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1 **The big bad pig: niche conservatism and the invasive potential**
2 **of the wild boar**

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23 **Summary**

- 24 1. Niche conservatism, i.e. the retention of a species fundamental niche through
25 evolutionary time, is a cornerstone for biological invasion assessments. The fact that
26 species tend to maintain their original climate niche allows predictive maps of
27 invasion risk to anticipate potential invadable areas. Unraveling the mechanisms
28 driving niche shifts can shed substantial light on the management of invasive species.
- 29 2. Here, we assessed niche shifts in one of the world's worst invasive species: the wild
30 boar *Sus scrofa*. We also predicted potential invadable areas based on an ensemble of
31 three ecological niche modeling methods, and evaluated the performance of models
32 calibrated with native *vs* pooled (native plus invaded) species records. By
33 disentangling the drivers of change on the exotic wild boar population's niches, we
34 found strong evidence for niche conservatism during biological invasion.
- 35 3. Ecological niche models calibrated with native *vs* pooled range calibration scenario
36 predicted convergent areas. Also, observed niche shifts are mostly explained by niche
37 unfilling, i.e. there are unoccupied areas in the exotic range where climate is
38 analogous to the native range.
- 39 4. Niche unfilling is expected as a result of recent colonization and ongoing dispersal,
40 and was potentially stronger for the Neotropics, where a recent wave of introductions
41 for pig-farming and game-hunting has led to high wild boar population growth rates.
42 The invasive potential of wild boar in the Neotropics is probably higher than in other
43 regions, which has profound management implications if we are to prevent their
44 invasion into species-rich areas, such as Amazonia, coupled with expansion of
45 African swine fever and possibly great economic losses.
- 46 5. Although the originally Eurasian-wide distribution suggests a pre-adaptation to a
47 wide array of climates, the wild boar worldwide invasion does not exhibit evidence
48 of niche evolution. The invasive potential of the wild boar probably lies on the
49 reproductive, dietary and morphological characteristics of this species, coupled with
50 behavioral thermoregulation.

51 **Key-words** Biological invasion; conservation biogeography; feral pig; invasive alien
52 species; ecological niche models.

53 **Introduction**

54 Assessing invasion risk and managing invasive species is a worldwide conservation,
55 economic and social issue (Strubbe, Beauchard & Matthysen 2015) and niche shifts during
56 biological invasions are one of the hot topics of current scientific debate (Guisan *et al.* 2014).
57 In fact, understanding processes that drive changes in species fundamental niches is
58 important for ecology and evolution (Wiens & Graham 2005; Pyron *et al.* 2015), and pivotal
59 for understanding biological invasions (Broennimann *et al.* 2007; Guisan *et al.* 2014). A
60 species “fundamental niche” can be defined as the set of environmental conditions where a
61 species can persist indefinitely (Hutchinson 1957). Competition and other negative
62 interactions lead to reductions in the fundamental niche to create the “realized niche”
63 (Hutchinson 1957), or the “biotically reduced niche” (Peterson *et al.* 2011). In this sense, the
64 “invadable niche” would be the portions of the fundamental niche, non-restricted by biotic
65 interactions, but unreachable due to geographic dispersal limitations (Peterson *et al.* 2011).

66

67 Potentially invadable areas have historically been assessed through the study or models of
68 ecological niche, which are based on the assumption that climatic similarity between native
69 and exotic ranges is an *a priori* condition for the establishment of an alien species (Peterson
70 2003; Thuiller *et al.* 2005; Jiménez-Valverde *et al.* 2011). This assumption is possible
71 because species fundamental niches are not likely to change over short-to-moderate time
72 spans (Peterson 2011). Given that these niches exhibit little or no climatic niche
73 differentiation, this process of niche conservatism is expected during biological invasion
74 (Peterson 2003, 2011). Therefore, by determining climate tolerances from species native
75 geographic range, climatically matching regions in non-native ranges can be assessed and

76 mapped (Thuiller *et al.* 2005; Jiménez-Valverde *et al.* 2011). If climatic conditions therefore
77 pose long-term and stable constraints on species geographic distribution, potentially
78 invadable areas can be anticipated with relative confidence (Peterson 2003).

79

80 Although exciting in their potential for guiding management decisions, ecological niche
81 models can only accurately predict potentially invadable areas when niche conservatism is
82 supported. However, initial studies on niche conservatism revealed contrasting patterns of
83 niche shift due to tests of different null hypotheses (Peterson 1999; Graham *et al.* 2004).
84 After Warren *et al.* (2008), niche conservatism was thought to be best measured in terms of
85 statistical difference, i.e. “niche similarity” and “niche equivalence”. Despite their
86 transparency, the similarity and equivalence tests only reveal statistically significant
87 differences on species climatic niches, but not the causes underlying niche shifts (Petitpierre
88 *et al.* 2012; Strubbe *et al.* 2013; Guisan *et al.* 2014). Hence, absolute values of “equivalency”
89 and “similarity” have little biological meaning unless niche shifts are disentangled into their
90 main drivers of change, namely “niche unfilling” and “niche expansion” (Petitpierre *et al.*,
91 2012; Guisan *et al.*, 2014). In addition to detect of niche shifts, decomposing niche changes
92 in terms of niche expansion and unfilling can shed substantial light on the ecological
93 processes driving biological invasions (Broennimann *et al.*, 2012; Guisan *et al.*, 2014).

