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HISTÓRIA DA INVASÃO DO JAVALI (*Sus scrofa* L.) NO BRASIL CONTADA PELA DISPERSÃO E MORFOLOGIA, COM CENÁRIOS DE MANEJO DA ESPÉCIE

CARLA GRASIELE ZANIN HEGEL

Brasília, DF

2021

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“Se queres conhecer o passado, examina o presente que é o resultado; se queres conhecer o futuro, examina o presente que é a causa.”

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SUMÁRIO

RESUMO GERAL

O conhecimento da história e das rotas de dispersão dos javalis na América do Sul, e principalmente no Brasil, é indispensável para a compreensão dos processos de evolução morfológica da espécie nas áreas introduzidas, e no estabelecimento de métodos de manejo e controle mais eficazes da espécie. Meu objetivo geral nesta tese foi verificar se os fatores históricos do processo de introdução e dispersão, e a variação geográfica e ambiental das populações de javali, são refletidos na morfologia craniana da espécie. Além disso, propus cenários de manejo e controle da espécie baseados na caça direcionada ao sexo. Estruturei a tese em quatro capítulos formatados como artigos. No primeiro capítulo intitulado "Wild pigs (*Sus scrofa* L.) in Brazil - Spatial distribution and dispersion rate of invasion", fiz uma revisão da literatura, que possibilitou contar a história da invasão do javali no Brasil, mapeando sua acelerada distribuição espacial ao longo do tempo, além de criar modelos com taxas de dispersão da espécie. Dois eventos principais de introdução do javali foram responsáveis pela sua invasão: 1) no século XV, a forma doméstica da espécie foi trazida pelos colonizadores europeus durante o período de colonização; e 2) no século XX os javalis foram introduzidos para fins de caça, produção comercial e zoológicos. No Brasil as primeiras introduções do javali datam da década de 1960 e os primeiros casos de invasão pelas fronteiras com o Uruguai, são relatados ao final da década de 1980, com uma expansão rápida a partir dos anos 2000. As rotas traçadas no sentido do sul para o norte do país, variaram entre 50,62 km/ano e 89,90 km/ano, e mostram que possivelmente houve um efeito de aceleração da dispersão provocado pela ação humana e que essa velocidade não é natural à espécie. Já no segundo capítulo, intitulado "Do cranium and mandible reflect the wild pigs geographic variation in South America?", verifiquei por meio de técnicas de morfometria geométrica, se os javalis do Brasil, Argentina e Uruguai apresentavam diferenciação morfológica, na forma e tamanho de crânios e mandíbulas, em um gradiente latitudinal. Além disso, analisei se a diferenciação morfológica da espécie estava relacionada com variáveis ambientais específicas ou com a cobertura do solo. Os resultados das análises mostraram que os javalis têm variação morfológica de tamanho e forma da estrutura craniana ao longo da variação geográfica, com animais maiores nas áreas mais frias e em latitudes mais altas, concordando com a Regra de Bergmann. Entretanto, os modelos não mostraram nenhum efeito específico de uma variável climática ou ambiental agindo na diferenciação morfológica, mas sim um efeito fraco do ambiente como um todo sobre a morfologia da espécie. No terceiro capítulo, intitulado "Is there differentiation in the morphology of the skull of wild pigs (*Sus scrofa* L.) structured between native and introduced areas?", comparei pela morfometria geométrica, crânios e mandíbulas de javalis das áreas nativas com os de áreas introduzidas, e verifiquei se as caraterísticas morfológicas das linhagens nativas eram mantidas, ou variavam nos javalis de áreas onde foram introduzidos. Os resultados das análises mostraram que nem todos os grupos de javalis nas áreas introduzidas diferem quanto ao tamanho, ou à forma, em relação aos javalis das áreas nativas. Isso pode ser um efeito do processo histórico das introduções e hibridizações do passado. Nos capítulos 2 e 3, utilizei exemplares de javalis de diferentes localidades da América do Sul, América do Norte, Europa e Ásia provenientes de museus, coleções de Universidades e coleções particulares de controladores de javalis credenciados.

No total, comparei 294 crânios em vista dorsal, 254 crânios em vista lateral e 300 mandíbulas em vista dorsal, para o capítulo 2. No capítulo 3, o tamanho amostral foi de 407 crânios em vista dorsal, 359 crânios em vista lateral e 425 mandíbulas em vista dorsal. Por fim, no quarto capítulo, “Terminators of the future: Controlling population growth of the wild pigs (*Sus scrofa* L.)”, modelei 11 cenários de controle populacional do javali pela análise de viabilidade populacional (PVA) baseados na caça direcionada ao sexo. Os modelos mostraram que aumentar a pressão de caça sobre machos, não reduz o tamanho populacional dos javalis ao longo do tempo. Entretanto, aumentar a caça sobre fêmeas de 50% a 70%, parece ser uma estratégia eficaz para o manejo de javalis no Brasil.

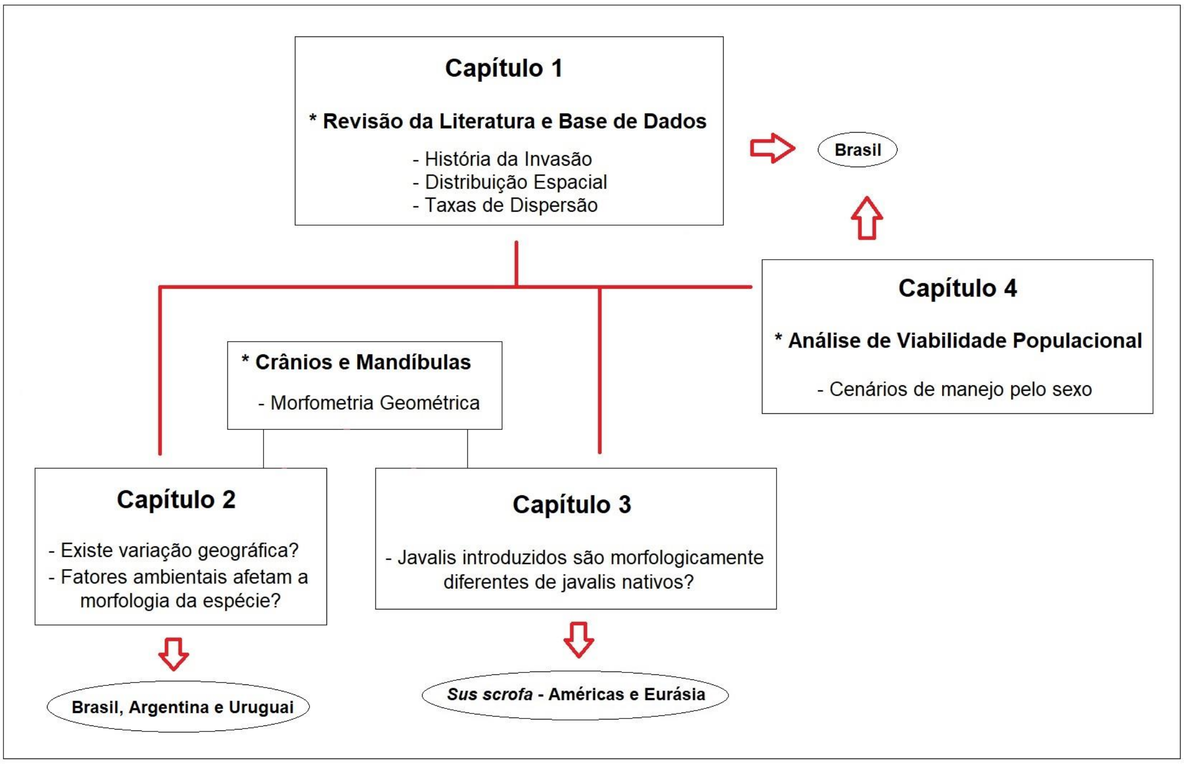
Palavras-chave: Controle populacional, Invasão biológica, Modelagem, Porcos ferais

ABSTRACT

Knowledge of the wild pigs' history and dispersal routes in South America and Brazil is essential for understanding the morphological evolution of the species in the introduced areas and setting up more effective management and control methods. The general aim of this thesis was to verify whether the historical factors of the introduction and dispersal process and the geographic and environmental variation of the wild pigs' population are reflected in the cranial morphology of the species. In addition, species management and control scenarios based on sex-oriented hunting are proposed. In the first chapter entitled "Wild pigs (*Sus scrofa* L.) in Brazil - Spatial distribution and dispersion rate of invasion", I reviewed the literature, which made it possible to tell the story of the wild pigs' invasion in Brazil, to map its accelerated spatial distribution throughout of time and create models with rates of dispersion of the species. Two main events of the introduction of the wild pigs were responsible for its invasion: 1) in the 15th century, European settlers brought the domestic form of the species during the colonization period, and 2) in the 20th century, wild pigs were introduced for hunting, commercial production, and zoological purposes. In Brazil, the first introductions of wild pigs date back to the 1960s, and the first cases of invasion across the borders with Uruguay are reported at the end of the 1980s, with a rapid expansion from the 2000s onwards. For the north of the country, they ranged between 50.62 km/year and 89.90 km/year, showing that there was possibly an acceleration effect in dispersion caused by human activity and that this speed is not natural to the species. The second chapter, entitled "Do cranium and mandible reflect the wild pigs geographic variation in South America?" It was verified through geometric morphometric techniques whether wild pigs from Brazil, Argentina, and Uruguay presented geographic differentiation in the shape and size of crania and mandibles in a latitudinal gradient. Furthermore, it was analyzed whether the morphological differences in the species was related to specific environmental variables or land cover. The analyzes showed that wild pigs have morphological differences in size and shape of the skulls across geographic variation, having larger animals in cooler areas and at higher latitudes, following Bergmann's rule. However, the models did not show a specific effect of a climatic or environmental variable acting on the morphological differentiation, but rather a weak effect of the environment as a whole on the morphology of the species. In the third chapter, entitled "Is there differentiation in the morphology of the skull of wild pigs (*Sus scrofa* L.) structured between native and introduced areas?", I compared by geometric morphometry, wild boars and wild pigs crania and mandibles from native and introduced areas, and verified whether morphological characteristics of native strains were maintained or varied from those introduced. The analyzes showed that not all groups of wild pigs in the introduced areas differ in size or shape compared to wild boars in native areas. This may be an effect of the historical process of past introductions and hybridizations. In chapters 2 and 3, it was used wild pigs and wild boars specimens from different locations in South America, North America, Europe, and Asia from museums, university collections, and private collections of accredited wild pigs controllers. In total, I used in chapter 2, 294 crania in the dorsal view, 254 crania in the side view, and 300 mandibles in the dorsal view. In chapter 3, the sample size was 407 crania in the dorsal view, 359 crania in the lateral view, and 425 mandibles in the dorsal view. Finally, in the fourth chapter, "Terminators of the future: Controlling population growth of the wild pigs (*Sus scrofa* L.)," I modeled 11 wild pigs population control scenarios based on sex-directed hunting, using population viability analysis (PVA). Increasing hunting pressure on males does not reduce wild pigs' population size over time while increasing female hunting from 50% to 70% seems to be an effective wild boar management strategy in Brazil.

Keywords: Biological invasion, Feral pigs, Modeling, Population control

RESUMO GERAL ESQUEMÁTICO



LISTA DE FIGURAS

INTRODUÇÃO GERAL

CAPÍTULO 1

CAPÍTULO 2

CAPÍTULO 3

CAPÍTULO 4

LISTA DE TABELAS

CAPÍTULO 1

CAPÍTULO 2

CAPÍTULO 3

CAPÍTULO 4

LISTA DE ANEXOS

CAPÍTULO 1

CAPÍTULO 2

CAPÍTULO 3

ANEXOS GERAIS

Introdução Geral

Invasões biológicas estão entre as maiores ameaças à biodiversidade e ao funcionamento dos ecossistemas naturais (Simberloff 2009). Nas últimas décadas, houve um aumento no número de espécies invasoras em todo o mundo (Blackburn et al. 2011), sendo que muitas foram introduzidas pelo ser humano de forma acidental ou intencional (Vitule et al. 2012). Espécies invasoras podem se tornar dominantes no ambiente onde foram introduzidas e podem provocar consequências negativas à medida que se adaptam a esse novo ambiente (Simberloff et al. 2013), causando alterações na estrutura das comunidades e na dinâmica dos ecossistemas naturais (Martin et al. 2009). Além disso, podem predar, competir ou disseminar doenças para as espécies nativas (Gurevitch e Padilla 2004; Simberloff 2009; Blackburn et al. 2011). Por isso, o manejo e controle das espécies invasoras tornou-se uma preocupação mundial (Simberloff et al. 2013).

O sucesso da invasão está principalmente relacionado aos atributos biológicos do organismo invasor (Kolar e Lodge 2001; Facon et al. 2006), à disponibilidade de recursos no ambiente (Petren e Case 1996) e a ausência de predadores ou parasitas nativos (Settle e Wilson 1990; Keane e Crawley 2002). Além disso, espécies invasoras geralmente são generalistas e beneficiadas pelas perturbações causadas pelo homem (Gurevitch e Padilla 2004; Blackburn et al. 2011). Essas espécies têm alta plasticidade em resposta às mudanças das condições ambientais, o que lhes permite ocupar novos ambientes (Bradshaw 1965; Richards et al. 2005). Assim, uma espécie invasora é capaz de se dispersar rapidamente pelo ambiente e se reproduzir atingindo expressivo tamanho populacional (Simberloff e Rejmánek 2011). Estudos ainda mostram que, durante o processo de invasão biológica, muitas populações introduzidas passaram por mudanças na morfologia e na genética, devido à variação geográfica, ambiental e/ou temporal (ver revisão de Mooney e Cleland 2001).

Animais de ampla distribuição geográfica em geral apresentam variação na morfologia (Mayr 1956; Thorpe 1987). Os padrões geralmente se manifestam por um gradiente contínuo de variação intraespecífica (clinas) gerados por gradientes ambientais, ou seja, quando a seleção natural favorece genótipos diferentes em ambientes diferentes (Brown e Lomolino 2006). Nesse sentido, variações no corpo, principalmente no tamanho, são fundamentais para a compreensão dos padrões macroecológicos das espécies (relações entre variáveis ecológicas medidas em grandes escalas de tempo e espaço) (Brown e Lomolino 2006). A variação da forma e tamanho do crânio e da mandíbula em mamíferos, por exemplo, podem revelar adaptações nos padrões e nos processos evolutivos e estes, geralmente, são influenciados por relações filogenéticas (Freckleton e Jetz 2009; Maestri et al. 2018) ou explicados por gradientes ambientais (Cardini et al. 2007; Bubadué et al. 2016).

No caso dos gradientes ambientais, a variação geográfica refletida na morfologia de mamíferos pode ser justificada principalmente pela Regra de Bergmann, pela plasticidade fenotípica da espécie ou pela Regra de Recursos. Na Regra de Bergmann, as variações na morfologia de animais endotérmicos são atribuídas à latitude, estabelecendo uma relação entre o tamanho do corpo e as diferentes regiões climáticas, onde as espécies tendem a ter indivíduos maiores em regiões frias e menores em regiões quentes, como forma de compensação de energia diante das condições climáticas locais (Bergmann 1847; Rensch 1938). Já a plasticidade fenotípica de uma espécie, refere-se às adaptações influenciadas pelas diferentes condições climáticas e ambientais. Ou seja, como um mesmo genótipo pode levar a diferentes fenótipos devido a diferenças no ambiente em que esse genótipo se desenvolve. Por consequência, a seleção natural que leva a espécie a aclimatação e futura incorporação dessas características fenotípicas, ou seja, a espécie adapta sua morfologia às condições locais (Bradshaw 1965; Turcotte e Levine 2016). Por fim, na Regra de Recursos (McNab 2010), a abundância e a disponibilidade de recursos controlam a massa corporal e o gasto de energia, considerando fatores geográficos (incluindo latitude - Regra de Bergmann), a vida em desertos ou em ilhas oceânicas (Regra da Ilha), a antecipação sazonal do inverno (Fenômeno de Dehnel), e uma tendência de aumento de massa corporal em algumas linhagens ao longo do tempo (Regra de Cope).

Em invasões biológicas, o javali (*Sus scrofa* L.) e seus híbridos, enquadram-se nesse contexto. A espécie possui uma das maiores áreas de distribuição geográfica entre os mamíferos terrestres, principalmente devido aos eventos de introdução do século passado (Barrios-García e Ballari 2012), e isso reflete em uma variação morfológica na espécie (Albarella et al. 2009). Devido à sua ampla distribuição geográfica, pode se dizer que os javalis são pré-adaptados para uma ampla gama de condições ambientais (Baskin e Danell 2003), ou adaptáveis e facilmente aclimatáveis a elas. A espécie apresenta pelo menos dezesseis subespécies com base em variações morfológicas (Groves 1981, 2007) e marcadores genéticos (Larson et al. 2005) em todo o mundo. Por isso, pesquisadores têm investido em estudos de morfologia para explicar quais são as causas das variações e diferenças na forma e no tamanho dos javalis; e compreender como os fatores históricos e ambientais vêm interferindo na morfologia da espécie (Endo et al. 2000; Albarella et al. 2009; Ježek et al. 2011).

A introdução do javali na América do Sul no século passado e consequentemente, a rápida expansão pelo Brasil nas últimas décadas (Barrios-García e Ballari 2012, Deberdt e Scherer 2007), provavelmente reflete na morfologia da espécie em resposta às condições climáticas e ambientais do novo continente. Nesse sentido, embora estudos para compreender como os javalis respondem morfologicamente aos novos ambientes após a introdução sejam extremamente necessários, eles continuam até o momento ausentes na literatura. O conhecimento da história e das rotas de dispersão dos javalis é fundamental para a compreensão dos processos de evolução morfológica da espécie em áreas introduzidas, como a América do Sul, e mais especificamente o Brasil. Serve também para embasar métodos de manejo e controle mais eficazes. Assim, meu objetivo geral nesta tese foi verificar se os fatores históricos do processo de introdução e dispersão, e a variação geográfica e ambiental das populações de javali, são refletidos na morfologia craniana da espécie. Além disso, propus cenários de manejo e controle da espécie baseados no aumento de caça direcionada para o sexo dos indivíduos.

A espécie estudada

O javali (*Sus scrofa* Linnaeus, 1758) é um mamífero pertencente à ordem Artiodactyla e à família Suidae, constituída por cinco gêneros. Um desses gêneros é o *Sus* (Bosma et al. 1996), ao qual a espécie *Sus scrofa* pertence. Atualmente, pela morfologia e genética, *Sus scrofa* representa 16 subespécies (Groves 1981; 2007).

O javali é nativo da Europa, Ásia e Norte da África e por intervenção humana tornou-se uma das espécies terrestres mais amplamente distribuídas no mundo (Oliver et al. 1993). A espécie é encontrada em todos os continentes, exceto na Antártida (Barrios-García e Ballari 2012) e habita uma gama diversificada de hábitats e condições climáticas, desde florestas boreais até desertos (Meijaard et al. 2011). As semelhanças das condições climáticas e ambientais entre as áreas nativas e as áreas onde foram introduzidos, facilitam o estabelecimento do javali nas novas áreas (Sales et al. 2017).

Os javalis têm hábitos alimentares generalistas, e a dieta varia de acordo com a localização geográfica ou a estação do ano (Genov 1981; Ballari e Barrios-García 2014). Eles se alimentam basicamente de matéria vegetal, mas também de invertebrados e vertebrados como anfíbios, répteis, aves e mamíferos (Irizar et al. 2004; Herrero et al. 2006; Giménez-Anaya et al. 2008; Cervo e Guadagnin 2020). Nas áreas invadidas, causam impactos na fauna e flora, nos ecossistemas naturais e nas culturas agrícolas (Ickes et al. 2001; Massei e Genov 2004; Herrero et al. 2006; Hegel e Marini 2013; Barrios-García et al. 2014). Competem com espécies nativas por alimento e alteram o ambiente natural por fuçar, removendo a vegetação nativa, alterando os solos e prejudicando o processo de regeneração natural da vegetação, causando sérios danos em longo prazo (Massei e Genov 2004; Cuevas et al. 2012). Por isso, é considerada atualmente uma das 100 piores espécies invasoras do mundo (Lowe et al. 2000; IUCN 2021).

Por apresentarem alta plasticidade, os javalis podem ser considerados tanto K quanto r-estrategistas (Bieber e Ruf 2005). Eles têm alto potencial reprodutivo e baixa taxa de predação (Heise-Pavlov et al. 2009). A puberdade é precoce, entre 5 e 10 meses de idade (Fonseca et al. 2011) e a gestação curta, com cerca de 108 a 120 dias (Henry 1968). O número de filhotes consiste em média de 4 a 6 leitões, variando até o máximo de 10 a 12 filhotes, com até duas gestaçoes por ano (Mendina-Filho et al. 2015). Podem reproduzir até aos 13 anos de idade (Rosell et al. 2001). O peso e o tamanho dos adultos são determinados por fatores ambientais (Fernández-Llario & Mateos-Quesada 1998), e podem variar de 50 a 350 kg, e 65 a 125 cm na altura do ombro (Meijaard et al. 2011). Os javalis possuem um comportamento agressivo, que juntamente com o grande peso e tamanho dificultam a sua predação. Apenas predadores de grande porte, como lobos, ursos, tigres, guepardos, leões, e crocodilos predam javalis (Jedrzejewski et al. 1992; Wolf e Conover 2003; Nores et al. 2008). Na América do Sul, apenas os pumas foram registrados como predadores até o momento (Branch 1995; Skewes et al. 2012; Hegel e Marini 2018). A ausência de grandes predadores nos países onde os javalis foram introduzidos, além de dificultar o controle do tamanho populacional, também facilita a invasão a novos ambientes (West et al. 2009).

