

[Click here to view linked References](#)

Contextualized niche shifts upon independent invasions by the dung beetle *Onthophagus taurus*

**Daniel P. Silva^{1*}, Bruno Vilela^{2,3}; Bruno A. Buzatto⁴; Armin P.
Moczek⁵; Joaquín Hortal^{6,7}**

¹ Instituto Federal Goiano, Departamento de Ciências Biológicas, Rodovia Geraldo
Silva Nascimento, KM 2,5, Urutaí – GO, Brazil – CEP: 75790-000.

² Programa de Pós-Graduação em Ecologia e Evolução, Departamento de Ecologia,
ICB, Universidade Federal de Goiás, Rodovia Goiânia-Nerópolis, Km 5, Campus II,
Setor Itatiaia, Goiânia – GO, Brazil- CEP: 74001-970.

³ Departamento de Ciencias de la Vida, Universidad de Alcalá, Madrid, Spain

⁴ Centre for Evolutionary Biology, School of Animal Biology (M092), The University
of Western Australia, 35 Stirling Highway, Crawley – WA 6009, Australia.

⁵ Department of Biology, Indiana University, 915 E. 3rd Street, Myers Hall 150,
Bloomington – IN, United States of America. P.O. Box 47405-7107.

⁶ Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias
Naturales (MNCN-CSIC), C/Jose Gutiérrez Abascal 2, 28006 Madrid, Spain

⁷ Departamento de Ecologia, ICB, Universidade Federal de Goiás, Rodovia Goiânia-
Nerópolis, Km 5, Campus II, Setor Itatiaia, Goiânia – GO, Brazil- CEP: 74001-970.

*E-mail: daniel.paivasilva@gmail.com

24 **ABSTRACT**

25 The historical contingencies of biological invasions may have important consequences
26 for final invasion outcomes. Here, we characterize the variations in the realized niche
27 during the invasions of the bull-headed dung beetle *Onthophagus taurus* (Coleoptera:
28 Scarabaeidae) from its native Mediterranean range following accidental (Eastern North
29 America) as well as deliberate (Western North America, Western Australia, and Eastern
30 Australia) releases into novel, exotic ranges approximately 50 years ago. Specifically,
31 we examined whether the climatic responses of exotic *O. taurus* have diverged from
32 those characterizing their native range, and if so, to what degree and in what
33 dimensions. We found that when compared to the native range, all exotic populations
34 exhibited similar overlap proportions regardless of invasion history. However, more
35 detailed analysis of climatic niche features showed that all three deliberately established
36 populations were characterized by overall similar climatic niche features, whereas the
37 accidentally-established Eastern North American populations have undergone
38 significant changes in their climatic niche. Specifically, when analog climates were
39 considered on the background of each pairwise range comparison, accidentally-
40 established Eastern North American populations showed a different climatic niche
41 expansion than their deliberately introduced Australian or Western North American
42 counterparts, in particular towards colder and more humid climates. We discuss our
43 results in the context of the widely divergent introduction histories of *O. taurus* in
44 Australia and North America, and highlight the possible roles of contrasting propagule
45 sizes, disparate genetic profiles and variances, adaptive processes and invadable
46 landscapes in shaping invasion outcomes in the different exotic ranges.

47 **Keywords:** niche conservatism; niche shift; invasive species; realized climatic niche;
48 multivariate niche analyses, dung beetles, Scarabaeidae

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

49 INTRODUCTION

50 A species' range can be defined by the intersection of the suitable biotic and abiotic
51 conditions accessible to its populations through migration ([Soberón and Peterson 2005](#);
52 [Soberón 2007](#)). Here, climatic conditions are generally considered the most important
53 determinants of species ranges ([Soberón and Nakamura 2009](#); [Soberón 2010](#); [Guisan et](#)
54 [al. 2014](#); [Lenoir and Svenning 2014](#)), after accounting for the effect of historical
55 processes that restrict the presence of the species to certain regions ([Jiménez-Valverde](#)
56 [et al. 2008](#); [Hortal et al. 2012](#)). The same factors delineate the outcome of invasion
57 events, except that in such cases the limitations normally imposed on natural migration
58 are reduced or eliminated via direct human-mediated dispersal and/or elimination of
59 dispersal boundaries ([Soberón 2007](#); [Jiménez-Valverde et al. 2011](#); [Guisan et al. 2014](#)).
60 Furthermore, pre-adaptions to the environmental conditions available in potential exotic
61 ranges, and the ability to rapidly evolve or otherwise adjust following initial
62 colonization further impact a species' success during the occupation of new ranges
63 ([Sakai et al. 2001](#); [Müller-Schärer and Steinger 2004](#); [Müller-Schärer et al. 2004](#); [Sax et](#)
64 [al. 2007](#)).

65 Current availability of species occurrences and climatological data ([Graham et](#)
66 [al. 2004](#); [Hijmans et al. 2005](#)) allowed species distribution models (SDMs from here on)
67 to be widely used to test for climatic niche evolution in invasion events ([Fitzpatrick et](#)
68 [al. 2007](#); [Bradley et al. 2010](#); [Da Mata et al. 2010](#); [Araújo and Peterson 2012](#); but see
69 [Jiménez-Valverde et al. 2011](#)). This practice, however, has recently come under
70 criticism ([Jiménez-Valverde et al. 2011](#); [Peterson et al. 2011](#); [Soberón and Peterson](#)
71 [2011](#); [Barve et al. 2011](#)). More specifically, SDMs rely on climatic niche conservation
72 between native and exotic ranges ([Pearman et al. 2008](#); [Colwell and Rangel 2009](#);
73 [Peterson 2011](#)), an assumption only partly supported by existing data ([Hortal et al.](#)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

74 2012; [Guisan et al. 2014](#)). Different SDMs also differ in how they weigh and emphasize
75 the climatic variables used to model species' potential distributions, thereby risking the
76 eventual elimination of important determinants of the distribution of the target organism
77 ([Broennimann et al. 2012](#)).