94

95 Currently present in all continents, except in Antarctica, the wild boar is a member of the
96 family Suidae from Eurasia and North Africa. The wild boar is the oldest intentionally
97 introduced mammal species (for bush meat) and is now one of the most widely distributed

98 species in the world (Long 2003). Biological traits of the species partially explain its invasive
99 success. Wild boars have fast population growth rates (Taylor *et al.* 1998) and feed
100 opportunistically on many plants and animals (Ballari & Barrios-García 2014). Population
101 top-down control by predators is limited throughout its native and exotic ranges due to
102 worldwide small density of large carnivores (Estes *et al.* 2011; Barrios-Garcia & Ballari
103 2012) and widespread defaunation of natural areas (Dirzo *et al.* 2014). Wild boars also
104 possess weaponry and a low centre of gravity that prevents their preferential capture by all
105 but the largest felids (Hayward, Jędrzejewski & Jędrzejewska 2012). Further, their extensive
106 native distribution across Eurasia and North Africa suggests a pre-adaptation to wide array
107 of climatic conditions (Long 2003; Barrios-Garcia & Ballari 2012). In this paper, we assessed
108 the invasive potential of the wild boar *Sus scrofa* globally. Our aim was to test whether wild
109 boars and their hybrids have substantially changed their climatic niches during their global
110 invasion. In addition, we mapped potentially invadable areas, where allowed by niche
111 conservatism assumptions.

112

113 **Materials and methods**

114 THE WILD BOAR

115 Wild boars (*Sus scrofa*) are ecosystem engineers that turn extensive areas of leaf litter, soil
116 and vegetation, and may ultimately affect fire regimes (Hayward *et al.* 2016). While the
117 impact of that rooting behavior on biodiversity is controversial (Siemann *et al.* 2009), the
118 same is not true for economic losses. Wild boar rooting damages crops and husbandry,
119 causing economic losses up to 800 million dollars a year in the USA alone (Pimentel, Zuniga

120 & Morrison 2005). Wild boars damage various vegetable crops (Pimentel *et al.* 2005; Herrero
121 *et al.* 2006; Ballari & Barrios-García 2014) and also transmit and are reservoirs for several
122 diseases to humans and livestock (Barasona *et al.* 2014). Impacts of wild boars on wildlife
123 span predation (Ballari & Barrios-García 2014) to habitat and nest destruction (Barrios-
124 Garcia & Ballari 2012). Competitive interaction with wild boar leads to native species
125 exclusion, especially peccaries (Gabor & Hellgren 2000) and other species of the genus *Sus*
126 (Frantz *et al.* 2016). Despite those negative effects, in some particular areas – such as the
127 Brazilian Pantanal – wild boars are supposed to be a preferential target for bush meat hunters
128 and may thus release native peccaries from over-harvesting (Desbiez *et al.* 2011), although
129 this lacks empirical validation.

130

131 As they are primarily raised for meat, domesticated pig breeds were selected to increase traits,
132 such as fecundity and population growth rate. Escaped domestic pigs hybridize with wild
133 populations and transmit to them those artificially selected traits, which enhances hybrid
134 fitness (Fulgione *et al.* 2016). Hybrid pigs have therefore inherited higher fertility rates and
135 larger litter size from their domestic relatives (Fulgione *et al.* 2016), while retaining
136 sociability, coupled with associated large group herds, and flexible climatic tolerance from
137 their wild ancestors (Marshall *et al.* 2014). The impact of hybrid pigs on both biodiversity
138 and the economy can therefore be even harder than that of wild populations, although those
139 effects are still to be addressed in the scientific literature (Barrios-Garcia & Ballari 2012).

140 DATA COLLECTION

141 We collected occurrence data for the wild boar and its hybrids [henceforth jointly named
142 “wild boars”] from different virtual databases, namely the Global Biodiversity Information
143 Facility (GBIF; www.gbif.org), the VertNet (www.vertnet.org), the Biodiversity Information
144 Serving Our Nation (BISON; www.bison.usgs.ornl.gov), the Berkeley Ecoinformatics
145 Engine (Ecoengine; www.ecoengine.berkeley.edu), the iNaturalist (www.inaturalist.org) and
146 the Invasive Species Compendium (ICS; www.cabi.org). In addition, we exhaustively
147 searched non-formal sources of wild boar occurrence information, primarily game hunting
148 or wildlife sightseeing websites, such as the “Rede Aqui Tem Javali” in Brazil
149 (aquitemjavali.blogspot.com.br), the “Wild Boars in Canada” (wildboarcanada.ca), and
150 “Feral Scan” in Australia (www.feralscan.org.au). A strong geographical bias towards
151 European countries was found in the distribution of wild boar occurrence records within
152 native distribution. Thus, to improve characterization of the niche space, we did a literature
153 survey on wild boar occurrences from less sampled regions within the native distribution (see
154 Table S1). All occurrences from virtual databases were downloaded with the function *occ*
155 from R package (R Development Core Team 2016) *spocc* (Scott *et al.* 2016), and occurrences
156 from other sources were downloaded manually.