O javali causa grandes impactos à economia. Os ataques às culturas agrícolas ocorrem com alta frequência e provocam danos bilionários aos plantios agrícolas (Honda 2009; West et al. 2009; Pedrosa et al. 2015), assim como na ovinocultura (Mendina-Filho et al. 2015). Javalis transmitem, tanto para a fauna nativa quanto para rebanhos domésticos, uma gama de doenças como brucelose, raiva, leptospirose e febre aftosa (Rosell et al. 2001). A espécie foi declarada nociva em vários países e no Brasil teve o abate autorizado por controladores credenciados, como uma medida de manejo e redução do tamanho populacional (IBAMA

2005; 2013). Estima-se que as densidades populacionais de javalis no Brasil variem de 0,22 a 22,3 indivíduos/km² nas regiões Sul e Sudeste (Oliveira 2012; Puertas 2015). Esses valores não são bem definidos reforçando ainda mais a necessidade de estudos e de controle da espécie no país, pois o número de novos registros em novos municípios tem aumentado consideravelmente ano após ano (Deberdt e Scherer 2007; Pedrosa et al. 2015; BRASIL - PAN Javali 2017; IBAMA 2019).

Figura 1. Javali (*Sus scrofa* L.) na Mata Atlântica. (Foto: Hegel C.G.Z., Município de Muitos Capões, 2015).

Referências Bibliográficas

Albarella U., Dobney K., Rowley-Conwy, P. (2009). Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environmental Archaeology*, 14:103–136.

Ballari S.A., Barrios-García M.N. (2014). A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mammal Review*, 44(2):124–134.

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

Barrios-García M.N., Classen A.T., Simberloff D. (2014). Disparate responses of above-and belowground properties to soil disturbance by an invasive mammal. *Ecosphere*, 5(4):1-13.

Baskin L.M., Danell K. (2003). *Ecology of ungulates: A handbook of species in Eastern Europe and Northern and Central Asia*. Berlin: Springer.

Bergmann C. (1847). Ober die Verhaltnisse der Warmeokonomie der Thiere zu ihrer Grosse. *Gottinger Studien*, 3:595-708.

Bieber C., Ruf T. (2005). Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology*, 42:1203-1213.

Blackburn T.M., Pyšek P., Bacher S., Carlton J.T., Duncan R.P., et al. (2011). A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, 26(7):333-339.

Bosma A.A., Haan N.A., Mellink C.H.M., Yerle M., Zijlstra C. (1996). Chromosome homology between the domestic pig and the babirusa (family Suidae) elucidated with the use of porcine painting probes. *Cytogenetic and Genome Research*, (75): 32-35.

Bradshaw A.D. (1965). Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, 13:115–155.

Branch L.C. (1995). Observations of predation by pumas and Geoffroy´s cats on the plains vizcacha in semi-arid scrub of central Argentina. *Mammalia*, 59:152-156.

BRASIL - PAN Javali. (2017). *Plano Nacional de Prevenção, Controle e Monitoramento do Javali (Sus scrofa) no Brasil.* Ministério do Meio Ambiente (MMA) & Ministério da Agricultura, Pecuária e Abastecimento (MAPA). Brasília, Brasil.

Brown J.H., Lomolino, M.V. (2006). *Biogeografia*. Funpec. 2ª Ed.

Bubadué J., Cáceres N., dos Santos Carvalho R., Meloro C. (2016). Ecogeographical Variation in Skull Shape of South-American Canids: Abiotic or Biotic Processes? *Evolutionary Biology*, 43:145-149.

Cardini A., Jansson A.U., Elton S. (2007). A geometric morphometric approach to the study of ecogeographical and clinal variation in vervet monkeys. *Journal of Biogeography*, 34:1663–1678.

Cervo I.B., Guadagnin D.L. (2020). Wild boar diet and its implications on agriculture and biodiversity in Brazilian forest–grassland ecoregions. *Animal Biodiversity and Conservation*, 43(1):123-136.

Cuevas M.F., Mastrantonio L., Ojeda R.A., Jaksic F.M. (2012). Effects of wild boar disturbance on vegetation and soil properties in the Monte Desert, Argentina. *Mammalian Biology*, 77:299–306.

Deberdt A.J., Scherer S.B. (2007). O javali asselvajado: ocorrência e manejo da espécie no Brasil. Natureza & Conservação, 5(2):31-44.

Endo H., Hayashi Y., Yamazaki K., Motokawa M., Pei J.-C.K., et al. (2002). Geographical Variation of Mandible Size and Shape in the Wild Pig (*Sus scrofa*) from Taiwan and Japan. *Zoological Studies*, 41:452-460.

Facon B., Genton B.J., Shykoff J., Jane P., Estoup A., et al. (2006). General ecoevolutionary framework for understanding bioinvasions. *Trends in Ecology and Evolution*, 21(3):130-135.

Fernández-Llario P., Mateos-Quesada P. (1998). Body size and reproductive parameters in the wild boar *Sus scrofa*. *Acta Theriologica*, 43:439–444.

Freckleton R.P., Jetz W. (2009). Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proceedings of the Royal Society of London B: Biological Sciences*, 276:21-30.

Fonseca C., Alves da Silva A., Alves J., Vingada J., Soares A.M.V.M. (2011). Reproductive performance of wild boar females in Portugal. *European Journal of Wildlife Research*, 57(2):363–371.

Genov P. (1981). Food composition of wild boar in North-eastern and Western Poland. *Acta Theriologica*, 26:185–205.

Giménez-Anaya A., Herrero J., Rosell C., Couto S., García-Serrano A. (2008). Food habits of wild boars (*Sus scrofa*) in a Mediterranean coastal wetland. *Wetlands*, 28:197–203.

Groves C. (1981). Ancestors for the pigs; taxonomy and phylogeny of the genus Sus. Department of Prehistory, Research School of Pacific Studies. *Australian Natural University Technical Bulletin*, 3:1-96.

Groves C.P. (2007). Current views on taxonomy and zoogeography of the genus Sus. *Pigs and humans*, 10:15-29.

Gurevitch J., Padilla D.K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution*, 19(9):470-474.

Hegel C.G.Z., Marini M.Â. (2013). Impact of the wild boar, *Sus scrofa*, on a fragment of Brazilian Atlantic Forest. *Neotropical Biology and Conservation, 8*, 17-24.

Hegel C.G.Z., Marini M.Â. (2018). Large felids as predators of wild boars in the Atlantic Forest: reconciling Verdade et al. and Rosa et al. *Animal Conservation*, 21(5):363-364.

Heise-Pavlov P.M., Heise-Pavlov S.R., Nelson J.E. (2009). *Sus scrofa*: Population structure, reproduction and condition in Tropical North-Eastern Australia. *Acta Silvatica et Ligniaria Hungarica*, 5:179-188.

Henry V.G. (1968). Length of estrous cycle and gestation in European wild hogs, *Journal of Wildlife Management*, 32:406–408.

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

Honda T. (2009). Environmental factors affecting the distribution of the wild boar, sika deer, Asiatic black bear and Japanese macaque in central Japan, with implications for human-wildlife conflict. *Mammal Study*, 34:107-116.

IBAMA. (2005). *Instrução Normativa Ibama Nº 71 de 04 de agosto de 2005 do Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (IBAMA).* Brasília: Ministério do Meio Ambiente (MMA).

IBAMA. (2013). *Instrução Normativa Ibama Nº 03 de 31 de janeiro de 2013 do Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (IBAMA).* Brasília: Ministério do Meio Ambiente (MMA).

IBAMA. (2019). Relatório sobre áreas prioritárias para o manejo de javalis: aspectos ambientais, socioeconômicos e sanitários. Batista G. O. (Org.). Brasília: Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (IBAMA).

Ickes K. (2001). Hyper-abundance of native wild pigs (*Sus scrofa*) in a lowland dipterocarp rain forest of Peninsular Malaysia. *Biotropica*, 33:682-690.

Irizar I., Laskurain N.A., Herrero J. (2004). Wild boar frugivory in the Atlantic Basque Country. *Galemys*, 16:125–133.

IUCN - International Union for Conservation of Nature. (2021). *The IUCN red list of threatened species.* Disponível em: http://www.iucnredlist.org/search/details. Acesso em 09 de maio de 2021.

Jedrzejewski W., Jedrzejewska B., Okarma H., Ruprecht A.L. (1992). Wolf predation and snow cover as mortality f actors in the ungulate community of the Białowieza National Park, Poland. *Oecologia*, 90(1):27-36.

Ježek M., Štípek K., Kušta T., Červený J., Vícha J. (2011). Reproductive and morphometric characteristics of wild boar (*Sus scrofa*) in the Czech Republic. *Journal of Forest Science*, 57:285–292.

Keane R.M., Crawley M.J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, 17(2):167-170.

Kolar C.S., Lodge D.M. (2001). Progress in invasion biology: predicting invaders. *Trends Ecology Evolution*, 16:199-204.

Larson G., Dobney K., Albarella U., Fang M., Matisoo-Smith E., et al. (2005). Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science*, 307(5715):1618-1621.

Lowe S., Browne M., Boudjelas S., De Poorter M. (2000). *100 of the World's Worst Invasive Alien Species a selection from the Global Invasive Species Database*. Published by The Invasive Species Specialist Group - ISSG, Species Survival Commission - SSC, World Conservation Union - IUCN. 12 p.

Maestri R., Monteiro L.R., Fornel R., de Freitas T.R.O., Patterson B.D. (2018). Geometric morphometrics meets metacommunity ecology: environment and lineage distribution affects spatial variation in shape. *Ecography*, 41(1):90-100.

Martin M.R., Tipping P.W., Sickman J.O. (2009). Invasion by an exotic tree alters above and belowground ecosystem components. *Biological Invasions*, 11(8):1883-1894.

Massei G., Genov P.V. (2004). The environmental impact of wild boar. *Galemys*, 16:135-145.

Mayr E. (1956). Geographical character gradients and climatic adaptation. *Evolution*, 10(1):105-108.

McNab B.K. (2010). Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia*, 164(1):13-23.

Meijaard E., d'Huart J., Oliver W.L.R. (2011). Family Suidae (Pigs). In book: *Handbook of the Mammals of the World*, Volume 2. Edition: Barcelona, Publisher: Lynx Edicions, Editors: Wilson, Mittermeier, pp. 248-291.

Mendina-Filho L.H., Wallau M.O., Dos Reis T.X. (2015). *O Javali no Pampa: contexto, biologia e manejo.* Pallotti, Santana do Livramento.

Mooney H.A., Cleland E.E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, 98(10):5446-5451.

Nores C., Llaneza L., Álvarez M.A. (2008). Wild boar *Sus scrofa* mortality by hunting and wolf *Canis lupus* predation: an example in northern Spain. *Wildlife Biology*, 14:44-51.

Oliveira, C.H.S. (2012). Ecologia e manejo de javali (*Sus scrofa* L.) na América do Sul. Tese, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil.

Oliver W.L.R., Brisbin I.L. (1993). *Introduced and Feral Pigs: Problems, Policy and Priorities.* In: Oliver WLR (ed) Status Survey and Conservation Action Plan. Pigs, Peccaries and Hippos. IUCN, pp. 159-191.

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

Petren K., Case T.J. (1996). An esperimental demonstration of exploitation competition in an ongoing invasion. *Ecology*, 77:118-132.

Puertas F.H.G. (2015). A invasão do javali na Serra da Mantiqueira: aspectos populacionais, uso do habitat e sua relação com o homem. Tese, Universidade Federal de Lavras, Lavras, Minas Gerais, Brasil.

Rensch B. (1938). Some problems of geographical variation and species-formation. *Proceedings of the Linnean Society of London*, 150(4):275-285.

Richards C.L., Pennings S.C., Donovan L.A. (2005). Habitat range and phenotypic variation in salt marsh plants. *Plant Ecology*, 176:263–273.

Rosell C., Fernández-Llario P., Herrero J. (2001). El jabalí (*Sus scrofa* Linnaeus, 1758). *Galemys*, 13:1–25.

Sales L.P., Ribeiro B.R., Hayward M.W., Paglia A., Passamani M., et al. (2017). Niche conservatism and the invasive potential of the wild boar. *Journal of Animal Ecology*, 86:1214-1223.

Settle W.H., Wilson L.T. (1990). Invasion by the Variegated Leafhopper and Biotic Interactions: Parasitism, Competition, and Apparent Competition. *Ecology*, 71(4):1461-1470.

Simberloff D. (2009). The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution and Systematics*, 40:81-102.

Simberloff D., Rejmánek M. (2011). *Encyclopedia of Biological Invasions*. University of California Press. Benkeley, Los Angeles, London.

Simberloff D., Martin J-L., Genovesi P., Maris V., Wardle D.A., et al. (2013). Impacts of Biological Invasions: What's What And The Way Forward. *Trends in Ecology and Evolution*, 28(1):58-66.

Skewes O., Moraga C.A., Arriagada P., Rau, J.R. (2012). El jabalí europeo (*Sus scrofa*): Un invasor biológico como presa reciente del puma (*Puma concolor*) en el sur de Chile**.** *Revista Chilena de Historia Natural*, 85:227-232.

Thorpe R.S. (1987). Geographic variation: a synthesis of cause, data, pattern and congruence in relation to subspecies, multivariate analysis and phylogenesis. *Italian Journal of Zoology*, 54(1):3-11.

Turcotte M.M., Levine J.M. (2016). Phenotypic plasticity and species coexistence. *Trends in Ecology and Evolution*, 31:803–813.

Vitule J.R.S., Freire C.A., Vazquez D.P., Nuñez M.A., Simberloff D. (2012). Revisiting the potential conservation value of non-native species**.** *Conservation Biology*, 26(6):1153-1155.

West B.C., Cooper A.L., Armstrong J.B. (2009). Managing wild pigs: A technical guide. *Human-Wildlife Interactions Monograph*, 1:1-55.

Wolf T., Conover M.R. (2003). *Feral pigs and the environment: an annotated bibliography*. Berryman Institute Publication 21, Utah State University, Logan; Mississippi State University, Starkville.

Wild pigs (*Sus scrofa* L.) in Brazil - Spatial distribution and dispersion rate of invasion

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ABSTRACT

Wild pigs (*Sus scrofa* L.) are considered one of the 100 worst invasive species, causing adverse social, economic, and environmental impacts worldwide. Knowing the wild pigs' dispersion rate and route of invasion can help early detection in areas yet to be invaded. Our goal was to update the information about the invasion history and distribution of wild pigs and calculate the dispersion rate of the species in Brazil. Using extant occurrence records in the literature, we built distribution maps and calculated the dispersion rate. We identified occurrences of wild pigs in 1,152 municipalities, primarily concentrated in the southeast region of Brazil (52.95%). The dispersion rate was estimated for five potential routes and varied between 50.62 km/year and 89.90 km/year. Our results revealed an accelerated increase of wild pigs in the last 30 years in Brazil, especially across the southern regions. Both the highly fragmented landscapes and natural open vegetation of the southern regions may ease wild pig movement. Some other locations, particularly the Amazon Forest, have experienced low dispersal rates and may resist invasion. This is the first research showing the dispersal rates and patterns of wild pigs in the country. Our results have straightforward implications in managing this critical invasive species, helping in preventing invasion from occurring in new areas.

Keywords: Wild boar, Neotropics, Dispersion route, Species Introduction, Biological Invasion

Introduction

During the European navigations of the Age of Discovery (1400 - 1600), domestic pigs from the genus *Sus* were used as bargaining chips and as a source of protein in the newly discovered territories as trade routes expanded (Oliver 1993). Given the wide range of environments suited for these pigs, their tremendous adaptive capacity, and fast reproduction rates, they quickly became an important species for the colonized areas. Pigs in domestic and wild forms have been set up worldwide and are found on every continent except Antarctica and several oceanic islands (Oliver 1993; Barrios-García and Ballari 2012). Wild boars, especially the *Sus scrofa* L. (native to Asia, Europe, and North Africa), were introduced much later. Domesticated pigs and wild boars eventually crossbred, resulting in a lineage of wild pigs that carry characteristics that make them one of the world's most successful invasive vertebrate species (Keiter et al. 2016; Melletti and Meijaard 2017). Given their ubiquitous distribution and adverse impact on biodiversity and natural ecosystems (e.g. Massei and Genov 2004; Herrero et al. 2006; Hegel and Marini 2013; Barrios-García et al. 2014; Hegel et al. 2019), wild pigs are considered one of the 100 worst invasive species in the world (Lowe et al. 2000).

In South America, European wild boars were introduced in the first decade of the 1900s to establish hunting grounds in Argentina, then Uruguay and Chile in the 1920s (Daciuk 1978; Navas 1987; García et al. 2011; Sagua et al. 2018). The species has since returned to nature through escapes and deliberate releases that formed wild populations, invading new areas and expanding its distribution to different regions (Jaksic 1998; Deberdt and Scherer 2007; Novillo and Ojeda 2008; García et al. 2011; Acosta et al. 2019). A similar process was observed in Oceania and North America where the species is also not native (Cucchi et al. 2009; Mayer 2009). In Brazil, raising pigs free range was a common practice since early colonial times, with many of those populations becoming feral (Mourão et al. 2002). Free range practices were eventually limited by conflicts with agricultural activities and sanitary regulations as commercial pig production expanded during the mid- and late-1900s.

A fast expansion and dispersion of wild pigs in Brazil started being documented in the late 1980s in the Rio Grande do Sul state (RS) (Deberdt and Scherer 2007), although many other geographically restricted and unverified reports date as far back as the 1960s (Salvador 2012). In the early 1990s, wild pigs were spread due to biological invasion and through introduction cycles for commercial and illegal hunting purposes (IBAMA 1995). The expansion of wild pigs is uneven throughout Brazil (Salvador 2012), resulting in multiple nuclei of dispersion. Four decades after the first official report, wild pigs are found in most country regions, causing significant ecological and economic damage (Pedrosa et al. 2015). Despite the known impact of the wild pig invasion, there is no estimate of the speed of dispersion of the species.

Studies analyzing the dispersal distances of wild pigs are necessary for understanding the genetic diversity, population structure, and probability of disease dispersion (Casas-Díaz et al. 2013; Jerina et al. 2014; Han et al. 2021) and are therefore needed for the effective implementation of population control strategies and public mitigation policy. The knowledge of dispersion and invasion behavior in individuals may help early detect new mammal invasions or reinvasions (Clout and Russell 2008) and aid in management efforts to control population growth and prevent invasion from occurring in new areas. Our goal is to update information about the invasion history and distribution of wild pigs and calculate the dispersion rate of the species in Brazil.

Methods

Data collection

To evaluate the historical process of invasion and spatial distribution of wild pigs in Brazil, we collected data from 15 official and peer-reviewed datasets (IBAMA 1995, 2002, 2004, 2019; Menezes 2002; Frankenberg 2005; Ladeia et al. 2006; Deberdt and Scherer 2007; Bach 2009; Fonseca et al. 2009; Salvador 2012; Pedrosa et al. 2015; BRASIL - PAN Javali 2017; SAA/SP 2018; Rosa et al. 2020). This research includes the revision of scientific papers, governmental reports, and Ph.D. theses holding information about geographic distribution. We evaluated a timeframe between 1990 to 2020 and considered the date on the record or the dataset publication date as the date of occurrence (e.g., when the event was recorded, but no specific date is available). We reviewed the compiled database to exclude errors including data with incomplete information (e.g., municipality without the date) or duplicates. We also excluded information collected by interviews made by non-specialist or untrained staff (e.g., unverified popular reports), and data with dubious collection methods.

Map generation

We compiled and reviewed the database and plotted the distribution of wild pigs through two approaches. First, we plotted all municipalities that reported wild pigs' presence in Brazil (spatial), then we plotted all reports as a function of time (temporal). This was done for four periods: before 1990, between 1990 and 2000, between 2000 and 2010, and after 2010. A third map was created to visualize the development of the distribution over time based on the most suitable routes and the species' biological capacity (see dispersion rate section). Maps were generated using QGis 3.16 (QGis Development Team 2020). The shapefiles were merged with geographic information from Brazil and elsewhere in South America collected from public repositories such as Instituto Brasileiro de Estatística e Geografia - IBGE (IBGE 2021).

Dispersion rate

We calculated the wild pigs’ dispersion rate following Bonino et al. (2010) and Faria et al. (2016), considering the routes follow in the north direction of the country. We excluded the historical data of introductions, and we considered the records of wild pigs invasion from Jaguarão (RS), from the border with Uruguay, in 1989.

We determined the municipalities on the route according to the following criteria 1) find a cluster of municipalities with the same reporting year; 2) in this cluster, determine which municipality has a more northerly location (Bonino et al. 2010, Faria et al. 2016). We observed if there were more than one conglomerate of records for the same year and they are in different directions, the same route can be divided. Thus, we considered the extreme geographical points (e.g., southernmost, and northernmost report), and intermediate points, to calculate the invasion routes. The intermediate points are necessary to trace small tracks in the south-north orientation to make one route. Those intermediate points are essential for accounting for the significant differences in landscape physiognomy and physical obstacles such as rivers, mountains, biome differences, urban areas, and agricultural areas.

To estimate the dispersion rate, we first calculated the dispersion rate of the track of municipalities in the same route. For this, we stipulated the differences in distance and timing between each municipality in the track of the route (e.g. distance and timing between municipality A and municipality B; distance and timing between municipality B and municipality C, and so on). After that, we calculated the route dispersion from the sum of the dispersion rate of each track of the route, divided by the total number of tracks in the same route. As a result, we obtained the dispersal rate in km/year for different routes between extreme municipalities. We used Google Sheets (Google Inc 2021) for data organization and calculations.

Results

Historical Data

Introduction, establishment, and invasion of the wild pigs: a brief history

The introduction, establishment, and invasion of the wild pigs in South America specifically in Brazil, went through different routes starting centuries ago with European naval expeditions and colonization (Salvador 2012; Table 1). In the late 15th century, the first European settlers brought multiple breeds of domestic pigs (Burgos-Paz et al. 2013). The first record of pigs in Brazil dates from 1532 by Martin Afonso de Souza (Mariante and Cavalcante 2006). Those animals were extensively raised free-range around settlements throughout the colonies and were used as sources of fat and meat. Some original wild pig populations from early domestic breeds are still (Donkin 1985; Long 2003), such as the feralized population of the Pantanal ecosystem (Mourão et al. 2002).

