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Niche conservatism and the invasive potential of the wild boar

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Abstract

1. Niche conservatism, i.e. the retention of a species' fundamental niche through evolutionary time, is 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. Unravelling the mechanisms driving niche shifts can shed 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 modelling 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 both native and pooled range records 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 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 world-wide invasion does not exhibit evidence of niche evolution. The invasive potential of the wild boar therefore probably lies on the reproductive, dietary and morphological characteristics of this species, coupled with behavioural thermoregulation.

KEYWORDS
biological invasion, conservation biogeography, ecological niche models, feral pig, invasive alien species

1 | 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, Petitpierre, Broennimann, Daehler, & Kueffer, 2014). In fact, understanding processes that drive changes in species' fundamental niches is important for ecology and evolution (Pyron, Costa, Patten, & Burbrink, 2015; Wiens & Graham, 2005), but is 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).

Potential 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 (Jiménez-Valverde et al., 2011; Peterson, 2003; Thuiller et al., 2005). This assumption is possible because species' fundamental niches are not likely to change over short-to-moderate time spans (Peterson, 2011). Given that these climatic niches exhibit little or no differentiation, the 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 mapped (Jiménez-Valverde et al., 2011; Thuiller et al., 2005). If climatic conditions therefore pose long-term and stable constraints on species geographic distribution, potential invadable areas can be anticipated with relative confidence (Peterson, 2003).

Although exciting in their potential for guiding management decisions, ecological niche models can only accurately predict potential invadable areas when niche conservatism is supported. However, initial studies on niche conservatism revealed contrasting patterns of niche shift due to tests of different null hypotheses (Graham, Ron, Santos, Schneider, & Moritz, 2004; Peterson, 1999). After Warren, Glor, and Turelli (2008), niche conservatism was thought to be best measured in terms of statistical difference, i.e. "niche similarity" and "niche equivalence." Despite their transparency, the similarity and equivalence tests only reveal statistically significant differences on species' climate niches, but not the causes underlying such niche shifts (Guisan et al., 2014; Petitpierre et al., 2012; Strubbe, Broennimann, Chiron, & Matthysen, 2013). Hence, absolute values of "equivalence" and "similarity" have little biological meaning unless niche shifts are disentangled into their main drivers of change, namely "niche unfilling" and "niche expansion" (Broennimann et al., 2012; Guisan et al., 2014). In addition to detecting niche shifts, decomposing the changes in terms of niche expansion and unfilling can shed substantial light on the ecological processes driving biological invasions (Broennimann et al., 2012; Guisan et al., 2014).

Currently present in all continents, except in Antarctica, the wild boar is a member of the family Suidae from Eurasia and North Africa. The wild boar is the oldest intentionally introduced mammal species (for bush meat) and is now one of the most widely distributed species in the world (Long, 2003). Biological traits of the species partially explain its invasive success. Wild boars have fast population growth rates (Taylor, Hellgren, Gabor, & Ilse, 1998) and feed opportunistically on many plants and animals (Ballari & Barrios-García, 2014). Population top-down control by predators is limited throughout its native and exotic ranges due to world-wide small density of large carnivores (Barrios-Garcia & Ballari, 2012; Estes et al., 2011) and widespread defaunation of natural areas (Dirzo et al., 2014). Wild boars also possess weaponry and a low centre of gravity that prevents their preferential capture by all but the largest felids (Hayward, Jędrzejewski, & Jêdrzejewska, 2012). Further, their extensive native distribution across Eurasia and North Africa suggests a pre-adaptation to a wide array of climatic conditions (Barrios-Garcia & Ballari, 2012; Long, 2003). In this paper, we assessed the invasive potential of the wild boar *Sus scrofa* globally. Our aim was to test whether wild boars and their hybrids have substantially changed their climatic niches during their global invasion. In addition, we mapped potential invadable areas, where allowed by niche conservatism assumptions.