157

158 Native distribution was defined based on the IUCN range map for *Sus scrofa* (Oliver & Leus
159 2008), obtained at www.iucnredlist.org. The use of IUCN range maps to identify species
160 native distribution is considered useful for large-scale modeling studies, as well as to
161 conservation planning, management and wildlife monitoring (Rodrigues *et al.* 2006). We also
162 included occurrences up to 200 km from the existing border of the species native range map.

163 Occurrences farther than that to the native polygon were removed from the “native dataset”.
164 By doing so, we accounted for possible uncertainties on the borders of IUCN range maps, to
165 consider highly updated – though perhaps imprecise – species records. A total of 2283
166 occurrence records was then collected, from which 688 belonged to native distribution, 168
167 of them to the Australian region, 609 to the Nearctic region, and 736 to the Neotropical region
168 (Fig. 1, Appendix S1). Those records cover years 1970 to 2016. Spatial autocorrelation was
169 minimized by randomly removing occurrences less than 0.5 degree of latitude/longitude from
170 each other, from the whole dataset (both native and exotic ranges). This procedure has
171 minimized problems related to spatial autocorrelation in other niche shift studies at the
172 biogeographical scale (Broennimann *et al.* 2012; Strubbe *et al.* 2015).

173

174 Climate data was produced from interpolation of ground weather stations, from year 1950 to
175 2000, downloaded from the WorldClim website (www.worldclim.org/version1) and
176 downscaled to 0.5 degrees of latitude/longitude. All WorldClim bioclimatic predictors were
177 used for tests of niche equivalence/similarity between native and exotic ranges, but only five
178 were used to predict potentially invadable areas for the wild boar. A factor analysis with
179 Varimax rotation was used to select uncorrelated variables and to avoid collinearity issues
180 (Table S2). Five non-correlated variables were used to fit ecological niche models: BIO2:
181 Mean Diurnal Range (Mean of monthly (max temp - min temp)); BIO5: Max Temperature
182 of Warmest Month; BIO14: Precipitation of Driest Month; BIO15: Precipitation Seasonality
183 (Coefficient of Variation); BIO16: Precipitation of Wettest Quarter.

184

185 NICHE EQUIVALENCE/SIMILARITY TESTS

186 We used all predictors at first because tests of niche equivalence/similarity are best performed
187 with the PCA-env method (Broennimann *et al.* 2012). The PCA-env is calibrated with the
188 full background, i.e. environmental conditions of both native and exotic range, and reduces
189 environmental data dimensionality to the first two main axes of the principal component
190 analysis (PCA). That full background is then compared to the areas effectively occupied by
191 species on each of its ranges. Niche overlap between native and exotic range is measured in
192 terms of Schoener's *D*, which ranges from no overlap, 0, to complete overlap, 1 (Schoener
193 1974; Warren *et al.* 2008).

194

195 The observed niche overlap is then compared to random measures of niche overlap. Niche
196 equivalence and similarity tests are based on comparisons of observed measures of niche
197 overlap to random overlap values, although different null hypotheses are thereby tested.
198 Niche equivalence tests, as initially proposed by Graham *et al.* (2004), ask whether the
199 compared niches are indistinguishable from each other. Rejection of the null hypothesis on
200 niche equivalency tests indicates that native and exotic niches are not identical (Broennimann
201 *et al.* 2012; Strubbe *et al.* 2015). Niche similarity tests, on other hand, were first used in
202 Peterson *et al.*'s (1999) work, and test whether niche models calibrated for one species (or
203 population, in our case) predict other species occurrences better than expected by chance.
204 The niche similarity null hypothesis is that of retained niche resemblance and its rejection
205 indicates that niches are more different than expected by chance. Null hypotheses tests were
206 repeated 1000 times for each biogeographical region and *p*-values were computed at a 5%
207 level of confidence.

208

209 Following Broennimann et al. (2012), niche changes between native and exotic populations
210 were directly measured in a gridded environmental space, not in the geographic space. Kernel
211 density functions were used to produce smoothed densities of both occurrences and
212 environmental availability. Explicitly incorporating environmental availability into niche
213 shift measures reduces erroneous detections of niche changes due to uneven distribution of
214 climate conditions on native and exotic ranges (Guisan *et al.* 2014). Niche shift analyses were
215 done using the *ecospat* R package (Randin *et al.* 2016).