Table 1. Review of the history of two primary forms of *Sus scrofa* (domestic pig and wild boars) introductions since the beginning of European settlement (late 15th century) in South America and in Brazil.

Form	Year	Origin	Destination	Reason
Domestic Pigs	1493-1900	Iberic Peninsula[1,2,3]	Whole continent (including coastal and oceanic islands)	extensive farming for meat and fat
	1900-1970	Many national and imported naturalized breeds[4-9]		
	1970-	Few national and imported naturalized breeds[4-9]		intensive farming for meat
Wild boar	1904-1909	Siberia or Europe[10-12]	Argentina	game
	1924-1928	Uruguay[11,12]	Argentina	game
	1917-1956	Argentina[10,13-16]	Chile	dispersion
	1950	Germany[15-16]	Chile	zoo
	1924-1928	Caucasus[10,17,18]	Uruguay	game
	1961-4 and 1983	Germany[10,26]	Brazil	zoo
	1989	Uruguay[17-21,25]	Brazil	dispersion
	1992-1998	Argentina and Uruguay[21,24-26]	Brazil	farming for meat
	1997	France[21,23,26]	Brazil	farming for meat
	1998-2010	Brazil[21,23,26]	Brazil	farming for meat
		Unknown[24,25]	Colombia and Peru	unknown
	2011-	Argentina and Uruguay (via Brazil)[26]	Paraguay	game and dispersion
		Argentina and Uruguay [26]	Argentina, Uruguay, Brazil and Paraguay	game and dispersion

Source: Salvador (2012): 1-(Donkin 1985); 2-(Zadik 2005); 3-(Rodero et al. 1992);4-(Silva Filha 2008); 5-(Bach 2009); 6-(Castro et al. 2002); 7-(Mariante and Cavalcani 2006); 8-(Mariante et al. 2003); 9-(Primo 2004); 10-(Daciuk 1978); 11-(Navas 1987); 12-(Canevari and Vaccaro 2007); 13-(Jaksic 1998); 14-(GISD 2016); 15-(Skewes and Morales 2006); 16-(Skewes 2010); 17-(Ghione et al. 2008); 18-(García et al. 2011); 19-(Valério 1999); 20-(Porto 1994); 21-(Deberdt and Scherer 2007); 22-(Fonseca et al. 2009); 23-(Oliveira 1996); 24-(IASI 2016); 25-(IABIN 2016); 26-(Salvador 2012).

The first reports of wild boars' introductions in South America are from the beginning of the 20th century. These animals were brought from Europe to Argentina to set up hunting farms (Daciuk 1978; Navas 1987; Canevari and Vaccaro 2007; see Table 1). Through escapes or deliberate introductions, those animals later dispersed into other territories (Salvador 2012; Sagua et al. 2018; Acosta et al. 2019). It is estimated that by as early as 1914, wild boars were already introduced throughout much of the Argentinian territory (Navas 1987). The first introduction of wild boars in Uruguay was in 1920 at the department of Colonia (García et al. 2011).

In Brazil, reports of deliberate introductions of wild boars go back to the mid-1960s, where animals were imported from different countries such as Uruguay, Germany, and France for setting up hunting grounds, commercial meat production, or zoos. This occurred in various parts of the country. These commercial imports were intended for breeding pure lineages, avoiding miscegenation with wild pigs. Introductions would have occurred in regions such as Rio de Janeiro state (Rio de Janeiro, RJ) around 1961, and municipalities such as Palmeira, Campo Largo, and Ponta Grossa in Paraná state (Paraná, PR) around 1966 (Bach 2009; Salvador 2012). In this period, free-ranging wild pigs were restricted to only a few regions in Brazil.

A rapid expansion of wild pigs in Brazil was first noted around the late 1980s in Jaguarão (Rio Grande do Sul, RS; Deberdt and Scherer 2007). Deberdt and Scherer (2007) commented that the invasion might have been associated with a significant drought in 1989. This episode would have lowered the water level of the Jaguarão river that divides the border between Brazil and Uruguay, allowing animals to cross. They add, however, that it is currently believed that animals were brought from Uruguay into the country by road, transported illegally for farming or for setting up hunting grounds. Other records suggest a later date for the invasion through the same region (Jaguarão or Herval), that date being between 1991 and 1992 (Fonseca et al. 2009). In studies developed before those dates, Pereira-Neto et al. (1992) did not register wild pigs in this region.

Nevertheless, reports of conflicts and damage to crops and livestock were already present. Wild pigs found a favorable breeding ground for expanding, with a mosaic of agriculture and native forest supplying ample resources and little competition. The expansion of wild pigs seems to have followed the main river basins, which offered shelter, food, and water. In the country's southern region, an abundance of native species, such as *Araucaria angustifolia* (Bertol.) Kuntze, also serves as an essential food source (Deberdt and Scherer 2007).

The popularity of wild pigs as game animals and exotic meat increased in 1990, when commercial breeding accelerated their distribution. In this period, several breeding and rearing facilities, both legal and illegal, were set up in the South and Southeastern regions (Salvador 2012). In the northeast part of Rio Grande do Sul state, wild pigs breeding sites would have been installed in municipalities like Caxias do Sul (RS). In the late 1990s, these wild pigs would have been sold to other states in Brazil, such as São Paulo (SP), Santa Catarina (SC), Paraná (PR), Minas Gerais (MG), Mato Grosso do Sul (MS), and Bahia (BA) (Salvador 2012). New genetic (pure) lineages were also imported from Europe to refresh the bloodlines, such as in the late 1990s when wild boars were imported from France to Serra Azul (SP) (Oliveira 1996; Paiva 1996; Deberdt and Scherer 2007; Salvador 2012). Nowadays, there are at least six different origins in space and time of wild pigs in Brazil and South America (Table 1). Despite earlier introductions in Brazil between the 1960s and 1990s, the invasion sped up only in the 2000s, when wild pigs became a country-wide problem (Deberdt and Scherer 2007; Pedrosa et al. 2015; BRASIL - PAN Javali 2017) (Figure 1 and 2).

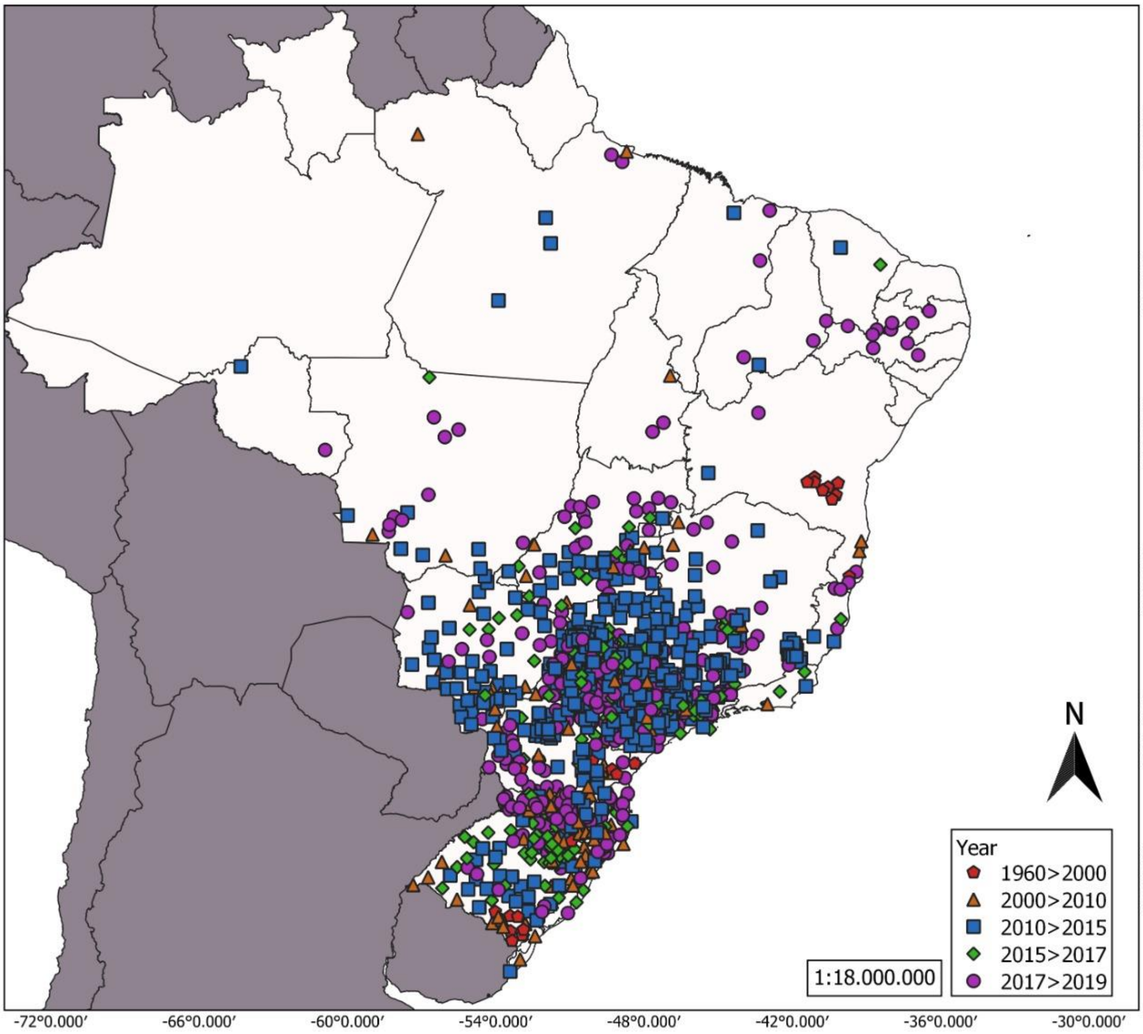

Figure 1. Wild pigs' occurrences in Brazil extracted from databases considering the year on record (IBAMA 1995, 2002, 2004, 2019; Menezes 2002; Frankenberg 2005; Ladeia et al. 2006; Deberdt and Scherer 2007; Bach 2009; Fonseca et al. 2009; Salvador 2012; Pedrosa et al. 2015; BRASIL - PAN Javali 2017; SAA/SP 2018; Rosa et al. 2020).

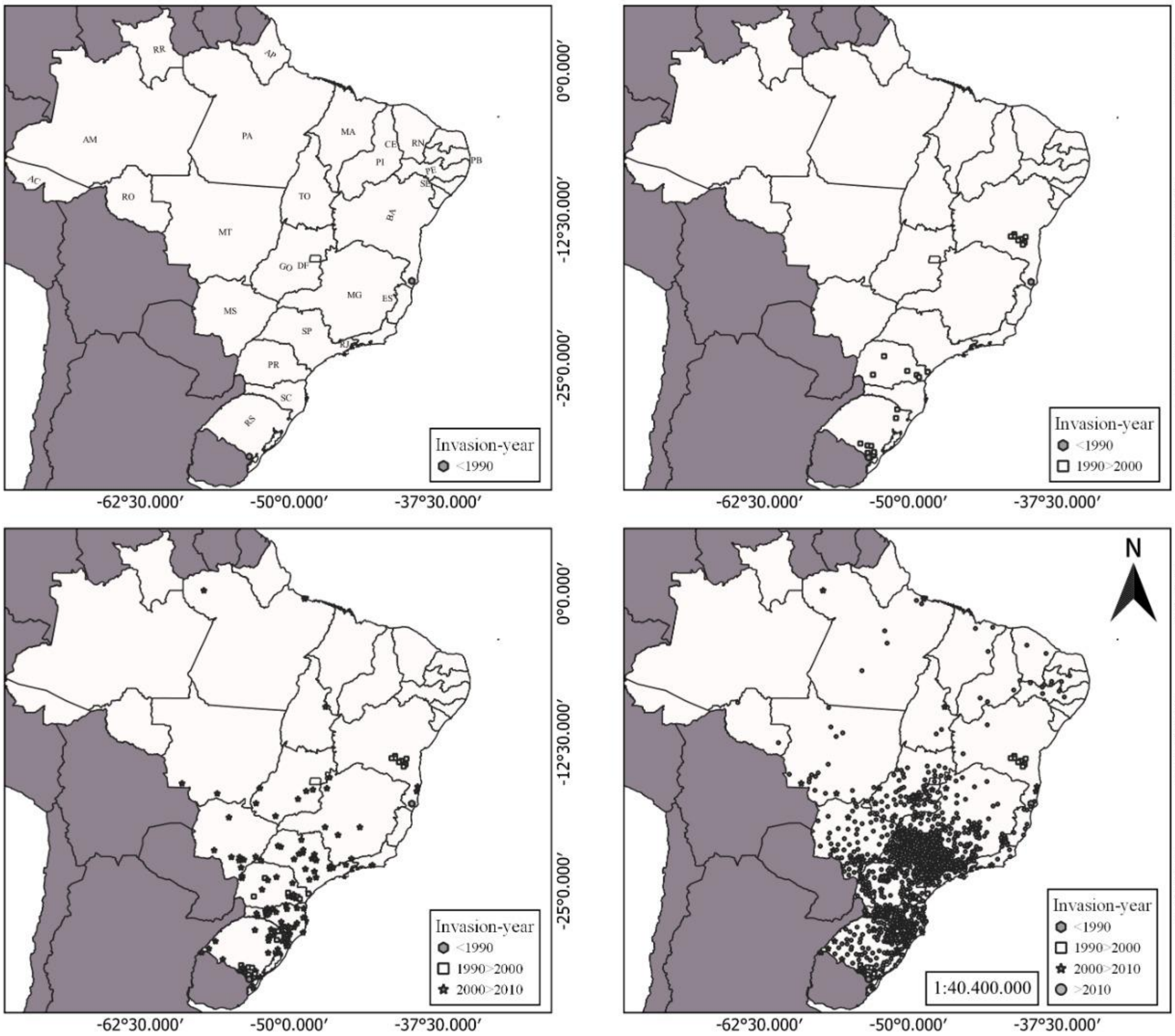

Figure 2. The distribution of wild pigs: A) before 1990, B) from 1990 to 2000, C) from 2000 to 2010, D) after 2010.

Wild pigs: a pest species in Brazil

In 1995, the problems caused by wild pigs in Southern Brazil became more prevalent, and the federal environmental agency (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis - IBAMA) allowed for population control in specific invaded areas in RS state (Ordinance 7/1995; IBAMA 1995). The legislation set up in 1998 prohibited the installation of new commercial wild boar farms (Ordinance 102/1998; IBAMA 1998b) and suspended all animal imports (Ordinance 92/1998; IBAMA 1998a).

From around 2000 to 2005, the imposed restrictions and economic issues led to the shutdown of commercial meat production, likely resulting in the widespread release of those animals into the wild (Salvador 2012). After the 2000s, wild pigs were already present in most of the Brazilian states except Alagoas (AL), Amapá (AP), Amazônia (AM), Rio Grande do Norte (RN), Roraima (RR) and Sergipe (SE) (Figure 2) (IBAMA 1995, 2002, 2004, 2019; Menezes 2002; Frankenberg 2005; Ladeia et al. 2006; Deberdt and Scherer 2007; Bach 2009; Fonseca et al. 2009; Salvador 2012; Pedrosa et al. 2015; BRASIL - PAN Javali 2017; SAA/SP 2018; Rosa et al. 2020). Most reports were from the South (29.43%) and Southeast (52.95%) regions where the first introductions and invasions occurred. An interesting fact that may have contributed to this distribution is land use and occupation. These regions contain most of the Brazilian population, suggesting that more anthropized areas may be more favorable for dispersion of invasive species such as wild pigs, as previously reported. The characteristic abundance of food (e.g. garbage and agricultural products) and absence of predators (Van der Windt and Swart 2008; Hulme 2009) in those regions are favorable for wild pigs.

Reports on the presence and damage caused by wild pigs escalated between 2000 and 2015. The number of invaded municipalities increased from 20 in 2000 to 91 in 2007, 370 in 2012, and 472 in 2015 (IBAMA 2002; Salvador 2012; Pedrosa et al. 2015). In 2013, IBAMA declared wild pigs harmful and allowed lethal population control as the principal management strategy in all national territory. The Inter-Institutional Committee on Management and Monitoring of wild pig populations were formed (IBAMA 2013).

In 2017 the Brazilian Ministry of the Environment (Ministério do Meio Ambiente, MMA) and Ministry of Agriculture (Ministério de Agricultura, Pecuária e Abastecimento, MAPA) organized a series of meetings to discuss a national plan for wild pigs control and mitigation of damages (BRASIL - PAN Javali 2017). The general goal was to establish a plan to contain wild pigs territorial and demographic expansion and reduce their impacts, especially in priority areas of environmental, social, and economic interest. In 2019, because of this national effort, IBAMA indicated that 1,563 municipalities in all country regions were affected by wild pigs (IBAMA 2019).

Current distribution and Dispersion rate and routes

We identified 1,152 municipalities with occurrences of wild pigs in Brazil (Supplementary material 1; Figure 2), an increase of 244% of municipalities from the survey developed by Pedrosa et al. (2015). Most records were in the Southeast (52.95%) and South (29.43%), followed by the Northeast (13.89%), Midwest (2.95%), and North (0.78%) (Figure 1). Concerning Brazilian biomes, the Atlantic Forest accounts for more than half of records (60.42%), followed by Cerrado (29.69%), Pampa (5.46%), Amazon (1.91%), Caatinga (1.91%), and Pantanal (0.61%). In relative terms, the Atlantic Forest and Pampa correspond to about 15% and 2% of Brazilian territory, respectively.

Five proposed routes of dispersion were spread between Jaguarão (RS) and the extreme points. All routes share a similar path until Teodoro Sampaio (SP) (Figure 3), where they then branched out in different directions. We identified the routes as follows: South-Midwest-North (RSMN), South-Midwest-Northeast (RSMNE), South-Southeast-Northeast (RSSNE), South-West (RSW) and South-West-North (RSWN).

The route between Jaguarão (RS) and Teodoro Sampaio (SP) was a standard track for all routes, with a 51.17 km/year dispersion rate. The routes RSW and RSWN share the stretch between Jaguarão in RS and Barra do Bugres in Mato Grosso state (MT), but each trajectory has a different northernmost record and dispersion rate, 50.62 km/year for RSMNE and 89.90 km/year, for RSWN (Table 2). The fastest rate of invasion was RSWN. Despite having a lower dispersion rate than other routes, RSMNE has a large concentration of municipalities, denoting potentially intensive lateralization from the mainstream. We considered a municipality the central point of a small region in the routes, but wild pigs are not restricted to geographical limits. It is also possible that many other municipalities are not mentioned in our table, as wild pigs may have already expanded their occurrence area since the last reports. RSWN also presents significant advances in space in a short time (e.g. Barra do Bugres (MT) to Paranaíta (MT), 626.21 km/year) and the longest total distance traveled (5,465.83 km) (Supplementary material 2).

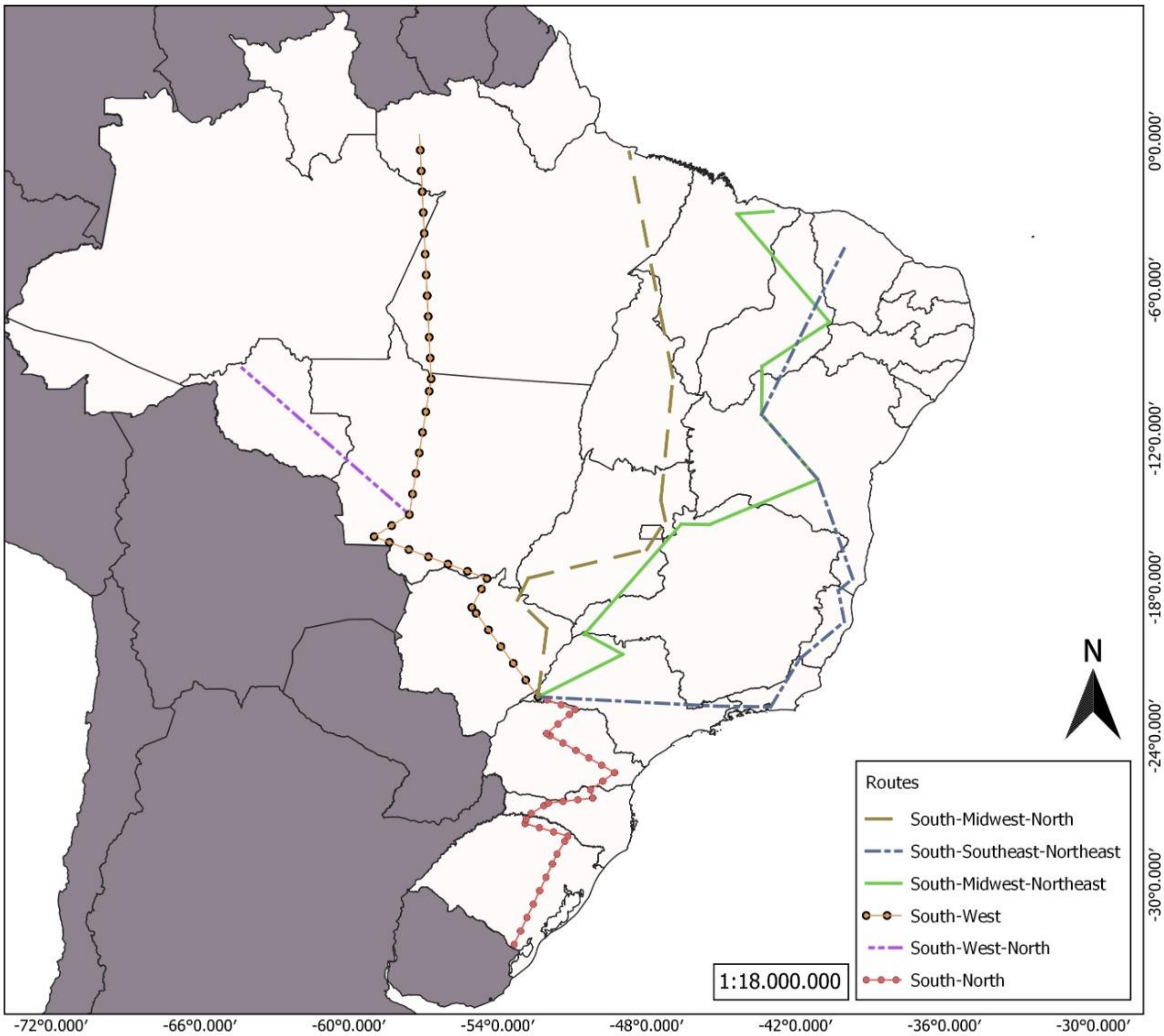

Figure 3. The five routes of wild pigs dispersion and invasion in Brazil: The South-Midwest-North (RSMN), South-Midwest-Northeast (RSMNE), South-Southeast-Northeast (RSSNE), South-West (RSW), and South-West-North (RSWN).

