

1 **Do global distribution patterns provide evidence of niche-shift by the introduced**
2 **African dung beetle *Digitonthophagus gazella* (Coleoptera: Scarabaeidae)?**

3
4 **Running title:** Introduced African dung beetle niche-shift

5
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42

43 **Abstract**

44 The introduction of cattle into different regions of the world has led to dung beetle
45 relocation programs to reduce pasture fouling and to control dung-breeding flies. One of
46 these beetles, *Digitonthophagus gazella* (Fabricius, 1787) (Coleoptera: Scarabaeidae), is
47 native to southeast Africa and has been introduced into the Americas, Australia, and
48 New Zealand. Distribution records for this species have been used by several authors to
49 develop climate models of potential future establishment. Recent studies, however,
50 identify *D. gazella* as a complex comprised of seven species. Taking into account this
51 revision, we developed climate models to identify factors contributing to the ability of
52 this species to establish in many different regions. We compared the climatic conditions
53 of *D. gazella* in its origin with climatic conditions where the species has or has not
54 established. In Africa, Central, and South America, our results indicate that *D. gazella* is
55 absent in regions where it could potentially establish. We speculate that its African
56 distribution is limited due to competitive exclusion. The introduction of *D. gazella* in
57 Central and South America is relatively recent, such that the full extent of its
58 distribution may yet to be realized. In Australia and North America, *D. gazella* is
59 present in regions not predicted by the native climatic conditions. This discrepancy may
60 reflect a lack of competitive exclusion, phenotypic plasticity, and (or) genetic adaptation.
61 Our analyses suggest that the species has the ability to adapt to new conditions and a
62 wide range of climatic regions that are extremely different from those in the native
63 region.

64

65 *Key words:* climate modelling, colonization, environmental niche, invasive species,
66 natural range, Onthophagini, Scarabaeinae, spatial distribution

67

68 **Introduction**

69 What are the mechanisms that allow invasive species to expand their distributions into
70 new geographic regions? This has been a persistent and challenging question in
71 biogeographical studies (Crisp & Cook, 2012; Boucher et al., 2014; Pyron et al., 2015)
72 with important implications for the spread (Broennimann et al., 2007; Petitpierre et al.,
73 2012; Hill et al., 2017) and management (Hugall et al., 2002) of invasive species. Many
74 species expand into new geographic regions when given the opportunity, often the result
75 of human-aided transport (*e.g.*, emerald ash borer *Agrilus planipennis* Fairmaire, 1888;
76 spotted vinegar fly *Drosophila suzukii* (Matsumura, 1931); red fire ant *Solenopsis*
77 *invicta* Buren, 1972) or, increasingly, of climate change (Stachowicz et al., 2002;
78 McGeoch et al., 2010; Turbelin et al., 2016). Such examples do not require a change in
79 the species' fundamental niches, but rather reflect their establishment into regions for
80 which they are potentially pre-adapted (Simberloff, 1989). Thus, the native range of a
81 species has often been used as a proxy to predict regions of potential future
82 establishment (Broennimann et al., 2007; Boucher et al., 2014). However, the
83 fundamental niche of a species may also allow it to establish in new locations
84 characterized by abiotic or biotic conditions absent in the native range (Prentis et al.,
85 2008; Wilson et al., 2009; Blackburn et al., 2011; Keller et al., 2011; Sultan et al.,
86 2013). In such cases, predicting distribution solely on a species' native range can
87 underestimate potential future areas of establishment (Urban et al., 2007; Beaumont et
88 al., 2009; Parker et al. 2013). In addition, the ability of a species to expand into new
89 regions can be aided by genetic change, that may alter the boundaries of its fundamental
90 niche to allow it to shift its realized niche (Jezkova & Wiens, 2016; Chapman et al.,
91 2017). Examples of genetic changes include crop cultivars bred to withstand a wider
92 range of drought, temperature, and saline conditions (Matsui & Omasa, 2002; Olesen et
93 al., 2011). Thus, predictions of where species may establish outside their native ranges
94 are confounded by the extent of knowledge of its native range, its unsuspected
95 physiological attributes and phenotypic plasticity, and potential genetic changes.

96 *Digitonthophagus gazella* (Fabricius, 1787) is an African dung beetle species
97 (Coleoptera: Scarabaeidae: Scarabaeinae: Onthophagini) that is now widely distributed
98 in North America, Central and South America, Australia and the southwest Pacific, with

99 records from Japan (see Table 1). Its range expansion has been aided by redistribution
100 programs established to accelerate the degradation of cattle dung on pastures. Adult
101 beetles arrive at fresh dung pats to remove and bury dung in tunnels beneath the pat.
102 This behaviour removes dung pats as breeding sites for parasites and arthropods
103 affecting livestock (Blume & Aga, 1978; Fincher et al., 1983; Doube et al., 1991).
104 Additionally, buried dung restores soil nutrients and the tunnels increase soil
105 bioturbation, soil aeration, and water percolation (Nichols et al., 2008).
106 *Digitonthophagus gazella* displays broad tolerance to different ecosystems and regions,
107 particularly non-forested cattle pastures in tropical, subtropical and semi-arid regions
108 (Montes de Oca & Halffter, 1998). It also has a high dispersal rate (Seymour, 1980;
109 Barbero & López-Guerrero, 1992; Kohlmann, 1994; Álvarez et al., 2009; Noriega et al.,
110 2011) and a relatively short generation time (Lee & Peng, 1981; 1982; Floate et al.,
111 2015). Because of these attributes, *D. gazella* has become a dominant member of the
112 dung beetle community in many locations (Doube et al., 1991; Lobo & Montes de Oca,
113 1997; Aidar et al., 2000; Marchiori et al., 2003; Koller et al., 2007; Matavelli &
114 Louzada, 2008). It has also become dominant in dung beetle literature. Génier & Davis
115 (2017) report the existence of at least 1120 scientific publications that reference the
116 study of this dung beetle species.

117 Models that predict regions of potential establishment for *D. gazella* are of
118 interest for two reasons. First, they are useful as a tool to aid future programs of
119 intentional release. Second, they can be used to identify regions where native dung
120 beetle faunas may be at risk by possible competitive interactions with *D. gazella*.
121 Duncan et al. (2009) used climatic parameters from its native range to predict the
122 occurrence of *D. gazella* in Australia at sites where the species is known to occur.
123 However, their model indicated discrepancies between the species' predicted and actual
124 Australian distributions. Medina (2016) compared climatic parameters from *D.*
125 *gazella*'s native range with that of its global invaded range. His results showed a high
126 degree of overlap between the two sets of parameters, suggesting that the climatic niche
127 of the species is stable between native and invaded regions. Floate et al. (2017) used
128 bioclimatic models to predict the potential distribution of *D. gazella* and two other
129 Onthophagini species in North America. Results for *D. gazella* indicated that it has
130 likely already reached the North American limits of its potential distribution.

131 Models previously developed to predict the distribution of *D. gazella* may be
132 compromised by new taxonomic insights. In their recent revision of the genus, Génier &
133 Moretto (2017) identified *D. gazella* as a complex of cryptic species with Indo-African
134 distribution. The species now specifically recognized as *D. gazella* has a restricted
135 native range from central to southern Africa and it is the only member of the species
136 complex that has been widely introduced outside of Africa (Génier & Moretto, 2017).
137 Thus, one of the main results of this revision is that the native range of *D. gazella* is
138 actually more restricted than previously thought. In addition, the name *D. gazella* has
139 been misapplied and is a synonym of a strictly Indomalayan species, *D. catta*
140 (Fabricius, 1787). To preserve current usage and stability in nomenclature an
141 application is currently under consideration by the International Commission of
142 Zoological Nomenclature requesting that the name *D. gazella* be retained for the widely
143 distributed African species (Génier & Krell, 2017: Case 3722). Our assumption in this
144 work is that the application will be successful.

145 In the current study, we revisited previous models that predict sites of potential
146 establishment for *D. gazella* based on climatic parameters from its native range.
147 Whereas these previous models used native site localities for *D. gazella* and other
148 members of the species complex, we used only the native site localities for *D. gazella* as
149 reported in Génier & Moretto (2017). Specifically, we asked whether *D. gazella* has
150 successfully invaded regions where climate models predict establishment to be unlikely.
151 A negative answer would indicate that the modelled realized niche of *D. gazella* is the
152 same in both its native and expanded range as concluded by Medina (2016). A positive
153 answer would suggest a shift in the realized niche with the establishment of the species
154 in regions outside its native range. If the latter is the case, then future research would be
155 warranted to verify and identify underlying mechanisms enabling this niche shift.

156

157 **Materials and methods**

158 **Species data**

159 We compiled a database of 2582 unique locality records for *D. gazella* in both its native
160 and invaded ranges, which represent a larger data set for this species compared to
161 previous studies (see Appendix S1). Records in this database were obtained from Génier
162 & Moretto (2017) and reviewed by François Génier, who checked male genitalia of at

163 least one specimen from each collecting event from 27 countries around the world (for
164 more details see Génier & Moretto, 2017). This examination determined that the species
165 redistributed outside Africa is *D. gazella* and does not include any other members of the
166 *D. gazella* species complex (Génier & Davis, 2017). Additional records for *D. gazella*
167 were obtained from the scientific literature, unpublished records provided by colleagues,
168 and from specimen labels in private and public collections. Each locality was associated
169 with its longitude and latitude (in decimal degrees) following the WGS 84 coordinates
170 reference system. The database included locality information for specimens collected in
171 51 countries across six big regions around the world (Africa – 19.6%, Asia – 0.3%,
172 North America – 26.8%, Central America and the Caribbean – 3.3%, South America –
173 21.9%, and Oceania – 28.1%).

174

175 **Environmental predictors**

176 A total of 27 environmental variables at a resolution of 2.5 minutes (approximately 25
177 km²) were used as predictors: five topographic (elevation, elevation diversity, slope,
178 slope diversity, and aspect diversity), one edaphic (soil or edaphic diversity), and 21
179 climatic (see Appendix S2). Elevation was calculated from a digital elevation model
180 (DEM) downloaded from the USGS EROS Data Center (www.eros.usgs.gov). This
181 DEM was used to calculate both a slope and an aspect map, and to estimate the diversity
182 of slopes and aspects in a 7 x 7 pixel window using the classic Shannon diversity index.
183 In the same manner as that for topographic variables, we used the world map of soil
184 orders from the U.S. Natural Resource Conservation Service (www.nrcs.usda.gov) to
185 calculate the diversity of soils. Finally, the 19 bioclimatic variables of WorldClim were
186 also used (see www.worldclim.org; Hijmans et al., 2005), adding aridity and
187 continentality as calculated by Valencia-Barrera et al. (2002).