216

217 Niche equivalence and similarity tests only verify whether niche shifts have occurred, but do
218 not address their causal mechanisms. To understand the wild boar invasion process, we
219 disentangled niche changes into the processes of unfilling and expansion. Niche unfilling is
220 observed when some environmental conditions within the native niche are available, but
221 unoccupied in the exotic climate (Guisan *et al.* 2014). Those unoccupied areas probably result
222 from recent colonization and ongoing dispersal. In niche unfilling, the exotic niche is a subset
223 of the native niche, and the species will eventually occupy all available niche space within
224 exotic range, unless biological interactions restrict range expansion (Guisan *et al.* 2014).
225 Niche expansion, on the other hand, is the result of occupancy of non-analogous climatic
226 conditions to the native range. In other words, niche expansion is observed when the species
227 occupies climate conditions to which it is not supposedly adapted, based on its native
228 distribution climatic limits. Such occupancy in non-analogous climates is probably due to
229 ecological or evolutionary changes on its fundamental niche (Guisan *et al.* 2014).

230

231 Observed niche expansion can also be the outcome of the constrained nature of a species
232 realized niche. Across an accessible geographic distribution, a species may not occupy its
233 full fundamental niche due to extant or past biotic interactions (Soberón & Peterson 2005;
234 Soberón 2007; Peterson *et al.* 2011). Also, there may be environmental conditions that are
235 favorable to a species persistence, but non-existent throughout the species geographic range
236 (Barve *et al.* 2011). All those conditions may limit the observed occupancy of certain
237 environmental conditions that do belong to the fundamental niche (Hutchinson 1957).
238 Therefore, observed niche expansion can also result from occupancy of regions within a
239 species fundamental niche, but outside its geographically accessible area and/or restricted by
240 negative biotic interactions. Also, the correlative nature of the techniques used to disentangle
241 niche shifts into unfilling and expansion implies that a species niche will be always calibrated
242 using observed occurrences from the realized niche (Guisan *et al.* 2014). Assessing the whole
243 fundamental niche and knowing for sure all the exact conditions favorable for a species is
244 nearly impossible. Therefore, asserting niche expansions may be a doubtful task.

245

246 Predicting potentially invadable areas for invasive species is only possible when: 1) changes
247 in a species climatic niche are not observed or 2) observed niche differences are not caused
248 by evolutionary changes in the species fundamental niche (Jiménez-Valverde *et al.* 2011;
249 Strubbe *et al.* 2013, 2015). If the exotic niche is a subset of the native one, and niche shifts
250 are therefore caused by niche unfilling rather than expansion, then an ecological niche model
251 calibrated with climatic conditions where the species is known to occur may accurately
252 predict invasion potential (Peterson 2011; Jiménez-Valverde *et al.* 2011; Strubbe *et al.* 2015).

253 Otherwise, the essential assumption of equilibrium between the species distribution and
254 climate tolerances is violated (Early & Sax 2014). In cases where climatic equilibrium is not
255 supported, forecasts of invasion risk based on correlative models may not be reliable (Early
256 & Sax 2014).

257

258 ECOLOGICAL NICHE MODELS

259 For cases exhibiting evidence for niche conservatism or niche unfilling as the main driver of
260 niche changes, we predicted potentially invadable areas for the wild boar using ecological
261 niche models. Ecological niche models are correlation procedures that capture environmental
262 conditions within which the species is known to be present, based on occurrence and
263 environmental data from geographic information systems (Broennimann & Guisan 2008;
264 Jiménez-Valverde *et al.* 2011). Original invasion risk assessments attempted to predict
265 potentially invadable areas from climatic conditions present in the species native range
266 (Peterson 2003; Thuiller *et al.* 2005). The idea behind this approach is that evolutionary
267 changes on species fundamental niches are not likely to occur within the timescale of
268 anthropogenic species invasions (Peterson 1999, 2011). Therefore, if climatic constraints
269 create evolutionary markers carried away during species transportations, then species are
270 supposed to preferentially occupy areas climatically similar to those where they evolved
271 (Peterson 2011).

272

273 Although the predictive accuracy of ecological niche models can often be high, the native-
274 based approach does not incorporate possible niche shifts that may occur during biological

275 invasions (Tingley *et al.* 2014). To allow for less restrictive models in terms of niche
276 conservatism, the use of all occurrences from locations where a species is known to occur
277 has been suggested as a step forward on invasion risk assessments (Peterson 2011; Jiménez-
278 Valverde *et al.* 2011). By using distributional data from both native and other invaded ranges,
279 possibly small niche shifts could be incorporated into ecological niche models.