2 | MATERIALS AND METHODS

2.1 | The wild boar

Wild boars (*S. scrofa*) are ecosystem engineers that turn extensive areas of leaf litter, soil and vegetation, which may ultimately affect fire regimes (Hayward et al., 2016). While the impact of that rooting behaviour on biodiversity is controversial (Siemann, Carrillo, Gabler, Zipp, & Rogers, 2009), the same is not true for economic losses. Wild boar rooting damages crops and husbandry, causing economic losses up to 800 million dollars a year in the USA alone (Pimentel, Zuniga, & Morrison, 2005). Wild boars damage various vegetable crops (Ballari & Barrios-García, 2014; Herrero, García-Serrano, Couto, Ortuño, & García-González, 2006; Pimentel et al., 2005) and also transmit and are reservoirs for several diseases to humans and livestock (Barasona et al., 2014). Impacts of wild boars on wildlife span predation (Ballari & Barrios-García, 2014) to habitat and nest destruction (Barrios-Garcia & Ballari, 2012). Competitive interaction with wild boar leads to native species exclusion, especially peccaries (Gabor & Hellgren, 2000) and other species of the genus *Sus* (Frantz et al., 2016). Despite those negative effects, in some particular areas—such as the Brazilian Pantanal—wild boars are supposed to be a preferential target for bush meat hunters and may thus release native peccaries from over-harvesting (Desbiez, Keuroghlian, Piovezan, & Bodmer, 2011), although this lacks empirical validation.

As they are primarily raised for meat, domesticated pig breeds were selected to increase traits, such as fecundity and population growth rate. Escaped domestic pigs hybridize with wild populations and transmit to them those artificially selected traits, which enhances

FIGURE 1 Distribution of wild boar *Sus scrofa* around the world. Violet polygon indicates the species' native distribution, according to the IUCN. Dark pigs indicate wild boar occurrences considered native in this study, and pale pigs represent occurrences considered exotic. Only some occurrences used in this work are shown [Colour figure can be viewed at wileyonlinelibrary.com]

hybrid fitness (Fulgione et al., 2016). Hybrid pigs have therefore inherited higher fertility rates and larger litter size from their domestic relatives (Fulgione et al., 2016), while retaining sociability, coupled with associated large group herds, and flexible climatic tolerance from their wild ancestors (Marshall, Dobney, Denham, & Capriles, 2014). The impact of hybrid pigs on both biodiversity and the economy can therefore be even higher than that of wild populations, although those effects are still to be addressed in scientific literature (Barrios-Garcia & Ballari, 2012).

2.2 | Data collection

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

Native distribution was defined based on the IUCN range map for *Sus scrofa* (Oliver & Leus, 2008), obtained at www.iucnredlist.org. The use of IUCN range maps to identify species native distribution is considered useful for large-scale modelling studies, as well as to conservation planning, management and wildlife monitoring (Rodrigues, Pilgrim, Lamoreux, Hoffmann, & Brooks, 2006). We also included occurrences up to 200 km from the existing border of the species native range map. Occurrences farther than that to the native polygon were removed from the "native dataset". By doing so, we accounted for possible uncertainties on the borders of IUCN range maps, to consider highly updated—though perhaps imprecise—species records. A total of 2283 occurrence records was then collected, from which 688 belonged to native distribution, 168 of them to the Australian region, 609 to the Nearctic region, and 736 to the Neotropical region (Figure 1 and Figure S1), covering years from 1970 to 2016. Remaining occurrences were scattered around the globe and not used in this study. Spatial autocorrelation was minimized by randomly removing occurrences less than 0.5 degree of latitude/longitude from each other, from the whole dataset (both native and exotic ranges). This procedure has minimized problems related to spatial autocorrelation in other niche shift studies at geographic scale (Broennimann et al., 2012; Strubbe et al., 2015).

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

2.3 | Niche equivalence/similarity tests

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

The observed niche overlap is then compared to random measures of niche overlap. Niche equivalence and similarity tests are based on comparisons of observed measures of niche overlap to random overlap values, although different null hypotheses are thereby tested. Niche equivalence tests, as initially proposed by Graham et al. (2004), ask whether the compared niches are indistinguishable from each other. Rejection of the null hypothesis on niche equivalence tests indicates that native and exotic niches are not identical (Broennimann et al., 2012; Strubbe et al., 2015). Niche similarity tests, on other hand, were first used in Peterson (1999) work, and test whether niche models calibrated for one species (or population, in our case) predict other species' occurrences better than expected by chance. The niche similarity null hypothesis is that of retained niche resemblance and its rejection indicates that niches are more different than expected by chance. Null hypotheses tests were repeated 1,000 times for each biogeographical region and *p*-values were computed at a 5% level of confidence.

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 performed using the *ecospat* R package (Di Cola et al., 2017).

