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

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Summary

1. Niche conservatism, i.e. the retention of a species fundamental niche through evolutionary time, is a cornerstone for biological invasion assessments. The fact that species tend to maintain their original climate niche allows predictive maps of invasion risk to anticipate potential invadable areas. Unraveling the mechanisms driving niche shifts can shed substantial light on the management of invasive species.

2. Here, we assessed niche shifts in one of the world's worst invasive species: the wild boar *Sus scrofa*. We also predicted potential invadable areas based on an ensemble of three ecological niche modeling methods, and evaluated the performance of models calibrated with native *vs* pooled (native plus invaded) species records. By disentangling the drivers of change on the exotic wild boar population's niches, we found strong evidence for niche conservatism during biological invasion.

3. Ecological niche models calibrated with native *vs* pooled range calibration scenario predicted convergent areas. Also, observed niche shifts are mostly explained by niche unfilling, i.e. there are unoccupied areas in the exotic range where climate is analogous to the native range.

4. Niche unfilling is expected as a result of recent colonization and ongoing dispersal, and was potentially stronger for the Neotropics, where a recent wave of introductions for pig-farming and game-hunting has led to high wild boar population growth rates. The invasive potential of wild boar in the Neotropics is probably higher than in other regions, which has profound management implications if we are to prevent their invasion into species-rich areas, such as Amazonia, coupled with expansion of African swine fever and possibly great economic losses.

5. Although the originally Eurasian-wide distribution suggests a pre-adaptation to a wide array of climates, the wild boar worldwide invasion does not exhibit evidence of niche evolution. The invasive potential of the wild boar probably lies on the reproductive, dietary and morphological characteristics of this species, coupled with behavioral thermoregulation.

Introduction

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

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

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

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

216

Niche equivalence and similarity tests only verify whether niche shifts have occurred, but do not address their causal mechanisms. To understand the wild boar invasion process, we disentangled niche changes into the processes of unfilling and expansion. Niche unfilling is observed when some environmental conditions within the native niche are available, but unoccupied in the exotic climate (Guisan *et al.* 2014). Those unoccupied areas probably result from recent colonization and ongoing dispersal. In niche unfilling, the exotic niche is a subset of the native niche, and the species will eventually occupy all available niche space within exotic range, unless biological interactions restrict range expansion (Guisan *et al.* 2014). Niche expansion, on the other hand, is the result of occupancy of non-analogous climatic conditions to the native range. In other words, niche expansion is observed when the species occupies climate conditions to which it is not supposedly adapted, based on its native distribution climatic limits. Such occupancy in non-analogous climates is probably due to 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 *kernlab* (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   ($Stability_{mean} = 0.99 \pm 0.006$) and niche expansion was low ($Expansion_{mean} = 0.01 \pm 0.006$)

371   in all regions. Niche shifts indicated by rejection of null hypotheses of niche similarity were

372   explained by the process of niche unfilling ($Unfilling_{mean} = 0.12 \pm 0.14$). 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 ($TSS_{mean}=0.62\pm0.1$ and $TSS_{mean}=0.68\pm0.06$,

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

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 conservatisms 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

18

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 stablished

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

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.

Data Accessibility

Climate data used in this work can be downloaded at www.worldclim.org/version1. Wild

boar occurrences were collected on freely available web sources, listed in M&M section.

Additional data was obtained from a literature survey, which is provided as supplementary

material, alongside with the spreadsheet containing all occurrences collected in this work.

All R codes used in this paper are based open-source packages, available at The

Comprehensive R Archive Network (cran.r-project.org). All R scripts used in niche overlap

and ENM assessments can be downloaded at

http://www.unil.ch/ecospat/home/menuguid/ecospat-resources/tools.html.

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

554   **References**

555   Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models:
556   prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232.

557   Ballari, S.A. & Barrios-García, M.N. (2014) A review of wild boar *Sus scrofa* diet and factors affecting food
558   selection in native and introduced ranges. *Mammal Review*, **44**, 124–134.