78 Since occurrence records constitute the main source of data used to describe
79 species' potential distributions, optimal and suboptimal locations are pooled together as
80 equally relevant under the “presence” category. This complicates quantifying a species'
81 true climatic niche, because sink populations are not distinguishable from those
82 inhabiting suitable conditions (see [Soberón and Nakamura 2009](#)). Additionally, using
83 SDMs to test for climatic niche shifts in an invasive species requires accepting the
84 assumption of equilibrium of its native distribution with the climatic conditions, which
85 is often not true ([Araújo and Pearson 2005](#); [Colwell and Rangel 2009](#); [McInerney and](#)
86 [Etienne 2012a](#)), especially in invasive species ([Jiménez-Valverde et al. 2011](#)). Finally,
87 comparisons restricted only to the geographic projections generated by SDMs may also
88 vary depending, for instance, on the distribution of climatic gradients in the study area
89 ([Broennimann et al. 2012](#)). Given these constraints, there can be uncertainty about
90 whether a calculated distribution truly corresponds to the one occupied by a given
91 exotic species, thereby limiting the confidence with which climatic niche shifts can be
92 assessed ([Jiménez-Valverde et al. 2011](#); [Araújo and Peterson 2012](#)).

93 Even though it remains affected by some of these issues, the ordination method
94 proposed by [Broennimann et al. \(2012\)](#) reduces the impact of these shortcomings by
95 equally weighting all environmental variables thought to be important in determining
96 the climatic niche features of the target species, optimizing the description of the
97 species' geographic and environmental spaces. Moreover, this method also accounts for
98 sampling biases in the occurrence data (from unsystematic sampling designs) and

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

99 corrects the densities of known species occurrences considering the environmental
100 space available for the species. Finally, the method relies solely on the species'
101 environmental space, without generating projections onto geographic space. Taken
102 together, these characteristics allow us to evaluate climatic niche features of invasive
103 species currently occupying new ranges while avoiding many of the shortcomings of
104 traditional SDM approaches, and put us in a position to utilize species invasions as
105 “natural experiments” to gain insights into the evolutionary ecology of niche
106 differentiation (Sax et al. 2007; Prentis et al. 2008). Here we utilize this approach to
107 evaluate and contrast post-invasion niche shifts across diverse populations of the bull-
108 headed dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae) during their
109 invasions of both Australia and North America.

110 *Onthophagus taurus* originally exhibited a Mediterranean distribution
111 (Balthasar 1964; Figure 1A). However, following a series of accidental and deliberate
112 releases, it is now well established in both Eastern and Western portions of Australia
113 (Figure 1B), as well as parts of the Eastern and Western US (Figure 1C). The
114 introduction to the Eastern US is believed to have occurred accidentally via a single and
115 small founding population of unknown Mediterranean origin, first discovered in
116 Northern Florida in 1971 (Fincher and Woodruff 1975; Hoebeke and Beuchke 1997).
117 Following its initial detection in the Florida panhandle, the species has spread rather
118 rapidly north- and west-ward, though no deliberate redistribution efforts have been
119 recorded. In contrast, *O. taurus* was released deliberately, and around the same time,
120 into Eastern and Western Australia (Figure 1C), as well as the Western US, to help
121 control cow dung and dung-breeding flies ([Waterhouse 1974](#); [Tyndale-Biscoe 1990](#);
122 [Doubt et al. 1991](#); [Hoebeke and Beuchke 1997](#); [Anderson and Loomis 1998](#); [Evans and](#)
123 [Hogue 2004](#)). All three planned introductions are well documented and derive from the

124 same source populations collected originally in Spain, Greece, and Turkey, which were
125 combined and bred collectively in quarantine facilities of the *Commonwealth Scientific*
126 *Research Organization (CSIRO)* of Australia (AMRC 1982; [Tyndale-Biscoe 1990](#);
127 1996), with the resulting offspring being used to fuel individual releases in all three
128 regions.

129 For Eastern and Western Australia, at least 36 releases with 500–1800
130 individuals per release were recorded to have taken place between 1969 and 1983
131 (Tyndale-Biscoe 1996). No deliberate re-distributions of *O. taurus* from Eastern to
132 Western Australia or *vice versa* have been documented, and natural migration is likely
133 to be minimal or absent given the vast expanses of arid environment separating both
134 Australian ranges. Lastly, in the Western US *O. taurus* was released in California,
135 beginning in 1973 as part of a collaboration between state agricultural authorities, the
136 University of California at Davis, the US Department of Agriculture, and the CSIRO,
137 which provided the initial breeding stock of *O. taurus* (Hoebeke and Beuchke 1997;
138 Anderson and Loomis 1998; Evans and Hogue 2004). Releases involved up to four
139 different species depending on year including *O. taurus*, and totaled an estimated
140 680,000 beetles from 1974-77, after which the program was terminated (Anderson and
141 Loomis 1997; Evans and Hogue 2004). In summary, a single and small introduction
142 event in the early 1970s is believed to have initiated *O. taurus*' introduction to the
143 Eastern US, whereas three roughly simultaneously conducted deliberate introduction
144 programs utilizing the same Mediterranean source populations were responsible for the
145 introductions of *O. taurus* to the Eastern US, Eastern Australia, and Western Australia.

146 Here, we use these similarities and differences in introduction histories to
147 examine the potential influences of invasion mode on realized niches and potential
148 niche differentiation. Specifically, we predict that the single and accidental introduction

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

149 of *O. taurus* into the Eastern US would have resulted in a strong founder effect and the
150 likely failure to representatively capture the genetic diversity present within the native
151 range. Consequently, the realized niche of North American *O. taurus*' populations may
152 be predicted to either represent a fraction of that of the populations in the native
153 Mediterranean range (reflecting the fraction of the native genetic diversity retained in
154 this population) or, alternatively, depart altogether from the native realized climatic
155 niche (due to founder effect-mediated rapid evolution). In contrast, the planned and
156 repeated introduction of a genetically diverse pool of *O. taurus* individuals into Eastern
157 and Western Australia as well as the Western US should have reduced the probability of
158 founder effects, causing the realized climatic niche of these populations to resemble
159 more closely that of the species' native range.