280

281 To compare the invasion risk maps produced with both calibration scenarios, we fitted
282 ecological niche models using data from the native and the pooled range for the wild boar.
283 Our niche models were therefore calibrated with: 1) occurrences from the wild boar's native
284 distribution (native-based models); or 2) occurrences from all distribution information
285 available (pooled-range-based models) (see Fig. S1). All models were projected worldwide.
286 We randomly partitioned wild boar occurrence data into two subsets of calibration (75% of
287 data), and validation (remaining 25%). That data-splitting process was repeated 100 times,
288 in a cross-validation procedure, maintaining the species observed prevalence unchanged.
289 Those occurrences, coupled with the five previously chosen environmental predictors, were
290 used to model the wild boar potential distribution.

291

292 Diverse techniques have been proposed for estimating species climate niches and potential
293 distributions (Franklin 2009). These methods usually aim to provide a mathematical link
294 between occurrence information for the species and the environmental predictors associated
295 to the location of those occurrences. In this work, ecological niche models are solely meant
296 to provide estimates of the wild boar distributional potential. Niche comparisons were

297 performed using the methods described in the previous section, following Broennimann
298 (2012). We therefore chose methods best suited to estimate the potential distribution of a
299 species, or invasion risk maps (Jiménez-Valverde *et al.* 2011). In this work, chosen methods
300 do not strongly rely on true absence information and usually lead to overprediction, an
301 intrinsic artifact to the very nature of invasive species (Jiménez-Valverde *et al.* 2011).

302

303 Three different presence-only and presence-pseudoabsence modeling techniques were used:
304 Bioclim, Mahalanobis distance and Support Vector Machine. In Bioclim, environmental
305 predictors of species occurrences are treated as multiple distributions of uni-tailed
306 percentiles. The values of each cell grid are evaluated to determine their position in the
307 distribution percentiles. Bioclim then compares the predictor values in a grid cell to the
308 distribution percentiles of the known occurrences of the species to calculate the relative
309 suitability of a given grid cell (Graham & Hijmans 2006; Hijmans *et al.* 2013). Therefore,
310 values of predictor variables closer to the 50th percentile (the median) are considered the most
311 suitable for species. Distribution tails are not distinguished, that is, the 10th percentile is
312 equivalent to the 90th percentile.

313

314 Species distribution models based on Mahalanobis distance consider the correlations of
315 environmental variables, are scale-independent and useful to determine the similarity
316 between a known sample and an unknown sample (Hijmans *et al.* 2013). Calculations in the
317 mahal algorithm are based on the Mahalanobis distance (Mahalanobis 1936). The highest
318 possible value is a function of the correlation between variables in the data set. Consequently,

319 similarity values are not dependent on the scale of measurements. Bioclim and Mahalanobis
320 distance are presence-only methods (Franklin 2009). Bioclim models were fitted with the
321 *bioclim* function, and Mahalanobis distance models with the *mahal* function, from the R
322 package *dismo* (Hijmans *et al.* 2013).

323

324 Support Vector Machine models are a machine-learning technique to analyze data and
325 recognize patterns (e.g. species presences) (Karatzoglou, Smola & Hornik 2016). Support
326 Vector Machine are useful for classification and regression analysis, and usually exhibits
327 good performance under several conditions (Karatzoglou *et al.* 2016). Support Vector
328 Machine is a presence-background method (Franklin 2009), for which models were fitted
329 using the function *ksvm* from R package *kernelab* (Karatzoglou *et al.* 2016). We used an
330 epsilon regression (*eps-svr*) with binary numeric response. All non-binary variables were
331 scaled to mean zero plus variance. The argument *kpar* contains the parameters to be passed
332 on to the kernel function and calculates the appropriate sigma value for the regression. The
333 *ksvm* function, i.e. the kernel function, was used in both training and prediction. Model fitting
334 is performed on output data, via a 3-fold cross-validation on the training dataset, which is the
335 suggested procedure (Karatzoglou *et al.* 2016).

336

337 Continuous predictions of habitat suitability derived from the three previously described
338 ecological niche models were converted to binary projections. For that, we found the
339 threshold with maximum sensitivity and specificity values in the relative operating
340 characteristic (ROC curve). Then, we calculated the True Skills Statistics (TSS), a measure

341 of model performance that corrects for the dependence on the prevalence of the modelled.
342 The TSS is the measure of choice for presence-absence predictions and ranges from -1 to +1
343 (Allouche, Tsoar & Kadmon 2006). Values close to +1 indicate good prediction and values
344 equal or smaller than zero are not better than random predictions (Allouche *et al.* 2006).

345

346 Ensembles of forecasts tend to produce more robust predictions and reduce variability related
347 to modeling methods used (Diniz-Filho *et al.* 2009). We therefore created an ensemble of
348 gridded potential distribution maps, originated from the three methods we used here.
349 Ensembles were then created by weighting each model projection (habitat suitability map)
350 according to model performance to discriminate them in terms of accuracy, and only models
351 with $TSS > 0.5$ were used in final models of potential distribution.