559 Barasona, J.A., Latham, M.C., Acevedo, P., Armenteros, J.A., Latham, A.D.M., Gortazar, C., Carro, F.,
560   Soriguer, R.C. & Vicente, J. (2014) Spatiotemporal interactions between wild boar and cattle:
561   implications for cross-species disease transmission. *Veterinary Research*, **45**, 122.

562 Barrios-Garcia, M.N. & Ballari, S.A. (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native
563   range: a review. *Biological Invasions*, **14**, 2283–2300.

564 Barve, N., Barve, V., Jimenez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberon, J. &
565   Villalobos, F. (2011) The crucial role of the accessible area in ecological niche modeling and species
566   distribution modeling. *Ecological Modelling*, **222**, 1810–1819.

567 Bengsen, A.J., Gentle, M.N., Mitchell, J.L., Pearson, H.E. & Saunders, G.R. (2014) Impacts and management
568   of wild pigs *Sus scrofa* in Australia. *Mammal Review*, **44**, 135–147.

569 Bracke, M.B.M. (2011) Review of wallowing in pigs: Description of the behaviour and its motivational basis.
570   *Applied Animal Behaviour Science*, **132**, 1–13.

571 Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W.,
572   Fortin, M.-J., Randin, C., Zimmermann, N.E., Graham, C.H. & Guisan, A. (2012) Measuring ecological
573   niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, **21**,
574   481–497.

575 Broennimann, O. & Guisan, A. (2008) Predicting current and future biological invasions: both native and
576   invaded ranges matter. *Biology Letters*, **4**, 585–589.

577 Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007)
578   Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701–709.

579 Colwell, R.K. & Rangel, T.F. (2009) Hutchinson's duality: The once and future niche. *Proceedings of the
580   National Academy of Sciences*, **106**, 19651–19658.

581 Desbiez, A.L.J., Keuroghlian, A., Piovezan, U. & Bodmer, R.E. (2011) Invasive species and bushmeat
582   hunting contributing to wildlife conservation: the case of feral pigs in a Neotropical wetland. *Oryx*, **45**,
583   78–83.

584 Diniz-Filho, J.A.F., Mauricio Bini, L., Fernando Rangel, T., Loyola, R.D., Hof, C., Nogués-Bravo, D. &
585   Araújo, M.B. (2009) Partitioning and mapping uncertainties in ensembles of forecasts of species
586   turnover under climate change. *Ecography*, **32**, 897–906.

587 Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the
588   Anthropocene. *Science*, **345**, 401–406.

589 Early, R. & Sax, D.F. (2014) Climatic niche shifts between species' native and naturalized ranges raise
590   concern for ecological forecasts during invasions and climate change. *Global Ecology and*

591   *Biogeography*, **23**, 1356–1365.

592   Estes, J. a, Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E.,
593   Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple,
594   W.J., Sandin, S. a, Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soule, M.E., Virtanen,
595   R. & Wardle, D. a. (2011) Trophic Downgrading of Planet Earth. *Science*, **333**, 301–306.

596   Fernández-Llario, P. (2005) The sexual function of wallowing in male wild boar (*Sus scrofa*). *Journal of*
597   *Ethology*, **23**, 9–14.

598   Franklin, J. (2009) *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge University
599   Press.

600   Frantz, L., Meijaard, E., Gongora, J., Haile, J., Groenen, M.A.M. & Larson, G. (2016) The Evolution of
601   Suidae. *Annual Review of Animal Biosciences*, **4**, 61–85.

602   Fulgione, D., Rippa, D., Buglione, M., Trapanese, M., Petrelli, S. & Maselli, V. (2016) Unexpected but
603   welcome. Artificially selected traits may increase fitness in wild boar. *Evolutionary Applications*, **9**,
604   769–776.

605   Gabor, T.M.. & Hellgren, E.C.. (2000) Variation in Peccary Populations: Landscape Composition or
606   Competition by an Invader? *Ecology*, **81**, 2509–2524.