160

161 **METHODS**

162 We gathered occurrence data records for *O. taurus* from: 1) the Global Biodiversity
163 Information Facility and related institutions (GBIF; <http://www.gbif.org>; see additional
164 list); 2) the BANDASCA database (Lobo and Martín-Piera 1991); 3) literature records
165 (Supplementary Information); 4) confirmed identified photographs with a minimum of
166 nearest city as geographic reference information from BugGuide.net
167 (<http://www.bugguide.net>); 5) records from A. Moczek's, K. Floate's, and J. Ridsdill-
168 Smith's personal collections; and 6) Published literature papers. A full list of all studies
169 used to obtain records of *O. taurus*, as well as entomological collections that provided
170 occurrences to the GBIF database, are found in the Supplementary Files. We used
171 Google Earth (Google Inc. 2015) and Global Gazetteer version 2.2
172 (<http://www.fallingrain.com>) to obtain proxy coordinates from the city halls for records
173 with city/county lacking geographic coordinates. We assembled 1,272 records for *O.*

174 *taurus*. We applied a 10 km buffer around each one to minimize geographical sampling
175 biases, using the spThin R package ([Aiello-Lammens et al. 2015](#)), which resulted in
176 1,058 geographically unique occurrences considering the thinning distance applied in
177 our analyses. Then, we considered a minimum convex polygon around the occurrences
178 and the estimated annual dispersion rates for *O. taurus* (130 to 200 km; Hanski and
179 Cambefort 1991) to define five different geographical backgrounds, as the region
180 defined by a buffer of one degree width around the occurrences in each separate region.
181 Considering the wide niche breadth of this species (Martin-Piera and Lobo 1996), which
182 as a generalist dung beetle is able to consume a variety of dung types, we assumed that
183 species dispersal was not limited by dung availability. The five geographical
184 backgrounds considered (Figure 1) were: 1) Native Mediterranean Range (hereafter just
185 referred as Native; $n=785$), 2) Eastern Australian Range (AUSe; $n=164$), 3) Western
186 Australian Range (AUSw; $n=69$), 4) Eastern North American Range (NAe; $n=29$), and
187 5) Western North American Range (NAw; $n=11$).

188 We considered a grid of cells of 0.16° size in all analyses. We gathered 19
189 environmental variables from WorldClim (<http://www.worldclim.org>) and cropped
190 them according to the above mentioned background regions. Considering the methods
191 proposed by Broennimann et al. (2012), we evaluated *O. taurus* climatic niche features
192 among all of its five occupied ranges calibrated on each available geographical
193 background.

194 We used the methods developed by Broennimann et al. (2012) to assess
195 whether the environmental niche of this dung beetle species changed when it dispersed
196 from its Native range into the four other ranges it currently occupies. We chose the
197 PCA-env approach outlined by Broennimann et al. (2012) to consider all ranges
198 occupied by *O. taurus* simultaneously. As a first step, this method considers the density

199 of occurrences of the species, using a smooth kernel density function to correct for
200 potential sampling biases ([Broennimann et al. 2012](#)). Second, it considers the
201 environmental variables available within the entire background defined by the species
202 annual dispersal rates. Next, this method transforms the correlated environmental
203 variables into orthogonal (independent) new principal components, thereby allowing the
204 comparison between the environmental spaces available for the species in the different
205 biogeographic regions it occupies. The first two axes from the PCA-env are later
206 considered as the available environmental space for the species to disperse, while the
207 known occurrences for the beetles are used to generate the conditions occupied by the
208 species in each invaded range alongside the environmental niche overlap between them.
209 Finally, the analysis executes pairwise comparisons of all five different ranges occupied
210 by the species.

211 We compared the environmental conditions available for the species within
212 each of the four exotic ranges (AUS_e, AUS_w, NAE, and NAW) to those found within
213 the Native range as well as between each pair of exotic ranges. In these comparisons,
214 our approach generated occurrence density models, while correcting for the
215 environmental conditions available in the spatial scale for the analyzed species, and
216 calculated observed niche overlap scores using Schoener's *D* ([Schoener 1970](#);
217 [Broennimann et al. 2012](#)), which varies from 0 (complete dissimilarity between the
218 compared environmental niches) to 1 (complete overlap). We then tested for niche
219 equivalency between the compared ranges by randomizing the occurrence records in
220 both backgrounds and recalculating Schoener's *D* 100 times in order to produce a null
221 distribution of overlap scores, which we then compared to the observed value, as
222 proposed by [Warren et al. \(2008\)](#).

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

223 An observed overlap score that is significantly smaller than one obtained with
224 the null distribution of overlap scores suggests that the focus species is occupying
225 different environmental spaces in the considered ranges. We thus measured niche
226 similarity between each pair of ranges by comparing the overlap of one range with
227 randomized occurrences on the background conditions of the other ($1 \rightarrow 2$), keeping the
228 original number of occurrences, and vice-versa ($1 \leftarrow 2$). We repeated this process 100
229 times in order to produce a null distribution of overlap scores, which was then compared
230 to the observed value. Significantly higher overlap scores indicate more similar
231 environmental conditions across two occupied ranges than expected by chance
232 ([Broennimann et al. 2012](#)), whereas significantly lower overlap scores denote more
233 dissimilar environmental niches and the use of unique environmental space across two
234 occupied ranges. We used the package *ecospat* (Broennimann et al. 2014) in R (R
235 Development Core Team 2015) to obtain the proportion of climatic niche in each
236 comparison that was either in expansion, stabilized, or unfilled, following analyses
237 proposed by Guisan et al. (2014). Despite the overwhelming amount of results that can
238 be generated in this kind of analyses, here we will only discuss the differences between
239 the climatic niche of *O. taurus* in its native range and that observed in the exotic ranges
240 after the invasion events (direction $1 \rightarrow 2$, considering only the comparisons of the native
241 vs. the exotic ranges).

242 The rationale for this method is based on comparisons between both native and
243 invaded ranges and comparisons of all the climatic conditions available and occupied by
244 the species in both ranges. Considering environmental conditions found in both ranges,
245 if the overlap of the occupied conditions is considerable, the climatic niche of the
246 populations in the invaded range would be considered as stabilized. If the overlap of
247 available conditions in both ranges is small, but all environmental conditions in the

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
248 invaded range overlap with those of the native one, the niche of the species in the
249 invaded range is considered unfilled, when compared to the native one. On both of these
250 scenarios, no niche shift is expected to have occurred during the invasion process.
251 Finally, still considering only the similar conditions available in both ranges, if the
252 overlap between the pair of occupied ranges that is compared is very small or inexistent,
253 then it can be assumed that there was a niche expansion in the populations of the
254 invaded range in comparison to the native one. Throughout the text, we depict the
255 Native range of *O. taurus* in red and the invaded ranges in Western Australia (AUSw),
256 Eastern Australia (AUSe), Western North America (NAw), and the Eastern North
257 America (NAe) in light green, dark green, light blue, and purple, respectively. A file
258 including a detailed description of our methods and analyses, including all R code used
259 to generate the results, is available in the Supplementary Files.