352

353 **Results**

354 Patterns of niche shift during wild boar invasion were not similar across all studied regions
355 (Table 1). Niche overlap (in terms of Schoener's D) between native and invaded niches was
356 overall low (Table 1). The wild boar populations from Australasian region presented the
357 highest values of niche overlap with the native populations of the species (Schoener's $D =$
358 0.4 ± 0.03), compared to the Neotropical (Schoener's $D = 0.3 \pm 0.06$) and the Nearctic
359 (Schoener's $D = 0.2 \pm 0.02$). However, we found no evidence that the invaded populations'
360 niches from any of the analyzed regions are identical to their native counterparts, although in
361 the Nearctic they were more similar than expected by chance (Figs. S2, S3 and S4).

362

363 The hypothesis that native and exotic niches are indistinguishable (i.e. niche equivalence)
364 was rejected for all biogeographical regions. However, the hypothesis that niche overlap falls
365 within the 95% confidence limits of the null distributions (i.e. niche similarity) was rejected
366 only for the Neotropical and Australasian region. In these regions, the wild boar's realized
367 niche was apparently different from the one belonging to native populations.

368

369 Although some apparent niche shifts were observed, niche stability was high overall
370 ($\text{Stability}_{\text{mean}} = 0.99 \pm 0.006$) and niche expansion was low ($\text{Expansion}_{\text{mean}} = 0.01 \pm 0.006$)
371 in all regions. Niche shifts indicated by rejection of null hypotheses of niche similarity were
372 explained by the process of niche unfilling ($\text{Unfilling}_{\text{mean}} = 0.12 \pm 0.14$). The proportion of
373 climate conditions present in the native range, but unoccupied by exotic populations ranged
374 from 1% in the Nearctic, to 8% in Australasia and up to 28% in the Neotropics.

375

376 Because we found evidence for niche conservatism, we created invasion risk maps based on
377 climate suitability, using ecological niche models. Native-based models had a slightly poorer
378 accuracy than pooled-range-based models ($\text{TSS}_{\text{mean}}=0.62\pm0.1$ and $\text{TSS}_{\text{mean}}=0.68\pm0.06$,
379 respectively). Native-based models also accurately predicted most areas where wild boar is
380 known to have invaded in all but the Australasian region (Fig. 2). The Afrotropical
381 biogeographical region was not used for niche comparison in this work due to the small
382 number of valid occurrences ($n = 2$). Although we did not calibrate models with occurrences
383 for that region, both ecological niche model calibration scenarios used here (native vs pooled

384 range) indicated high climatic suitability for the wild boar on central and southeastern Africa
385 (Fig. 2).

386

387 **Discussion**

388 We found that during the wild boar invasion into the Neotropical, Nearctic and Australian
389 regions, niche stability was high and niche expansion was low. Although native and exotic
390 populations' niches were not equivalent (*sensu* Peterson et al., 1999), climatic matches
391 among occupied ranges were greater than expected by chance (*sensu* Graham et al., 2004) in
392 only one out of three regions analyzed. Niche stability was however corroborated by niche
393 overlap measures (*sensu* Broennimann et al., 2012) and also by congruent broad-scale
394 predictions of ecological niche models calibrated with native and pooled range data (*sensu*
395 Peterson, 2003). Niche conservatism is arguably one of the main processes that allows for a
396 species to invade different areas across the globe (Peterson 2011; Strubbe *et al.* 2015; Pyron
397 *et al.* 2015). Although phylogenetic changes in species fundamental niches are expected
398 during the speciation processes (Pyron *et al.* 2015), such changes are rarely observed at the
399 timescale of man-made introductions (Peterson 2011).

400

401 Even though niche conservatism seems to be an *a priori* assumption for predicting potentially
402 invadable areas (Jiménez-Valverde *et al.* 2011), observation of niche changes are
403 increasingly reported (Broennimann *et al.* 2007; Tingley *et al.* 2014; Early & Sax 2014). The
404 validity of those changes is however questioned due to the recent unraveling of processes
405 driving niche shifts (Guisan *et al.* 2014). If species, in their invaded range, only occupy a

406 subset of the environmental conditions that they are usually found in their native range,
407 classic statistical tests may indeed find differences among realized climatic niches. Those
408 differences nevertheless do not arise from expansion into non-analogous climate, as expected
409 from evolutionary adaptation. Niche unfilling might indeed be the pure result of ongoing
410 colonization and slow dispersal (Petitpierre *et al.* 2012; Guisan *et al.* 2014; Strubbe *et al.*
411 2015). A single snapshot in time may therefore not be sufficient to capture nuances of these
412 processes. Observed changes on realized niches may in fact mislead understanding of niche
413 shifts during biological invasions. Here, comparisons of native *vs* exotic populations revealed
414 that niches were more similar than expected by chance in the Nearctic, although not
415 equivalent in any analyzed region, and that differences may be explained by niche unfilling,
416 rather than niche expansion (Guisan *et al.* 2014). Observed niche shifts due to unfilling of
417 environmental space have already been reported for several non-native vertebrate species,
418 including the wild boar (Strubbe *et al.* 2013, 2015).