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 the exotic range, unless biological interactions restrict range expansion (Guisan et al., 2014). Niche expansion, on 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).

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

Predicting potential invadable areas for invasive species is only possible when: (1) changes in a species' climatic niche are not observed or (2) observed niche differences are not caused by evolutionary changes in the species fundamental niche (Jiménez-Valverde et al., 2011; Strubbe et al., 2013, 2015). If the exotic niche is a subset of the native one, and niche shifts are therefore caused by niche unfilling rather than expansion, then an ecological niche model calibrated with climatic conditions where the species is known to occur may accurately predict invasion potential (Jiménez-Valverde et al., 2011; Peterson, 2011; Strubbe et al., 2015). Otherwise, the essential assumption of equilibrium between the species' distribution and climate tolerances is violated (Early & Sax, 2014). In cases where climatic equilibrium is not supported, forecasts of invasion risk based on correlative models may not be reliable (Early & Sax, 2014).

2.4 | Ecological niche models

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

Although the predictive accuracy of ecological niche models can often be high, the native-based approach does not incorporate possible niche shifts that may occur during biological invasions (Tingley, Vallinoto, Sequeira, & Kearney, 2014). To allow for less restrictive models in terms of niche conservatism, the use of all occurrences from locations where a species is known to occur has been suggested as a step forward on invasion risk assessments (Jiménez-Valverde et al., 2011; Peterson, 2011). Using distributional data from both native and invaded ranges, possibly small niche shifts could be incorporated into ecological niche models.

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

Diverse techniques have been proposed for estimating species climate niches and potential distributions (Franklin, 2009). These methods usually aim to provide a mathematical link between occurrence information for the species and the environmental predictors associated to the location of those occurrences. In this work, ecological niche models are solely meant to provide estimates of the wild boar distributional potential. Niche comparisons were performed using the methods described in the previous section, following Broennimann et al. (2012). We therefore chose methods best suited to estimate the potential distribution of a species, or invasion risk maps (Jiménez-Valverde et al., 2011). In this work, chosen methods do not strongly rely on true absence information and usually lead to overprediction, an intrinsic artefact to the very nature of invasive species (Jiménez-Valverde et al., 2011).

Three different presence-only and presence-pseudoabsence modeling techniques were used: Bioclim, Mahalanobis distance and Support Vector Machine. In Bioclim, environmental predictors of species' occurrences are treated as multiple distributions of uni-tailed percentiles. The values of each cell grid are evaluated to determine their position in the distribution percentiles. Bioclim then compares the predictor values in a grid cell to the distribution percentiles of the known occurrences of the species to calculate the relative suitability of a given grid cell (Graham & Hijmans, 2006; Hijmans, Phillips, Leathwick, & Elith, 2011). Therefore, values of predictor variables closer to the 50th percentile (the median) are considered the most suitable for species. Distribution tails are not distinguished, i.e. the 10th percentile is equivalent to the 90th percentile.

Species distribution models based on Mahalanobis distance consider the correlations of environmental variables, are scale-independent and useful to determine the similarity between a known sample and an unknown sample (Hijmans et al., 2011). Calculations in the mahal algorithm are based on the Mahalanobis distance (Mahalanobis, 1936). The highest possible value is a function of the correlation between variables in the dataset. Consequently, similarity values are not dependent on the scale of measurements. Bioclim and Mahalanobis distance are presence-only methods (Franklin, 2009). Bioclim models were fitted with the *bioclim* function, and Mahalanobis distance models with the *mahal* function, from the R package *dismo* (Hijmans et al., 2011).

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

Continuous predictions of habitat suitability derived from the three previously described ecological niche models were converted to binary projections. For that, we found the threshold with maximum sensitivity and specificity values in the relative operating characteristic (ROC curve). Then, we calculated the True Skills Statistics (TSS), a measure of model performance that corrects for the dependence on the prevalence of the modelled. The TSS is the measure of choice for presence-absence predictions and ranges from −1 to +1 (Allouche, Tsoar, & Kadmon, 2006). Values close to +1 indicate good prediction and values equal or smaller than zero are not better than random predictions (Allouche et al., 2006).