31 **RESULTS**

32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
262 The first two PCA axes generated in our multivariate analyses combined explain
263 64.47% of the original environmental variation (41.41% for the first and 23.06% for the
264 second one; Figure S1A). The most important variables according to our density plots
265 were Annual Mean Temperature (bio 1), Mean Temperature of the Coldest Quarter (bio
266 11), Mean Temperature of Warmest Quarter (bio 10), Maximum temperature of
267 Warmest Period (bio 5), and Mean Diurnal Range (bio 2). The contributions of each
268 variable to each of the two PCA axes are shown in Figure S1B-C. All pairwise
269 comparisons between the five *O. taurus* ranges yielded variable proportions of overlap,
270 ranging from 0.161 to 0.442 (Table 1; Table S1-S2; Figure S1). When compared only to
271 the Native range, the accidental NAe range exhibited the smallest overlap proportion
272 (0.180), followed by all three deliberately established exotic ranges: AUSw (0.182),

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

273 AUSE (0.299), and finally NAW (0.442). In general, while the planned introductions
274 (AUSw, AUSE, and NAW) resulted in populations occupying slightly more humid
275 climatic conditions than those found in the Native range, populations in the accidental
276 NAe range occupied areas that were considerably colder and more humid (Figure 2).
277 Furthermore, both AUSw and NAW ranges exhibited realized climatic niches that were
278 significantly more similar to the Native range than expected by chance (assuming an
279 alpha of 0.05 in the niche stability test, keeping the native range fixed and randomizing
280 the invaded range), whereas the climatic conditions inhabited by *O. taurus* within the
281 NAe and AUSE ranges did not exhibit high similarity to the Native range (Table 1).
282 Figure 3 illustrates the proportion of overlap among all ranges considered in this
283 analysis.

284 Lastly, the climatic niches of the invaded ranges of *O. taurus* showed high
285 degrees of filling of the niche space (Native [1] → Invaded ranges [2]; Table 1) and
286 niche expansion (Table 1) when compared to the Native range. At the same time,
287 environmental niche stability with the Native range was high in all comparisons to
288 exotic *O. taurus* ranges (Table 1; Table S3-S5). Still, the niche similarity of the native
289 range was statistically significant to that observed in both NAW and AUSw ranges,
290 while it was not in the comparisons between the native range and NAe and AUSE. The
291 lack of similarity between native and NAe ranges conforms with the notion that this
292 exotic range is showing different environmental features than that observed in the native
293 one (Table S2). Although a D value of 0.299 was found between the native range and
294 AUSE, the lack of similarity indicates that this value is not different from what would be
295 expected from a random invasion process. Therefore, such overlap may be explained by
296 the similar climate conditions available on AUSE when compared to the native range.

297

298 **DISCUSSION**

1
2 299 Our results show that the independent invasions of *O. taurus* resulted in significantly
3
4 300 different realized niches, possibly due to the particular invasion context in each of its
5
6
7 301 ranges. Specifically, both Australian (AUSw and AUSe) and North American (NAw
8
9 302 and NAe) populations expanded their environmental niches beyond the climatic
10
11 303 boundaries of the species' within its native Mediterranean range. Furthermore, and
12
13 304 consistent with our initial predictions, both Western Australian and Western North
14
15 305 American populations exhibit a similar realized niche to that observed for the original
16
17 306 Mediterranean range of *O. taurus*. Eastern Australian populations failed to yield a
18
19 307 significant similarity test with the native range, yet examination of their respective
20
21 308 climatic niche breadths nevertheless supports the existence of significant similarities
22
23 309 and overlap in realized niches between Eastern Australian and native *O. taurus*
24
25 310 populations.

26
27
28
29
30
31 In contrast, despite similar overlapping proportions, the accidentally established
32
33 312 NAe population expanded towards colder and more humid climates not occupied in any
34
35 313 of the other region, consequently showing a greater niche divergence than all the other
36
37 314 studied ranges. Differences between the climatic space occupied by Mediterranean,
38
39 315 Australian, and Western North American populations could be partially attributed to
40
41 316 small differences in the available climates in both continents (as in Gouveia et al. 2014),
42
43 317 since some of the climatic domains occupied by *O. taurus* populations in the
44
45 318 Mediterranean range are simply not available in these exotic regions. Although some
46
47 319 areas in the NAe range have environmental features very similar to those found in the
48
49 320 native range of *O. taurus*, in the former there is also a wide availability of new
50
51 321 environmental conditions that do not occur in the latter. Therefore, differences in the
52
53 322 realized niche between the deliberate releases (AUSe, AUSw, NAw) and the accidental
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

323 one (NAe) when compared to the native range may be attributed by the lack of adequate
324 climates for the species in the NAe range.

325 The limited influence of climate availability on niche expansion raises the
326 possibility that differences in the realized niche may be due to the different histories of
327 colonization in Australia and North America. While both Australian as well as the
328 Western North American introductions involved numerous releases of large numbers of
329 genetically heterogeneous individuals from different Mediterranean source populations,
330 the Eastern North American introduction was seeded by a single event of a modest
331 number of individuals from a single Mediterranean source population. Previous work
332 has shown that the number of introduced individuals and the frequency of introductions
333 are key factors for the success of invasive species when expanding into new ranges
334 (Lockwood et al. 2005; [Drake et al. 2005](#); [Simberloff 2009](#); [Deacon et al. 2011](#);
335 Forsman 2014). Invasions involving large numbers of individuals, diverse original
336 populations and/or high frequency of introductions (\approx smaller propagule pressure) are
337 generally more resistant to stochastic events and produce more genetically and
338 phenotypically diverse populations. This could in turn enable more significant niche
339 evolution following initial colonization ([Simberloff 2009](#); [Deacon et al. 2011](#)).
340 However, invasions with higher propagule pressure and low individual abundances may
341 result in Allee effects and genetic disruptions that, when transcended, may result in even
342 more pronounced genetic differences between native and introduced populations
343 ([Courchamp et al. 1999](#); [Kanarek and Webb 2010](#)). This could also increase the
344 probability of fixing adaptive genetic variants conducive to using new niche space after
345 colonization. It is thus conceivable that the divergent introduction histories of *O. taurus*
346 in North America and Australia may have led to the emergence of different realized
347 niches for *O. taurus* in both exotic ranges.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