188

189 **Modelling procedure**

190 Georeferenced localities in the native range of *D. gazella* were used at a resolution of
191 2.5 minutes to identify regions of the globe with abiotic conditions similar to those in
192 the native range or potential distribution (*i.e.*, a provisional image of the inhabited
193 localities when the set of contingent factors preventing the colonization of suitable
194 regions have not affected the distribution; see Lobo, 2016). To identify regions of
195 potential *D. gazella* establishment outside the native range, we accounted for three main

196 disadvantages of the procedures frequently used to estimate these distributions: i) the
197 lack of reliable absence data, ii) the use of complex modelling techniques, and iii) the
198 arbitrary selection of a geographical extent. We excluded the use of pseudo-absences
199 selected at random from the studied area that are generally used when reliable absence
200 data is lacking (Hastie & Fithian, 2013; Iturbide et al., 2018). We also establish an
201 appropriate geographic area of analysis, which is fundamental to correctly selecting the
202 appropriate predictors of distribution (VanDerWal et al., 2009; Barve et al., 2011;
203 Acevedo et al., 2012), in order to generate reliable models and assessments of their
204 accuracy (Lobo et al., 2008; Hijmans, 2012; Somodi et al., 2017).

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

223 To identify variables with the highest predictive value, we firstly excluded those
224 with a Variance Inflation Factor (VIF) lower than five. In statistics, VIF quantifies the
225 multicollinearity of predictors. This step eliminates twelve variables from further
226 consideration because they are correlated with the other variables (see Appendix S2).
227 The remaining 15 variables were then screened to identify those with the highest
228 capacity to discriminate between the environmental conditions in the presence cells

229 against those prevailing in the GB area. An Instability Index, included within the
230 ModestR software, was estimated by dividing each continuous predictor into bins and
231 compares the relative frequency of the cells with presence data against those of GB for
232 each bin (Guisande et al., 2017). The explanatory variables showing greatest percentage
233 of contribution to the Instability Index are assumed to be those that have the highest
234 capacity to discriminate the cells of occurrence in the selected region (Guisande et al.,
235 2006, 2017). As a result of this screening, six additional variables were eliminated from
236 consideration (see Appendix S2). The remaining nine variables were retained: (i)
237 precipitation of the wettest month, (ii) precipitation of the warmest quarter, (iii)
238 precipitation of the driest month, (iv) precipitation seasonality, (v) continentality (*i.e.*,
239 the degree to which the climate of a region exemplifies that of the interior of a
240 landmass), (vi) mean diurnal range of temperature, (vii) isothermality, (viii) mean
241 temperature of the wettest quarter, and (ix) edaphic diversity. The so selected
242 explanatory variables are not intended to be those that are causally and micro-
243 environmentally linked to the occurrence and abundance of the studied species. These
244 true causal variables can change spatially, may be difficult to detect in absence of
245 ecophysiological knowledge, and should reflect the environmental requirements of all
246 development stages of an insect species. Given the frequent correlation between
247 different environmental variables, the followed process of selection only aims to
248 diminish the number correlated variables and reject those with a reduced capacity of
249 being explanatory for the target species at the examined resolution. Thus, it is assumed
250 that at least some of the selected predictors direct influence demographic processes that
251 are important for the species (Austin, 1980).

252 The values of the nine selected climatic predictors were used to generate a map
253 of potential distribution according to a simple multidimensional envelope or generalized
254 intersection procedure (see Jiménez-Valverde et al., 2011; Booth et al., 2014). This
255 binary suitability map was generated by estimating the maximum and minimum
256 environmental values in cells of species presence for each selected environmental
257 variable. For each variable, we assume that the species may colonize areas showing
258 conditions within and up to these extremes at which native occurrences are observed.
259 Therefore, the map would show the potential world distribution based on similar
260 environmental conditions to those existing in the observed area of occurrence (potential
261 distribution). To asses continuous suitability representation of this potential distribution,

262 the formerly selected environmental variables were used to calculate the scale-invariant
263 Mahalanobis distance (MD; Farber & Kadmon, 2003), thus measuring the
264 environmental distance between the observations of *D. gazella* in its native range and
265 all the remaining world cells. The upper quartile MD value in the native range has been
266 considered the cut-off value to discriminate the most suitable localities within this
267 potential distribution.

268 The potential global distribution derived from native occurrences was considered
269 to represent a global geographical projection of the realized niche of the species, given
270 the used predictors and the available observations. Derived in such a way, the potential
271 distribution cannot be subjected to classic validation procedures because reliable
272 absences are lacking, and also because occurrence data cannot be used to validate
273 potential distributions (Lobo, 2016); reliable absences can be obtained in favourable
274 locations predicted as presences due to the role played contingent factors, biotic
275 interactions or dispersal limitations. The geographic area currently occupied by *D.*
276 *gazella* (realized distribution) can only be estimated using known observations (Figure
277 1). Thus, an α -shape procedure was applied (Pateiro-López & Rodríguez-Casal, 2011)
278 to generate non-convex polygons by incorporating discontinuities in species
279 distributions. The overlap of the so obtained potential and realized distributions allow us
280 to identify three types of areas outside the GB area: i) environmentally suitable areas
281 that have been successfully invaded (suitable invaded areas - SIAs), ii) environmentally
282 suitable areas not yet invaded (SNIAs), and iii) environmentally unsuitable areas that
283 have been successfully invaded (UIAs). All of the analyses were conducted using
284 ModestR (García-Roselló et al., 2103; 2014; www.ipez.es/ModestR) and STATISTICA
285 packages (StatSoft Inc. v12.0).

286

287 **Results**

288 The potential distribution derived from the multidimensional enveloping procedure
289 (Figure 2) suggests that several regions of the Americas, Africa, and Australia have
290 environmental conditions similar to those existing in the native range of *D. gazella*.
291 Suitable conditions also occur in Madagascar and in north of its current reported
292 distribution in Africa, mostly avoiding arid and tropical areas. Environmentally
293 favourable conditions are predicted to occur in a sizeable part of South and Central
294 America, northern and eastern Australia, and even southern India and Indochina. In total,

295 the potential distribution of *D. gazella* could encompass around 27.8 million km². Of
296 this area, approximately 20.2 million km² (72.7%) still remains un-colonized, but this
297 percentage corresponds mainly to *a priori* suitable areas in Africa and South America.

298 About half (47.6%) of the presence cells (Table 2) appear under *a priori*
299 environmentally favourable conditions but a slightly higher number of cells (52.4%)
300 occur in unfavourable areas (n=567). *Digitonthophagus gazella* seems to have invaded
301 favourable areas (*i.e.*, SIAs) with conditions falling within extremes similar to those
302 experienced in the native area (see maximum and minimum values in Table 2), but with
303 different average values. Invaded localities have slightly higher edaphic diversity and
304 isothermality values (the range of temperatures throughout a day in comparison to
305 annual variations is higher). Above all, they have (i) a higher mean diurnal range of
306 temperature, (ii) a higher mean temperature during the wettest quarter, (iii) a
307 significantly greater precipitation during the driest month, (iv) the wettest month, and (v)
308 the warmest quarter, and (vi) a lower seasonality in monthly precipitation (Table 2).

309 The overlap of realized and potential distributions (Figure 3) indicates that large
310 regions of North America and central Australia have been invaded without harbouring
311 the *a priori* suitable climatic conditions of the native occurrences, based on climate
312 matching from the native range (southeast Africa, around 6 million km²). The
313 worldwide invaded localities where climatic characteristics are outside the favourable
314 climatic values of the native observations (UIAs) seem to show consistently
315 significantly higher average values of continentality and precipitation during the driest
316 month (Table 2). In addition, these invaded localities indicate that the extreme
317 conditions reached by some occurrences greatly exceed those existing in the native area.
318 This occurs for all of the selected variables, but especially for precipitation-related
319 variables. Invasive *D. gazella* populations seem to inhabit wetter, warmer, and more
320 continental areas than populations in their native range (Table 2). When mapping the
321 particular climatic conditions of the invaded localities that are not shared with those
322 present in the native area, there is no suitable 2.5 minute cell in Africa (*e.g.*, only in
323 some equatorial and Malagasy areas it is possible to observe rain values higher than 60
324 mm/m² during the driest month, and mean temperatures over 30°C during the wettest
325 quarter can only be experienced in the Sahel and the Horn of Africa).

326

327 **Discussion**

328 In this study we analyse the distribution and the associated probable niche shift of *D.*
329 *gazella*, an invasive species introduced into several regions around the world. We base
330 our analysis on recent clarification of its native distribution using all the available
331 information in order to evaluate the magnitude and tendency of the environmental niche
332 shift experienced by this species. Our results indicate that about half of the distribution
333 records for *D. gazella* are centered on regions with differing climatic conditions to its
334 native range in Africa. These results are consistent with a substantial shift in the realized
335 environmental niche of the species. As a result, *D. gazella* is the most widespread dung
336 beetle in tropical and subtropical pastures around the globe. The current study indicates
337 that *D. gazella* has successfully established itself in geographic regions that could not be
338 entirely predicted based on environmental conditions in its native range. The global
339 invasion of *D. gazella* seems to have occurred in regions predicted *a priori* to be both
340 suitable and unsuitable for establishment. A combination of processes may explain this
341 observation, (i) relaxation of competition, (ii) ecological adaptation, (iii) physiological
342 plasticity, (iv) genetic variability, (v) anthropic disturbance and introduced exotic
343 resources, and (vi) short-term evolutionary processes.

344

345 **Competitive interactions**

346 In its native range, *D. gazella* populations co-occur with seven closely-related species
347 that occupy the same functional guild (Génier & Moretto, 2017). These latter species
348 are absent in all of the regions into which *D. gazella* has been introduced (*i.e.*, Australia,
349 North America, Central America, and South America). Evaluation of potential negative
350 interactions between *D. gazella* and other native dung beetles (*i.e.*, competition, spatial
351 displacements, or local extinctions), is generally inconclusive, especially in saturated
352 dung beetle assemblages (Noriega et al., 2017). Although reports from USA, Mexico,
353 West Indies, and Brazil suggest that introduced *D. gazella* have caused a decline of
354 native species (Howden & Scholtz, 1986; Montes de Oca & Halfpeter, 1995; Young,
355 2007; Ivie & Philips, 2008; Filho et al., 2017), this is disputed by other findings from
356 the USA, Mexico, and Nicaragua (Lobo & Montes de Oca, 1994; Howden & Howden,
357 2001; Horgan, 2008; Tiberg & Floate, 2011). However, further findings from the USA
358 and Brazil report clear changes in abundance structure of assemblages (Fincher et al.,
359 1986; Filho et al., 2017) or dominance of *D. gazella* in terms of abundance in
360 assemblages of the USA and Australia (Edwards, 2003; Kaufman & Wood, 2012).