Table 2. Routes of dispersion for invasions and dispersion rates found for each route in Brazil. BA - Bahia state; CE - Ceará state; GO - Goiás state; MA - Maranhão State; MG - Minas Gerais State; MS - Mato Grosso do Sul state; MT - Mato Grosso state; PA - Pará state; PI - Piauí state; PR - Paraná state; RJ - Rio de Janeiro state; RO - Roraima state; RS - Rio Grande do Sul state; RSMN - South-Midwest-North; RSMNE - South-Midwest-Northeast; RSSNE - South-Southeast-Northeast; RSW - South-West; RSWN - South-West-North; SC - Santa Catarina state; SP - São Paulo state; TO - Tocantins state.

Identification	Route	Distance (km)	Dispersion rate (km/year)
RSW	Jaguarão, RS → Nova Prata, RS → Esmeralda do Sul, RS → Trindade do Sul, RS → Nonoai, RS → Chapecó, SC → Passos Maia, SC → Papanduva, SC → Três Barras, SC → Curitiba, PR → Fênix, PR → Sertaneja, PR → Teodoro Sampaio, SP → Rio Verde de Mato Grosso, MS → Sonora, MS → Porto Esperidião, MT → Barra do Bugres, MT → Porto Velho, RO	4,218.17	77.44
RSWN	Jaguarão, RS → Nova Prata, RS → Esmeralda do Sul, RS → Trindade do Sul, RS → Nonoai, RS → Chapecó, SC → Passos Maia, SC → Papanduva, SC → Três Barras, SC → Curitiba, PR → Fênix, PR → Sertaneja, PR → Teodoro Sampaio, SP → Rio Verde de Mato Grosso, MS → Sonora, MS → Porto Esperidião, MT → Barra do Bugres, MT → Paranaíta, MT → Oriximiná, PA	4,937.11	89.90
RSMN	Jaguarão, RS → Nova Prata, RS → Esmeralda do Sul, RS → Trindade do Sul, RS → Nonoai, RS → Chapecó, SC → Passos Maia, SC → Papanduva, SC → Três Barras, SC → Curitiba, PR → Fênix, PR → Sertaneja, PR → Teodoro Sampaio, SP → Inocência, MS → Costa Rica, MS → Mineiros, GO → Luziânia, GO → Formosa, GO → São João d'Aliança, GO → Lizarda, TO → Soure, PA	4,788.89	66.79
RSMNE	Jaguarão, RS → Nova Prata, RS → Esmeralda do Sul, RS → Trindade do Sul, RS → Nonoai, RS → Chapecó, SC → Passos Maia, SC → Papanduva, SC → Três Barras, SC → Curitiba, PR → Fênix, PR → Sertaneja, PR → Teodoro Sampaio, SP → Olímpia, SP → Ouroeste, SP → Populina, SP → Buritis, MG → Chapada Gaúcha, MG → Barra da Estiva, BA → Barra, BA → Caracol, PI → Caldeirão Grande do Piauí, PI → Bacabeira, MA → Barreirinhas, MA	5,465.83	50.62

RSSNE	Jaguarão, RS → Nova Prata, RS → Esmeralda do Sul, RS → Trindade do Sul, RS → Nonoai, RS → Chapecó, SC → Passos Maia, SC → Papanduva, SC → Três Barras, SC → Curitiba, PR → Fênix, PR → Sertaneja, PR → Teodoro Sampaio, SP → Guaratinguetá, SP → Rio de Janeiro, RJ → Varre-sai, RJ → Linhares, ES → Montanha, ES → Caravelas, BA → Barra da Estiva, BA → Barra, BA → Santa Quitéria, CE	5,208.35	62.18

The rate of dispersion is variable and dependent on multiple factors. In natural areas, wild boar dispersal distance for four years varied between 30 km and 89.8 km in Spain (Casas-Díaz et al. 2013). A monitored sow covered 60 km in two months in Slovenia, later establishing at 100 km from its pre-dispersion home range (Jerina et al. 2014). In this study, we did not evaluate if the dispersion of wild pigs in Brazil is related to its home range (natal or reproductive dispersion). However, the dispersion rates found by Casas-Díaz et al. (2013) and Jerina et al. (2014) are very similar to our results. In our case, the extreme dispersion rate found is unlikely to be natural, as it would be improbable to achieve 1,152 populations in a period of a few decades over such a geographical dimension only by increasing the home range of their individuals like a metapopulation case. This suggests that latent populations that were not previously noxious expanded at similar rates in multiple places in the country, suddenly creating conflicts and human interference with the dispersion process, especially at extreme points.

Without direct human interference, we expect abiotic factors such as temperature, elevation, latitude, and rainfall to be the main factors influencing the movements and distribution of wild pigs (Ballari and Barrios-García 2014; Schlichting et al. 2016; Sales et al. 2017). The climate may not define the distribution limits of a species due to species tolerances to heat, cold, or drought, but it may affect the distribution and availability of key resources and, consequently, species spread (Gross and Price 2000). Nevertheless, the size of dispersion stretches between intermediate points that resulted in dispersion rates of over 500 km/year, which shows that the wild pig dispersion in Brazil is very unlikely to be considered only a geographic expansion by its own biological capability (e.g., without anthropic interference, intentional or consequential).

We cannot disregard that the lack of information about wild pig introduction data in Brazil may result in gaps that influence the high values found in dispersal rates. Human action facilitates the introduction of species and biological invasion (Blackburn et al. 2011). Humans have traded and transported alien species for millennia with three notable step-changes: the end of the Middle Ages (post-1500), the beginning of the Industrial Revolution (19th century), and in the Era of Globalization (post-1990; Hulme 2009). Some routes (e.g., RSW) coincide with large Brazilian highways, such as the BR-163. This highway connects the municipalities of Sinop (MT) to Santarém (PA), showing that wild pigs are most likely having their dispersal facilitated by human interference. Reports are presented by hunters of animals being carried from one region to another for cynegetic purposes, as this species is the only one that can be legally hunted in Brazil (Rosa et al. 2018). Besides direct human interference, roads, railways, rivers, or canals can ease invasive species dispersion and establishment (Hulme 2009) since they are viewed as habitat corridors that help direct the movement of organisms, facilitating gene flow and thus population persistence (Van der Windt and Swart 2008).

The southeast region of Brazil is undeniably one of the regions most affected by the invasion of wild pigs (Pedrosa et al. 2015; Rosa et al. 2017), where crops are an essential food source for the species (Beca et al. 2017). Wild pigs' density is directly affected by the availability of resources (Geisser and Reyer 2005; Frauendorf et al. 2016). Therefore, it is expected that with a larger population, there will be an acceleration of the species' dispersion to other areas since dispersion occurs when individuals leave their social group or home range by population (e.g., scarcity of resources) or social (e.g., reproductive) pressure, redistributing into the new ground (Ronce 2007). We showed in this study that the distribution of wild pigs in Brazil expanded through all biomes except the Amazon Forest, as had been predicted by climate-based models (Sales et al. 2017). This may suggest that the Amazon Rainforest is a geographic and environmental barrier to dispersal for wild pigs. Some studies in Europe suggest that physical barriers such as rivers, valleys, highways, and mountains may influence dispersal movements and the genetic structure of wild boar populations through distance isolation (Ferreira et al. 2006; Nikolov et al. 2009; Velickovic et al. 2012). Another hypothesis is that the Amazon Rainforest, as one of the last wilderness regions in Brazil, may still host well-preserved native local biotas, which prevents invasional meltdown (Green et al. 2011). However, the results could be a mere historical contingency because the invasion started in the South and Southern part of Brazil and might not have extended to the far regions of Amazon. Most of the rainforest is still sparsely populated and has therefore had no reports of conflict with agricultural activities. The Amazon case would be an important issue to be investigated in future research.

Despite not being included in the calculation of dispersal rate given the methodological challenges, it is still essential to consider the commercial introductions (post-1900). Those indeed helped accelerate the dispersion and distribution of wild pigs in the Brazilian territory in multiple ways, first, by colonizing surrounding areas shortly after release and potentially overloading the natural ecosystem, pushing the invasion further. Second, by introducing new and improved bloodlines with greater adaptation capacity and reproductive rates, many hybridized with domestic lineages. Once introduced into a region, an invasive species may spread via natural means to other regions (Hulme 2009). Without these introduction events, the municipalities in the north-central region of the country would probably have taken longer to register the presence of the wild pigs if they followed the natural route of dispersion of the species starting from southern Brazil.

Our results bring an important warning about the accelerated increase of wild pigs in Brazil in the last 30 years. The impressive ability for quick geographical expansion and adaptation to new biomes that present different vegetation types, climate, and temperature, reinforces the need for urgent population control. Knowing the dispersion rate and route of invasion can help early detection of wild pigs into areas not currently invaded, especially the Amazon Forest. Furthermore, the analysis of the dispersion rate in each invasion route will aid in implementing population management and prevent new areas from being invaded. This can improve the development of more effective population control strategies and public mitigation policies. Thus, we suggest that the environmental agencies responsible for immediate control in the North of Brazil pay more attention to the problem of the wild pigs invasion and start implementing strategies for population control and management before wild pigs expand into the region. In agreement with Rosa et al. (2018), we suggest the immediate use of lethal control methods and reinforcing priority control in municipalities and regions suggested by IBAMA (2019).

References

Acosta D.B., Figueroa C.E., Fernández G.P., Carpinetti B.N., Merino M.L. (2019). Genetic diversity and phylogenetic relationships in feral pig populations from Argentina. *Mammalian Biology*, 99(1):27-36.

Bach A.M. (2009). Porcadeiros. Ed. Estúdio Texto. Ponta Grossa.

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

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

Barrios-García M.N., Classen A.T., Simberloff D. (2014). Disparate responses of above-and belowground properties to soil disturbance by an invasive mammal. *Ecosphere*, 5(4):1-13.

Blackburn T.M., Pyšek P., Bacher S., Carlton J.T., Duncan R.P. et al. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution,* 26(7):333-339.

Bonino N., Cossíos D., Menegheti J. (2010). Dispersal of the European hare, *Lepus europaeus* in South America. *Folia Zoologica,* 59:9-15.

BRASIL - PAN Javali. (2017). Plano Nacional de Prevenção, Controle e Monitoramento do Javali (*Sus scrofa*) no Brasil. Ministério do Meio Ambiente (MMA) & Ministério da Agricultura, Pecuária e Abastecimento (MAPA). Brasília, Brasil.

Burgos-Paz W., Souza C.A., Megens H.J., Ramayo-Caldas Y., Melo M., et al. (2013). Porcine colonization of the Americas: a 60k SNP story. *Heredity*, 110(4):321-330.

Canevari M., Vaccaro O. (2007). Guía de mamíferos del sur de América del Sur. Literature of Latin America (LOLA), Buenos Aires.

Casas-Díaz E., Closa-Sebastià F., Peris A., Miño A., Torrentó J., et al. (2013). Recorded dispersal of wild boar (*Sus scrofa*) in Northeast Spain: implications for disease-monitoring programs. *Wildlife Biology in Practice*, 9(3):19-26.

Castro S.T.R., Albuquerque M.S.M., Germano J.L. (2002). Census of Brazilian naturalized swine breeds. *Archivos de Zootecnia*, 51:235-237.

Clout M.N., Russell J.C. (2008). The invasion ecology of mammals: a global perspective. *Wildlife Research*, 35:180-184.

Cucchi T., Fujita M., Dobney K. (2009). New insights into pig taxonomy, domestication and human dispersal in Island South East Asia: molar shape analysis of Sus remains from Niah Caves, Sarawak. *International Journal of Osteoarchaeology,* 19(4):508–530.

Daciuk J. (1978). Estado actual de las especies de mamíferos introducidos en la Subregión Aracuana (Rep. Argentina) y grado de coacción ejercido en algunos ecosistemas surcordilleranos. *Anales de Parques Nacionales*, 105–130.

Deberdt A.J., Scherer S.B. (2007). O javali asselvajado: ocorrência e manejo da espécie no Brasil. *Natureza & Conservação,* 5(2):31-44.

Donkin R.A. (1985). The peccary: with observations on the introduction of pigs to the New World. *Proceedings of the American Philosophical Society*, 75:1–152.

Faria G.M.M., Rosa C.A., Corrêa G.L.C., Puertas F., Jiménez K.M.O., et al. (2016). Geographic distribution of the European hare (Lepus europaeus) in Brazil and new records of occurrence for the Cerrado and Atlantic Forest biomes. *Mammalia*, 80(5):497-505.

Ferreira E., Souto L., Soares A.M.V.M., Fonseca C. (2006.) Genetic structure of the wild boar (*Sus scrofa* L.) population in Portugal. *Wildlife Biology in Practice*, 2:17–25.

Fonseca C., Neves M.P., Silva V.G., Scherer S., Campelo A.D.A., et. al. (2009). Status and distribution of wild boar in Rio Grande do Sul, Southern Brazil. In Proceedings of the 7th International Symposium on Wild Boar, pp.20-29.

Frankenberg S.T. (2005). Levantamento e avaliação da Portaria 138/02 e Instrução Normativa 25/04, que regulamentaram o controle do javali (*Sus scrofa*) no Rio Grande do Sul no período compreendido entre 2003 e 2005. Produto PNUD, Projeto BRA/01/037. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, Porto Alegre.

García G., Vergara J., Lombardi R. (2011). Genetic characterization and phylogeography of the wild boar *Sus scrofa* introduced into Uruguay. *Genetics and Molecular Biology*, 34(2):329-37.

Ghione S., Martino D., Aldabe J., Bartesaghi L., Blanco D., et al. (2008). Biodiversidad. In PNUMA/CLAVES/DINAMA, editor. GEO *Uruguay: informe del estado del ambiente.* Programa de Naciones Unidas para el Medio Ambiente (PNUMA)/ Centro Latino Americano de Ecología Social (CLAES)/ Dirección Nacional de Medio Ambiente (DINAMA), Montevideo, pp.180–241.

GISD. (2016). Global Invasive Species Database: *Sus scrofa*. <www.issg.org/database/species/distribution.asp?si=73&fr=1&sts=sss&lang=EN>. Accessed 4 Jan 2016.

Google Inc (2021). Google Sheets. https://www.google.com/sheets/about/.

Green P.T., O'Dowd D.J., Abbott K.L., Jeffery M., Retallick K., et. al. (2011). Invasional meltdown: invader–invader mutualism facilitates a secondary invasion. *Ecology*, 92(9):1758-1768.

Gross S.J., Price T.D. (2000). Determinants of the northern and southern range limits of a warbler. *Journal of Biogeography*, 27:869–878.

Han S.W., Park H.C., Kim J.H., Suh J.H., Lee H., et. al. (2021). Population Genetic Structure of Wild Boar and Dispersal Performance Based on Kinship Analysis in the Northern Region of South Korea. Res Square (Version online).

Hegel C.G.Z., Marini M.Â. (2013). Impact of the wild boar, *Sus scrofa*, on a fragment of Brazilian Atlantic Forest. *Neotropical Biology and Conservation*, 8:17-24.

Hegel C.G.Z., Santos L.R., Marinho J.R., Marini M.Â. (2019). Is the wild pig the real “big bad wolf”? Negative effects of wild pig on Atlantic Forest mammals. *Biological Invasions*, 21:3561-3574.

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

Hulme P.E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, 46(1):10-18.

IABIN. (2016). Inter-American Biodiversity Information Network. http://www.iabin.net. Accessed 4 Jan 2016.

IASI. (2016). *Data base of Invasive Alien Species Indicator.* http://academic.sun.ac.za/cib/iasi/index.asp. Accessed 4 Jan 2016.

IBGE. (2021). Instituto Brasileiro de Estatística e Geografia – IBGE. https://downloads.ibge.gov.br/. Accessed 9 Jun 2021.

IBAMA. (1995). *Portaria Ibama Nº 7 de 26 de janeiro de 1995 do Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (IBAMA).* Brasília: Ministério do Meio Ambiente (MMA).

IBAMA. (1998a). *Portaria Ibama Nº 93 de 7 de julho de 1998 do Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA).* Brasília: Ministério do Meio Ambiente.

IBAMA. (1998b). *Portaria Ibama Nº 102 de 15 de julho de 1998 do Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA).* Brasília: Ministério do Meio Ambiente.

IBAMA. (2002). *Portaria Ibama N° 138 de 14 de outubro de 2002 do Instituto Brasileiro do Meio Ambiente e dos Recurso Naturais Renováveis (IBAMA).* Diário Oficial da União 200:114. Brasília.

IBAMA. (2004). *Instrução Normativa Nº 25 de 31 de março de 2004. Page 91 in. Diario Oficial da União N° 63 de 1 de abril de 2004.* Instituto Brasileiro do Meio Ambiente e dos Recurso Naturais Renováveis (IBAMA), Brasília.

IBAMA. (2013). *Instrução Normativa Ibama Nº 03 de 31 de janeiro de 2013 do Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (IBAMA).* Brasília: Ministério do Meio Ambiente (MMA).

IBAMA. (2019). *Relatório sobre áreas prioritárias para o manejo de javalis: aspectos ambientais, socioeconômicos e sanitários.* Batista G. O. (Org.). Brasília: IBAMA.

Jaksic F.M. (1998). Vertebrate invaders and their ecological impacts in Chile. *Biodiversity and Conservation*, 7(11):1427–1445.

Jerina K., Pokorny B., Stergar M. (2014). First evidence of long-distance dispersal of adult female wild boar (*Sus scrofa*) with piglets. *European Journal of Wildlife Research*, 60(2):367-370.

Keiter D.A., Mayer J.J., Beasley J.C. (2016). What is in a “common” name? A call for consistent terminology for nonnative *Sus scrofa*. *Wildlife Society Bulletin*, 40:384-387.

Ladeia R.E.F., Almeida O.B., Santos P.C.O. (2006). *Relatório técnico sobre ocorrência de javali (Sus scrofa) na Bahia.* Vitória da Conquista: IBAMA. 8 p.

Long J.L, (2003). Introduced mammals of the world: their history, distribution and influence. CISOR, Collingwood.

Lowe S., Browne M., Boudjelas S., De Poorter M. (2000). *100 of the World's Worst Invasive Alien Species a selection from the Global Invasive Species Database.* Published by The Invasive Species Specialist Group - ISSG, Species Survival Commission - SSC, World Conservation Union - IUCN. 12 p.

Mariante A.S., Castro S.T.R., Albuquerque M.S.M., Paiva S.R., Germano J.L. (2003). Pig biodiversity in Brazil. *Archivos de Zootecnia*, 52:245–248.

Mariante A.S., Cavalcante N. (2006). *Animals of the discovery: domestic breeds in the history of Brazil*. Embrapa: Brasília-DF, Brazil.

Massei G., Genov P.V. (2004). The environmental impact of wild boar. *Galemys*, 16:135-145.

Mayer J.J. (2009). Wild pig population biology. In JJ Mayer & IL Brisbin (eds.) *Wild pigs: biology, damage, control techniques and management*. Aiken: Savannah River National Laboratory, 157-192.

Melletti M., Meijaard E. (2017). *Ecology, Conservation and Management of Wild Pigs and Peccaries.* Cambridge: Cambridge University Press.

Menezes G.P. (2002). *Implicações ambientais, sanitárias e zootécnicas da criação de javonteiro.* Universidade Anhanguera – Uniderp.

Mourão G.M., Coutinho M.E., Mauro R.A., Tomás W.M., et. al. (2002). *Levantamentos aéreos de espécies introduzidas no Pantanal: porcos ferais (porco monteiro), gado bovino e búfalos*. Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Corumbá.

Navas J.R. (1987). Los vertebrados exóticos introducidos en la Argentina. *Revista del Museum Argentino de Ciências Naturales Zoologia*, 2:7–37.

Nikolov I.S., Gum B., Markov G., Kuehn R. (2009). Population genetic structure of wild boar *Sus scrofa* in Bulgaria as revealed by microsatellite analysis. *Acta Theriologica*, 54:193–205.

Novillo A., Ojeda R.A. (2008). The exotic mammals of Argentina. *Biological Invasions*, 10(8):1333-1344.

Oliveira M.O. (1996). *Criação de javali. Série Animais Silvestre.* Vídeo. Centro de Produções Técnicas, Viçosa, Viçosa.

Oliver W.L. (Ed.) (1993). *Pigs, peccaries and hippos: status survey and conservation action plan.* Island Pr.

Paiva R. (1996). O porco de sangue azul. *Globo Rural*, 10:39-44.

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

Pereira-Neto O.A., Riet-Correa F., Méndez M.D.C. (1992). Javali: um predador a ser evitado no Rio Grande do Sul. In A. L. Schild, F. Riet-Correa, M. D. C. Méndez, and J. L. M. Ferreira, editors. *Laboratório Regional de Diagnóstico: Doenças diagnosticadas no ano de 1991.* Editora Universitária, Pelotas 42–48.

Porto A. (1994). Fronteiras rompidas. *Globo Rural,* 1:32–38.

Primo A.T. (2004). *América - conquista e colonização. A fantástica história dos conquistadores ibéricos e seus animais na era dos descombrimentos.* Movimento, Porto Alegre.

QGIS Development Team. (2020). *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

Rodero A., Delgado J.V., Rodero E. (1992). Primitive Anadalusian livestock and their implications in the discovery of America. *Zootecnia,* 41:384–400.

Rosa C.A.D., Wallau M.O., Pedrosa F. (2018). Hunting as the main technique used to control wild pigs in Brazil. *Wildlife Society Bulletin*, 42(1):111-118.