348 Alternatively, or in addition, pre-existing ecological differences between
349 Australian and North American ranges may have shaped differential niche evolution in
350 both ranges. Prior to the introduction of *O. taurus* in North America, cow dung was
351 already used by many native *Onthophagus* and other dung beetle species, which in turn
352 provided an important resource for specialized dung beetle predators, parasitoids, and
353 brood parasites ([Davis 1958](#); [Kohlmann 1991](#)). Pre-existing competitors, predators, and
354 parasites may therefore have both reduced the accessibility of available niche space in
355 Eastern North America and generated selection pressure on invading *O. taurus* to
356 diversify into novel niche ranges. In contrast, for both Western and Eastern Australian
357 populations, cow dung is as exotic a resource as is *O. taurus* as a dung beetle
358 ([Bornemissza 1976](#)). Even though more than 200 *Onthophagus* species are native to
359 Australia ([Matthews 1972](#); [Storey and Weir 1988](#); [Storey and Weir 1990](#)), nearly all are
360 specialized to feed and breed on marsupial dung and for the most part do not use cow
361 dung as a resource ([Matthews 1972](#); [Moczek 2003](#)). As a consequence, *O. taurus*
362 released into Australia were likely to have encountered an ecological space rich in
363 resources but largely free of native competitors, predators, parasites, or other biotic
364 pressures that otherwise would have forced a more significant niche expansion. That
365 said, *O. taurus* was one of ultimately 52 species of dung beetles introduced into
366 Australia between 1969 and 1984 to help control cattle dung abundances ([Bornemissza](#)
367 [1976](#); [Tyndale-Biscoe 1996](#); [Duncan et al. 2009](#)). Even though many of these
368 introductions failed ([Duncan et al. 2009](#)), those that led to established heterospecific
369 populations could have exerted at least some competitive pressure on *O. taurus* in
370 selected locations. Finally, differences in the type and densities of large herbivore
371 communities in North America (hoofed mammals) and Australia (dominated by

1
2 372 marsupials) may have further contributed to providing different opportunities for niche
3 373 expansion in different exotic ranges.

4
5 374 Finally, it is worth noting that while the smoothed kernel method utilized in
6
7 375 this study constitutes a useful approach, in part due to its ability to allow for the
8
9 376 comparison of “entities” (*sensu* Broennmiann et al. 2012) from different taxonomic,
10
11 377 geographic or temporal perspectives, it also suffers from significant limitations, such as
12
13 378 a strong dependency on occurrence data and the diverse biases inherent to surveys
14
15 379 (Reddy and Davalos 2003; Sastre and Lobo 2009; Pyke and Ehrlich 2010).
16
17 380 Consequently, the observed ranges and/or environmental conditions defining the
18
19 381 distribution of a species provide a likely incomplete estimation of its true realized niche
20
21 382 ([Broennimann et al. 2012](#)). For invasive species, as is the case of *O. taurus*, the reality is
22
23 383 possibly even more complex, because such species are likely not in equilibrium with the
24
25 384 environmental conditions of their newly invaded range (Araújo and Pearson 2005;
26
27 385 Colwell and Rangel 2009; McNerny and Etienne 2012a). In this study, however, the
28
29 386 range with the smallest number of occurrences, and thus the greatest probability of
30
31 387 sampling bias, was NAW ($n=11$), followed by NAe ($n=29$), followed lastly by both
32
33 388 Australian ranges (more than fifty occurrences each). Despite the small amount of
34
35 389 occurrences for NAW, this range emerged as very similar to both the native and the
36
37 390 Australian ranges. In contrast, NAe - with almost three times the number of
38
39 391 occurrences than NAW, differed significantly from all other ranges, whether inhabited
40
41 392 by native and deliberate released populations. Thus, we would expect our results to be
42
43 393 robust even if more occurrences are sampled in future studies.
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

395 *Concluding remarks*

1
2 396 Our results illustrate that an evaluation of niche evolution that is based on approaches
3
4 397 that only consider a species' known occurrences and realized niche are prone to
5
6
7 398 disregard biological processes (e.g. competition, mutualisms, predation, parasitism) that
8
9 399 may have shaped a species' realized niche (Soberón 2007; Soberón 2010; Hortal et al.
10
11 400 2012; McInerny and Etienne 2012a; McInerny and Etienne 2012b; McInerny and
12
13 401 Etienne 2012c; Guisan et al. 2014). Without being able to fully consider the
14
15 402 fundamental niche of an invasive species, a meaningful assessment of the causes of
16
17 403 invasion success or failure thus remains difficult (Soberón and Peterson 2005; Soberón
18
19 404 2007; Jiménez-Valverde et al. 2011; Araújo and Peterson 2012; Guisan et al. 2014).
20
21
22 405 With the increasing availability of occurrence records, many studies have attempted to
23
24 406 substantiate niche evolution using SDMs and multivariate analyses (Fitzpatrick et al.
25
26 407 2007; [Petitpierre et al. 2012](#); [Strubbe et al. 2013](#); [Higgins and Richardson 2014](#); Strubbe
27
28 408 et al. 2015). However, the available evidence suggests that the majority of invasive
29
30 409 species considered in these studies may in fact be failing to fill the climatic space
31
32 410 available in their native ranges, rather than exhibiting true niche shifts in the exotic ones
33
34 411 (e.g. plants: [Petitpierre et al. 2012](#); Faleiro et al. 2015; birds: Strubbe et al. 2013;
35
36 412 Strubbe and Matthysen 2014, mammals Strubbe et al. 2015; but see Ancillotto et al.
37
38 413 2015).

39
40
41 414 This is particularly important when we consider the North American
42
43 415 populations of *O. taurus*: without knowing their precise origin and how their
44
45 416 abundances may have oscillated through time and space, it is impossible to fully
46
47 417 determine the climatic requirements that regulate their densities. Therefore, additional
48
49 418 data and physiological experiments involving sample populations from all five ranges
50
51 419 (Native and all four exotic ones), are necessary to better evaluate the species'

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

420 physiological responses within each particular range ([Tingley et al. 2014](#)). Such
421 experiments would be especially useful in order to predict the behavior of *O. taurus* in
422 yet another and very recently established new range: New Zealand ([Dymock 1993](#)).