607   Graham, C.H. & Hijmans, R.J. (2006) A comparison of methods for mapping species ranges and species
608   richness. , 578–587.

609   Graham, C.H., Ron, S.R., Santos, J.C., Schneider, C.J. & Moritz, C. (2004) Integrating phylogenetics and
610   environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution;*
611   *international journal of organic evolution*, **58**, 1781–93.

612   Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C. & Kueffer, C. (2014) Unifying niche shift studies:
613   insights from biological invasions. *Trends in Ecology & Evolution*, **29**, 260–269.

614   Hayward, M.W., Jędrzejewski, W. & Jêdrzejewska, B. (2012) Prey preferences of the tiger Panthera tigris (ed
615   A Kitchener). *Journal of Zoology*, **286**, 221–231.

616   Hayward, M.W., Ward-Fear, G., L'Hotellier, F., Herman, K., Kabat, A.P. & Gibbons, J.P. (2016) Could
617   biodiversity loss have increased Australia's bushfire threat? *Animal Conservation*.

618   Herrero, J., García-Serrano, A., Couto, S., Ortuño, V.M. & García-González, R. (2006) Diet of wild boar *Sus*
619   *scrofa L.* and crop damage in an intensive agroecosystem. *European Journal of Wildlife Research*, **52**,
620   245–250.

621   Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2013) dismo: Species distribution modeling.

622 Hutchinson, G.E. (1957) Concluding remarks. *Cold spring harbor symposium on quantitative biology*, pp.
623   415–427.

624 Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P. & Lobo, J.M. (2011) Use of
625   niche models in invasive species risk assessments. *Biological Invasions*, **13**, 2785–2797.

626 Karatzoglou, A., Smola, A. & Hornik, K. (2016) kernlab: Kernel-Based Machine Learning Lab.

627 Long, J.L. (2003) *Introduced Mammals of the World: Their History, Distribution and Influence.* CSIRO
628   Publishing, Collingwood Victoria, Australia.

629 Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2000) 100 of the World's Worst Invasive Alien
630   Species. *Published by The Invasive Species Specialist Group ISSG a specialist group of the Species*
631   *Survival Commission SSC of the World Conservation Union IUCN 12pp First published as special*
632   *liftout in Aliens*, **12**, 12.

633 Mahalanobis, P.C. (1936) On the generalized distance in statistics. *Proceedings of the National Institute of*
634   *Sciences (Calcutta)*, **2**, 49–55.

635 Manner, M.J. & McCrea, M. (1963) Changes in the chemical composition of sow-reared piglets during the
636   first month of life. *British Journal of Nutrition*, **17**, 495–513.

637 Marshall, F.B., Dobney, K., Denham, T. & Capriles, J.M. (2014) Evaluating the roles of directed breeding
638   and gene flow in animal domestication. *Proceedings of the National Academy of Sciences*, **111**, 6153–
639   6158.

640 Meurk, C. (2015) Contesting Death: Conservation, Heritage and Pig Killing in Far North Queensland,
641   Australia. *Environmental Values*, **24**, 79–104.

642 Olczak, K., Nowicki, J. & Klocek, C. (2015) Pig behaviour in relation to weather conditions – a review.
643   *Annals of Animal Science*, **15**, 601–610.

644 Oliver, W. & Leus, K. (2008) Sus scrofa. The IUCN Red List of Threatened Species 2008: Downloaded on 16
645   March 2017.

646 Pedrosa, F., Salerno, R., Padilha, F.V.B. & Galetti, M. (2015) Current distribution of invasive feral pigs in
647   Brazil: economic impacts and ecological uncertainty. *Natureza & Conservação*, **13**, 84–87.

648 Peterson, A.T. (1999) Conservatism of Ecological Niches in Evolutionary Time. *Science*, **285**, 1265–1267.

649 Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *The*
650   *Quarterly Review of Biology*, **78**, 419–433.

651 Peterson, A.T. (2011) Ecological niche conservatism: A time-structured review of evidence. *Journal of*
652   *Biogeography*, **38**, 817–827.