361

362 **Ecological adaptation**

363 Another interesting research matter to explore is the study of potential differences
364 between native and invasive populations of *D. gazella* that are living outside the limits
365 of the predictive range areas. Under a global climate change scenario it is highly
366 probable that *D. gazella* will be favoured (in some specific areas) and will be able to
367 colonize higher elevations, northern and southern latitude areas that could be warmer in
368 the future, taking in consideration regional precipitation changes. However, additional
369 studies of the interactions between a changing climate and biological restrictions are
370 needed (Simberloff, 2000). Studies of other taxa suggest that the potential adaptation of
371 invasive species to novel and extreme conditions is strongly connected to genetic
372 plasticity (Sexton et al., 2002; Geng et al., 2007). Distribution programs for *D. gazella*
373 began in the 1960s (Bornemissza, 1970; Edwards, 2007), providing a 50 year period of
374 culturing the species. A short generation time combined with multiple generations per
375 year (Tyndale-Biscoe, 1990; Floate et al., 2015) could facilitate genetic changes
376 between native and redistributed populations. Molecular analyses seem warranted to
377 assess the potential genetic differences between local ecotypes, regional, and
378 intercontinental populations (the different climate strains referred to by Edwards, 2007).
379 Further molecular studies (*i.e.*, epigenetic analyses of recognized heat/cold tolerance
380 genes) are needed to compare genetic differences between native and worldwide-
381 introduced populations and identify probable genetic changes experienced by invaders.
382 This suggestion receives some support from Whipple et al. (2012) who report high
383 genetic diversity between South African and Puerto Rican populations of *D. gazella*
384 with genetic differentiation best explained by geographic isolation in the absence of
385 evidence for inbreeding depression.

386

387 **Potential areas of colonization by *D. gazella* around the world**

388 Based on conditions occurring in its native range, our results suggest that vast areas of
389 the Americas, Africa, Australia, India, and Indochina have environmentally favourable
390 conditions for *D. gazella*, making the invasion of new areas highly probable. More than
391 27.8 million km² (almost three times the size of USA) could be part of the potential
392 distribution area of the species, following a very conservative estimation. These new
393 areas to be invaded (especially those that are different from the native conditions and

394 were not predicted to be suitable) expand the potential range conditions (showing a
395 higher continentality, a higher edaphic diversity, a higher isothermality, a highest
396 diurnal range and wettest quarter temperature, a highest precipitation of the warmest
397 quarter, of the driest, and wettest month, and a lower precipitation seasonality). This
398 invadable area could be much higher if the climatic conditions in the invaded areas now
399 detected as unsuitable are considered as favourable, thus increasing the potential ability
400 of the species to invade new regions with more extreme climatic conditions.

401 The study of the colonization limits of *D. gazella* is important, particularly in
402 terms of latitude, elevation, and physiological restrictions. The highest elevational
403 records are around 1500 m a.s.l. in the native range (Génier & Moreto, 2017) versus
404 1920 m a.s.l. in the Americas (Anduaga, 2004), although high elevation sites typically
405 range from 1200-1500 m a.s.l (Vidaurre et al., 2008; Noriega et al., 2010). The northern
406 latitudinal limit in North America corresponds to Missouri - USA (38° N; Floate et al.,
407 2017). The southern latitude limit in South America is in Chillan – Chile (36° S). Its
408 establishment in Victoria – Australia at 36° S (Edwards, 2003) and parts of New
409 Zealand (34° – 47° S) (Forgie et al., 2018) demonstrate the ability of *D. gazella* to
410 survive in more southerly latitudes. Floate et al. (2015) report that *D. gazella* does not
411 have an obligatory diapause and that the minimum temperature for egg development is
412 18°C (with an average egg-to-adult development time of 52.2 days at 22 °C, a
413 development threshold of 18°C equates to 209 degree days). Tyndale-Biscoe (1990)
414 suggests that the species overwinter in Australia in both adult and larval stages. This
415 combination of factors could limit the northernmost extent of its range. Some authors
416 think that the species has reached the maximum extent of its potential distribution in
417 North America (Floate et al., 2017). However, it is possible that the species could
418 expand its actual distribution even further to colonize new areas, including regions that
419 are outside of the actual potential distribution zone that we have established here.

420 Given its membership in a “complex of seven morphologically almost
421 indistinguishable species” (Génier & Moreto, 2017), careful examination of all
422 specimens recovered outside of Africa is encouraged to establish species identity.
423 Examination of male genitalia support the contention that the species recovered outside
424 of Africa (*e.g.*, American and Australian specimens) is *D. gazella*, but we do not
425 exclude the possibility that other species in this complex may have been relocated off of
426 the continent due to many different introduction programs. For example, Maes, et al.

427 (1997) reported the presence of the species in the Natural Reserve of Bosawas (north-
428 eastern of Nicaragua). However, in that paper they mention the small size of the species
429 (0.5 cm, the average size of *D. gazella* is around 1 cm) and also the collection of just
430 one specimen in an area without human and cattle activity (primary rain forest) that is
431 very unusual for this species. For these reasons, we believed that this initial report
432 represented a probable confusion with *Onthophagus gazellinus* Bates, 1887, a native
433 species that has a similar overall shape and colour pattern but that it is smaller than *D.*
434 *gazella* and inhabits rainforest. However, we have now the confirmation of the presence
435 of *D. gazella* in Nicaragua (A. Solís pers. comm.).

436

437 **Environmental developers and barriers to colonization**

438 The speed with which *D. gazella* has established in different suitable invaded areas
439 (SIA's) has been variable (Barbero & López-Guerrero, 1992; Kohlmann, 1994; Noriega
440 et al., 2011). This partially may reflect different levels of competition from native
441 species. Establishment success would be hindered in regions where the functional guild
442 of *D. gazella* (*i.e.*, crepuscular-nocturnal fast tunnelers in grassland environments) in
443 cattle dung is already occupied by native species. Conversely, the absence of native
444 species in this functional guild may explain the dominance of *D. gazella* in Central
445 America (and possibly South America) (Horgan, 2008). Even if there are no studies that
446 evaluate the importance of biotic interactions as potential barriers (*e.g.*, competitors,
447 predators, parasitoids) to the invasion of *D. gazella*, we suggest that the main reason for
448 the species' absence in some potential areas of Africa is due to biotic interactions (*i.e.*,
449 resource competition) with other very similar species that would act as an ecological
450 barrier to its expansion. The existence of seven neighbouring species could prevent the
451 expansion of the species, particularly as they occur within the northern and southern
452 limits of the distribution of *D. gazella* (Génier & Moretto, 2017). Another possible
453 element that could affect the distribution pattern of *D. gazella* outside its native range is
454 reduced predation pressure. Doube (1991) suggested that the low numbers of
455 individuals of *D. gazella* in African populations in comparison to those recorded in
456 Australia (North Queensland) might be related to the frequent predation on pats by
457 termites that are common in African grasslands but lack functional equivalents in
458 Australia.

459 One of the most evident barriers to the distribution of the species in many
460 regions is vegetation cover. *Digitonthophagus gazella* possesses a broad distribution
461 range occupying many different ecosystems: savannas, pastures, and several different
462 altered and open landscapes, especially associated with livestock (Noriega et al., 2017).
463 In its native range, *D. gazella* strongly favour grassland (75%) over woodland (18%)
464 and shaded thickets (7%) with a bias to finer-grained rather than coarser-grained soils
465 (77% sandy clay loam: 23% deep sand, n=402; Davis 1996). It appears unable to invade
466 and colonize forest areas (Lobo & Montes de Oca, 1994; Noriega et al., 2010; Davis et
467 al., 2014; Noriega et al., 2017). However, Matavelli & Louzada (2008) report that in
468 Brazil *D. gazella* has been able to invade inter-Amazonian grasslands that are
469 geographically isolated from cattle pastures by an extensive barrier of rainforest.
470 Although some of these introductions could result from individuals hitchhiking rides
471 within cattle dung during cattle transportation from one pasture to another. In the case
472 of inland zones of Australia, Floate et al. (2017) suggested that irrigation programs in
473 dry regions could allow *D. gazella* to colonize and expand into these new areas that
474 were previously not suitable for the species. However, some of the new localities
475 outside its predicted range are almost entirely non-irrigated (SOE, 2017), so something
476 different is facilitating this expansion. Vidaurre et al. (2008) mention that it could be
477 difficult for the species to invade dry inter-Andean valleys and below Puna regions
478 because of climatic conditions. However, in Colombia the species has been recovered in
479 an inter-Andean valley (Noriega, 2016) in a very dry environment (Tatacoa desert, 30°
480 C, 60% humidity, and less than 1000 mm annually), which implies the high plasticity of
481 this species to adapt to extreme conditions.

482 It is almost certain that the success of *D. gazella* in many regions is due to the
483 conversion of forests into grasslands on which cattle have been introduced. It is to be
484 expected that within a future scenario of an increase in anthropogenic disturbance (*e.g.*,
485 deforestation, conversion of forestland to agricultural systems, and the spread of
486 grassland areas for cattle production), the establishment and invasion of *D. gazella* will
487 be favoured. These new open-areas create suitable habitat conditions, having available
488 food resources that the species needs. Most of the new country and establishment
489 records of the species in Central and South America are attributed to cattle breeding
490 intensification and cattle movement between countries (Noriega, 2002; Vidaurre et al.,
491 2008; Noriega et al., 2010; 2017; Pablo-Cea et al., 2017). Besides, it is very interesting

492 that the native range of *D. gazella* in Africa matches to the more diverse areas of the
493 native distribution of bovids (Deshler, 1963; Heywood, 2010). Furthermore, in some
494 regions of Australia the presence of *D. gazella* is used as a clear indicator of disturbance
495 of native woodlands (Gollan et al., 2010). In addition, Wallace & Richardson (2005)
496 and Cave (2005) found that *D. gazella* is able to adapt to city environments and can use
497 dung of domestic animals (dogs), favouring the potential expansion of the species from
498 rural to urban areas.