423 **ACKNOWLEDGEMENTS**

1
2 424 We thank two anonymous reviewers for their thoughtful and constructive comments
3
4 425 which significantly improved the manuscript, and Kevin Floate, James Ridsdill-Smith,
5
6
7 426 and Jorge M. Lobo for providing us with with occurrence data for *O. taurus* in its North
8
9 427 American, Australian, and native ranges, respectively. DPS received a doctorate
10
11 428 fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico
12
13 429 (CNPq) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).
14
15
16 430 BV received a doctorate fellowship from CAPES. BAB was funded by a Discovery
17
18 431 Early Career Researcher Award (DE150101521) from the Australian Research Council.
19
20
21 432 JH was funded by a Spanish DGcyT Ramón y Cajal grant, the CSIC/CNPq Co-
22
23 433 operation project 2011BR0071, and the Brazilian CNPq PVE grant 401471/2014-4.
24
25
26 434

28
29 435 **REFERENCES**

- 30
31 436 [Aiello-Lammens ME, Boria RA, Radosavljevic A, et al \(2015\) spThin: an R package](#)
32 437 [for spatial thinning of species occurrence records for use in ecological niche](#)
33 438 [models. *Ecography* 38:541–545.](#)
34
35 439 AMRC (1982) Australian Meat Research Committee. Workshop Report. The biological
36 440 control of dung in Australia. Commonwealth Scientific Research Organization.
37 441 Canberra, Australia
38
39 442 [Ancillotto L, Strubbe D, Menchetti M, Mori E \(2015\) An overlooked invader?](#)
40 443 [Ecological niche, invasion success and range dynamics of the Alexandrine](#)
41 444 [parakeet in the invaded range. *Biol Invasions*. doi: 10.1007/s10530-015-1032-y](#)
42
43 445 Anderson JR, Loomis EC (1998) Exotic dung beetles in pasture and range land
44 446 ecosystem. *Calif Agric* 2:21–31.
45
46 447 [Araújo MB, Pearson RG \(2005\) Equilibrium of species' distributions with climate.](#)
47 448 [Ecography 28:693–695.](#)
48
49 449 [Araújo MB, Peterson AT \(2012\) Uses and misuses of bioclimatic envelope modeling.](#)
50 450 [Ecology 93:1527–1539.](#)
51
52 451 [Balthasar V \(1964\) Monographie der Scarabaeidae und Aphodiidae der palaearktischen](#)
53 452 [und orientalischen Region \(Coleoptera: Lamellicornia\). Band 2, Coprinae. Verlag](#)
54 453 [der tschechoslowakischen Akademie der Wissenschaften, Praga](#)
55
56 454 Barve N, Barve V, Jiménez-Valverde A, et al (2011) The crucial role of the accessible
57
58
59
60
61
62
63
64
65

455 area in ecological niche modeling and species distribution modeling. *Ecol Modell*
456 222:1810–1819.

457 [Bornemissza GF \(1976\) The Australian dung beetle project, 1965-1975. *Aust Meat Res*
458 *Commitee Rev* 30:1–30.](#)

459 [Bradley BA, Blumenthal DM, Wilcove DS, Ziska LH \(2010\) Predicting plant invasions
460 in an era of global change. *Trends Ecol Evol* 25:310–8.](#)

461 [Broennimann O, Fitzpatrick MC, Pearman PB, et al \(2012\) Measuring ecological niche
462 overlap from occurrence and spatial environmental data. *Glob Ecol Biogeogr*
463 21:481–497.](#)

464 Broennimann O, Petitpierre B, Randin CF, et al (2014) ecospat: Spatial ecology
465 miscellaneous methods. R package version 1.0. [http://CRAN.R-](http://CRAN.R-project.org/package=ecospat)
466 [project.org/package=ecospat](http://CRAN.R-project.org/package=ecospat).

467 [Colwell RK, Rangel TF \(2009\) Hutchinson’s duality: the once and future niche. *Proc*
468 *Natl Acad Sci U S A* 106:19651–19658.](#)

469 Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the
470 Allee effect. *Trends Ecol Evol* 14:405–410.

471 [Da Mata RA, Tidon R, Côrtes LG, et al \(2010\) Invasive and flexible: niche shift in the
472 drosophilid *Zaprionus indianus* \(Insecta, Diptera\). *Biol Invasions* 12:1231–1241.](#)

473 [Davis L V \(1958\) The Scarabaeidae of Durham and Orange Counties, North Carolina.
474 Durham, North Carolina: Duke University](#)

475 [Deacon AE, Ramnarine IW, Magurran AE \(2011\) How reproductive ecology
476 contributes to the spread of a globally invasive fish. *PLoS One* 6:e24416.](#)

477 Doube BM, Macqueen A, Ridsdill-Smith TJ, Weir T (1991) Native and introduced dung
478 beetles in Australia. In: Hanski I, Cambefort Y (eds) *Dung Beetle Ecology*, 1st
479 edn. Princeton University Press, pp 255–278

480 [Drake JM, Baggenstos P, Lodge DM \(2005\) Propagule pressure and persistence in
481 experimental populations. *Biol Lett* 1:480–3.](#)

482 [Duncan RP, Cassey P, Blackburn TM \(2009\) Do climate envelope models transfer? A
483 manipulative test using dung beetle introductions. *Proc R Soc B Biol Sci*
484 276:1449–1457. doi: 10.1098/rspb.2008.1801](#)

485 [Dymock J \(1993\) A case for the introduction of additional dung burying beetles
486 \(Coleoptera: Scarabaeidae\) into New Zealand. *New Zeal J Agric Res* 36:163–171.](#)

487 Evans A V, Hogue JN (2004) *Introduction to California beetles*, 1st edn. University of
488 California Press, Berkeley

489 Faleiro F V, Silva DP, Carvalho RA, et al (2015) Ring out the bells, we are being
490 invaded! Niche conservatism in exotic populations of the Yellow Bells, *Tecoma*
491 *stans* (Bignoniaceae). *Nat Conserv* 13:24–29.

492 Fincher GT, Woodruff RE (1975) A European dung beetle, *Onthophagus taurus*
493 Schreber, new to the U.S. (Coleoptera: Scarabaeidae). *Coleopt Bull* 29:349–350.

494 Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR (2007) The biogeography of

495 prediction error: why does the introduced range of the fire ant over-predict its
496 native range? *Glob Ecol Biogeogr* 16:24–33.

497 [Forsman A \(2014\) Effects of genotypic and phenotypic variation on establishment are](#)
498 [important for conservation, invasion, and infection biology. *Proc Natl Acad Sci U*](#)
499 [S A 111:302–7.](#)

500 Google Inc. (2015) Google Earth, version 7.0.3.8542.

501 Gouveia SF, Hortal J, Tejedo M, et al (2014) Climatic niche at physiological and
502 macroecological scales: the thermal tolerance-geographical range interface and
503 niche dimensionality. *Glob Ecol Biogeogr* 23:446–456.