Rosa C.A., Ribeiro B.R., Bejarano V., Puertas F.H., Bocchiglieri A., et al. (2020). Neotropical Alien Mammals: a data set of occurrence and abundance of alien mammals in the Neotropics. *Ecology,* e03115.

SAA/SP. (2018). *Relatório do Grupo de Trabalho da Resolução SAA n° 42/2018*. Secretaria de Agricultura e Abastecimento do Estado de São Paulo, São Paulo.

Sagua M.I., Figueroa C.E., Acosta D.B., Fernández G.P., Carpinetti B.N., et al. (2018). Inferring the origin and genetic diversity of the introduced wild boar (*Sus scrofa*) populations in Argentina: an approach from mitochondrial markers. *Mammal Research*, 63(4):467-476.

Sales L.P., Ribeiro B.R., Hayward M.W., Paglia A., Passamani M., et al. (2017). Niche conservatism and the invasive potential of the wild boar. *Journal of Animal Ecology,* 86(5):1214-1223.

Salvador C.H. (2012). *Ecologia e manejo de javali (Sus scrofa L.) na América do Sul.* PhD Thesis. Rio de Janeiro: Universidade Federal do Rio de Janeiro.

Schlichting P.E., Fritts S.R., Mayer J.J., Gipson P.S., Dabbert C.B. (2016). Determinants of variation in home range of wild pigs. *Wildlife Society Bulletin,* 40(3):487-493.

Silva Filha O.L. (2008). Brazilian experiences on local pig rearing. *Revista Computadorizada de Producción Porcina,* 15:41–53.

Skewes O., Morales R. (2006). Crianza de jabali (*Sus scrofa* L.) en Chile. Distribucion, tamaño y aspectos basicos de manejo wild boar. *Agro-Ciência,* 22:29–36.

Skewes O. (2010). European wild boar (*Sus scrofa scrofa*) in Chile, history of introduction and colonization. In *The 10th Mammalogical Congress*. International Federation of Mammalogist (IFM), Mendonza. 1982–1982.

Valério L.A.J. (1999). *Ocorrência e alimentação da linhagem javali (Sus scrofa MAMMALIA, ARTIODACTYLA) em estado silvestre no sudoeste do Rio Grande do Sul*. Master Thesis. Porto Alegre: Universidade Federal do Rio Grande do Sul.

Van Der Windt H.J., Swart J.A.A. (2008). Ecological corridors, connecting science and politics: the case of the Green River in the Netherlands. *Journal of Applied Ecology*, 45(1):124-132.

Velickovic N., Djan M., Obreht D., Vapa L. (2012). Population genetic structure of wild boars in the West Balkan region. *Russian Journal of Genetics*, 48:859–863.

Zadik B.J. (2005). *The Iberian pig in Spain and the Americas at the time of Columbus.* Ph.D. Thesis, Berkele: University of California.

Supplementary material 1. Records of wild pigs in Brazil according to the database.

State	Municipality	Coordinate X	Coordinate Y	Year	Reference
BA	Alcobaça	-39,410	-17,469	2019	IBAMA 2019
	Barra	-43,366	-11,031	2019	IBAMA 2019
	Barra da Estiva	-41,098	-13,650	2000	Ladeia et al 2006, Deberdt and Scherer 2007
	Boa Nova	-40,230	-14,360	2000	Ladeia et al 2006; Deberdt and Scherer 2007
	Caravelas	-39,689	-17,658	1990-1992	Rosa et al 2020
	Contendas do Sincorá	-41,094	-13,838	2000	Ladeia et al 2006; Deberdt and Scherer 2007
	Correntina	-45,396	-13,467	2015	Pedrosa et al 2015
	Ituaçu	-41,390	-13,837	2000	Ladeia et al 2006; Deberdt and Scherer 2007
	Jequié	-40,146	-13,878	2000	Ladeia et al 2006; Deberdt and Scherer 2007
	Manoel Vitorino	-40,548	-14,051	2000	Ladeia et al 2006, Deberdt and Scherer 2007
	Mirante	-40,764	-14,168	2000	Ladeia et al 2006; Deberdt and Scherer 2007
	Nova Viçosa	-39,715	-17,900	2019	IBAMA 2019
	Poções	-40,383	-14,536	2000	Ladeia et al 2006; Deberdt and Scherer 2007
	Porto Seguro	-39,279	-16,625	2009	Rosa et al 2020
	Santa Cruz Cabrália	-39,201	-16,229	2009	Rosa et al 2020
CE	Morada Nova	-38,433	-5,035	2017	Rosa et al 2020
DF	Brasília	-47,797	-15,781	2019	IBAMA 2019
ES	Afonso Cláudio	-41,127	-20,089	2015	Pedrosa et al 2015
	Aracruz	-40,176	-19,766	2019	IBAMA 2019
	Dores do Rio Preto	-41,812	-20,635	2015	Pedrosa et al 2015
	Linhares	-40,029	-19,383	2017	Rosa et al 2020
	Montanha	-40,275	-18,139	2019	IBAMA 2019
	Pedro Canário	-40,037	-18,182	2019	IBAMA 2019
	São José do Calçado	-41,656	-20,983	2015	Pedrosa et al 2015

	Vitória	-39,088	-20,304	2015	Rosa et al 2020
GO	Abadiânia	-48,714	-16,187	2015	Pedrosa et al 2015
	Água Fria de Goiás	-47,795	-14,907	2019	IBAMA 2019
	Alexânia	-48,482	-16,089	2015	Pedrosa et al 2015
	Aloândia	-49,465	-17,693	2019	IBAMA 2019
	Aporé	-52,045	-18,768	2019	IBAMA 2019
	Aragoiânia	-49,419	-16,952	2019	IBAMA 2019
	Araguapaz	-50,440	-15,139	2019	IBAMA 2019
	Aruanã	-50,937	-14,806	2019	IBAMA 2019
	Baliza	-52,438	-16,360	2008	Rosa et al 2020
	Bela Vista de Goiás	-48,912	-16,957	2017	BRASIL - PAN Javali 2017
	Britânia	-51,208	-15,237	2019	IBAMA 2019
	Caçu	-51,131	-18,701	2009	Rosa et al 2020
	Caiapônia	-51,815	-17,007	2015	Pedrosa et al 2015
	Caldas Novas	-48,647	-17,709	2015	Pedrosa et al 2015
	Campo Alegre de Goiás	-47,768	-17,551	2019	IBAMA 2019
	Catalão	-47,665	-17,931	2015	Pedrosa et al 2015
	Cezarina	-49,757	-17,086	2019	IBAMA 2019
	Chapadão do Céu	-52,634	-18,465	2017	BRASIL - PAN Javali 2017
	Cocalzinho de Goiás	-48,603	-15,656	2017	BRASIL - PAN Javali 2017
	Córrego do Ouro	-50,582	-16,366	2019	IBAMA 2019
	Cristalina	-47,518	-16,698	2015	Pedrosa et al 2015
	Crixás	-50,065	-14,640	2019	IBAMA 2019
	Cromínia	-49,357	-17,241	2015	Pedrosa et al 2015
	Edealina	-49,742	-17,422	2017	BRASIL - PAN Javali 2017
	Edéia	-49,964	-17,477	2015	Pedrosa et al 2015
	Faina	-50,370	-15,436	2019	IBAMA 2019
	Flores de Goiás	-46,905	-14,652	2019	IBAMA 2019
	Formosa	-47,248	-15,308	2015	Pedrosa et al 2015
	Gameleira de Goiás	-48,673	-16,403	2019	IBAMA 2019
	Goiatuba	-49,660	-17,994	2019	IBAMA 2019

Guapó	-49,573	-16,911	2015	Pedrosa et al 2015
Hidrolândia	-49,267	-17,012	2019	IBAMA 2019
Indiara	-49,968	-17,185	2019	IBAMA 2019
Ipameri	-48,055	-17,506	2019	IBAMA 2019
Itajá	-51,320	-19,101	2019	IBAMA 2019
Itapirapuã	-50,771	-15,703	2017	BRASIL - PAN Javali 2017
Itarumã	-51,331	-18,844	2017	BRASIL - PAN Javali 2017
Itumbiara	-49,417	-18,353	2019	IBAMA 2019
Ivolândia	-51,034	-16,676	2015	Pedrosa et al 2015
Jandaia	-50,182	-17,092	2015	Pedrosa et al 2015
Jataí	-51,732	-17,910	2015	Pedrosa et al 2015
Luziânia	-47,992	-16,482	2006	Deberdt and Scherer 2007
Mairipotaba	-49,458	-17,300	2015	Pedrosa et al 2015
Mimoso de Goiás	-48,309	-15,017	2019	IBAMA 2019
Mineiros	-52,766	-17,631	2002	Rosa et al 2020
Moiporá	-50,773	-16,508	2019	IBAMA 2019
Montividiu	-51,190	-17,318	2015	Pedrosa et al 2015
Morrinhos	-49,129	-17,775	2015	Pedrosa et al 2015
Mozarlândia	-50,587	-14,843	2019	IBAMA 2019
Niquelândia	-48,402	-14,499	2019	IBAMA 2019
Orizona	-48,195	-17,008	2015	Pedrosa et al 2015
Paraúna	-50,638	-17,047	2015	Pedrosa et al 2015
Perolândia	-52,225	-17,494	2019	IBAMA 2019
Piracanjuba	-48,993	-17,332	2019	IBAMA 2019
Pires do Rio	-48,389	-17,272	2015	Pedrosa et al 2015
Planaltina	-47,752	-15,284	2017	BRASIL - PAN Javali 2017
Pontalina	-49,538	-17,531	2015	Pedrosa et al 2015
Professor Jamil	-49,246	-17,273	2006	Deberdt and Scherer 2007
Rio Verde	-51,039	-17,739	2015	Pedrosa et al 2015
Sanclerlândia	-50,375	-16,285	2019	IBAMA 2019
Santa Cruz de Goiás	-48,593	-17,360	2019	IBAMA 2019

	Santa Rita do Araguaia	-53,069	-17,244	2017	BRASIL - PAN Javali 2017
	Santo Antônio da Barra	-50,631	-17,525	2017	BRASIL - PAN Javali 2017
	São João d'Aliança	-47,423	-14,486	2019	IBAMA 2019
	São Simão	-50,591	-19,011	2015	Pedrosa et al 2015
	Senador Canedo	-49,108	-16,706	2017	IBAMA 2019
	Serranópolis	-52,212	-18,225	2015	Pedrosa et al 2015
	Silvânia	-48,558	-16,607	2006	Deberdt and Scherer 2007
	Turvelândia	-50,313	-17,755	2017	BRASIL - PAN Javali 2017
	Urutaí	-48,196	-17,436	2019	IBAMA 2019
	Varjão	-49,611	-17,078	2015	Pedrosa et al 2015
	Vianópolis	-48,442	-16,813	2015	Pedrosa et al 2015
MA	Bacabeira	-44,358	-2,936	2013	Rosa et al 2020
	Barreirinhas	-42,910	-2,840	2019	IBAMA 2019
	Caxias	-43,300	-4,867	2019	IBAMA 2019
MG	Água Comprida	-48,084	-20,005	2015	Pedrosa et al 2015
	Aiuruoca	-44,648	-21,955	2011	Rosa et al 2020
	Alfenas	-45,966	-21,389	2019	IBAMA 2019
	Alterosa	-46,154	-21,225	2015	Pedrosa et al 2015
	Alto Caparaó	-41,865	-20,458	2015	Pedrosa et al 2015
	Alto Jequitibá	-41,949	-20,437	2014	Rosa et al 2020
	Araguari	-48,222	-18,577	2015	Rosa et al 2020
	Araxá	-46,972	-19,636	2007	Deberdt and Scherer 2007
	Arinos	-45,989	-15,751	2019	IBAMA 2019
	Bambuí	-45,999	-20,111	2019	IBAMA 2019
	Belo Vale	-44,060	-20,425	2019	IBAMA 2019
	Betim	-44,199	-19,947	2019	IBAMA 2019
	Boa Esperança	-45,621	-21,049	2019	IBAMA 2019
	Bocaina de Minas	-44,483	-22,216	2019	IBAMA 2019
	Bom Despacho	-45,286	-19,685	2015	Pedrosa et al 2015
	Bom Sucesso	-44,784	-21,026	2015	Pedrosa et al 2015

Bonfim	-44,215	-20,321	2019	IBAMA 2019
Botelhos	-46,419	-21,636	2015	Pedrosa et al 2015
Brasilândia de Minas	-45,902	-16,957	2015	Pedrosa et al 2015
Brasília de Minas	-44,439	-16,243	2019	IBAMA 2019
Brumadinho	-44,123	-20,178	2015	Pedrosa et al 2015
Buritis	-46,604	-15,453	2007	Deberdt and Scherer 2007
Buritizeiro	-45,192	-17,286	2019	IBAMA 2019
Cachoeira de Minas	-45,793	-22,362	2019	IBAMA 2019
Cachoeira Dourada	-49,479	-18,608	2015	Pedrosa et al 2015
Caiana	-41,908	-20,725	2015	Pedrosa et al 2015
Caldas	-46,364	-21,891	2015	Pedrosa et al 2015
Cambuí	-46,078	-22,583	2017	BRASIL - PAN Javali 2017
Campestre	-46,221	-21,710	2015	Pedrosa et al 2015
Campina Verde	-49,810	-19,479	2015	Pedrosa et al 2015
Canápolis	-49,272	-18,758	2015	Pedrosa et al 2015
Caparaó	-41,950	-20,527	2015	Pedrosa et al 2015
Capelinha	-42,492	-17,693	2015	Pedrosa et al 2015
Capim Branco	-44,168	-19,570	2015	Pedrosa et al 2015
Capinópolis	-49,582	-18,687	2015	Pedrosa et al 2015
Capitólio	-46,144	-20,613	2015	Pedrosa et al 2015
Carangola	-42,088	-20,703	2015	Pedrosa et al 2015
Carmo do Paranaíba	-46,185	-18,908	2015	Pedrosa et al 2015
Carmo do Rio Claro	-46,099	-20,972	2015	Pedrosa et al 2015
Carneirinho	-50,830	-19,750	2015	Pedrosa et al 2015
Catas Altas	-43,408	-20,075	2019	IBAMA 2019
Centralina	-49,162	-18,633	2015	Pedrosa et al 2015
Chapada Gaúcha	-45,459	-15,469	2019	IBAMA 2019
Conceição das Pedras	-45,425	-22,147	2015	Pedrosa et al 2015
Conceição do Pará	-44,872	-19,786	2019	Rosa et al 2020
Conquista	-47,624	-19,884	2015	Pedrosa et al 2015
Consolação	-45,916	-22,536	2019	IBAMA 2019

Coromandel	-47,137	-18,413	2015	Pedrosa et al 2015
Divino	-42,175	-20,590	2015	Pedrosa et al 2015
Divinópolis	-44,931	-20,124	2019	IBAMA 2019
Dom Joaquim	-43,259	-18,928	2019	IBAMA 2019
Doresópolis	-45,887	-20,292	2007	Deberdt and Scherer 2007
Esmeraldas	-44,308	-19,733	2015	Pedrosa et al 2015
Espera Feliz	-41,930	-20,597	2015	Pedrosa et al 2015
Estiva	-46,014	-22,458	2019	IBAMA 2019
Estrela do Sul	-47,726	-18,715	2015	Pedrosa et al 2015
Extrema	-46,290	-22,825	2017	BRASIL - PAN Javali 2017
Faria Lemos	-42,036	-20,781	2015	Pedrosa et al 2015
Fortuna de Minas	-44,504	-19,558	2015	Pedrosa et al 2015
Fronteira	-49,159	-20,229	2015	Rosa et al 2020
Frutal	-49,000	-20,036	2019	IBAMA 2019
Ibertioga	-43,959	-21,450	2019	IBAMA 2019
Ibiá	-46,596	-19,558	2015	Pedrosa et al 2015
Igarapé	-44,322	-20,059	2016	Rosa et al 2020
Iguatama	-45,753	-20,156	2015	Pedrosa et al 2015
Ijaci	-44,934	-21,178	2015	Pedrosa et al 2015
Indianópolis	-47,850	-18,952	2015	Pedrosa et al 2015
Itamarandiba	-42,877	-17,856	2015	Pedrosa et al 2015
Itamonte	-44,758	-22,289	2007	Deberdt and Scherer 2007
Itanhandu	-44,921	-22,320	2019	IBAMA 2019
Itapagipe	-49,423	-19,795	2017	Rosa et al 2020
Ituiutaba	-49,544	-18,993	2015	Pedrosa et al 2015
Iturama	-50,345	-19,716	2015	Pedrosa et al 2015
Jacutinga	-46,601	-22,288	2015	Pedrosa et al 2015
Janaúba	-43,397	-15,799	2015	Pedrosa et al 2015
Jeceaba	-44,047	-20,552	2019	IBAMA 2019
Jequitibá	-44,001	-19,212	2015	Pedrosa et al 2015
João Pinheiro	-45,934	-17,605	2015	Pedrosa et al 2015

Lavras	-45,038	-21,265	2015	Pedrosa et al 2015
Liberdade	-44,333	-22,016	2017	BRASIL - PAN Javali 2017
Limeira do Oeste	-50,648	-19,407	2015	Pedrosa et al 2015
Luisburgo	-42,074	-20,436	2019	IBAMA 2019
Machado	-45,920	-21,666	2015	Pedrosa et al 2015
Madre de Deus de Minas	-44,332	-21,485	2015	Pedrosa et al 2015
Manhuaçu	-42,107	-20,195	2015	Pedrosa et al 2015
Manhumirim	-41,939	-20,347	2015	Pedrosa et al 2015
Maravilhas	-44,671	-19,501	2017	BRASIL - PAN Javali 2017
Minduri	-44,614	-21,675	2015	Pedrosa et al 2015
Monte Alegre de Minas	-48,887	-18,845	2015	Pedrosa et al 2015
Monte Carmelo	-47,461	-18,709	2015	Pedrosa et al 2015
Munhoz	-46,304	-22,632	2015	Pedrosa et al 2015
Nepomuceno	-45,261	-21,228	2015	Pedrosa et al 2015
Onça de Pitangui	-44,736	-19,708	2017	BRASIL - PAN Javali 2017
Orizânia	-42,213	-20,515	2015	Pedrosa et al 2015
Ouro Fino	-46,384	-22,255	2015	Pedrosa et al 2015
Ouro Preto	-43,610	-20,391	2019	IBAMA 2019
Papagaios	-44,691	-19,376	2017	BRASIL - PAN Javali 2017
Pará de Minas	-44,608	-19,834	2017	BRASIL - PAN Javali 2017
Paracatu	-46,884	-17,173	2019	IBAMA 2019
Paraopeba	-44,453	-19,272	2019	IBAMA 2019
Passa Quatro	-44,968	-22,406	2019	IBAMA 2019
Passos	-46,622	-20,719	2015	Pedrosa et al 2015
Patrocínio	-47,051	-18,971	2015	Pedrosa et al 2015
Pedra Dourada	-42,155	-20,828	2015	Pedrosa et al 2015
Pedro Leopoldo	-44,053	-19,640	2007	Deberdt and Scherer 2007
Perdizes	-47,196	-19,400	2015	Pedrosa et al 2015
Perdões	-45,065	-21,076	2015	Pedrosa et al 2015
Piedade do Rio Grande	-44,155	-21,484	2015	Pedrosa et al 2015

	Piedade dos Gerais	-44,246	-20,474	2019	IBAMA 2019
	Piranguçu	-45,515	-22,557	2015	Pedrosa et al 2015
	Piumhi	-46,050	-20,441	2015	Pedrosa et al 2015
	Poços de Caldas	-46,563	-21,808	2015	Pedrosa et al 2015
	Pompéu	-44,924	-19,131	2019	IBAMA 2019
	Prata	-48,954	-19,330	2015	Pedrosa et al 2015
	Pratinha	-46,403	-19,760	2019	IBAMA 2019
	Ribeirão Vermelho	-45,073	-21,148	2015	Pedrosa et al 2015
	Rio Manso	-44,345	-20,267	2015	Pedrosa et al 2015
	Rio Paranaíba	-46,299	-19,240	2015	Pedrosa et al 2015
	Sacramento	-47,266	-19,904	2015	Pedrosa et al 2015
	Santa Juliana	-47,509	-19,380	2015	Pedrosa et al 2015
	Santa Rita de Caldas	-46,271	-22,024	2015	Pedrosa et al 2015
	Santo Antônio do Monte	-45,292	-20,083	2015	Pedrosa et al 2015
	São Francisco de Sales	-49,859	-19,797	2015	Pedrosa et al 2015
	São João del Rei	-44,274	-21,263	2015	Pedrosa et al 2015
	São Roque de Minas	-46,514	-20,187	2015	Pedrosa et al 2015
	São Vicente de Minas	-44,474	-21,667	2015	Pedrosa et al 2015
	Serrania	-46,093	-21,554	2015	Pedrosa et al 2015
	Sete Lagoas	-44,253	-19,437	2015	Pedrosa et al 2015
	Tapira	-46,868	-19,916	2015	Pedrosa et al 2015
	Tiros	-45,824	-18,860	2015	Pedrosa et al 2015
	Tombos	-42,064	-20,882	2015	Pedrosa et al 2015
	Três Corações	-45,205	-21,686	2019	IBAMA 2019
	Tupaciguara	-48,755	-18,535	2015	Pedrosa et al 2015
	Uberaba	-47,977	-19,581	2015	Pedrosa et al 2015
	Uberlândia	-48,332	-19,028	2015	Pedrosa et al 2015
	Unaí	-46,820	-16,376	2007	Deberdt and Scherer 2007
	Varjão de Minas	-45,935	-18,467	2015	Pedrosa et al 2015
MS	Jardim	-56,286	-21,576	2007	Deberdt and Scherer 2007