499 It is also crucial to study more about the natural history and ecology of this
500 species in order to assess differences in its reproductive rate and phenology between
501 populations in its native and expanded ranges. Given that the main reason for their
502 introduction to several regions is the “assumed” capacity of *D. gazella* to work as an
503 excellent dung removal recycler and also act as an efficient biological control agent for
504 flies and gastrointestinal helminths (Doube et al., 1991; Miranda et al., 2000), we know
505 very little about the ecosystem services that this species performs in invaded
506 communities. It would be very important to validate and quantify the functional role of
507 this species in the introduced regions.

508 In conclusion, if we place together all the environmental, climatic, and biotic
509 elements that we know might restrict the spread and invasion of *D. gazella*, the main
510 geographical barriers could be: 1) vegetation cover (secondary and primary forests; such
511 as in the entire Amazon region), 2) elevation (most of the records are below 2000 m
512 a.s.l.), 3) extremes in average annual temperatures (*i.e.*, more than 30 C°, or less than 6
513 C°), 4) extremes in average annual precipitation (*i.e.*, more than 4400 mm, or less than
514 90 mm), 5) latitude (between 40-45° N and 40-45° S), and 6) saturated assemblages with
515 similar functional species (crepuscular-nocturnal fast tunnelers). However, the
516 surprising large differences between the SIA’s and the UIA’s suggest that the species
517 has the ability to adapt to new conditions that are extremely different from those that
518 exist in the original African native region.

519 Finally, one evident conclusion of this study is the crucial relevance of a correct
520 taxonomical identification and the importance of using an extensive and accurate
521 locality database of the native and actual distributional ranges for the species in question.
522 Using incomplete or wrong data that do not correspond to the native range, incorrect
523 localities, or mistaken data because of a poor taxonomic classification could generate a
524 wrong estimation. For example, using the data of other species that were included

525 erroneously in the “*D. gazella*” complex (Génier & Moretto, 2017) could generate a lot
526 of noise. This may explain discrepancies between results of the current study and those
527 of Medina (2016). Results of our model identify a greater than expected capacity for *D.*
528 *gazella* to establish in a wide range of climatic regions. This discrepancy may reflect a
529 lack of competitive exclusion, phenotypic plasticity, genetic adaptation, and (or)
530 weaknesses in the climate model. Genetic and developmental studies comparing
531 geographically isolated populations of *D. gazella* will help clarify the factors underlying
532 this species’ distribution.

533

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540

541 **References**

- 542 Acevedo P, Jiménez-Valverde A, Lobo JM & Real R (2012) Delimiting the
543 geographical background in species distribution modelling. *Journal of*
544 *Biogeography* 39: 1383–1390.
- 545 Aidar T, Koller WW, Rodrigues SR, Correa AM, da Silva JCC, Balta OS, de Oliveira
546 JM & Oliveira JL (2000) Besouros coprófagos (Coleoptera: Scarabaeidae)
547 coletados em Aquidauana, MS, Brasil. *Anais da Sociedade Entomológica do*
548 *Brasil* 29: 817–820.
- 549 Álvarez MC, Damborsky MP, Bar ME & Ocampo FC (2009) Registros y distribución
550 de la especie afroasiática *Digitonthophagus gazella* (Coleoptera: Scarabaeidae:
551 Scarabaeinae) en Argentina. *Revista de la Sociedad Entomológica Argentina* 68:
552 373–376.
- 553 Anderson JR & Loomis S (1978) Exotic dung beetles in pasture and rangeland
554 ecosystems. *California Agriculture* 32: 31–32.
- 555 Anduaga S (2004) Impact of the activity of dung beetles (Coleoptera: Scarabaeidae:
556 Scarabaeinae) inhabiting pastureland in Durango, Mexico. *Environmental*
557 *Entomology* 33: 1305–1312.

- 558 Austin MP (1980) Searching for a model for use in vegetation analysis. *Vegetatio* 42:
559 11–21.
- 560 Barbero E & López-Guerrero Y (1992) Some considerations on the dispersal power of
561 *Digitonthophagus gazella* (Fabricius 1787) in the New World (Coleoptera,
562 Scarabaeidae, Scarabaeinae). *Tropical Zoology* 5: 115–120.
- 563 Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT et al.
564 (2011) The crucial role of the accessible area in ecological niche modeling and
565 species distribution modeling. *Ecological Modelling* 222: 1810–1819.
- 566 Beaumont L, Gallagher J, Thuiller RV, Downey W, Leishman PO & Hughes MR (2009)
567 Different climatic envelopes among invasive populations may lead to
568 underestimations of current and future biological invasions. *Diversity and*
569 *Distributions* 15: 409–420.
- 570 Bianchin I, Alves RGO & Koller W (1998) Efeito de carrapaticidas / inseticidas
571 “Pour-on” sobre adultos do besouro coprófago africano *Onthophagus gazella*
572 Fabr. (Coleoptera: Scarabaeidae). *Anais da Sociedade Entomológica do Brasil*
573 27: 275–279.
- 574 Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V et al. (2011) A
575 proposed unified framework for biological invasions. *Trends in Ecology &*
576 *Evolution* 26: 333–339.
- 577 Blume RR (1985) A checklist, distributional record, and annotated bibliography of the
578 insects associated with bovine droppings on pastures in America North of
579 Mexico. *Southwestern Entomologist* 9: 1–55.
- 580 Blume RR & Aga A (1978) *Onthophagus gazella*: Progress of experimental releases in
581 South Texas. *Folia Entomológica Mexicana* 39–40: 190–191.
- 582 Boilly O & Vaz-de-Mello FZ (2013) Les Scarabaeinae de Guyane: clé illustrée des
583 genres (Coleoptera, Scarabaeidae). *ACOREP-France: Coléoptères de Guyane*,
584 pp. 103–112.
- 585 Booth TH, Nix HA, Busby JR & Hutchinson MF (2014) BIOCLIM: the first species
586 distribution modelling package, its early applications and relevance to most
587 current MAXENT studies. *Diversity and Distributions* 20: 1–9.

- 588 Bornemissza GF (1970) Insectary studies on the control of dung breeding flies by the
589 activity of the dung beetle, *Onthophagus gazella* F. (Coleoptera: Scarabaeinae).
590 Journal of the Australian Entomological Society 9: 31–41.
- 591 Boucher FC, Thuiller W, Davies TJ & Lavergne S (2014) Neutral biogeography and the
592 evolution of climatic niches. American Naturalist 183: 573–584.
- 593 Broennimann O, Treier UA, Muller-Scharer H, Thuiller W, Peterson AT & Guisan A
594 (2007) Evidence of climatic niche shift during biological invasion. Ecology
595 Letters 10: 701–709.
- 596 Cave RD (2005) Observations of urban dung beetles utilizing dog feces (Coleoptera:
597 Scarabaeidae). The Coleopterists Bulletin 59: 400–401.
- 598 Chapman DS, Scalone R, Štefani E & Bullock JM (2017) Mechanistic species
599 distribution modeling reveals a niche shift during invasion. Ecology 98: 1671–
600 1680.
- 601 Crisp MD & Cook LG (2012) Phylogenetic niche conservatism: what are the underlying
602 evolutionary and ecological causes? New Phytologist 196: 681–694.
- 603 Davis ALV (1996) Habitat associations in a South African, summer rainfall, dung
604 beetle community (Coleoptera: Scarabaeidae, Aphodiidae, Staphylinidae,
605 Histeridae, Hydrophilidae). Pedobiologia 40: 260–280.
- 606 Davis ALV, Swemmer AM, Scholtz CH, Deschodt CM & Tshikae BP (2014) Roles of
607 environmental variables and land usage as drivers of dung beetle assemblage
608 structure in mopane woodland. Austral Ecology 39: 313–327.
- 609 Deloya C (2000) Escarabajos exóticos (Coleoptera: Scarabaeidae) para la fauna de los
610 estados de Morelos y Oaxaca, México. Folia Entomológica Mexicana 108: 125–
611 126.
- 612 Deshler W (1963) Cattle in Africa: Distribution, types, and problems. Geography
613 Review 53: 52–58.
- 614 Doube BM (1991) Dung beetles of Southern Africa. In I Hanski & Y Cambefort (Eds.)
615 Dung beetle ecology. Princeton University Press, New Jersey, pp. 133–155.
- 616 Doube BM, Macqueen A, Ridsdill-Smith TJ & Weir TA (1991) Native and introduced
617 dung beetles in Australia. In I Hanski & Y Cambefort (Eds.), Dung beetle
618 ecology. Princeton University Press, New Jersey, pp. 255–278.
- 619 Downie NM (1984) *Onthophagus gazella* Fabricius, new to Florida (Coleoptera:
620 Scarabaeidae). The Coleopterists Bulletin 38: 304.

- 621 Duncan RP, Cassey P & Blackburn TM (2009) Do climate envelope models transfer? A
622 manipulative test using dung beetle introductions. *Proceedings of the Royal*
623 *Society B* 276: 1449–1457.
- 624 Edwards PB (2003) Improving sustainable land management systems in Queensland
625 using dung beetles. Final report of the 2001-2002 Queensland Dung Beetle
626 Project.
- 627 Edwards P (2007) Introduced dung beetles in Australia 1967-2007, current status and
628 future directions. Landcare Australia Project, Maleny, Queensland.
- 629 ERMA (Environmental Risk Management Authority) (2011) Decision: application
630 ERMA200599. Wellington, New Zealand.
- 631 Farber O & Kadmon R (2003) Assessment of alternative approaches for bioclimatic
632 modelling with special emphasis on the Mahalanobis distance. *Ecological*
633 *Modelling* 160: 115–130.
- 634 Filho WM, Flechtmann CAH, Godoy WAC & Bjornstad ON (2017) The impact of the
635 introduced *Digitonthophagus gazella* on a native dung beetle community in
636 Brazil during 26 years. *Biological Invasions* 20: 963–979.
- 637 Fincher GT, Stewart TB & Hunter JS III (1983) The 1981 distribution of *Onthophagus*
638 *gazella* Fabricius from releases in Texas and *Onthophagus taurus* Schreber from
639 an unknown release in Florida. *The Coleopterists Bulletin* 37: 159–163.
- 640 Fincher GT, Blume RR, Hunter JS III & Beerwinkle KR (1986) Seasonal distribution
641 and diel flight activity of dung-feeding scarabs in open and wooded pasture in
642 East-Central Texas. *Southwestern Entomology* 10: 1–35.
- 643 Floate KD, Watson DW, Coghlin P & Olfert O (2015) Degree-day models for
644 development of the dung beetles *Onthophagus nuchicornis*, *O. taurus*, and
645 *Digitonthophagus gazella* (Coleoptera: Scarabaeidae), and the likelihood of *O.*
646 *taurus* establishment in southern Alberta, Canada. *The Canadian Entomologist*
647 147: 617–627.
- 648 Floate KD, Watson DW, Weiss RM & Olfert O (2017) Bioclimatic analyses for the
649 distributions of *Onthophagus nuchicornis*, *O. taurus* and *Digitonthophagus*
650 *gazella* (Coleoptera: Scarabaeidae) in North America. *The Canadian*
651 *Entomologist* 149: 504–524.