504 [Graham CH, Ferrier S, Huettman F, et al \(2004\) New developments in museum-based](#)
505 [informatics and applications in biodiversity analysis. *Trends Ecol Evol* 19:497–](#)
506 [503.](#)

507 [Guisan A, Petitpierre B, Broennimann O, et al \(2014\) Unifying niche shift studies:](#)
508 [insights from biological invasions. *Trends Ecol Evol* 29:260–269.](#)

509 Hanski I, Cambefort Y (eds) (1991) *Dung beetle ecology*, 1st edn. Princeton University
510 Press, New Jersey

511 [Higgins SI, Richardson DM \(2014\) Invasive plants have broader physiological niches.](#)
512 [*Proc Natl Acad Sci U S A* 111:10610–10614.](#)

513 [Hijmans RJ, Cameron SE, Parra JL, et al \(2005\) Very high resolution interpolated](#)
514 [climate surfaces for global land areas. *Int J Climatol* 25:1965–1978.](#)

515 [Hoebcke ER, Beuchke K \(1997\) Adventive *Onthophagus* \(Coleoptera: Scarabaeidae\) in](#)
516 [North America: Geographic ranges, diagnoses, and new distributional records.](#)
517 [*Entomol News* 108:345–362.](#)

518 [Hortal J, Lobo J, Jiménez-Valverde A \(2012\) Basic questions in biogeography and the](#)
519 [\(lack of\) simplicity of species distributions: Putting species distribution models in](#)
520 [the right place. *Nat Conserv* 10:108–118.](#)

521 [Jiménez-Valverde A, Lobo JM, Hortal J \(2008\) Not as good as they seem: the](#)
522 [importance of concepts in species distribution modelling. *Divers Distrib* 14:885–](#)
523 [890.](#)

524 [Jiménez-Valverde A, Peterson AT, Soberón J, et al \(2011\) Use of niche models in](#)
525 [invasive species risk assessments. *Biol Invasions* 13:2785–2797.](#)

526 [Kanarek AR, Webb CT \(2010\) Allee effects, adaptive evolution, and invasion success.](#)
527 [*Evol Appl* 3:122–135.](#)

528 [Kohlmann B \(1991\) Dung beetles in Subtropical North America. In: Hanski I,](#)
529 [Cambefort Y \(eds\) *Dung Beetle Ecology*, 1st edn. Princeton University Press,](#)
530 [Princeton, New Jersey, pp 116–132](#)

531 [Lenoir J, Svenning J-C \(2014\) Climate-related range shifts - a global multidimensional](#)
532 [synthesis and new research directions. *Ecography* 37:1–14.](#)

533 Lobo JM, Martín-Piera F (1991) La creación de un banco de datos zoológico sobre los
534 Scarabaeidae (Coleoptera: Scarabaeoidea) Íbero-Baleares: Una experiencia piloto.
535 *Elytron* 5:31–38.

- 1 536 Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in
2 537 explaining species invasions. *Trends Ecol Evol* 20:223–228.
- 3 538 [Martin-Piera F, Lobo JM \(1996\) A comparative discusion of trophic preferences in](#)
4 539 [dung beetles communities. *Misc Zool* 19:13–31.](#)
- 5
6 540 [Matthews EG \(1972\) A revision of the scabraeinae dung beetles of Australia. I. Tribe](#)
7 541 [Onthophagini. *Aust J Zool Suppl Ser* 9:1–330.](#)
- 8
9 542 [McInerny GJ, Etienne RS \(2012a\) Ditch the niche - is the niche a useful concept in](#)
10 543 [ecology or species distribution modelling? *J Biogeogr* 39:2096–2102.](#)
- 11 544 [McInerny GJ, Etienne RS \(2012b\) Pitch the niche - taking responsibility for the](#)
12 545 [concepts we use in ecology and species distribution modelling. *J Biogeogr*](#)
13 546 [39:2112–2118.](#)
- 14
15
16 547 [McInerny GJ, Etienne RS \(2012c\) Stitch the niche - a practical philosophy and visual](#)
17 548 [schematic for the niche concept. *J Biogeogr* 39:2103–2111.](#)
- 18
19 549 [Moczek AP \(2003\) The behavioral ecology of threshold evolution in a polyphenic](#)
20 550 [beetle. *Behav Ecol* 14:841–854.](#)
- 21
22 551 [Müller-Schärer H, Schaffner U, Steinger T \(2004\) Evolution in invasive plants:](#)
23 552 [implications for biological control. *Trends Ecol Evol* 19:417–422.](#)
- 24
25 553 [Müller-Schärer H, Steinger T \(2004\) Predicting evolutionary change in invasive, exotic](#)
26 554 [plants and its consequences for plant–herbivore interactions. In: Ehler L, Sforza R,](#)
27 555 [Mateille T \(eds\) *Genetics, Evolution and Biological Control*, 1st edn. CABI](#)
28 556 [Publishing, Wallingford, UK, pp 137–162](#)
- 29
30
31 557 Newbold T (2010) Applications and limitations of museum data for conservation and
32 558 ecology, with particular attention to species distribution models. *Prog Phys Geogr*
33 559 34:3–22.
- 34
35 560 Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space
36 561 and time. *Trends Ecol Evol* 23:149–158.
- 37
38 562 [Peterson AT \(2011\) Ecological niche conservatism: a time-structured review of](#)
39 563 [evidence. *J Biogeogr* 38:817–827.](#)
- 40
41 564 [Peterson AT, Soberón J, Pearson RG, et al \(2011\) *Ecological niches and geographic*](#)
42 565 [distributions, 1st edn. Princeton University Press, Princeton](#)
- 43
44 566 [Petitpierre B, Kueffer C, Broennimann O, et al \(2012\) Climatic niche shifts are rare](#)
45 567 [among terrestrial plant invaders. *Science* 335:1344–1348.](#)
- 46
47 568 Prentis PJ, Wilson JRU, Dormontt EE, et al (2008) Adaptive evolution in invasive
48 569 species. *Trends Plant Sci* 13:288–294.
- 49
50 570 [Pyke GH, Ehrlich PR \(2010\) Biological collections and ecological/environmental](#)
51 571 [research: A review, some observations and a look to the future. *Biol Rev* 85:247–](#)
52 572 [266.](#)
- 53
54
55 573 [R Development Core Team \(2015\) *R: A language and environment for statistical*](#)
56 574 [computing. R Foundation for Statistical Computing.](#)
- 57
58 575 Reddy S, Davalos LM (2003) Geographical sampling bias and its implications for