653   Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo,

654   M.B. (2011) *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton,

655   New Jersey.

656   Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C. & Guisan, A. (2012) Climatic Niche

657   Shifts Are Rare Among Terrestrial Plant Invaders. *Science*, **335**, 1344–1348.

658   Pimentel, D., Zuniga, R. & Morrison, D. (2005) Update on the environmental and economic costs associated

659   with alien-invasive species in the United States. *Ecological Economics*, **52**, 273–288.

660   Pyron, R.A., Costa, G.C., Patten, M.A. & Burbrink, F.T. (2015) Phylogenetic niche conservatism and the

661   evolutionary basis of ecological speciation. *Biological Reviews*, **90**, 1248–1262.

662   R Development Core Team. (2016) R: A language and environment for statistical computing.

663   Randin, C., Engler, R., Pio, D., Garcia, R., Dubuis, A., Scherrer, D., Maiorano, L., Ndiribe, C., Salamin, N.,

664   Guisan, A., Valeria, M. & Cola, D. (2016) Package " ecospat ."

665   Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M. & Brooks, T.M. (2006) The value of the

666   IUCN Red List for conservation. *Trends in Ecology and Evolution*, **21**, 71–76.

667   Schoener, T.W. (1974) Some methods for calculating competition coefficients from resource-utilization

668   spectra. *American Naturalist*, **108**, 332–340.

669   Scott, A., Ram, K., Hart, T. & Chamberlain, S. (2016) Package "spocc": Interface to Species Occurrence Data

670   Sources. , 1–29.

671   Siemann, E., Carrillo, J.A., Gabler, C.A., Zipp, R. & Rogers, W.E. (2009) Experimental test of the impacts of

672   feral hogs on forest dynamics and processes in the southeastern US. *Forest Ecology and Management*,

673   **258**, 546–553.

674   Skewes, O. & Jaksic, F.M. (2015) History of the introduction and present distribution of the European wild

675   boar (*Sus scrofa*) in Chile. *Mastozoología Neotropical*, **22**, 113–124.

676   Soberón, J. (2007) Grinnellian and Eltonian niches and grographic distribution of species. *Ecology Letters*,

677   **10**, 1115–1123.

678   Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: Concepts, methods, and assumptions.

679   *Proceedings of the National Academy of Sciences*, **106**, 19644–19650.

680   Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species'

681   distributional areas. *Biodiversity Informatics*, 1–10.

682   Spencer, P.B.S. & Hampton, J.O. (2005) Illegal translocation and genetic structure of feral pigs in Western

683   Australia. *Journal of Wildlife Management*, **69**, 377–384.

684   Strubbe, D., Beauchard, O. & Matthysen, E. (2015) Niche conservatism among non-native vertebrates in
685   Europe and North America. *Ecography*, **38**, 321–329.

686   Strubbe, D., Broennimann, O., Chiron, F. & Matthysen, E. (2013) Niche conservatism in non-native birds in
687   Europe: niche unfilling rather than niche expansion. *Global Ecology and Biogeography*, **22**, 962–970.

688   Taylor, R.B., Hellgren, E.C., Gabor, T.M. & Ilse, L.M. (1998) Reproduction of Feral Pigs in Southern Texas.
689   *Journal of Mammalogy*, **79**, 1325–1331.

690   Thuiller, W., Richardson, D.M., Pysek, P., Midgley, G.F., Hughes, G.O. & Rouget, M. (2005) Niche-based
691   modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change*
692   *Biology*, **11**, 2234–2250.

693   Tingley, R., Vallinoto, M., Sequeira, F. & Kearney, M.R. (2014) Realized niche shift during a global
694   biological invasion. *Proceedings of the National Academy of Sciences*, **111**, 10233–10238.

695   Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus conservatism:
696   Quantitative approaches to niche evolution. *Evolution*, **62**, 2868–2883.

697   Wiens, J.J. & Graham, C.H. (2005) Niche Conservatism: Integrating Evolution, Ecology, and Conservation
698   Biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

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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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