419

420 Colonization history and propagule pressure also affect observed niche changes during
421 biological invasions. Niche unfilling seems to be larger for species introduced recently and
422 into a small number of locations, compared to those with ancient colonization history and
423 introduced in several points in space (Strubbe *et al.* 2015). In this work, niche unfilling was
424 substantially higher for the Neotropics, compared to other locations. Wild boar importation
425 into the Neotropics has a 200 year long history (Skewes & Jaksic 2015). However, recent
426 waves of introduction on the 1990s for pig-farming and game hunting, followed by escape
427 and inter-country dispersal (Skewes & Jaksic 2015; Pedrosa *et al.* 2015) have led to explosive
428 population growth in the Neotropics (Pedrosa *et al.* 2015). Because we found 28% of niche

429 unfilling for the Neotropical region, our results indicate that the invasive potential of wild
430 boar might be larger than expected so far. Preventing the expansion of wild boar distribution
431 into Neotropical species-rich areas such as the Amazon, coupled with potential economic
432 loss, thus requires specific management towards population control in areas already invaded.

433

434 Because the niche of non-native populations of wild boars is a subset of its native
435 counterparts' niche, ecological niche models should lead to accurate predictions of
436 potentially invadable areas (Strubbe *et al.* 2015). We found that models calibrated with
437 occurrences within the native distribution indeed predicted areas reportedly struggling with
438 wild boar population expansion, such as the south and southeastern Brazil (Pedrosa *et al.*
439 2015), eastern USA (Pimentel *et al.* 2005) and eastern Australia (Spencer & Hampton 2005).
440 In other words, models calibrated with native and pooled ranges led to convergent
441 predictions, thus suggesting that newly occupied areas are climatically similar to the ones the
442 wild boar was already adapted to. Those convergences imply that evolutionary markers from
443 climatic constraints across the native range are still evident on populations inhabiting exotic
444 ranges (Pyron *et al.* 2015).

445

446 We found a remarkable convergence on potentially invadable areas for the Afrotropical
447 region. Although no data from that region was used to calibrate ecological niche models,
448 both calibration scenarios predicted high climatic suitability for the wild boar in central and
449 southeastern Africa. The Suidae family is a monophyletic group of Cetartiodactyla,
450 composed of 17 species and originated in Africa (Frantz *et al.* 2016). That origin of extant

451 species is relatively recent – less than 5.3 Ma – and many lineages have and continue to
452 hybridize (Frantz *et al.* 2016). Climatic constraints on species realized niche may be the result
453 of adaptation to climates in which species have evolved (Pyron *et al.* 2015). If fundamental
454 niches are phylogenetically conserved and climate-related evolutionary markers are indeed
455 preserved on related lineages (Pyron *et al.* 2015), then the high climatic suitability exhibited
456 for the wild boar may in fact be shared with other Afrotropical Suidae species. Furthermore,
457 the diversity of Suidae species in Africa probably prevented wild boar invasion, because
458 humans bred other suids (such as the bushpig *Potamochoerus larvatus*) and transported them
459 through the mainland and towards Mayotte, Comoros, Madagascar and other islands (Frantz
460 *et al.* 2016). Testing whether phylogenetic niches are preserved among members of the
461 Suidae family is yet to be attempted, but could shed substantial light to the processes driving
462 speciation in that taxa.

463

464 One exception to the ecological niche models' predictive ability was nevertheless found.
465 Models calibrated with native occurrences were less able to predict wild boar's exotic
466 occurrences in Australasia, compared to the other regions. Domestic pigs were first established
467 in Australia in 1788 and recreational hunting has been common practice among Caucasian
468 and Aboriginal groups since then (Bengsen *et al.* 2014; Meurk 2015). Pig hunting is therefore
469 part of subsistence and social practices and contributes substantially to regional economies
470 (Meurk 2015), despite long-lasting attempts to eradicate feral pig populations in Australian
471 territory (Bengsen *et al.* 2014). Illegal transportation for game hunt and escapes from pig
472 farms probably increase propagule pressure all over Australia, thus leading to species
473 temporary occupancy of sub-optimal climates. Those populations occupying marginal

474 climates are characterized by sink dynamics and are not expected to persist in time (Colwell
475 & Rangel 2009; Soberón & Nakamura 2009).

476

477 Also, some of the records from central Australia are from pigs following flooding rivers
478 downstream into Lake Eyre. This is not driven by local climatic events, but rainfall far away
479 in the upstream reaches of the catchments, and so correlations between climate and
480 occurrence is less likely here. Because native-based models were less able to predict wild
481 boar occurrence in the Australasian region, we suggest that predictive maps of invasion risk
482 for that region should be calibrated with pooled range calibration scenarios. Although overall
483 broad-scale differences were small, including all known occurrences of an invasive species
484 allows incorporation of possible non-equilibrium source-sink dynamics and their outcomes,
485 which improves invasion risk assessments at regional scale (Peterson 2011; Jiménez-
486 Valverde *et al.* 2011).