- 652 Forgie SA, Paynter Q, Zhao Z, Flowers C & Fowler SV (2018) Newly released non-
653 native dung beetle species provide enhanced ecosystem services in New Zealand
654 pastures. *Ecological Entomology* 43: 431–439.
- 655 Gámez J, Mora E & de Ascencao A (1997) Coleópteros copronecrófilos (Scarabaeidae)
656 en un sistema agropastoril en el sur del Lago de Maracaibo. In Resumen XV
657 Congreso Venezolano de Entomología, Trujillo, Venezuela, p. 51.
- 658 García-Roselló E, Guisande C, González-Dacosta J, Heine J & Pelayo-Villamil P (2013)
659 ModestR: a software tool for managing and analyzing species distribution map
660 databases. *Ecography* 36: 1202–1207.
- 661 García-Roselló E, Guisande C, Juergen H, Pelayo-Villamil P, Manjarrés-Hernández A
662 (2014) Using ModestR to download, import and clean species distribution
663 records. *Methods in Ecology and Evolution* 5: 708–713.
- 664 Geng YP, Pan XY, Xu CY, Zhang WJ, Li B, Chen JK et al. (2007) Phenotypic
665 plasticity rather than locally adapted ecotypes allows the invasive alligator weed
666 to colonize a wide range of habitats. *Biological Invasions* 9: 245–256.
- 667 Génier F & Davis ALV (2017) *Digitonthophagus gazella* auctorum: an unfortunate case
668 of mistaken identity for a widely introduced species (Coleoptera: Scarabaeidae:
669 Scarabaeinae: Onthophagini). *Zootaxa* 4221: 497–500.
- 670 Génier F & Krell FT (2017) Case 3722 – *Scarabaeus gazella* Fabricius, 1787 (currently
671 *Digitonthophagus gazella* or *Onthophagus gazella*; Insecta, Coleoptera,
672 Scarabaeidae): proposed conservation of usage of the specific name by
673 designation of a neotype. *The Bulletin of Zoological Nomenclature* 74: 78–87.
- 674 Génier F & Moretto P (2017) *Digitonthophagus* Balthazar, 1959: taxonomy,
675 systematics, and morphological phylogeny of the genus revealing an African
676 species complex (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 4248: 1–
677 110.
- 678 Gollan JR, Reid CAM, Barnes PB & Wilkie L (2010) The ratio of exotic to native dung
679 beetles can indicate habitat quality in riparian restoration. *Insect Conservation*
680 and Diversity 4: 123–131.
- 681 Guisande C, Barreiro A, Maneir I, Riveiro I, Vergara AR & Vaamonde A (2006)
682 Tratamiento de datos. Ediciones Díaz de Santos, Vigo, España.
- 683 Guisande C, García-Roselló E, Heine J, González-Dacosta J, Gozález L, García BJ &
684 Lobo JM (2017) SPED InstabR: An algorithm based on a fluctuation index for

685 selecting predictors in species distribution modeling. *Ecological Informatics* 37:
686 18–23.

687 Gutiérrez J, Macqueen A & Brun LO (1988) Essais d'introduction de quatre espèces de
688 bousiers Scarabaeinae en Nouvelle Calédonie et au Vanuatu. *Acta Oecologica* 9:
689 39–53.

690 Hastie T & Fithian W (2013) Inference from presence-only data; the ongoing
691 controversy. *Ecography* 36: 864–867.

692 Heywood JJN (2010) Explaining patterns in modern ruminant diversity: contingency or
693 constraint? *Biological Journal of the Linnean Society* 99: 657–672.

694 Hijmans RJ (2012) Cross-validation of species distribution models: removing spatial
695 sorting and calibration with a null model bias. *Ecology* 93: 679–688.

696 Hijmans RJ, Cameron SE, Parra JL, Jones PG & Jarvis A (2005) Very high resolution
697 interpolated climate surfaces for global land areas. *International Journal of*
698 *Climatology* 25: 1965–1978.

699 Hill MP, Gallardo B & Terblanche JS (2017) A global assessment of climatic niche
700 shifts and human influence in insect invasions. *Global Ecology and*
701 *Biogeography* 26: 679–689.

702 Horgan FG (2008) Dung beetle assemblages in forests and pastures of El Salvador: A
703 functional comparison. *Biodiversity and Conservation* 17: 2961–2978.

704 Howden H & Howden A (2001) Change through time: A third survey of the
705 Scarabaeinae (Coleoptera: Scarabaeidae) at Welder Wildlife Refuge. *The*
706 *Coleopterists Bulletin* 55: 356–362.

707 Howden HF & Scholtz CH (1986) Changes in a Texas dung community between 1975
708 and 1985 (Coleoptera: Scarabaeidae, Scarabaeinae). *The Coleopterists Bulletin*
709 40: 313–316.

710 Huchet JB (1992) Un scarabée nouveau pour les Petites Antilles: *Digitonthophagus*
711 *gazella* (Fabricius). *Entomologiste* 48: 297–303.

712 Hugall A, Moritz C, Moussalli A & Stanisic J (2002) Reconciling paleodistribution
713 models and comparative phylogeography in the wet tropics rainforest land snail
714 *Gnarosophia bellendenkerensis* (Brazier 1875). *Proceedings of the National*
715 *Academy of Sciences of the USA* 99: 6112–6117.

- 716 Hunter JS & Fincher GT (1985) Five new state records for the Afro-Asian dung beetle
717 *Onthophagus gazella* (Coleoptera: Scarabaeidae). Journal of Entomological
718 Science 20: 24–25.
- 719 Iturbide M, Bedia J & Gutiérrez JM (2018) Background sampling and transferability of
720 species distribution model ensembles under climate change. Global and
721 Planetary Change 166: 19–29.
- 722 Ivie MA & Philips TK (2008) Three new species of *Canthonella* Chapin from
723 Hispaniola, with new records and nomenclatural changes for West Indian dung
724 beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Zootaxa 1701: 1–14.
- 725 Jezkova T & Wiens JJ (2016) Rates of change in climatic niches in plant and animal
726 populations are much slower than projected climate change. Proceedings of the
727 Royal Society B 283: 2016–2104.
- 728 Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragón P & Lobo JM (2011)
729 Use of niche models in invasive species risk assessments. Biological Invasions
730 13: 2785–2797.
- 731 Kaufman PE & Wood LA (2012) Indigenous and exotic dung beetles (Coleoptera:
732 Scarabaeidae and Geotrupidae) collected in Florida cattle pastures. Annals of the
733 Entomological Society of America 105: 225–231.
- 734 Keller RP, Drake JM, Drew MB & Lodge DM (2011) Linking environmental
735 conditions and ship movements to estimate invasive species transport across the
736 global shipping network. Diversity and Distributions 17: 93–102.
- 737 Kohlmann B (1994) A preliminary study of the invasion and dispersal of
738 *Digitonthophagus gazella* (Fabricius, 1787) in Mexico (Coleoptera:
739 Scarabaeidae: Scarabaeinae). Acta Zoológica Mexicana 61: 35–42.
- 740 Koller WW, Gomes A, Rodrigues SR & de Oliveira RG (1999) Besouros coprófagos
741 (Coleoptera: Scarabaeidae) coletados em Campo Grande, MS, Brasil. Anais da
742 Sociedade Entomológica do Brasil 28: 403–412.
- 743 Koller WW, Gomes A, Rodrigues SR & Iziq PF (2007) Scarabaeidae e Aphodiidae
744 coprófagos em pastagens cultivadas em área do cerrado sul-mato-grossense.
745 Zoociências 9: 81–93.
- 746 Lee JM & Peng YS (1981) Influence of adult size of *Onthophagus gazella* on manure
747 pat degradation, nest construction, and progeny size. Environmental Entomology
748 10: 626–630.

- 749 Lee JM & Peng YS (1982) Influence of manure availability and nesting density on the
750 progeny size of *Onthophagus gazella*. Environmental Entomology 11: 38–41.
- 751 Legner EF (1978) Diptera-Muscidae. In Clausen CP (Ed.) Introduced parasites and
752 predators of arthropod pests and weeds; a world review. Agriculture handbook,
753 US Department of Agriculture, pp. 346–355.
- 754 Lobo JM (2016) The use of occurrence data to predict the effects of climate change on
755 insects. Current Opinion in Insect Science 17: 62–68.
- 756 Lobo JM & Montes de Oca E (1994) Distribución local y coexistencia de
757 *Digitonthophagus gazella* (Fabricius, 1787) y *Onthophagus batesi* Howden,
758 Cartwright, 1963 (Coleoptera: Scarabaeidae). Elytron 8: 117–127.
- 759 Lobo JM & Montes de Oca E (1997) Spatial microdistribution of two introduced dung
760 beetle species *Digitonthophagus gazella* (F.) and *Euoniticellus intermedius*
761 (Reiche) (Coleoptera Scarabaeidae) in an arid region of Northern Mexico
762 (Durango, Mexico). Acta Zoológica Mexicana 71: 17–32.
- 763 Lobo JM, Jiménez-Valverde A & Real R (2008) AUC: a misleading measure of the
764 performance of predictive distribution models. Global Ecology and
765 Biogeography 17: 145–151.
- 766 MacRae TC & Penn SR (2001) Additional records of adventive *Onthophagus* Latreille
767 (Coleoptera: Scarabaeidae) in North America. The Coleopterists Bulletin 55:
768 49–50.
- 769 Maes JM, Ratcliffe BC & Jameson ML (1997) Fauna entomológica de la Reserva
770 Natural Bosawas, Nicaragua. XI. Escarabajos (Coleoptera: Scarabaeidae) nuevos
771 para la fauna de Nicaragua. Revista Nicaraguense de Entomología 39: 41–45.
- 772 Marchiori CH, de Oliveira AT & Linhares AX (2001) Artrópodes associados a massas
773 fecais bovinas no sul do estado de Goiás. Neotropical Entomology 30: 19–24.
- 774 Marchiori CH, Caldas ER & Almeida KGS (2003) Sucesion of Scarabaeidae on bovine
775 dung in Itumbiara, Goiás, Brazil. Neotropical Entomology 32: 173–176.
- 776 Markin GP & Yoshioka ER (1998) Biological control of the horn fly, *Haematobia*
777 *irritans* L., in Hawai'i (Diptera: Muscidae). Proceedings of the Hawaiian
778 Entomological Society 33: 43–50.
- 779 Matavelli RA & Louzada J (2008) Invasão de áreas de savanna intra-amazônicas por
780 *Digitonthophagus gazella* (Fabricius, 1787) (Insecta: Coleoptera: Scarabaeidae).
781 Acta Amazonica 38: 153–158.