- 576 conservation priorities in Africa. *J Biogeogr* 30:1719–1727.
- 1
2 577 Sakai AK, Allendorf FW, Holt JS, et al (2001) The population biology of invasive
3 578 species. *Annu Rev Ecol Syst* 32:305–332.
- 4
5 579 Sastre P, Lobo JM (2009) Taxonomist survey biases and the unveiling of biodiversity
6 580 patterns. *Biol Conserv* 142:462–467.
- 7
8 581 Sax DF, Stachowicz JJ, Brown JH, et al (2007) Ecological and evolutionary insights
9 582 from species invasions. *Trends Ecol Evol* 22:465–471.
- 10
11 583 Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats.
12 584 *Ecology* 51:408–418.
- 13
14 585 Simberloff D (2009) The Role of Propagule Pressure in Biological Invasions. *Annu Rev*
15 586 *Ecol Evol Syst* 40:81–102.
- 16
17 587 Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of
18 588 species. *Ecol Lett* 10:1115–23.
- 19
20 589 Soberón J, Nakamura M (2009) Niches and distributional areas: Concepts, methods, and
21 590 assumptions. *Proc Natl Acad Sci U S A* 106:19644–19650.
- 22
23 591 Soberón J, Peterson AT (2005) Interpretation of models of fundamental ecological
24 592 niches and species' distributional areas. *Biodivers Informatics* 2:1–10.
- 25
26 593 Soberón J, Peterson AT (2011) Ecological niche shifts and environmental space
27 594 anisotropy: A cautionary note. *Rev Mex Biodivers* 82:1348–1355.
- 28
29 595 Soberón JM (2010) Niche and area of distribution modeling: a population ecology
30 596 perspective. *Ecography* 33:159–167.
- 31
32 597 Storey RI, Weir TA (1990) New species of *Onthophagus* Latreille (Coleoptera:
33 598 Scarabaeidae) from Australia. *Invertebr Taxon* 3:783–815.
- 34
35 599 Storey RI, Weir TA (1988) New localities and biological notes for the genus
36 600 *Onthophagus* Latreille (Coleoptera: Scarabaeidae) in Australia. *Aust Entomol Mag*
37 601 15:17–24.
- 38
39 602 Strubbe D, Beauchard O, Matthysen E (2015) Niche conservatism among non-native
40 603 vertebrates in Europe and North America. *Ecography* 38:321–329. doi:
41 604 [10.1111/ecog.00632](https://doi.org/10.1111/ecog.00632)
- 42
43 605 Strubbe D, Broennimann O, Chiron F, Matthysen E (2013) Niche conservatism in non-
44 606 native birds in Europe: niche unfilling rather than niche expansion. *Glob Ecol*
45 607 *Biogeogr* 22:962–970.
- 46
47
48 608 Strubbe D, Matthysen E (2014) Patterns of niche conservatism among non-native birds
49 609 in Europe are dependent on introduction history and selection of variables. *Biol*
50 610 *Invasions* 16:759–764.
- 51
52 611 Tingley R, Vallinoto M, Sequeira F, Kearney MR (2014) Realized niche shift during a
53 612 global biological invasion. *Proc Natl Acad Sci U S A* 111:10233–10238.
- 54
55 613 Tyndale-Biscoe M (1990) Common dung beetles in pastures of south-eastern Australia.
56 614 *CSIRO Press, Canberra, Australia*
- 57
58 615 Tyndale-Biscoe M (1996) Australia's introduced dung beetles: original releases and

616 redistributions. Technical Report No. 62. Canberra, Australia

1
2 617 Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus
3 618 conservatism: quantitative approaches to niche evolution. Evolution (N Y)
4 619 62:2868–83.

5
6 620 Waterhouse DF (1974) The biological control of dung. Sci Am 230:1000–1009.

7
8 621

9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

622 **FIGURES CAPTIONS**

1
2 623 **Figure 1** – Geographic distribution of the dung beetle *Onthophagus taurus*. Stars
3
4
5 624 represent the occurrence data gathered for each of the geographical backgrounds
6
7 625 considered in A) its Native Mediterranean Range – Native (red); B) Western (light
8
9 626 green) and Eastern Australian (dark green) exotic ranges (AUSw and AUSe,
10
11 627 respectively); and C) Western (light blue) and Eastern North American (purple) exotic
12
13 628 ranges (NAw and NAe, respectively).
14
15
16
17

18 629 **Figure 2** – Climatic conditions occupied by *Onthophagus taurus* in all of its known
19
20 630 distributional ranges, showing the results obtained from the environmental niche
21
22 631 analysis. The solid and the dashed lines illustrate, respectively, 100% and 50% of the
23
24 632 available (background) climate for *O. taurus* in each one of its ranges. The shading
25
26 633 follows the same scheme used in Figure 1, where the Native range is represented in red,
27
28 634 Western Australia (AUSw) is in light green, Eastern Australia (AUSe) is in dark green,
29
30 635 Western North America (NAw) is in light blue, and Eastern North America (NAe) is in
31
32 636 purple.
33
34
35
36
37
38

39 637 **Figure 3** – Overlap of the realized climatic niches of *Onthophagus taurus* in all its
40
41 638 considered (native and invaded) ranges. Native: red; Western North America (NAw):
42
43 639 light blue; Eastern North America (NAe): purple; Western Australia (AUSw): light
44
45 640 green; Eastern Australia (AUSe): dark green. The solid line represents 10% of the
46
47 641 occurrence density.
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

642 **TABLES**

643 **Table 1** – Pairwise comparisons of niche overlap (D), niche similarity, niche unfilling
 644 (i.e., lack of filling the available climatic space), niche stability, and niche expansion
 645 between each one of the invaded ranges of *Onthophagus taurus* when compared to its
 646 native range, according to the framework of Broennimann et al. (2012). Bold values
 647 represent significant p-values (alpha = 0.05). Note that the niche similarity test verifies
 648 whether the niche overlap between two ranges is greater than expected by chance.

IRs	Overlap (D)	Similarity test Native→IRs (p-values)	Niche unfilling Native→ IRs	Niche stability Native→IRs	Niche expansion Native→IRs
NAw	0.442	0.050	0.000	0.931	0.069
NAe	0.180	0.119	0.000	0.948	0.052
AUSw	0.182	0.020	0.022	0.963	0.037
AUSE	0.299	0.317	0.016	0.980	0.020

Native: Native Mediterranean Range; AUSE: Eastern Australian Range; AUSw: Western Australian Range; NAe: Eastern North American Range; NAw: Western North American Range; IRs: Invaded Ranges;
 649