487

488 Wild boars, like other Suidae members, have a limited ability to eliminate heat. They lack
489 functional sweat glands, have a thick hairy skin and tend to accumulate subcutaneous fat
490 (Manner & McCrea 1963; Fernández-Llario 2005; Bracke 2011). We expected that wild
491 boars would thus preferentially occupy low temperature sites, such as high altitudes and high
492 latitudes, to prevent hyperthermia. However, all models predicted high climatic suitability in
493 warm areas, such as tropical America and Africa. Also, the wild boars' native distribution
494 includes the low-latitude Indian horn, southern China and The Philippines. The occupancy
495 of warm climates suggests that mechanisms other than physiology have evolved in wild boars

496 to prevent overheating. In response to increased temperature, pigs usually exhibit a series of
497 behavioral patterns, of which the most obvious is wallowing (Olczak, Nowicki & Klocek
498 2015). Wallowing helps wild boars eliminate heat and may have a sexual function in males
499 (Fernández-Llario 2005). We believe that behavioral flexibility may further allow the wild
500 boars to occupy a wide range of climate conditions and thus overcome many physiological
501 limitations, while also enhancing its invasive potential.

502

503 The wild boar is considered one of the worst invasive alien species in the world (Lowe *et al.*
504 2000). Its rapid and large-scale spread into many places worldwide is an issue of great
505 concern for areas as diverse as agriculture, economy and biodiversity conservation. We found
506 that, while niche conservatism explains invasion patterns, the broad native distribution of
507 wild boar is suggestive of a pre-adaptation to a wide array of climate conditions. That large
508 climatic tolerance is probably related to the species successful invasive potential, which can
509 have unprecedented proportions on newly colonized regions, such as the Neotropics. Our
510 results explain the observed invasive success of the species on several parts of the world, and
511 highlight potentially invadable areas to the wild boar.

512

513 **Authors' contributions**

514 LPS, BRR, MWH, AP, MP and RL conceived the ideas and designed the methods; LPS and
515 MWH collected the data; LPS and BRR analysed the data; LPS led the writing; BRR, MWH,
516 AP, MP and RL assisted writing and reviewed the manuscript. All authors contributed
517 critically to the drafts and gave final approval for publication.

518

519 **Data Accessibility**

520 Climate data used in this work can be downloaded at www.worldclim.org/version1. Wild
521 boar occurrences were collected on freely available web sources, listed in M&M section.
522 Additional data was obtained from a literature survey, which is provided as supplementary
523 material, alongside with the spreadsheet containing all occurrences collected in this work.
524 All R codes used in this paper are based open-source packages, available at The
525 Comprehensive R Archive Network (cran.r-project.org). All R scripts used in niche overlap
526 and ENM assessments can be downloaded at
527 <http://www.unil.ch/ecospat/home/menuguid/ecospat-resources/tools.html>.

528

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536

537 **Supporting Information**

538 Additional Supporting Information may be found in the online version of this article:

539

540 **Appendix S1.** Full occurrence dataset, plus their biogeographical origin, used in the
541 modeling procedures of this work

542 **Table S1.** Supplementary literature.

543 **Table S2.** Summary of loadings from factorial analysis.

544 **Fig. S1.** Distribution of wild boar occurrences and calibration scenarios.

545 **Fig. S2.** Summary of niche equivalence and similarity tests for comparisons between native
546 and Neotropical populations.

547 **Fig. S3.** Idem Fig. S2, for comparisons between wild boar populations from native and
548 Australasian region.

549 **Fig. S4.** Idem Figs. S1 and S2, for comparisons between wild boar populations from native
550 and Nearctic region.

551 **Fig. S5.** Niche shifts observed during wild boar invasion into the Neotropical, Australasian
552 and Nearctic biogeographical regions.

553

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710 *Figure legends*

711 **Fig. 1.** Distribution of wild boar *Sus scrofa* around the world. Violet polygon indicates the
712 species native distribution, according to the IUCN. Dark pigs indicate wild boar occurrences
713 considered native in this study, and pale pigs represent occurrences considered exotic. Only
714 some occurrences used in this work are shown.

715 **Fig. 2.** Climate suitability and potentially invadable areas for the wild boar *Sus scrofa*. On
716 the left, predictions are based on models calibrated solely with occurrences within the species
717 native range (native-based models). On the right, models were calibrated with all locations
718 where the wild boar is known to occur (pooled-range-based models). Continuous predictions
719 are shown on top, where reddish colors indicate high suitability and bluish colors, low
720 suitability. Binary predictions are presented on the downside of the picture, where red color
721 indicates predicted presence and white color, absence.

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