- 782 Matsui T & Omasa K (2002) Rice (*Oryza sativa* L.) cultivars tolerant to high
783 temperature at flowering: anther characteristics. *Annals of Botany* 89: 683–687.
- 784 McGeoch MA, Butchart SHM, Spear D, Marais E, Kleynhans EJ, Symes A, et al. (2010)
785 Global indicators of biological invasion: species numbers, biodiversity impact
786 and policy responses. *Diversity and Distributions* 16: 95–108.
- 787 Medina AM (2016) What can an invasive dung beetle tell us about niche conservatism?
788 *Environmental Entomology* 45: 1141–1145.
- 789 Miranda CH, dos Santos JC & Bianchin I (2000) The role of *Digitonthophagus gazella*
790 in pasture cleaning and production as a result of burial of cattle dung. *Pasturas*
791 *Tropicales* 22: 14–18.
- 792 Montes De Oca E (2001) Escarabajos coprófagos de un escenario ganadero típico de la
793 región de los Tuxtlas, Veracruz, México: Importancia del paisaje en la
794 composición de un gremio funcional. *Acta Zoologica Mexicana* 82: 111–132.
- 795 Montes de Oca EG & Halffter G (1995) Daily and seasonal activities of a guild of the
796 coprophagous, burrowing beetle (Coleoptera Scarabaeidae Scarabaeinae) in
797 tropical grasslands. *Tropical Zoology* 8: 159–180.
- 798 Montes de Oca EG & Halffter G (1998) Invasion of Mexico by two dung beetles
799 previously introduced into the United States. *Studies on Neotropical Fauna and*
800 *Environment* 33: 37–45.
- 801 Morales CJ, Ruiz R & Delgado L (2004) Primer registro de *Euoniticellus intermedius*
802 (Reiche, 1849) y datos nuevos de distribución de *Digitonthophagus gazella*
803 (Fabricius, 1787) (Coleoptera: Scarabaeidae) e *Hybosorus illigeri* Reiche, 1853
804 (Coleoptera: Hybosoridae) para el estado de Chiapas. *Dugesiana* 11: 21–23.
- 805 Morón MA, Deloya C, Ramírez A & Hernández S (1998) Fauna de Coleoptera
806 Lamellicornia de la región de Tepic, Nayarit, México. *Acta Zoológica Mexicana*
807 79: 77–102.
- 808 Nascimento YA, Blanchin I & Honer MR (1990) Instruções para a criação do besouro
809 *Onthophagus gazella* em laboratório. Empresa Brasileira de Pesquisa
810 Agropecuaria (EMBRAPA). Comunicado Técnico No 33.
- 811 Navarro IL, Román AK, Gómez FH & Pérez HA (2009) Primer registro de
812 *Digitonthophagus gazella* (Fabricius, 1787) para el departamento de Sucre,
813 Colombia. *Revista Colombiana de Ciencia Animal* 1: 60–64.

814 Nichols E, Spector S, Louzada J, Larsen T, Amézquita S, Favila ME & The
815 Scarabaeinae Research Network (2008) Ecological functions and ecosystem
816 services provided by Scarabaeinae dung beetles. *Biological Conservation* 141:
817 1461–1474.

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

820 Noriega JA (2016) First report of *Latrodectus geometricus* Koch (Araneae: Theridiidae)
821 as a predator of *Digitonthophagus gazella* (Fabricius) (Coleoptera:
822 Scarabaeidae). *The Coleopterists Bulletin* 70: 407–408.

823 Noriega JA, Delgado O, Blanco JI, Gámez J & Clavijo J (2017) Introduction,
824 establishment, and invasion of *Digitonthophagus gazella* (Fabricius, 1787)
825 (Coleoptera: Scarabaeinae) in the savannas of Venezuela and Colombia. *Natural*
826 *Resources* 8: 370–381.

827 Noriega JA, Horgan FG, Larsen TH & Valencia G (2010) Records of an invasive dung
828 beetle species, *Digitonthophagus gazella* (Fabricius, 1787) (Coleoptera:
829 Scarabaeidae), in Peru. *Acta Zoológica Mexicana* 25: 451–456.

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

834 Noriega JA, Solís C, Quintero I, Pérez LG, García H & Ospino DA (2006) Registro
835 continental de *Digitonthophagus gazella* (Coleoptera: Scarabaeidae) en
836 Colombia. *Caldasia* 28: 379–381.

837 Ocampo FC & Ruiz-Manzanos E (2008) Scarabaeidae. In LE Claps, G Debandi & S
838 Roig-Juñeny (Eds.) *Biodiversidad de Artrópodos Argentinos*, pp. 535–557.

839 Okajima S & Araya K (2012) *The standard of Scarabaeoid beetles in Japan*. Gakken
840 publishing.

841 Olesen JE, Trnka M, Kersebaum KC, Skjelvag AO, Seguin B, Peltonen-Sainio P, et al.
842 (2011) Impacts and adaptation of European crop production systems to climate
843 change. *European Journal of Agronomy* 34: 96–112.

844 Pablo-Cea JD, Velado-Cano MA, Fuentes R, Cruz M & Noriega JA (2017) First report
845 of *Digitonthophagus gazella* (Fabricius, 1787) and new records for *Euoniticellus*

846 *intermedius* (Reiche, 1849) (Coleoptera: Scarabaeidae Latreille, 1802) in El
847 Salvador. *Acta Zoologica Mexicana* 33: 527–531.

848 Parker JD, Torchin ME, Hufbauer RA, Lemoine NP, Alba C, Blumenthal DM, et al.
849 (2013) Do invasive species perform better in their new ranges? *Ecology* 94:
850 985–994.

851 Pateiro-López B & Rodríguez-Casal A (2011) Alphahull: generalization of the convex
852 hull of a sample of points in the plane. Available at: [http://cran.r-](http://cran.r-project.org/web/packages/alphahull)
853 [project.org/web/packages/alphahull](http://cran.r-project.org/web/packages/alphahull) (accessed 16 June 2016).

854 Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C & Guisan A (2012)
855 Climatic niche shifts are rare among terrestrial plant invaders. *Science* 335:
856 1344–1348.

857 Prentis PJ, Wilson JRU, Dormontt EE, Richardson DM & Lowe AJ (2008) Adaptive
858 evolution in invasive species. *Trends in Plant Science* 13: 288–294.

859 Pyron AR, Costa GC, Patten MA & Burbrink FT (2015) Phylogenetic niche
860 conservatism and the evolutionary basis of ecological speciation. *Biological*
861 *Reviews* 90: 1248–1262.

862 Reid CAM, Shaw JJ & Jensen AR (2018) The Australian museum Lord Howe island
863 expedition 2017 – Coleoptera. *Technical Reports of the Australian Museum* 26:
864 53–67.

865 Ripa R & Rodríguez F (1990) Introducción de escarabajos coprófagos a Chile. In
866 Resúmenes, XII Congreso Nacional de Entomología, 27–30 Noviembre 1990,
867 Valparaíso, Chile, p. 51.

868 Ripa RS, Rojas PS & Velasco G (1995) Releases of biological control agents of insect
869 pests on Easter Island (Pacific Ocean). *Entomophaga* 40: 427–440.

870 Rivera C & Wolff M (2007) *Digitonthophagus gazella* (Coleoptera: Scarabaeidae):
871 Distribución en América y dos nuevos registros para Colombia. *Revista*
872 *Colombiana de Entomología* 33: 190–192.

873 Rivera-Cervantes LE & García-Real E (1991) New locality records for *Onthophagus*
874 *gazella* Fabricius (Coleoptera: Scarabaeidae) in Jalisco, Mexico. *The*
875 *Coleopterists Bulletin* 45: 370.

876 Ruiz MADV (2000) Levantamento populacional de besouros coprófagos
877 (Coleoptera Scarabaeidae) no Estado de Amambay, Republica do Paraguai. Tese

878 de Mestrado em Entomologia, Universidade de São Paulo, Piracicaba, Brazil, p.
879 80.

880 Scheffler PY (2005) Dung beetle (Coleoptera: Scarabaeidae) diversity and community
881 structure across three disturbance regimes in eastern Amazonia. *Journal of*
882 *Tropical Ecology* 21: 9–19.

883 Schiffler G, Vaz-de-Mello FZ & Oliveira C (2003) Scarabaeidae s.str. (Coleoptera) do
884 Delta do Rio Doce e Vale do Suruaca no Município de Linhares, Estado do
885 Espírito Santo, Brasil. *Revista Brasileira de Zoologia* 5: 205–211.

886 Sexton JP, McKay JK & Sala A (2002) Plasticity and genetic diversity may allow
887 salcedar to invade cold climates in North America. *Ecological Applications* 12:
888 1652–1660.

889 Seymour J (1980) Dung beetles get a little help from their friends. *Ecos* 26: 20–25.

890 Simberloff D (1989) Which insect introductions succeed and which fail? In JA Drake,
891 HA Mooney, F di Castri, RH Groves, FJ Kruger, M Rejmánek, et al.
892 (Eds.). *Biological Invasions*, New York: John Wiley & Sons, pp. 61–75.

893 Simberloff D (2000) Global climate change and introduced species in United States
894 forests. *Science of the Total Environment* 3: 253–261.

895 SOE (State of the Environment) (2017) SoE Land Australian land use at the national
896 scale, 2010-2011. Dataset, SOE, Australia. [https://data.gov.au/dataset/2016-soe-](https://data.gov.au/dataset/2016-soe-lan-aus-land-use)
897 [lan-aus-land-use](https://data.gov.au/dataset/2016-soe-lan-aus-land-use).

898 Somodi I, Lepesi N & Botta-Dukát Z (2017) Prevalence dependence in model goodness
899 measures with special emphasis on true skill statistics. *Ecology and Evolution* 7:
900 863–872.

901 Stachowicz JJ, Terwin JR, Whitlatch RB & Osman RW (2002) Linking climate change
902 and biological invasions: ocean warming facilitates nonindigenous species
903 invasions. *PNAS* 99: 15497–15550.