Água Clara	-52,927	-19,963	2019	IBAMA 2019
Amambai	-54,968	-23,158	2015	Pedrosa et al 2015
Anaurilândia	-52,805	-22,111	2007	Rosa et al 2020
Angélica	-53,866	-22,062	2015	Pedrosa et al 2015
Antônio João	-55,961	-22,209	2015	Pedrosa et al 2015
Aquidauana	-55,877	-19,746	2015	Pedrosa et al 2015
Aparecida do Taboado	-51,290	-20,076	2015	Rosa et al 2020
Aral Moreira	-55,450	-22,908	2015	Pedrosa et al 2015
Bandeirantes	-54,285	-19,805	2017	BRASIL - PAN Javali 2017
Batayporã	-53,178	-22,391	2015	Pedrosa et al 2015
Bela Vista	-56,535	-21,936	2015	Pedrosa et al 2015
Bodoquena	-56,699	-20,549	2015	Pedrosa et al 2015
Bonito	-56,483	-21,033	2015	Pedrosa et al 2015
Brasilândia	-52,434	-21,076	2016	Rosa et al 2020
Caarapó	-54,803	-22,588	2015	Pedrosa et al 2015
Camapuã	-53,870	-19,342	2017	BRASIL - PAN Javali 2017
Campo Grande	-54,249	-20,914	2019	IBAMA 2019
Cassilândia	-52,180	-19,095	2015	Rosa et al 2020
Chapadão do Sul	-52,698	-18,995	2015	Pedrosa et al 2015
Corguinho	-55,057	-19,808	2017	BRASIL - PAN Javali 2017
Coronel Sapucaia	-55,383	-23,348	2015	Pedrosa et al 2015
Corumbá	-56,722	-18,722	2015	Pedrosa et al 2015
Costa Rica	-53,203	-18,519	2015	Rosa et al 2020
Coxim	-54,674	-18,281	2015	Pedrosa et al 2015
Deodápolis	-54,152	-22,156	2007	Deberdt and Scherer 2007
Dois Irmãos do Buriti	-55,362	-20,600	2019	IBAMA 2019
Dourados	-54,839	-22,145	2007	Deberdt and Scherer 2007
Fátima do Sul	-54,440	-22,337	2015	Pedrosa et al 2015
Glória de Dourados	-54,192	-22,427	2007	Deberdt and Scherer 2007
Guia Lopes da Laguna	-55,996	-21,542	2015	Pedrosa et al 2015

Iguatemi	-54,538	-23,434	2019	IBAMA 2019
Inocência	-52,022	-19,658	2013	Rosa et al 2020
Itaporã	-54,873	-22,005	2015	Pedrosa et al 2015
Itaquiraí	-54,119	-23,342	2015	Pedrosa et al 2015
Ivinhema	-53,799	-22,371	2007	Deberdt and Scherer 2007
Jaraguari	-54,348	-20,227	2019	IBAMA 2019
Jateí	-53,957	-22,707	2015	Pedrosa et al 2015
Juti	-54,489	-22,776	2015	Pedrosa et al 2015
Ladário	-57,569	-19,103	2019	IBAMA 2019
Laguna Carapã	-55,132	-22,678	2015	Pedrosa et al 2015
Maracaju	-55,397	-21,543	2015	Pedrosa et al 2015
Miranda	-56,596	-20,121	2015	Pedrosa et al 2015
Naviraí	-54,026	-23,023	2007	Deberdt and Scherer 2007
Nioaque	-55,901	-21,101	2019	IBAMA 2019
Nova Alvorada do Sul	-54,216	-21,491	2015	Pedrosa et al 2015
Nova Andradina	-53,422	-21,926	2015	Pedrosa et al 2015
Novo Horizonte do Sul	-53,782	-22,603	2015	Pedrosa et al 2015
Paraíso das Águas	-53,130	-19,228	2017	BRASIL - PAN Javali 2017
Paranaíba	-51,396	-19,528	2019	IBAMA 2019
Pedro Gomes	-54,339	-17,914	2015	Pedrosa et al 2015
Ponta Porã	-55,584	-22,202	2015	Pedrosa et al 2015
Porto Murtinho	-57,384	-21,226	2015	Pedrosa et al 2015
Ribas do Rio Pardo	-53,544	-20,597	2015	Pedrosa et al 2015
Rio Brilhante	-54,558	-21,696	2015	Pedrosa et al 2015
Rio Verde de Mato Grosso	-55,043	-18,814	2007	Deberdt and Scherer 2007
São Gabriel do Oeste	-54,483	-19,169	2015	Pedrosa et al 2015
Selvíria	-51,758	-20,282	2019	IBAMA 2019
Sidrolândia	-54,942	-21,094	2015	Pedrosa et al 2015
Sonora	-54,432	-17,649	2015	Pedrosa et al 2015
Tacuru	-54,990	-23,649	2015	Pedrosa et al 2015

	Taquarussu	-53,431	-22,668	2015	Pedrosa et al 2015
	Três Lagoas	-52,211	-20,439	2019	IBAMA 2019
	Vicentina	-54,425	-22,467	2017	BRASIL - PAN Javali 2017
	Rio Negro	-54986,000	-19448,000	2019	IBAMA 2019
MT	Rio Branco	-58,000	-15,240	2019	IBAMA 2019
	Alto Araguaia	-53,467	-17,449	2013	Rosa et al 2020
	Barão de Melgaço	-56,027	-16,806	2010	Rosa et al 2020
	Barra do Bugres	-57,563	-15,067	2015	Pedrosa et al 2015
	Cáceres	-57,834	-16,537	2015	Pedrosa et al 2015
	Glória D'Oeste	-58,325	-15,839	2019	IBAMA 2019
	Ipiranga do Norte	-56,056	-12,013	2019	IBAMA 2019
	Itiquira	-54,607	-17,336	2012 a 2015	Rosa et al 2020
	Lambari D'Oeste	-57,784	-15,375	2019	IBAMA 2019
	Nortelândia	-56,720	-14,348	2019	IBAMA 2019
	Paranaíta	-56,682	-9,593	2016	Rosa et al 2020
	Poconé	-56,947	-16,791	2013	Rosa et al 2020
	Porto Esperidião	-58,982	-15,958	2001	Rosa et al 2020
	Rondonópolis	-54,685	-16,554	2011	Rosa et al 2020
	São José dos Quatro Marcos	-58,297	-15,567	2019	IBAMA 2019
	Sinop	-55,500	-11,712	2018	Rosa et al 2020
	Tabaporã	-56,497	-11,213	2019	IBAMA 2019
	Torixoréu	-52,890	-16,295	2019	IBAMA 2019
	Vila Bela da Santíssima Trindade	-59,990	-15,189	2013	Rosa et al 2020
PA	Altamira	-53,887	-6,486	2012	Rosa et al 2020
	Cachoeira do Arari	-48,877	-0,869	2019	IBAMA 2019
	Oriximiná	-57,150	0,255	2010	Rosa et al 2020
	Santa Cruz do Arari	-49,314	-0,583	2019	IBAMA 2019
	Senador José Porfírio	-51,774	-4,170	2012	Rosa et al 2020
	Soure	-48,698	-0,448	2005-2018	Rosa et al 2020
	Vitória do Xingu	-51,974	-3,135	2012	Rosa et al 2020

PB	Princesa Isabel	-38,005	-7,654	2019	IBAMA 2019
	Santa Inês	-38,577	-7,666	2019	IBAMA 2019
	Santana dos Garrotes	-37,960	-7,388	2019	IBAMA 2019
	São Vicente do Seridó	-36,450	-6,909	2019	IBAMA 2019
PE	Carnaubeira da Penha	-38,722	-8,409	2019	IBAMA 2019
	Exu	-39,748	-7,516	2019	IBAMA 2019
	Itapetim	-37,143	-7,398	2019	IBAMA 2019
	Pedra	-36,900	-8,697	2019	IBAMA 2019
	São José do Belmonte	-38,746	-7,866	2019	IBAMA 2019
	Sertânia	-37,337	-8,211	2019	IBAMA 2019
PI	Caldeirão Grande do Piauí	-40,623	-7,308	2019	IBAMA 2019
	Caracol	-43,347	-9,089	2015	Pedrosa et al 2015
	Cristino Castro	-43,962	-8,782	2019	IBAMA 2019
	Paulistana	-41,145	-8,110	2019	IBAMA 2019
PR	Altônia	-53,949	-23,903	2004	Rosa et al 2020
	Apucarana	-51,446	-23,572	2015	Pedrosa et al 2015
	Arapoti	-49,976	-24,093	2017	BRASIL - PAN Javali 2017
	Araucária	-49,441	-25,609	2001 e 2002	Rosa et al 2020
	Assis Chateaubriand	-53,586	-24,425	2019	IBAMA 2019
	Astorga	-51,700	-23,250	2015	Pedrosa et al 2015
	Balsa Nova	-49,689	-25,522	2007	Rosa et al 2020
	Barbosa Ferraz	-52,047	-24,082	2015	Pedrosa et al 2015
	Bituruna	-51,527	-26,171	2019	IBAMA 2019
	Bom Sucesso	-51,824	-23,713	2015	Pedrosa et al 2015
	Cafelândia	-53,364	-24,692	2019	IBAMA 2019
	Cafezal do Sul	-53,562	-23,939	2019	IBAMA 2019
	Cambé	-51,284	-23,180	2015	Pedrosa et al 2015
	Cambira	-51,567	-23,630	2019	IBAMA 2019
	Campina Grande do Sul	-48,845	-25,186	2019	IBAMA 2019
	Campo Largo	-49,619	-25,292	2007	Deberdt and Scherer 2007, Salvador

				2012
Campo Mourão	-52,381	-24,102	2015	Pedrosa et al 2015
Candói	-52,021	-25,524	2019	IBAMA 2019
Carambeí	-50,152	-24,894	2015	Pedrosa et al 2015
Cascavel	-53,380	-25,029	2017	BRASIL - PAN Javali 2017
Castro	-49,842	-24,800	2015	Pedrosa et al 2015
Cidade Gaúcha	-52,958	-23,383	2017	BRASIL - PAN Javali 2017
Clevelândia	-52,358	-26,345	2019	IBAMA 2019
Conselheiro Mairinck	-50,130	-23,597	2019	IBAMA 2019
Corbélia	-53,237	-24,743	2015	Pedrosa et al 2015
Cornélio Procópio	-50,624	-23,226	2015	Pedrosa et al 2015
Coronel Domingos Soares	-51,925	-26,182	2019	IBAMA 2019
Corumbataí do Sul	-52,142	-24,124	2015	Pedrosa et al 2015
Curitiba	-49,288	-25,478	1995 a 2018	Rosa et al 2020
Douradina	-53,290	-23,348	2015	Pedrosa et al 2015
Engenheiro Beltrão	-52,270	-23,760	2015	Pedrosa et al 2015
Fênix	-52,030	-23,901	1996	Rosa et al 2020
Fernandes Pinheiro	-50,510	-25,517	2015	Pedrosa et al 2015
Formosa do Oeste	-53,332	-24,293	2019	IBAMA 2019
General Carneiro	-51,392	-26,473	2009-2014	Rosa et al 2020
Godoy Moreira	-51,908	-24,160	2015	Pedrosa et al 2015
Guaraniaçu	-52,863	-25,055	2017	BRASIL - PAN Javali 2017
Guarapuava	-51,491	-25,371	2015	Pedrosa et al 2015
Guaraqueçaba	-48,367	-25,234	1996 a 1998	Rosa et al 2020
Guaratuba	-48,769	-25,818	2019	IBAMA 2019
Ibaiti	-50,287	-23,778	2015	Pedrosa et al 2015
Ibema	-53,024	-25,152	2019	IBAMA 2019
Ibiporã	-51,038	-23,236	2019	IBAMA 2019
Imbituva	-50,655	-25,226	2017	BRASIL - PAN Javali 2017
Ipiranga	-50,586	-24,988	2015	Pedrosa et al 2015
Itambé	-52,008	-23,707	2015	Pedrosa et al 2015

Jaguapitã	-51,556	-23,065	2019	IBAMA 2019
Jaguariaíva	-49,705	-24,331	2008	Rosa et al 2020
Jandaia do Sul	-51,685	-23,628	2015	Pedrosa et al 2015
Jardim Alegre	-51,767	-24,206	2015	Pedrosa et al 2015
Jundiaí do Sul	-50,232	-23,473	2015	Pedrosa et al 2015
Lapa	-49,871	-25,771	2015	Pedrosa et al 2015
Lidianópolis	-51,639	-24,086	2015	Pedrosa et al 2015
Lindoeste	-53,558	-25,261	2019	IBAMA 2019
Londrina	-51,110	-23,514	2019	IBAMA 2019
Lunardelli	-51,771	-24,080	2007	Deberdt and Scherer 2007
Marilândia do Sul	-51,284	-23,773	2015	Pedrosa et al 2015
Mariópolis	-52,581	-26,336	2019	IBAMA 2019
Maripá	-53,792	-24,445	2019	IBAMA 2019
Marquinho	-52,253	-25,101	2019	IBAMA 2019
Marumbi	-51,660	-23,754	2019	IBAMA 2019
Nova Aurora	-53,277	-24,503	2019	IBAMA 2019
Nova Esperança	-52,251	-23,191	2015	Pedrosa et al 2015
Nova Fátima	-50,538	-23,419	2019	IBAMA 2019
Novo Itacolomi	-51,533	-23,781	2019	IBAMA 2019
Palmas	-51,814	-26,451	2007	Deberdt and Scherer 2007
Palmeira	-50,058	-25,443	2007	Deberdt and Scherer 2007, Bach 2009, Salvador 2012
Palmital	-52,266	-24,876	2007	Deberdt and Scherer 2007
Palotina	-53,824	-24,275	2015	Pedrosa et al 2015
Pato Branco	-52,663	-26,169	2019	IBAMA 2019
Peabiru	-52,327	-23,931	2015	Pedrosa et al 2015
Piraí do Sul	-49,938	-24,470	2019	IBAMA 2019
Ponta Grossa	-50,081	-25,140	1999	Rosa et al 2020, Salvador 2012
Porto Amazonas	-49,895	-25,530	2015	Pedrosa et al 2015
Quedas do Iguaçu	-52,955	-25,457	1997	Rosa et al 2020
Quinta do Sol	-52,140	-23,830	2015	Pedrosa et al 2015
Ribeirão do Pinhal	-50,374	-23,448	2015	Pedrosa et al 2015

	Rolândia	-51,409	-23,271	2015	Pedrosa et al 2015
	Santa Tereza do Oeste	-53,606	-25,037	2019	IBAMA 2019
	Santo Antônio da Platina	-50,086	-23,297	2015	Pedrosa et al 2015
	São João do Ivaí	-51,848	-23,993	2015	Pedrosa et al 2015
	São Jorge do Patrocínio	-53,948	-23,739	2004	Rosa et al 2020
	São José dos Pinhais	-49,095	-25,664	1997	Rosa et al 2020
	São Mateus do Sul	-50,442	-25,908	2015	Pedrosa et al 2015
	São Miguel do Iguaçu	-54,262	-25,387	2019	IBAMA 2019
	São Pedro do Iguaçu	-53,891	-24,907	2019	IBAMA 2019
	São Pedro do Ivaí	-51,872	-23,846	2015	Pedrosa et al 2015
	Sengés	-49,456	-24,249	2019	IBAMA 2019
	Sertaneja	-50,875	-22,934	2015	Pedrosa et al 2015
	Sertanópolis	-51,072	-23,057	2015	Pedrosa et al 2015
	Tamarana	-51,052	-23,822	2007	Deberdt and Scherer 2007
	Teixeira Soares	-50,408	-25,313	2015	Pedrosa et al 2015
	Telêmaco Borba	-50,523	-24,250	2017	Rosa et al 2020
	Terra Roxa	-54,063	-24,209	2013	Pedrosa et al 2015
	Tibagi	-50,469	-24,656	2015	Pedrosa et al 2015
	Toledo	-53,778	-24,705	2015	Pedrosa et al 2015
	Três Barras do Paraná	-53,225	-25,439	2019	IBAMA 2019
	Tuneiras do Oeste	-52,843	-23,879	2015	Pedrosa et al 2015
	Umuarama	-53,414	-23,680	2019	IBAMA 2019
	Verê	-52,958	-25,875	2019	IBAMA 2019
	Virmond	-52,237	-25,410	2019	IBAMA 2019
RJ	Bom Jesus do Itabapoana	-41,683	-21,123	2015	Pedrosa et al 2015
	Cardoso Moreira	-41,500	-21,525	2016	Rosa et al 2020
	Itatiaia	-44,588	-22,442	2014	Rosa et al 2020
	Laje do Muriaé	-42,135	-21,250	2019	IBAMA 2019
	Nova Friburgo	-42,501	-22,319	2017	BRASIL - PAN Javali 2017

	Porciúncula	-41,970	-20,907	2015	Pedrosa et al 2015
	Quissamã	-41,444	-22,105	2015	Rosa et al 2020
	Resende	-44,485	-22,441	2019	IBAMA 2019
	São Gonçalo	-42,997	-22,826	2010	Rosa et al 2020
	Varre-Sai	-41,830	-20,893	2015	Pedrosa et al 2015
RO	Chupinguaia	-60,898	-12,537	2019	IBAMA 2019
	Porto Velho	-64,307	-9,154	2011 a 2013	Rosa et al 2020
RS	Aceguá	-54,139	-31,691	2004	IBAMA 2004; Deberdt and Scherer 2007
	Alegrete	-55,836	-29,764	2015	Pedrosa et al 2015
	Almirante Tamandaré do Sul	-52,908	-28,130	2019	IBAMA 2019
	André da Rocha	-51,504	-28,594	2015	Pedrosa et al 2015
	Antônio Prado	-51,317	-28,882	2017	BRASIL - PAN Javali 2017
	Arroio dos Ratos	-51,752	-30,193	2004	IBAMA 2004; Deberdt and Scherer 2007
	Arroio Grande	-52,920	-32,188	1995	IBAMA 1995; Deberdt and Scherer 2007
	Bagé	-54,017	-31,236	1995	IBAMA 1995, Deberdt and Scherer 2007
	Barra do Quaraí	-57,335	-30,151	2007	Deberdt and Scherer 2007
	Barra do Ribeiro	-51,358	-30,374	2017	BRASIL - PAN Javali 2017
	Barros Cassal	-52,589	-29,113	2017	BRASIL - PAN Javali 2017
	Boa Vista do Cadeado	-53,838	-28,656	2015	Rosa et al 2020
	Bom Jesus	-50,423	-28,598	2002	IBAMA 2002, Deberdt and Scherer 2007
	Bom Princípio	-51,363	-29,470	2019	IBAMA 2019
	Butiá	-52,005	-30,184	2017	BRASIL - PAN Javali 2017
	Caçapava do Sul	-53,478	-30,593	2015	Pedrosa et al 2015
	Cacequi	-54,803	-29,920	2014	Rosa et al 2020
	Cachoeira do Sul	-52,986	-30,206	2015	Pedrosa et al 2015
	Camaquã	-51,789	-30,923	2015	Pedrosa et al 2015
	Cambará do Sul	-50,137	-29,063	2002	IBAMA 2002, Deberdt and Scherer 2007

Campestre da Serra	-51,099	-28,726	2017	BRASIL - PAN Javali 2017
Candiota	-53,746	-31,554	2004	IBAMA 2004, Deberdt and Scherer 2007
Canela	-50,775	-29,351	2015	Pedrosa et al 2015
Canguçu	-52,670	-31,217	2015	Pedrosa et al 2015
Capão Bonito do Sul	-51,389	-28,152	2017	BRASIL - PAN Javali 2017
Carazinho	-52,864	-28,278	2009	Rosa et al 2020
Carlos Barbosa	-51,505	-29,322	2017	BRASIL - PAN Javali 2017
Caseiros	-51,737	-28,248	2019	IBAMA 2019
Caxias do Sul	-51,024	-29,102	1992/2002	IBAMA 2002, Deberdt and Scherer 2007
Centenário	-52,003	-27,775	2019	IBAMA 2019
Cerrito	-52,796	-31,730	2004	IBAMA 2004, Deberdt and Scherer 2007
Chuí	-53,413	-33,653	2015	Rosa et al 2020
Coronel Pilar	-51,720	-29,263	2017	BRASIL - PAN Javali 2017
Coxilha	-52,332	-28,122	2017	BRASIL - PAN Javali 2017
Cristal	-52,030	-31,009	2019	IBAMA 2019
Dom Pedrito	-54,665	-31,057	2015	Pedrosa et al 2015
Encruzilhada do Sul	-52,672	-30,630	2015	Pedrosa et al 2015
Erechim	-52,257	-27,643	2019	IBAMA 2019
Esmeralda	-51,170	-28,038	2015	Rosa et al 2020
Espumoso	-52,827	-28,864	2017	BRASIL - PAN Javali 2017
Fagundes Varela	-51,717	-28,887	2004	IBAMA 2004, Deberdt and Scherer 2007
Farroupilha	-51,366	-29,210	2015	Pedrosa et al 2015
Flores da Cunha	-51,222	-29,031	2017	BRASIL - PAN Javali 2017
Garibaldi	-51,582	-29,241	2017	BRASIL - PAN Javali 2017
Giruá	-54,299	-28,030	2017	BRASIL - PAN Javali 2017
Gramado	-50,897	-29,386	2015	Pedrosa et al 2015
Gravataí	-50,947	-29,891	2007	Deberdt and Scherer 2007
Guabiju	-51,660	-28,578	2017	BRASIL - PAN Javali 2017
Guaíba	-51,434	-30,177	2015	Pedrosa et al 2015