Ensembles of forecasts tend to produce more robust predictions and reduce variability related to modelling methods used (Diniz-Filho et al., 2009). We therefore created an ensemble of gridded potential

TABLE 1 Summary of statistics describing niche shifts, and their main drivers, during wild boar invasion in the Neotropical, Australian and Nearctic biogeographical regions. Equivalence and Similarity (E→N: from exotic to native; N→E: from native to exotic) are measured in terms of observed niche overlap (Schoener's *D*). Asterisks indicate rejection of null hypothesis (*p*-value <.05), from comparisons of observed vs. random measures of niche overlap. Expansion and Stability are proportions of the exotic niche non-overlapping and overlapping, respectively, with the native niche. Unfilling is the proportion of the native niche, present but non-occupied in the exotic niche (details in text)

		Similarity				
	Equivalence	**E→N**	**N→E**	**Expansion**	**Stability**	**Unfilling**
Neotropical	0.36*	0.3*	0.3*	0.02	0.98	0.28
Australian	0.43*	0.4*	0.4*	0.01	0.99	0.08
Nearctic	0.22*	0.2	0.2	0.01	0.99	0.01

distribution maps, originated from the three methods we used here. Ensembles were then created by weighting each model projection (habitat suitability map) according to model performance to discriminate them in terms of accuracy, and only models with TSS > 0.5 were used in final models of potential distribution.

3 | RESULTS

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

The hypothesis that native and exotic niches are indistinguishable (i.e. niche equivalence) was rejected for all biogeographical regions. However, the hypothesis that niche overlap falls within the 95% confidence limits of the null distributions (i.e. niche similarity) was rejected only for the Neotropical and Australasian region. In these regions, the wild boar's realized niche was apparently different from the one belonging to native populations (Figure S5).

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

Because we found evidence for niche conservatism, we created invasion risk maps based on climate suitability, using ecological niche models. Native-based models had a slightly poorer accuracy than pooled-range-based models (TSS_{mean} = 0.62 ± 0.1 and TSS_{mean} = 0.68 ± 0.06 respectively). Native-based models also accurately predicted most areas where wild boar is known to have invaded in all but the Australasian region (Figure 2). The Afrotropical biogeographical region was not used for niche comparison in this work due to the small number of valid occurrences (*n* = 2). Although we did not calibrate models with occurrences for that region, both ecological niche model calibration scenarios used here (native vs. pooled range) indicated high climatic suitability for the wild boar on central and south-eastern Africa (Figure 2).

4 | DISCUSSION

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

Even though niche conservatism seems to be an a priori assumption for predicting potential invadable areas (Jiménez-Valverde et al., 2011), observation of niche changes are increasingly reported (Broennimann et al., 2007; Early & Sax, 2014; Tingley et al., 2014). The validity of those changes is however questioned due to recent unravelling of processes driving niche shifts (Guisan et al., 2014). If species, in their invaded range, only occupy a subset of the environmental conditions that they are usually found in their native range, classic statistical tests may indeed find differences among realized climatic niches. Those differences nevertheless do not arise from expansion into non-analogous climate, as expected from evolutionary adaptation. Niche unfilling might indeed be the pure result of ongoing colonization and slow dispersal (Guisan et al., 2014; Petitpierre et al., 2012; Strubbe et al., 2015). A single snapshot in time may therefore not be sufficient