904 Sultan SE, Horgan-Kobelski T, Nichols LM, Riggs CE & Waples RK (2013) A
905 resurrection study reveals rapid adaptive evolution within populations of an
906 invasive plant. *Evolutionary Applications* 6: 266–278.

907 Thomas DB (1993) Scarabaeidae (Coleoptera) of the Chiapanecan forests: a faunal
908 survey and chorographic analysis. *The Coleopterists Bulletin* 47: 363–408.

909 Tiberg K & Floate D (2011) Where went the dung-breeding insects of the American
910 bison? *The Canadian Entomologist* 143: 470–478.

- 911 Turbelin AJ, Malamud BD & Francis RA (2016) Mapping the global state of invasive
912 alien species: patterns of invasion and policy responses. *Global Ecology and*
913 *Biogeography* 26: 78–92.
- 914 Tyndale-Biscoe M (1990) Common dung beetles in pastures of south-eastern Australia.
915 CSIRO Australia, Division of Entomology Publishing, Clayton, Australia.
- 916 Urban MC, Phillips BL, Skelly DK & Shine R (2007) The cane toad's (*Chaunus [Bufo]*
917 *marinus*) increasing ability to invade Australia is revealed by a dynamically
918 updated range model. *Proceedings of the Royal Society B* 274: 1413–1419.
- 919 Valencia-Barrera R, Comtois P & Fernández GD (2002) Bioclimatic indices as a tool in
920 pollen forecasting. *International Journal of Biometeorology* 46: 171–175.
- 921 VanDerWal J, Shoo LP, Graham C & Williams SE (2009) Selecting pseudo-absence
922 data for presence-only distribution modeling: how far should you stray from
923 what you know? *Ecological Modelling* 220: 589–594.
- 924 Vidaurre T, Noriega JA & Ledezma MJ (2008) First report on the distribution of
925 *Digitonthophagus gazella* (Fabricius, 1787) (Coleoptera: Scarabaeidae) in
926 Bolivia. *Acta Zoologica Mexicana* 24: 217–220.
- 927 Vulinec K & Eudy SP (1993) A southern range extension for the introduced dung beetle
928 *Onthophagus taurus* Schreber (Coleoptera: Scarabaeidae). *The Coleopterists*
929 *Bulletin* 47: 129–131.
- 930 Wallace MG & Richardson RH (2005) Observations of urban dung beetles utilizing dog
931 feces (Coleoptera: Scarabaeidae). *The Coleopterists Bulletin* 59: 400–401.
- 932 Waterhouse DF (1974) The biological control of dung. *Scientific American* 230: 100–
933 109.
- 934 Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ & Richardson DM (2009) Something
935 in the way you move: dispersal pathways affect invasion success. *Trends in*
936 *Ecology and Evolution* 24: 136–144.
- 937 Whipple SD, Lindroth EJ, Hoback WW, Albrecht MC & Foster JE (2012) Genetic
938 variability of *Digitonthophagus gazella* (F.) (Coleoptera: Scarabaeidae) from
939 Vieques, Puerto Rico and South Africa. *The Coleopterists Bulletin* 66: 45–50.
- 940 Young OP (2007) Relationships between an introduced and two native dung beetle
941 species (Coleoptera: Scarabaeidae) in Georgia. *Southeastern Naturalist* 6: 491–
942 504.

943 Zunino M & Halffter G (1988) Análisis taxonómico, ecológico y biogeográfico de un
944 grupo Americano de *Onthophagus* (Coleoptera: Scarabaeidae). Bolletino Museo
945 Regionale di Scienze Naturali Torino 9: 1–211.
946

947 **Figure legends**

948

949 **Figure 1** World occurrences of *Digitonthophagus gazella* used in this study (2.5 minute
950 cells). Native occurrences are those records in mainland Africa with the exception of
951 those from Madagascar and the Comoros islands.

952

953 **Figure 2** Worldwide potential distribution of *Digitonthophagus gazella* using the data
954 of the selected climatic variables from its native occurrences and a multidimensional
955 enveloping procedure. The four regional maps, displayed in greater detail, show the
956 potential distribution of *D. gazella* and the observed occurrences (black points). The
957 colour gradient reflects the Mahalanobis distance (MD) from the conditions existing in
958 the native range. The upper MD quartile value of the native range represents the most
959 suitable localities within the potential distribution ($\blacktriangledown = 5.27$). Uncoloured areas lie
960 outside the potential distribution of the species.

961

962 **Figure 3** Mapping of the current and potential distribution of *Digitonthophagus gazella*
963 showing the extent and location of the environmentally suitable invaded areas
964 (equivalent to the native range in mainland Africa; SIAs in blue), the suitable not yet
965 invaded areas (SNIAs in orange), unsuitable invaded areas (UIAs in green), and
966 unsuitable not invaded (UNIAs without colour).

967

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 (chronologically) |
|-----------------|------------------------------------|-------|--|
| Asia | Japan ¹ | 1978 | Okajima & Araya, 2012 |
| Africa | Madagascar | 1885 | Génier & Moretto, 2017 |
| | France (Mayotte) | 1958 | Génier & Moretto, 2017 |
| | Comoros | 1958 | Génier & Moretto, 2017 |
| North America | US (Hawaii) | 1957 | Legner, 1978; Markin & Yoshioka, 1998; Génier & Moretto, 2017 |
| America | US | 1972 | Blume & Aga, 1978; Anderson & Loomis, 1978; Fincher et al., 1983; Downie, 1984; Blume, 1985; Hunter & Fincher, 1985; Fincher et al., 1986; 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 |
| (Greater | El Salvador | 2016 | Pablo-Cea et al., 2017 |
| | Nicaragua | <1996 | (A. Solís pers. comm.) |
|) | Cuba, Jamaica, Dominican Republic, | 1990 | Ivie & Philips, 2008; Génier & Moretto, 2017 |

| | | | |
|-------------------|---|-------|---|
| Antilles) | Puerto Rico (US) | | |
| (Lesser Antilles) | St Croix (US), Anguilla (UK), St. Kitts, Antigua, Montserrat (UK), Guadeloupe and Marie-Galante (France), Martinique (France), St Vincent, Union, Grenada | 1992 | Huchet ,1992; Kohlmann, 1994; Ivie & Philips, 2008; Génier & Moretto, 2017 |
| South America | Colombia | 1995 | Noriega, 2002; Noriega et al., 2006; Rivera & Wolff, 2007; Navarro et al., 2009; Noriega et al., 2011; Noriega, 2016; Noriega et al., 2017 |
| | Venezuela | 1996 | Gámez et al., 1997; Noriega et al., 2017 |
| | French Guiana | 2008 | Boilly & Vaz-de-Mello, 2013 |
| | Brazil | ~1990 | Nacimiento et al., 1990; Bianchin et al., 1998; Koller et al., 1999; Aidar et al., 2000; Miranda et al., 2000; Marchiori, de Oliveira & Linhares, 2001; 2003; Schiffler et al., 2003; Scheffler, 2005; Koller et al., 2007; Matavelli & Louzada, 2008; Génier & Moretto, 2017 |
| | 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 |
| Oceania | Australia | 1967 | Waterhouse, 1974; Génier & Moretto, 2017; Reid et al., 2018 |
| | Papua New Guinea | 1973 | Génier & Moretto, 2017 |

| | | |
|---------------|------|--|
| 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 Any specimen from this locality (Okinawa island, Japan) has been studied by F. Génier or by any of the co-authors. Further studies need to check if this record belongs to *D. gazella*.

Table 2 Mean values of the selected climatic variables (\pm 95% confidence intervals) for the 2.5-minute 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 last two numbers separated by a hyphen represent minimum and maximum climatic values. Temperatures are in decimal degrees and precipitation in mm

| Climatic variables | Native | Invaded | |
|--------------------------------------|----------------------------|----------------------------|----------------------------|
| | | SIAs (suitable) | UIAs (unsuitable) |
| Number of cells | 292 | 516 (47.64%) | 567 (52.35%) |
| Continentality | 9.05 \pm 0.65, 0-28 | 9.23 \pm 0.62, 0-28 | 22.93 \pm 1.32, 0-66 |
| Edaphic diversity | 0.57 \pm 0.05, 0-1.73 | 0.74 \pm 0.04, 0-1.70 | 0.62 \pm 0.04, 0-1.97 |
| Isothermallity | 58.55 \pm 0.65, 49-85 | 61.72 \pm 0.79, 50-84 | 51.83 \pm 0.92, 26-92 |
| Mean diurnal temperature range | 134.78 \pm 2.79, 62-172 | 118.74 \pm 1.87, 63-172 | 125.16 \pm 2.20, 61-190 |
| Mean temperature wettest quarter | 234.16 \pm 2.90, 96-286 | 254.79 \pm 2.04, 96-284 | 248.15 \pm 4.25, 33-327 |
| Precipitation of the driest month | 7.39 \pm 1.11, 0-59 | 17.42 \pm 1.28, 0-59 | 29.75 \pm 2.71, 0-244 |
| Precipitation seasonality | 83.59 \pm 2.33, 16-129 | 73.91 \pm 2.30, 27-126 | 62.64 \pm 2.75, 8-136 |
| Precipitation of the warmest quarter | 292.47 \pm 12.38, 25-884 | 407.03 \pm 13.79, 71-807 | 359.23 \pm 24.04, 3-1403 |
| Precipitation of the wettest month | 158.64 \pm 7.70, 39-465 | 218.74 \pm 8.61, 47-458 | 182.23 \pm 10.96, 17-648 |