Guaporé	-51,904	-28,855	2019	IBAMA 2019
Herval	-53,401	-32,021	1991	Deberdt and Scherer 2007
Hulha Negra	-53,889	-31,448	2004	IBAMA 2004, Deberdt and Scherer 2007
Ibiraiaras	-51,627	-28,380	2017	BRASIL - PAN Javali 2017
Ibirapuitã	-52,443	-28,625	2015	Pedrosa et al 2015
Ipê	-51,299	-28,718	2004	IBAMA 2004, Deberdt and Scherer 2007
Itaqui	-56,176	-29,214	2007	Deberdt and Scherer 2007
Itati	-50,164	-29,461	2007	Deberdt and Scherer 2007
Jaguarão	-53,336	-32,410	1989	Deberdt and Scherer 2007
Jaquirana	-50,361	-28,948	2004	IBAMA 2004, Deberdt and Scherer 2007
Lagoa Vermelha	-51,502	-28,226	2009	Rosa et al 2020
Lavras do Sul	-54,154	-30,772	2017	BRASIL - PAN Javali 2017
Manoel Viana	-55,557	-29,428	2017	BRASIL - PAN Javali 2017
Maquiné	-50,209	-29,634	2007	Deberdt and Scherer 2007
Marau	-52,269	-28,455	2019	IBAMA 2019
Monte Alegre dos Campos	-50,805	-28,700	2017	BRASIL - PAN Javali 2017
Mostardas	-50,729	-30,854	2017	Rosa et al 2020
Muitos Capões	-51,230	-28,385	2004	IBAMA 2004, Deberdt and Scherer 2007
Nonoai	-52,857	-27,370	2019	IBAMA 2019
Nova Araçá	-51,746	-28,651	2017	BRASIL - PAN Javali 2017
Nova Bassano	-51,754	-28,726	2017	BRASIL - PAN Javali 2017
Nova Bréscia	-52,035	-29,222	2017	BRASIL - PAN Javali 2017
Nova Prata	-51,608	-28,761	2004	IBAMA 2004, Deberdt and Scherer 2007
Nova Roma do Sul	-51,408	-28,989	2017	BRASIL - PAN Javali 2017
Palmares do Sul	-50,449	-30,362	2017	Rosa et al 2020
Palmeira das Missões	-53,382	-27,940	2017	BRASIL - PAN Javali 2017
Paraí	-51,788	-28,600	2017	BRASIL - PAN Javali 2017
Passo Fundo	-52,452	-28,269	2017	BRASIL - PAN Javali 2017

Pedras Altas	-53,691	-31,839	2004	IBAMA 2004, Deberdt and Scherer 2007
Pedro Osório	-52,873	-31,960	1997	IBAMA 2002, Deberdt and Scherer 2007
Pelotas	-52,341	-31,581	2015	Pedrosa et al 2015
Pinhal da Serra	-51,219	-27,854	2017	BRASIL - PAN Javali 2017
Pinheiro Machado	-53,413	-31,405	1995	IBAMA 1995, Deberdt and Scherer 2007
Piratini	-53,103	-31,439	1995	IBAMA 1995, Deberdt and Scherer 2007
Ponte Preta	-52,506	-27,655	2017	BRASIL - PAN Javali 2017
Protásio Alves	-51,487	-28,737	2017	BRASIL - PAN Javali 2017
Quaraí	-56,153	-30,279	2017	BRASIL - PAN Javali 2017
Quevedos	-54,065	-29,310	2017	Rosa et al 2020
Restinga Sêca	-53,344	-29,817	2014	Rosa et al 2020
Rio Grande	-52,405	-32,220	2008	Rosa et al 2020
Rio Pardo	-52,437	-30,023	2015	Pedrosa et al 2015
Roca Sales	-51,829	-29,257	2017	BRASIL - PAN Javali 2017
Rosário do Sul	-55,113	-30,326	2015	Rosa et al 2020
Santa Bárbara do Sul	-53,285	-28,374	2019	BRASIL - PAN Javali 2017
Santa Cecília do Sul	-51,898	-28,181	2017	BRASIL - PAN Javali 2017
Santa Margarida do Sul	-54,098	-30,371	2017	BRASIL - PAN Javali 2017
Santa Maria	-53,825	-29,785	2013	Rosa et al 2020
Santa Tereza	-51,711	-29,164	2004	IBAMA 2004, Deberdt and Scherer 2007
Santa Vitória do Palmar	-53,008	-33,164	2006	Rosa et al 2020
Santana da Boa Vista	-53,177	-30,817	2015	Pedrosa et al 2015
Sant'Ana do Livramento	-55,562	-30,738	2009	Rosa et al 2020
Santiago	-54,796	-29,127	2015	Rosa et al 2020
Santo Antônio da Patrulha	-50,559	-29,873	2019	IBAMA 2019
São Francisco de Assis	-55,131	-29,448	2019	IBAMA 2019

	São Francisco de Paula	-50,560	-29,200	2004	IBAMA 2004, Deberdt and Scherer 2007
	São Gabriel	-54,365	-30,305	2015	Pedrosa et al 2015
	São Jorge	-51,716	-28,498	2017	BRASIL - PAN Javali 2017
	São José do Ouro	-51,560	-27,772	2017	BRASIL - PAN Javali 2017
	São José dos Ausentes	-49,962	-28,649	2009	Rosa et al 2020
	São Lourenço do Sul	-52,123	-31,234	2019	IBAMA 2019
	São Luiz Gonzaga	-54,891	-28,418	2017	BRASIL - PAN Javali 2017
	São Marcos	-51,065	-28,963	2017	BRASIL - PAN Javali 2017
	São Miguel das Missões	-54,522	-28,673	2015	Pedrosa et al 2015
	São Nicolau	-55,248	-28,203	2017	BRASIL - PAN Javali 2017
	São Sepé	-53,620	-30,176	2017	BRASIL - PAN Javali 2017
	São Valentim do Sul	-51,761	-29,057	2017	BRASIL - PAN Javali 2017
	São Vicente do Sul	-54,754	-29,710	2019	IBAMA 2019
	Soledade	-52,537	-28,839	2017	BRASIL - PAN Javali 2017
	Tapes	-51,441	-30,664	2017	BRASIL - PAN Javali 2017
	Tavares	-51,075	-31,289	2019	IBAMA 2019
	Terra de Areia	-50,067	-29,602	2007	Deberdt and Scherer 2007
	Trindade do Sul	-52,899	-27,528	2015	Pedrosa et al 2015
	Tupanciretã	-54,003	-29,021	2015	Pedrosa et al 2015
	Unistalda	-55,159	-29,069	2017	BRASIL - PAN Javali 2017
	Uruguaiana	-56,729	-29,841	2007	Deberdt and Scherer 2007
	Vacaria	-50,924	-28,370	1994/2004	IBAMA 2004, Deberdt and Scherer 2007
	Viamão	-50,869	-30,167	2002	IBAMA 2002, Deberdt and Scherer 2007
	Vila Nova do Sul	-53,879	-30,346	2019	IBAMA 2019
SC	Abdon Batista	-51,056	-27,584	2019	IBAMA 2019
	Abelardo Luz	-52,256	-26,562	2015	Pedrosa et al 2015
	Água Doce	-51,612	-26,764	2007	Deberdt and Scherer 2007
	Alfredo Wagner	-49,331	-27,706	2010	Rosa et al 2020
	Anita Garibaldi	-51,080	-27,730	2019	IBAMA 2019

Antônio Carlos	-48,831	-27,497	2019	IBAMA 2019
Araquari	-48,758	-26,462	2007	Deberdt and Scherer 2007
Arvoredo	-52,442	-27,071	2019	IBAMA 2019
Atalanta	-49,743	-27,437	2019	IBAMA 2019
Balneário Barra do Sul	-48,653	-26,446	2019	IBAMA 2019
Belmonte	-53,618	-26,857	2019	IBAMA 2019
Benedito Novo	-49,435	-26,801	2019	IBAMA 2019
Blumenau	-49,097	-26,886	2019	IBAMA 2019
Bocaina do Sul	-49,909	-27,763	2019	IBAMA 2019
Bom Jardim da Serra	-49,652	-28,361	2019	IBAMA 2019
Bom Jesus	-52,390	-26,739	2019	IBAMA 2019
Bom Retiro	-49,563	-27,785	2016	Rosa et al 2020
Botuverá	-49,124	-27,219	2017	BRASIL - PAN Javali 2017
Brunópolis	-50,845	-27,347	2019	IBAMA 2019
Caçador	-51,085	-26,763	2010	Rosa et al 2020
Calmon	-51,007	-26,622	2015	Pedrosa et al 2015
Campo Belo do Sul	-50,771	-27,847	2015	Pedrosa et al 2015
Campos Novos	-51,245	-27,413	2013	Rosa et al 2020
Canelinha	-48,802	-27,235	2007	Deberdt and Scherer 2007
Capão Alto	-50,607	-28,062	2008	Salvador 2012
Capinzal	-51,631	-27,412	2019	IBAMA 2019
Catanduvas	-51,696	-27,045	2019	IBAMA 2019
Celso Ramos	-51,308	-27,652	2019	IBAMA 2019
Cerro Negro	-50,932	-27,776	2015	Pedrosa et al 2015
Chapecó	-52,650	-27,125	2005	Rosa et al 2020
Concórdia	-52,007	-27,239	2017	Rosa et al 2020
Coronel Freitas	-52,725	-26,883	2008	Rosa et al 2020
Correia Pinto	-50,378	-27,597	2019	IBAMA 2019
Corupá	-49,327	-26,440	2003	Rosa et al 2020
Curitibanos	-50,618	-27,293	2015	Pedrosa et al 2015
Descanso	-53,479	-26,858	2019	IBAMA 2019

Doutor Pedrinho	-49,554	-26,706	2019	IBAMA 2019
Faxinal dos Guedes	-52,244	-26,847	2015	Pedrosa et al 2015
Florianópolis	-48,508	-27,578	2015	BRASIL - PAN Javali 2017
Formosa do Sul	-52,794	-26,634	2019	IBAMA 2019
Forquilhinha	-49,493	-28,782	2019	IBAMA 2019
Fraiburgo	-50,872	-27,038	2015	Pedrosa et al 2015
Frei Rogério	-50,766	-27,192	2019	IBAMA 2019
Galvão	-52,659	-26,449	2017	Rosa et al 2020
Gaspar	-48,966	-26,931	2019	IBAMA 2019
Guaraciaba	-53,571	-26,580	2019	IBAMA 2019
Ibiam	-51,215	-27,208	2019	IBAMA 2019
Ibirama	-49,529	-27,018	2017	BRASIL - PAN Javali 2017
Ilhota	-48,857	-26,859	2019	IBAMA 2019
Iporã do Oeste	-53,489	-27,000	2019	IBAMA 2019
Ipuaçu	-52,476	-26,679	2019	IBAMA 2019
Ipumirim	-52,153	-27,040	2019	IBAMA 2019
Irani	-51,918	-27,025	2007	Deberdt and Scherer 2007
Jaborá	-51,773	-27,142	2019	IBAMA 2019
Jacinto Machado	-49,848	-28,995	2019	IBAMA 2019
Jardinópolis	-52,871	-26,717	2019	IBAMA 2019
Lages	-50,341	-28,020	2007	Deberdt and Scherer 2007
Laguna	-48,826	-28,486	2010	Rosa et al 2020
Lebon Régis	-50,703	-26,858	2015	Pedrosa et al 2015
Lindóia do Sul	-52,052	-27,032	2019	IBAMA 2019
Macieira	-51,353	-26,804	2019	IBAMA 2019
Mafra	-49,890	-26,201	2015	Pedrosa et al 2015
Maracajá	-49,456	-28,864	2019	IBAMA 2019
Matos Costa	-51,142	-26,481	2019	IBAMA 2019
Meleiro	-49,602	-28,842	2019	IBAMA 2019
Mondaí	-53,446	-27,099	2019	IBAMA 2019
Monte Carlo	-50,928	-27,194	2019	IBAMA 2019

Monte Castelo	-50,292	-26,661	2019	IBAMA 2019
Morro Grande	-49,740	-28,722	2019	IBAMA 2019
Orleans	-49,372	-28,280	2019	IBAMA 2019
Otacílio Costa	-49,972	-27,517	2015	Pedrosa et al 2015
Painel	-50,072	-27,964	2007	Deberdt and Scherer 2007
Palhoça	-48,662	-27,772	2017	BRASIL - PAN Javali 2017
Palmeira	-50,162	-27,563	2019	IBAMA 2019
Palmitos	-53,180	-27,093	2019	IBAMA 2019
Papanduva	-50,172	-26,502	2009	Rosa et al 2020
Paraíso	-53,678	-26,663	2019	IBAMA 2019
Passos Maia	-51,961	-26,706	2007	Deberdt and Scherer 2007
Ponte Alta	-50,299	-27,410	2019	IBAMA 2019
Ponte Alta do Norte	-50,419	-27,180	2019	IBAMA 2019
Ponte Serrada	-51,928	-26,862	2007	Deberdt and Scherer 2007
Porto União	-51,008	-26,384	2019	IBAMA 2019
Praia Grande	-49,990	-29,182	2015	BRASIL - PAN Javali 2017
Presidente Getúlio	-49,714	-27,063	2015	Pedrosa et al 2015
Rio das Antas	-51,063	-26,909	2019	IBAMA 2019
Rio dos Cedros	-49,368	-26,618	2019	IBAMA 2019
Rio Negrinho	-49,596	-26,443	2015	Pedrosa et al 2015
Rio Rufino	-49,753	-27,914	2019	IBAMA 2019
Riqueza	-53,344	-26,978	2019	IBAMA 2019
Santa Cecília	-50,446	-26,926	2015	Pedrosa et al 2015
São Carlos	-53,031	-27,030	2019	IBAMA 2019
São Cristóvão do Sul	-50,349	-27,295	2015	Pedrosa et al 2015
São Domingos	-52,555	-26,539	2017	Rosa et al 2020
São João Batista	-48,859	-27,329	2019	IBAMA 2019
São Joaquim	-50,014	-28,298	2009	Rosa et al 2020
São José do Cerrito	-50,650	-27,598	2010	Rosa et al 2020
São Martinho	-48,972	-28,125	2019	IBAMA 2019
Siderópolis	-49,527	-28,583	2019	IBAMA 2019

	Tangará	-51,147	-27,147	2019	IBAMA 2019
	Timbé do Sul	-49,868	-28,807	2019	IBAMA 2019
	Timbó Grande	-50,666	-26,624	2015	Pedrosa et al 2015
	Três Barras	-50,255	-26,170	2010	Rosa et al 2020
	Treviso	-49,490	-28,499	2019	IBAMA 2019
	Urubici	-49,577	-28,039	2010	Rosa et al 2020
	Urupema	-49,901	-28,024	2015	Pedrosa et al 2015
	Vargeão	-52,124	-26,779	2019	IBAMA 2019
	Vargem	-50,950	-27,467	2019	IBAMA 2019
	Vargem Bonita	-51,757	-26,945	2008 a 2010	Rosa et al 2020
	Xanxerê	-52,410	-26,872	2019	IBAMA 2019
	Xavantina	-52,322	-27,021	2019	IBAMA 2019
	Zortéa	-51,536	-27,477	2019	IBAMA 2019
SP	Adamantina	-51,057	-21,577	2018	SAA-SP 2018
	Adolfo	-49,653	-21,289	2017	MAPA 2019
	Aguaí	-47,040	-22,050	2015	Pedrosa et al 2015
	Águas de Lindóia	-46,604	-22,475	2015	Rosa et al 2020
	Águas de Santa Bárbara	-49,261	-22,858	2015	Rosa et al 2020
	Águas de São Pedro	-47,876	-22,599	2018	SAA-SP 2018
	Agudos	-49,109	-22,572	2015	Rosa et al 2020
	Alambari	-47,869	-23,549	2015	IBAMA 2019
	Altair	-49,094	-20,533	2016	IBAMA 2019
	Altinópolis	-47,386	-21,018	2017	Rosa et al 2020
	Alto Alegre	-50,192	-21,613	2013	Pedrosa et al 2015
	Álvares Florence	-49,920	-20,290	2013	Pedrosa et al 2015
	Álvares Machado	-51,515	-22,132	2015	Rosa et al 2020
	Alvinlândia	-49,759	-22,453	2018	SAA-SP 2018
	Americana	-47,289	-22,723	2015	Pedrosa et al 2015
	Américo de Campos	-49,768	-20,289	2013	Pedrosa et al 2015
	Amparo	-46,799	-22,699	2013	Pedrosa et al 2015
	Analândia	-47,678	-22,121	2016	IBAMA 2019

Andradina	-51,330	-20,836	2019	IBAMA 2019
Angatuba	-48,459	-23,437	2013	Pedrosa et al 2015
Anhembi	-48,175	-22,800	2015	IBAMA 2019
Anhumas	-51,428	-22,362	2016	IBAMA 2019
Aparecida d'Oeste	-50,922	-20,479	2015	Rosa et al 2020
Araçatuba	-50,574	-21,114	2013	Pedrosa et al 2015
Araçoiaba da Serra	-47,652	-23,544	2015	Rosa et al 2020
Aramina	-47,821	-20,145	2018	SAA-SP 2018
Arandu	-49,064	-23,178	2015	Rosa et al 2020
Araraquara	-48,181	-21,792	2014	Pedrosa et al 2015
Araras	-47,324	-22,346	2013	Pedrosa et al 2015
Arco-Íris	-50,431	-21,766	2015	Rosa et al 2020
Arealva	-48,982	-22,076	2015	IBAMA 2019
Artur Nogueira	-47,132	-22,561	2011-2012	Rosa et al 2020
Aspásia	-50,728	-20,184	2015	Rosa et al 2020
Assis	-50,421	-22,602	2017	BRASIL - PAN Javali 2017
Atibaia	-46,587	-23,123	2007	Deberdt and Scherer 2007
Auriflama	-50,580	-20,644	2018	SAA-SP 2018; IBAMA 2019
Avaí	-49,316	-22,187	2013	Pedrosa et al 2015
Avanhandava	-49,947	-21,461	2019	IBAMA 2019
Avaré	-48,894	-23,075	2013	Pedrosa et al 2015
Balbinos	-49,333	-21,892	2013	Pedrosa et al 2015
Bálsamo	-49,552	-20,710	2016	Rosa et al 2020
Barão de Antonina	-49,572	-23,583	2018	SAA-SP 2018
Bariri	-48,719	-22,067	2016	IBAMA 2019
Barra Bonita	-48,542	-22,479	2016	IBAMA 2019
Barretos	-48,652	-20,514	2014	Pedrosa et al 2015
Bastos	-50,744	-21,950	2018	SAA-SP 2018, IBAMA 2019
Batatais	-47,575	-20,868	2015	Rosa et al 2020
Bauru	-49,126	-22,254	2015	Pedrosa et al 2015
Bebedouro	-48,511	-20,940	2014	IBAMA 2019

Bilac	-50,479	-21,428	2015	IBAMA 2019
Birigui	-50,351	-21,262	2013	Pedrosa et al 2015
Boa Esperança do Sul	-48,464	-21,935	2016	IBAMA 2019
Bocaina	-48,529	-22,105	2015	IBAMA 2019
Bofete	-48,286	-23,129	2014	Rosa et al 2020
Boituva	-47,675	-23,288	2019	IBAMA 2019
Bom Jesus dos Perdões	-46,479	-23,173	2015	Rosa et al 2020
Bom Sucesso de Itararé	-49,165	-24,316	2018	SAA-SP 2018
Borborema	-49,072	-21,611	2015	IBAMA 2019
Borebi	-48,992	-22,681	2015	IBAMA 2019
Botucatu	-48,468	-22,863	2015	Pedrosa et al 2015
Bragança Paulista	-46,556	-22,938	2007	Deberdt and Scherer 2007
Braúna	-50,339	-21,553	2016	IBAMA 2019
Brejo Alegre	-50,210	-21,177	2016	IBAMA 2019
Brodowski	-47,628	-21,050	2015	IBAMA 2019
Brotas	-48,081	-22,273	2007	Deberdt and Scherer 2007
Buri	-48,575	-23,752	2012	Rosa et al 2020, Pedrosa et al 2015
Buritama	-50,200	-21,049	2019	IBAMA 2019
Buritizal	-47,693	-20,209	2015	Pedrosa et al 2015
Cabreúva	-47,080	-23,301	2015	Rosa et al 2020
Caçapava	-45,713	-23,104	2015	IBAMA 2019
Cafelândia	-49,549	-21,731	2013	Pedrosa et al 2015
Cajobi	-48,839	-20,874	2013	Pedrosa et al 2015
Cajuru	-47,310	-21,276	2015	Rosa et al 2020
Campina do Monte Alegre	-48,442	-23,607	2013	Pedrosa et al 2015
Campinas	-47,044	-22,884	2015	Pedrosa et al 2015
Campos do Jordão	-45,533	-22,702	2015	Pedrosa et al 2015
Campos Novos Paulista	-50,010	-22,611	2016	BRASIL - PAN Javali 2017
Cândido Mota	-50,422	-22,809	2013	Pedrosa et al 2015

Cândido Rodrigues	-48,629	-21,343	2014	Rosa et al 2020
Capão Bonito	-48,290	-24,039	2007	Deberdt and Scherer 2007
Capela do Alto	-47,731	-23,467	2015	Rosa et al 2020
Capivari	-47,478	-22,981	2017	IBAMA 2019
Caraguatatuba	-45,488	-23,640	2018	SAA-SP 2018
Cardoso	-49,948	-20,067	2015	Pedrosa et al 2015
Casa Branca	-47,088	-21,801	2015	IBAMA 2019
Catanduva	-48,964	-21,134	2015	Pedrosa et al 2015
Catiguá	-49,053	-21,063	2015	IBAMA 2019
Cerqueira César	-49,144	-23,059	2015	Rosa et al 2020
Cerquilho	-47,757	-23,187	2015	Rosa et al 2020
Cesário Lange	-47,904	-23,217	2013	Pedrosa et al 2015
Charqueada	-47,746	-22,530	2015	Pedrosa et al 2015
Clementina	-50,460	-21,570	2013	Pedrosa et al 2015
Colina	-48,589	-20,746	2013	Pedrosa et al 2015
Colômbia	-48,722	-20,267	2013	Pedrosa et al 2015
Conchal	-47,141	-22,369	2015	Pedrosa et al 2015
Conchas	-48,047	-22,966	2016	IBAMA 2019
Cordeirópolis	-47,415	-22,480	2015	IBAMA 2019
Coroados	-50,303	-21,376	2016	IBAMA 2019
Coronel Macedo	-49,307	-23,630	2015	Rosa et al 2020
Corumbataí	-47,611	-22,236	2013	Rosa et al 2020
Cosmorama	-49,775	-20,443	2013	Pedrosa et al 2015
Cravinhos	-47,745	-21,340	2015	Pedrosa et al 2015
Cristais Paulista	-47,401	-20,371	2013	BRASIL - PAN Javali 2017
Cruzália	-50,769	-22,738	2016	IBAMA 2019
Cruzeiro	-45,006	-22,551	2015	Rosa et al 2020
Descalvado	-47,655	-21,881	2013	Pedrosa et al 2015
Diadema	-46,611	-23,697	2019	IBAMA 2019
Dirce Reis	-50,628	-20,448	2018	SAA-SP 2018
Dobrada	-48,357	-21,516	2015	Pedrosa et al 2015