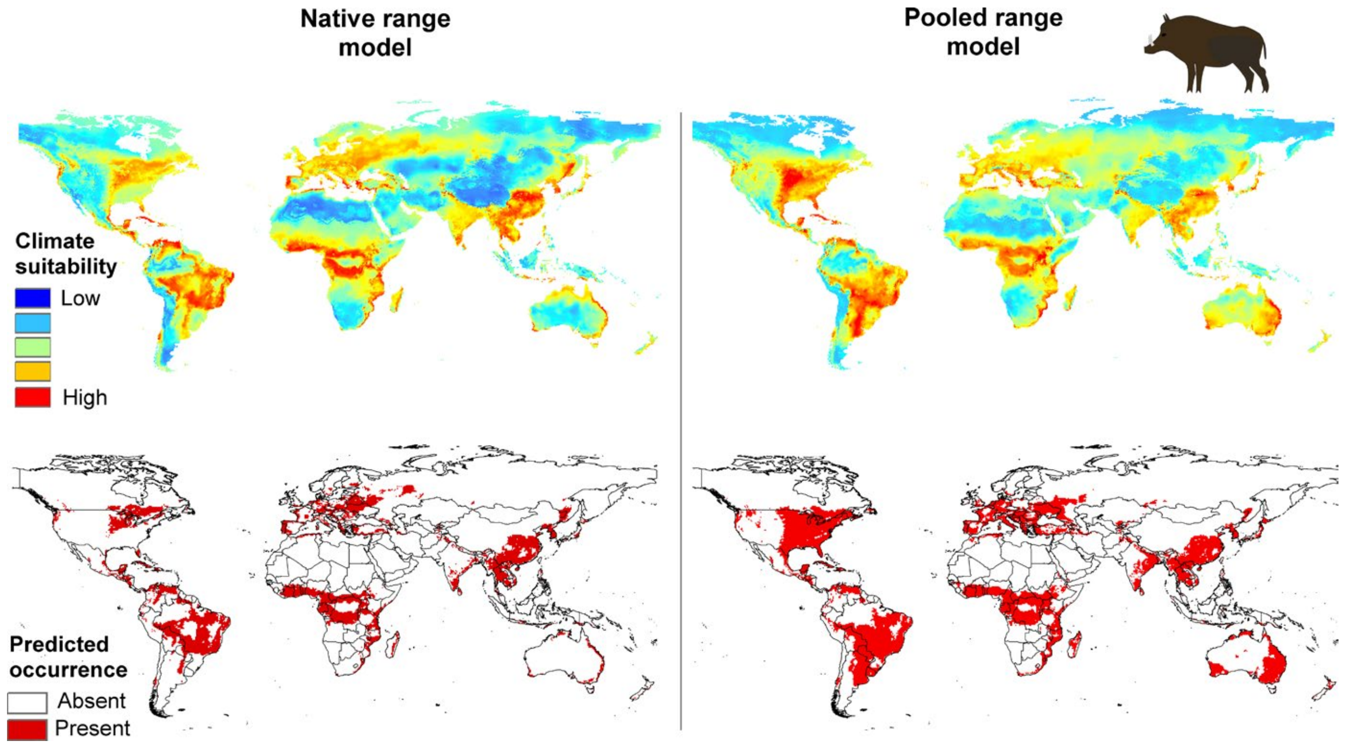

FIGURE 2 Climate suitability and potential invadable areas for the wild boar *Sus scrofa*. On the right, predictions are based on models calibrated solely with occurrences within the species native range (native-based models). On the right, models were calibrated with all locations where the wild boar is known to occur (pooled-range-based models). Continuous predictions are shown on top, where reddish colors indicate high suitability and bluish colors, low suitability. Binary predictions are presented on the downside of the picture, where red color indicates predicted presence and white color, absence [Colour figure can be viewed at wileyonlinelibrary.com]

to capture nuances of these processes. Observed changes on realized niches may in fact mislead understanding of niche shifts during biological invasions. Here, comparisons of native vs. exotic populations revealed that niches were more similar than expected by chance in the Nearctic, although not equivalent in any analysed region, and that differences may be explained by niche unfilling, rather than niche expansion (Guisan et al., 2014). Observed niche shifts due to unfilling of environmental space have already been reported for several non-native vertebrate species, including the wild boar (Strubbe et al., 2013, 2015).

Colonization history and propagule pressure also affect observed niche changes during biological invasions. Niche unfilling seems to be larger for species introduced recently and into a small number of locations, compared to those with ancient colonization history and introduced in several points in space (Strubbe et al., 2015). In this work, niche unfilling was substantially higher for the Neotropics, compared to other locations. Wild boar importation into the Neotropics has a 200-year long history (Skewes & Jaksic, 2015). However, recent waves of introduction on the 1990s for pig-farming and game hunting, followed by escape and inter-country dispersal (Pedrosa, Salerno, Padilha, & Galetti, 2015; Skewes & Jaksic, 2015) have led to explosive population growth in the Neotropics (Pedrosa et al., 2015). Because we found 28% of niche unfilling for the Neotropical region, our results indicate that the invasive potential of wild boar in this region might therefore be extremely high. Preventing expansion of wild boar distribution into Neotropical species-rich areas such as the Amazon, coupled with potential economic losses and the spread of swine fever, thus requires specific management towards population control in areas already invaded.

