution of this and other invasive species based on purely environmental conditions from species' native ranges.

Acknowledgements

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