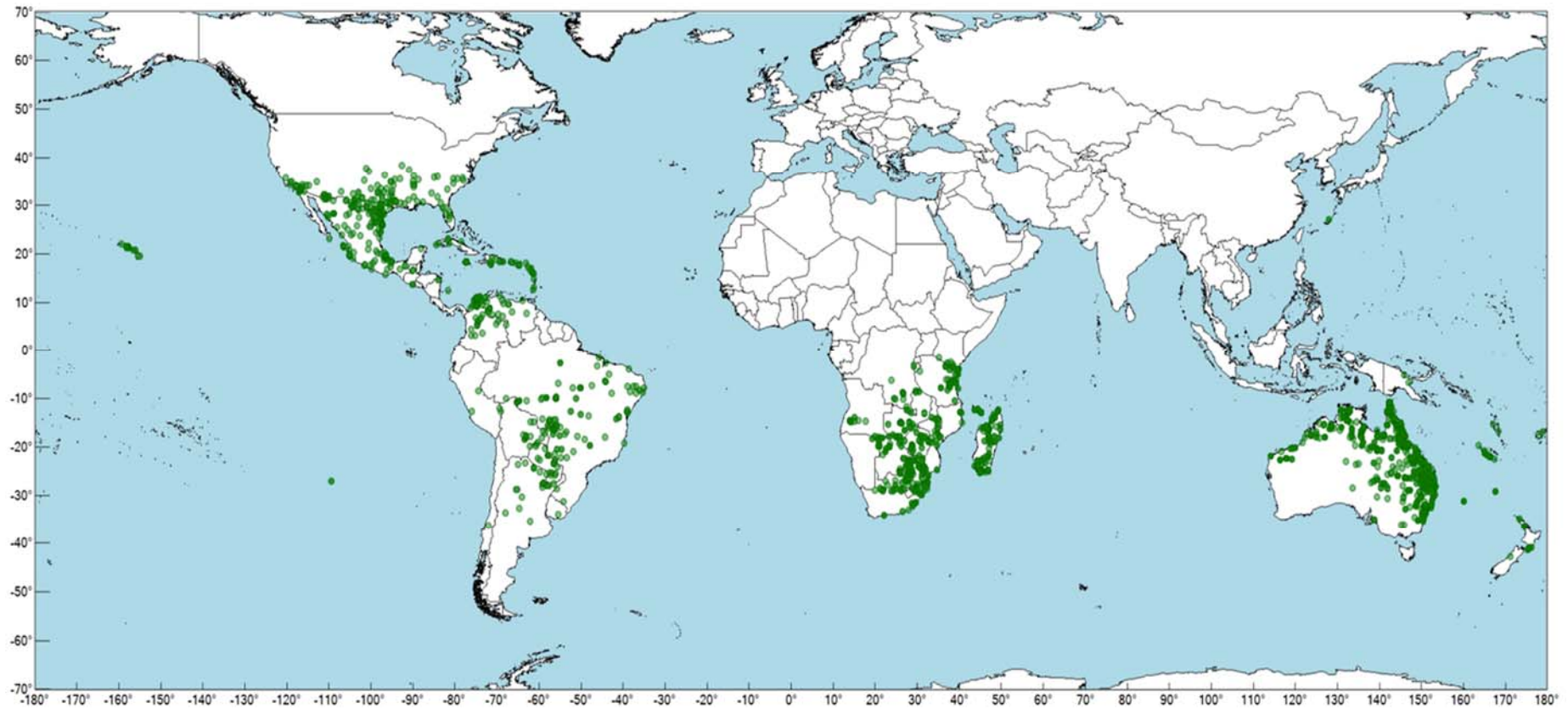


Figure 1 World occurrences of *Digitonthophagus gazella* used in this study (2.5 minute cells). Native occurrences are those records in mainland Africa with the exception of those from Madagascar and the Comoros islands.

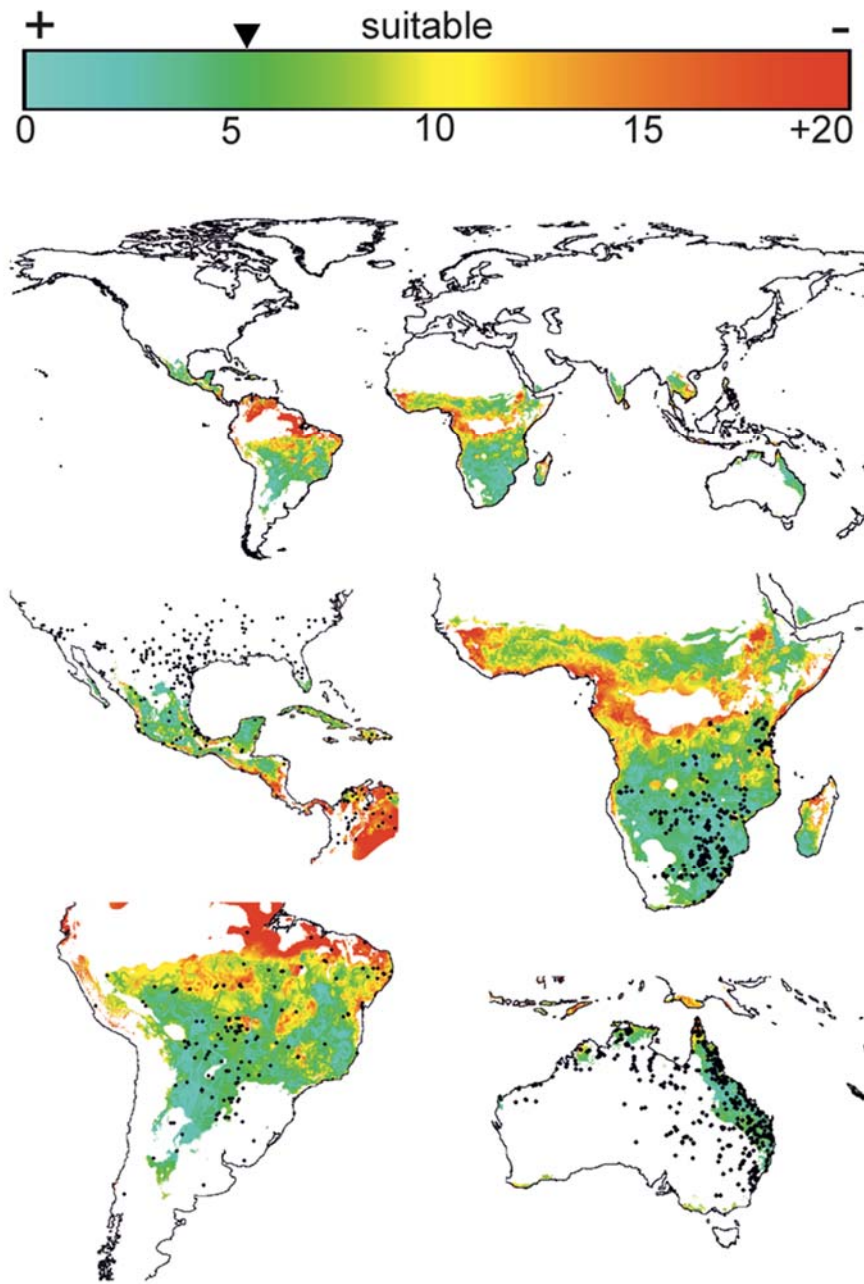


Figure 2 Worldwide potential distribution of *Digitonthophagus gazella* using the data of the selected climatic variables from its native occurrences and a multidimensional enveloping procedure. The four regional maps, displayed in greater detail, show the potential distribution of *D. gazella* and the 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.

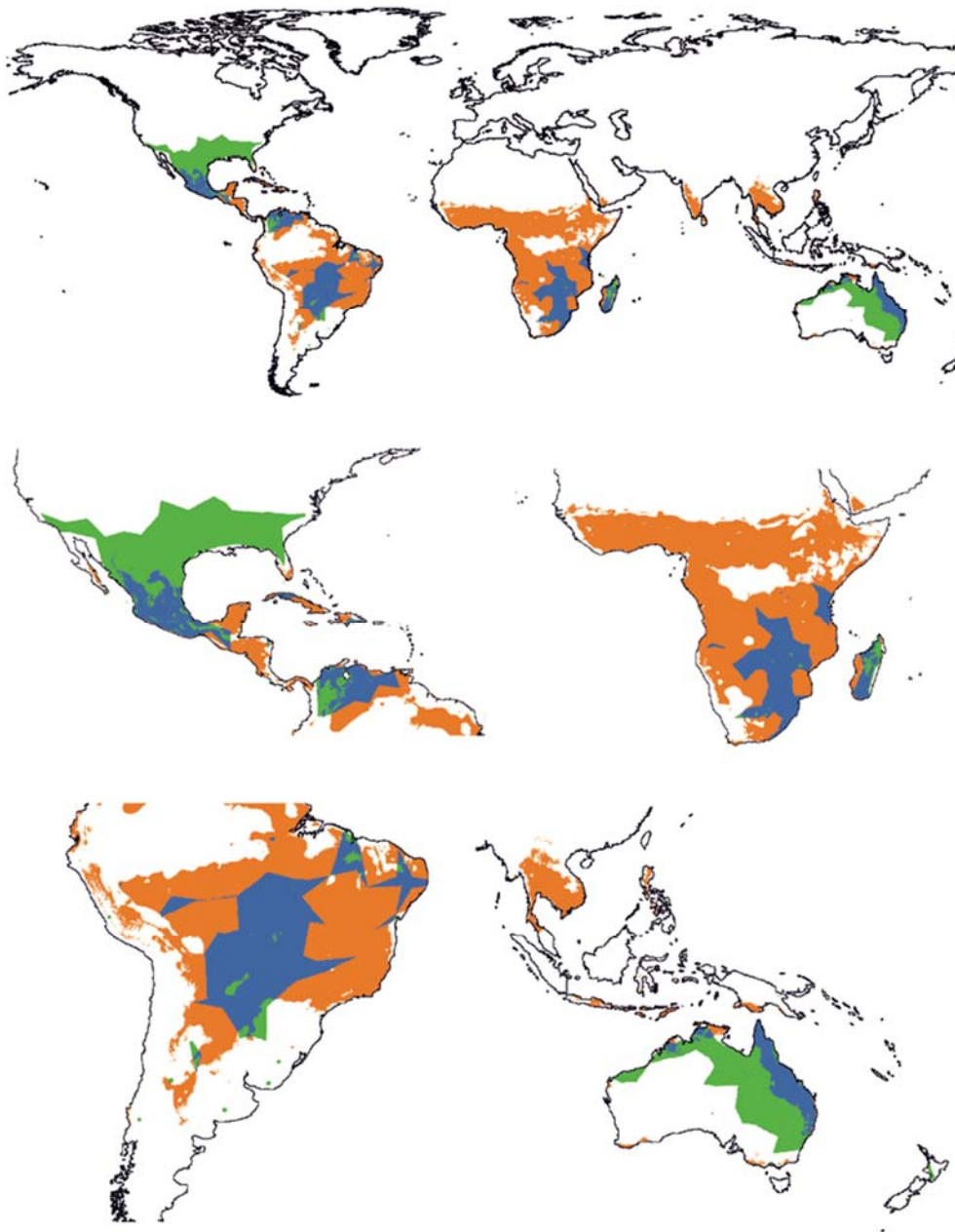


Figure 3 Mapping of the current and potential distribution of *Digitonthophagus gazella* showing the extent and location of the environmentally suitable invaded areas (equivalent to the native range in mainland Africa; SIAs in blue), the suitable not yet invaded areas (SNIAs in orange), unsuitable invaded areas (UIAs in green), and unsuitable not invaded (UNIAs without colour).