Because the niche of non-native populations of wild boars is a subset of its native counterparts' niche, ecological niche models should lead to accurate predictions of potential invadable areas (Strubbe et al., 2015). We found that models calibrated with occurrences within the native distribution indeed predicted areas reportedly struggling with wild boar population expansion, such as the south and southeastern Brazil (Pedrosa et al., 2015), eastern USA (Pimentel et al., 2005) and eastern Australia (Spencer & Hampton, 2005). Such correspondence probably implies that newly occupied areas are climatically similar to the ones the wild boar is already adapted to. Therefore, evolutionary markers from climatic constraints across the native range may still be evident on populations inhabiting exotic ranges (Pyron et al., 2015).

We also found a remarkable convergence on potential invadable areas for the Afrotropical region. Although no data from that region were used to calibrate ecological niche models, both calibration scenarios predicted high climatic suitability for the wild boar in central and southeastern Africa. The Suidae family is a monophyletic group of Cetartiodactyla, composed of 17 species and originated in Africa (Frantz et al., 2016). That origin of extant species is relatively recent—less than 5.3 Ma—and many lineages have and continue to hybridize (Frantz et al., 2016). Climatic constraints on species realized niche may be the result of adaptation to climates in which species have evolved (Pyron et al., 2015). If fundamental niches are phylogenetically conserved and climate-related evolutionary markers are indeed preserved on related lineages (Pyron et al., 2015), then the high climatic suitability exhibited for the wild boar may in fact be shared with other Afrotropical Suidae species. Furthermore, the diversity of Suidae species in Africa probably prevented wild boar invasion, because humans bred other suids (such as the bush pig *Potamochoerus larvatus*) and transported them through the mainland and towards Mayotte, Comoros, Madagascar and other islands (Frantz et al., 2016). Testing whether phylogenetic niches are preserved among members of the Suidae family is yet to be attempted, but could shed substantial light to the processes driving speciation in that taxa.

One exception to the ecological niche models' predictive ability was nevertheless found. Models calibrated with native occurrences were less able to predict wild boar's exotic occurrences in Australasia, compared to the other regions. Domestic pigs were first established in Australia in 1788 and recreational hunting has been common practice among Caucasian and Aboriginal groups since then (Bengsen, Gentle, Mitchell, Pearson, & Saunders, 2014; Meurk, 2015). Pig hunting is therefore part of subsistence and social practices and contributes substantially to regional economies (Meurk, 2015), despite long-lasting attempts to eradicate feral pig populations in Australian territory (Bengsen et al., 2014). Illegal transportation for game hunt and escapes from pig farms probably increased propagule pressure all over Australia, thus leading to species temporary occupancy of suboptimal climates. Those populations occupying marginal climates are characterized by sink dynamics and are not expected to persist in time (Colwell & Rangel, 2009; Soberón & Nakamura, 2009).

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

Wild boars, like other Suidae members, have a limited ability to eliminate heat. They lack functional sweat glands, have a thick hairy skin and tend to accumulate subcutaneous fat (Bracke, 2011; Fernández-Llario, 2005; Manner & McCrea, 1963). We expected that wild boars would thus preferentially occupy low temperature sites, such as high altitudes and high latitudes, to prevent hyperthermia. However, all models predicted high climatic suitability in warm areas, such as tropical America and Africa. Also, the wild boars' native distribution includes the low-latitude Indian horn, southern China and The Philippines. The occupancy of warm climates suggests that mechanisms other than physiology have evolved in wild boars to prevent overheating. In response to increased temperature, pigs usually exhibit a series of behavioural patterns, of which the most obvious is wallowing (Olczak, Nowicki, & Klocek, 2015). Wallowing helps wild boars eliminate heat and may have a sexual function in males (Fernández-Llario, 2005). We believe that behavioural flexibility may further allow the wild boars to occupy a wide range of climate conditions and thus overcome many physiological limitations, while also enhancing its invasive potential.

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

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AUTHORS' CONTRIBUTIONS

L.P.S., B.R.R., M.W.H., A.P., M.P. and R.L. conceived the ideas and designed the methods; L.P.S. and M.W.H. collected the data; L.P.S. and B.R.R analysed the data; L.P.S. led the writing; B.R.R., M.W.H., A.P., M.P. and R.L. assisted writing and reviewed the manuscript. All authors contributed 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 the Materials and methods section. Additional data were obtained from a literature survey, which is provided as Supporting Information. The final spreadsheet containing all occurrences used in this work is archived in the Dryad Digital Repository https://doi.org/10.5061/dryad.1v3c2 (Sales et al., 2017). 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.

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