Dois Córregos	-48,341	-22,396	2015	IBAMA 2019
Dolcinópolis	-50,528	-20,117	2018	SAA-SP 2018
Dourado	-48,334	-22,117	2016	IBAMA 2019
Dracena	-51,584	-21,557	2015	Rosa et al 2020
Duartina	-49,413	-22,393	2018	IBAMA 2019
Dumont	-47,980	-21,247	2019	IBAMA 2019
Eldorado	-48,234	-24,495	2013	Rosa et al 2020
Elisiário	-49,092	-21,161	2013	Pedrosa et al 2015
Embaúba	-48,848	-20,953	2013	Pedrosa et al 2015
Embu-Guaçu	-46,831	-23,854	2015	Pedrosa et al 2015
Engenheiro Coelho	-47,175	-22,487	2018	SAA-SP 2018
Espírito Santo do Pinhal	-46,793	-22,192	2013	Pedrosa et al 2015
Espírito Santo do Turvo	-49,433	-22,671	2019	IBAMA 2019
Estiva Gerbi	-46,943	-22,236	2019	IBAMA 2019
Estrela do Norte	-51,669	-22,486	2019	IBAMA 2019
Estrela d'Oeste	-50,411	-20,266	2015	Pedrosa et al 2015
Fartura	-49,520	-23,390	2017	IBAMA 2019
Fernandópolis	-50,283	-20,272	2015	Pedrosa et al 2015
Fernão	-49,542	-22,366	2016	IBAMA 2019
Flora Rica	-51,374	-21,698	2013	Pedrosa et al 2015
Floreal	-50,155	-20,670	2015	Pedrosa et al 2015
Flórida Paulista	-51,171	-21,540	2015	IBAMA 2019
Florínea	-50,695	-22,881	2015	Rosa et al 2020
Franca	-47,381	-20,555	2013	Pedrosa et al 2015
Gabriel Monteiro	-50,565	-21,500	2015	Rosa et al 2020
Gália	-49,578	-22,320	2007	Deberdt and Scherer 2007
Garça	-49,690	-22,231	2016	IBAMA 2019
Gastão Vidigal	-50,203	-20,804	2015	Rosa et al 2020
Gavião Peixoto	-48,448	-21,792	2015	Rosa et al 2020
General Salgado	-50,416	-20,638	2015	Pedrosa et al 2015

Getulina	-50,028	-21,783	2015	Pedrosa et al 2015
Guaiçara	-49,763	-21,570	2018	IBAMA 2019
Guaimbê	-49,861	-21,879	2019	IBAMA 2019
Guaíra	-48,364	-20,314	2013	Pedrosa et al 2015
Guapiaçu	-49,190	-20,743	2019	IBAMA 2019
Guapiara	-48,556	-24,213	2013	Rosa et al 2020
Guará	-47,775	-20,483	2018	SAA-SP 2018
Guaraçaí	-51,279	-21,086	2013	Pedrosa et al 2015
Guaraci	-49,003	-20,375	2016	IBAMA 2019
Guarani d'Oeste	-50,345	-20,067	2013	Pedrosa et al 2015
Guarantã	-49,588	-21,916	2018	IBAMA 2019
Guararapes	-50,695	-21,285	2007	Deberdt and Scherer 2007
Guararema	-46,059	-23,428	2015	Pedrosa et al 2015
Guaratinguetá	-45,233	-22,794	2006-2007	Rosa et al 2020
Guareí	-48,219	-23,370	2013	Rosa et al 2020
Guariba	-48,227	-21,396	2015	Rosa et al 2020
Guatapará	-47,980	-21,453	2018	IBAMA 2019
Guzolândia	-50,714	-20,628	2017	IBAMA 2019
Herculândia	-50,373	-21,962	2016	IBAMA 2019
Hortolândia	-47,208	-22,878	2015	Rosa et al 2020
Iacri	-50,619	-21,800	2014	BRASIL - PAN Javali 2017
Ibaté	-48,027	-21,951	2015	Pedrosa et al 2015
Ibirá	-49,220	-21,075	2013	Pedrosa et al 2015
Ibirarema	-50,077	-22,813	2016	IBAMA 2019
Ibitinga	-48,848	-21,793	2007	Deberdt and Scherer 2007
Icém	-49,185	-20,367	2016	IBAMA 2019
Iepê	-51,057	-22,649	2014	IBAMA 2019
Igarapava	-47,682	-20,064	2015	Pedrosa et al 2015
Igaratá	-46,150	-23,135	2019	IBAMA 2019
Iguape	-47,474	-24,550	2019	IBAMA 2019
Ilha Solteira	-51,259	-20,431	2015	Rosa et al 2020

Ilhabela	-45,323	-23,848	2016	IBAMA 2019
Indaiatuba	-47,203	-23,106	2015	Rosa et al 2020
Indiaporã	-50,264	-19,948	2015	Rosa et al 2020
Inúbia Paulista	-50,957	-21,739	2015	Rosa et al 2020
Iperó	-47,629	-23,404	2019	IBAMA 2019
Ipeúna	-47,716	-22,424	2007	Deberdt and Scherer 2007
Ipiguá	-49,404	-20,648	2015	Pedrosa et al 2015
Iporanga	-48,546	-24,513	2013	Rosa et al 2020
Ipuã	-48,066	-20,417	2015	IBAMA 2019
Iracemápolis	-47,524	-22,594	2015	Pedrosa et al 2015
Irapuã	-49,397	-21,268	2013	Pedrosa et al 2015
Itaberá	-49,142	-23,871	2013	Pedrosa et al 2015
Itaí	-49,054	-23,471	2013	Pedrosa et al 2015
Itajobi	-49,054	-21,356	2015	Rosa et al 2020
Itaju	-48,794	-21,952	2018	SAA-SP 2018
Itapecerica da Serra	-46,859	-23,737	2015	Pedrosa et al 2015
Itapetininga	-48,123	-23,645	2014	IBAMA 2019
Itapeva	-48,872	-23,914	2013	Pedrosa et al 2015
Itapira	-46,772	-22,432	2015	Pedrosa et al 2015
Itápolis	-48,815	-21,548	2004	Deberdt and Scherer 2007
Itaporanga	-49,458	-23,673	2018	SAA-SP 2018
Itararé	-49,304	-24,081	2015	Pedrosa et al 2015
Itatiba	-46,814	-23,007	2015	Pedrosa et al 2015
Itatinga	-48,629	-23,154	2003	Deberdt and Scherer 2007
Itirapina	-47,834	-22,295	2007	Deberdt and Scherer 2007
Itirapuã	-47,169	-20,658	2018	SAA-SP 2018
Itobi	-46,922	-21,749	2019	IBAMA 2019
Ituverava	-47,810	-20,330	2015	Pedrosa et al 2015
Jaborandi	-48,416	-20,650	2013	Pedrosa et al 2015
Jaboticabal	-48,288	-21,218	2015	Pedrosa et al 2015
Jacareí	-45,991	-23,299	2017	IBAMA 2019

Jaguariúna	-47,013	-22,692	2015	Rosa et al 2020
Jales	-50,554	-20,286	2016	IBAMA 2019
Jambeiro	-45,711	-23,279	2016	IBAMA 2019
Jardinópolis	-47,826	-20,992	2013	Pedrosa et al 2015
Jarinu	-46,721	-23,112	2015	Pedrosa et al 2015
Jaú	-48,556	-22,296	2015	IBAMA 2019
Jeriquara	-47,574	-20,340	2018	SAA-SP 2018
Joanópolis	-46,209	-22,939	2016	IBAMA 2019
João Ramalho	-50,799	-22,278	2016	IBAMA 2019
José Bonifácio	-49,779	-21,089	2014	IBAMA 2019
Jundiaí	-46,913	-23,195	2013	Pedrosa et al 2015
Junqueirópolis	-51,435	-21,449	2015	IBAMA 2019
Lagoinha	-45,207	-23,086	2016	IBAMA 2019
Laranjal Paulista	-47,866	-23,012	2019	IBAMA 2019
Lavínia	-51,033	-21,151	2018	IBAMA 2019
Lavrinhas	-44,889	-22,520	2016	IBAMA 2019
Leme	-47,338	-22,172	2017	IBAMA 2019
Lençóis Paulista	-48,825	-22,676	2015	Rosa et al 2020
Limeira	-47,364	-22,599	2015	Pedrosa et al 2015
Lins	-49,683	-21,650	2016	BAMA 2019
Lourdes	-50,234	-20,949	2019	IBAMA 2019
Louveira	-46,937	-23,084	2017	IBAMA 2019
Lucélia	-50,992	-21,644	2015	Rosa et al 2020
Lucianópolis	-49,550	-22,473	2018	IBAMA 2019
Luís Antônio	-47,782	-21,553	2015	Pedrosa et al 2015
Luiziânia	-50,351	-21,673	2014	IBAMA 2019
Lutécia	-50,385	-22,325	2018	IBAMA 2019
Macatuba	-48,719	-22,487	2015	IBAMA 2019
Macedônia	-50,182	-20,098	2015	Rosa et al 2020
Magda	-50,230	-20,596	2015	Pedrosa et al 2015
Mairinque	-47,229	-23,508	2015	Rosa et al 2020

Maracaí	-50,745	-22,652	2017	IBAMA 2019
Mariápolis	-51,172	-21,779	2018	IBAMA 2019
Marília	-49,983	-22,178	2018	SAA-SP 2018
Marinópolis	-50,832	-20,480	2018	SAA-SP 2018
Martinópolis	-51,123	-22,172	2015	Rosa et al 2020
Matão	-48,430	-21,610	2013	Pedrosa et al 2015
Meridiano	-50,187	-20,398	2013	Pedrosa et al 2015
Mesópolis	-50,615	-19,957	2019	IBAMA 2019
Miguelópolis	-48,105	-20,185	2015	Pedrosa et al 2015
Mineiros do Tietê	-48,433	-22,463	2013	Pedrosa et al 2015
Mira Estrela	-50,124	-19,952	2013	Pedrosa et al 2015
Miracatu	-47,395	-24,195	2019	IBAMA 2019
Mirandópolis	-51,131	-21,081	2015	IBAMA 2019
Mirante do Paranapanema	-51,998	-22,349	2018	SAA-SP 2018
Mirassol	-49,504	-20,828	2014	IBAMA 2019
Mirassolândia	-49,487	-20,595	2017	IBAMA 2019
Mococa	-47,033	-21,449	2015	Pedrosa et al 2015
Mogi Guaçu	-47,029	-22,232	2015	Pedrosa et al 2015
Mogi Mirim	-46,988	-22,451	2019	IBAMA 2019
Mombuca	-47,602	-22,943	2019	IBAMA 2019
Monte Alegre do Sul	-46,668	-22,704	2018	IBAMA 2019
Monte Alto	-48,533	-21,259	2015	IBAMA 2019
Monte Aprazível	-49,766	-20,737	2016	IBAMA 2019
Monte Azul Paulista	-48,681	-20,909	2013	Pedrosa et al 2015
Monte Castelo	-51,571	-21,255	2018	SAA-SP 2018
Monte Mor	-47,307	-22,953	2015	Pedrosa et al 2015
Monteiro Lobato	-45,804	-22,937	2015	IBAMA 2019
Morro Agudo	-48,153	-20,689	2013	IBAMA 2019
Morungaba	-46,783	-22,894	2013	Pedrosa et al 2015
Motuca	-48,170	-21,514	2015	IBAMA 2019
Murutinga do Sul	-51,301	-20,997	2018	SAA-SP 2018

Nazaré Paulista	-46,366	-23,191	2018	IBAMA 2019
Neves Paulista	-49,647	-20,870	2015	IBAMA 2019
Nhandeara	-50,047	-20,673	2016	IBAMA 2019
Nipoã	-49,778	-20,892	2015	Rosa et al 2020
Nova Aliança	-49,516	-21,063	2017	IBAMA 2019
Nova Campina	-48,973	-24,191	2018	SAA-SP 2018
Nova Canaã Paulista	-50,911	-20,372	2018	IBAMA 2019
Nova Castilho	-50,346	-20,778	2018	IBAMA 2019
Nova Europa	-48,550	-21,774	2015	Pedrosa et al 2015
Nova Granada	-49,331	-20,476	2015	IBAMA 2019
Nova Luzitânia	-50,249	-20,869	2019	IBAMA 2019
Novais	-48,918	-20,989	2016	IBAMA 2019
Novo Horizonte	-49,284	-21,469	2018	IBAMA 2019
Ocauçu	-49,938	-22,438	2019	IBAMA 2019
Olímpia	-48,960	-20,705	2007	Deberdt and Scherer 2007
Onda Verde	-49,244	-20,617	2018	SAA-SP 2018
Orindiúva	-49,355	-20,202	2017	IBAMA 2019
Orlândia	-47,906	-20,698	2014	IBAMA 2019
Oscar Bressane	-50,257	-22,295	2013	Pedrosa et al 2015
Osvaldo Cruz	-50,874	-21,733	2015	Rosa et al 2020
Ourinhos	-49,852	-22,953	2019	IBAMA 2019
Ouroeste	-50,402	-19,922	2013	Pedrosa et al 2015
Palestina	-49,498	-20,321	2015	IBAMA 2019
Palmares Paulista	-48,827	-21,105	2016	IBAMA 2019
Palmeira d'Oeste	-50,749	-20,439	2017	IBAMA 2019
Panorama	-51,858	-21,463	2015	IBAMA 2019
Paraguaçu Paulista	-50,627	-22,459	2012	Rosa et al 2020
Paraíso	-48,765	-21,020	2015	Pedrosa et al 2015
Paranapanema	-48,795	-23,438	2015	Pedrosa et al 2015
Paranapuã	-50,594	-20,064	2013	Pedrosa et al 2015
Parapuã	-50,822	-21,853	2016	IBAMA 2019

Pardinho	-48,402	-23,102	2015	Pedrosa et al 2015
Parisi	-50,037	-20,272	2015	Pedrosa et al 2015
Patrocínio Paulista	-47,289	-20,704	2015	Pedrosa et al 2015
Paulicéia	-51,791	-21,198	2015	IBAMA 2019
Paulínia	-47,145	-22,748	2011-2012	Rosa et al 2020
Paulistânia	-49,306	-22,568	2016	Rosa et al 2020
Paulo de Faria	-49,463	-20,067	2016	Rosa et al 2020
Pederneiras	-48,861	-22,301	2013	Pedrosa et al 2015
Pedra Bela	-46,442	-22,776	2018	IBAMA 2019
Pedranópolis	-50,107	-20,210	2013	Pedrosa et al 2015
Pedregulho	-47,439	-20,206	2015	Pedrosa et al 2015
Pedrinhas Paulista	-50,802	-22,817	2015	Rosa et al 2020
Penápolis	-50,096	-21,405	2015	Pedrosa et al 2015
Pereiras	-47,979	-23,120	2015	Rosa et al 2020
Piacatu	-50,644	-21,571	2015	Rosa et al 2020
Piedade	-47,438	-23,787	1995/2015	Pedrosa et al 2015
Pilar do Sul	-47,728	-23,856	2007	Deberdt and Scherer 2007
Pindamonhangaba	-45,459	-22,880	2017	IBAMA 2019
Pindorama	-48,912	-21,210	2016	IBAMA 2019
Pinhalzinho	-46,573	-22,779	2013	Pedrosa et al 2015
Piquete	-45,174	-22,590	2019	IBAMA 2019
Piracaia	-46,302	-23,047	2007	Deberdt and Scherer 2007
Piracicaba	-47,784	-22,726	2015	Pedrosa et al 2015
Piraju	-49,366	-23,187	2019	IBAMA 2019
Pirajuí	-49,414	-21,958	2013	Pedrosa et al 2015
Pirangi	-48,669	-21,094	2017	IBAMA 2019
Pirassununga	-47,390	-21,996	2013	Pedrosa et al 2015
Piratininga	-49,192	-22,425	2019	IBAMA 2019
Pitangueiras	-48,249	-21,006	2013	Pedrosa et al 2015
Planalto	-49,936	-21,001	2016	IBAMA 2019
Platina	-50,213	-22,625	2018	IBAMA 2019

Poloni	-49,820	-20,752	2016	IBAMA 2019
Pompéia	-50,188	-22,029	2013	Pedrosa et al 2015
Pongaí	-49,359	-21,730	2015	Rosa et al 2020
Pontalinda	-50,525	-20,451	2019	IBAMA 2019
Pontes Gestal	-49,757	-20,175	2015	Pedrosa et al 2015
Populina	-50,517	-19,907	2015	Pedrosa et al 2015
Porangaba	-48,117	-23,174	2015	Rosa et al 2020
Porto Feliz	-47,517	-23,230	2019	IBAMA 2019
Porto Ferreira	-47,447	-21,843	2018	SAA-SP 2018
Praia Grande	-46,523	-24,015	2017	Rosa et al 2020
Pratânia	-48,697	-22,819	2019	IBAMA 2019
Presidente Alves	-49,432	-22,122	2013	IBAMA 2019
Presidente Prudente	-51,343	-21,993	2019	IBAMA 2019
Presidente Venceslau	-51,838	-21,793	2018	SAA-SP 2018
Promissão	-49,870	-21,525	2019	IBAMA 2019
Quadra	-48,039	-23,301	2015	Pedrosa et al 2015
Quatá	-50,645	-22,206	2016	IBAMA 2019
Queiroz	-50,245	-21,801	2014	IBAMA 2019
Quintana	-50,369	-22,100	2018	IBAMA 2019
Rafard	-47,584	-23,045	2018	IBAMA 2019
Rancharia	-50,928	-22,283	2013	Pedrosa et al 2015
Reginópolis	-49,180	-21,883	2007	Deberdt and Scherer 2007
Registro	-47,821	-24,504	2015	Rosa et al 2020
Restinga	-47,506	-20,648	2018	SAA-SP 2018
Ribeirão Bonito	-48,185	-22,060	2015	IBAMA 2019
Ribeirão Corrente	-47,573	-20,449	2015	Pedrosa et al 2015
Ribeirão do Sul	-49,923	-22,752	2018	SAA-SP 2018
Ribeirão Grande	-48,359	-24,189	2014	Pedrosa et al 2015
Ribeirão Preto	-47,821	-21,211	2017	IBAMA 2019
Rifaina	-47,441	-20,061	2015	Rosa et al 2020
Rincão	-48,032	-21,594	2015	IBAMA 2019

Rinópolis	-50,717	-21,681	2014	IBAMA 2019
Rio Claro	-47,580	-22,374	2013	Pedrosa et al 2015
Rio das Pedras	-47,598	-22,850	2018	IBAMA 2019
Riolândia	-49,709	-20,024	2015	Rosa et al 2020
Riversul	-49,448	-23,847	2015	Rosa et al 2020
Rubiácea	-50,786	-21,361	2014	IBAMA 2019
Rubinéia	-51,018	-20,250	2014	IBAMA 2019
Sagres	-50,990	-21,868	2015	Rosa et al 2020
Sales	-49,503	-21,347	2018	SAA-SP 2018
Sales Oliveira	-47,855	-20,832	2019	IBAMA 2019
Salmourão	-50,876	-21,588	2015	Rosa et al 2020
Saltinho	-47,732	-22,871	2018	IBAMA 2019
Sandovalina	-51,842	-22,478	2016	IBAMA 2019
Santa Adélia	-48,819	-21,318	2017	IBAMA 2019
Santa Albertina	-50,728	-20,014	2015	Rosa et al 2020
Santa Bárbara d'Oeste	-47,428	-22,801	2017	IBAMA 2019
Santa Clara d'Oeste	-50,908	-20,067	2015	Rosa et al 2020
Santa Cruz da Conceição	-47,486	-22,121	2018	IBAMA 2019
Santa Cruz das Palmeiras	-47,250	-21,855	2015	Pedrosa et al 2015
Santa Ernestina	-48,367	-21,453	2015	Rosa et al 2020
Santa Gertrudes	-47,521	-22,475	2019	IBAMA 2019
Santa Maria da Serra	-48,154	-22,565	2013	Pedrosa et al 2015
Santa Rita do Passa Quatro	-47,508	-21,682	2015	Pedrosa et al 2015
Santa Rita d'Oeste	-50,813	-20,097	2015	Rosa et al 2020
Santa Rosa de Viterbo	-47,366	-21,504	2018	IBAMA 2019
Santa Salete	-50,720	-20,259	2015	Rosa et al 2020
Santana da Ponte Pensa	-50,797	-20,261	2016	IBAMA 2019
Santo Antônio de Posse	-46,950	-22,603	2015	Pedrosa et al 2015

Santo Antônio do Aracanguá	-50,554	-20,873	2013	Pedrosa et al 2015
Santo Antônio do Jardim	-46,683	-22,130	2014	IBAMA 2019
Santo Antônio do Pinhal	-45,698	-22,832	2016	IBAMA 2019
Santópolis do Aguapeí	-50,518	-21,660	2016	IBAMA 2019
São Bento do Sapucaí	-45,687	-22,681	2017	IBAMA 2019
São Carlos	-47,867	-21,919	2007	Deberdt and Scherer 2007
São Francisco	-50,676	-20,366	2018	SAA-SP 2018
São João da Boa Vista	-46,802	-21,978	2015	Pedrosa et al 2015
São João das Duas Pontes	-50,383	-20,408	2015	Rosa et al 2020
São João de Iracema	-50,356	-20,521	2013-2018	IBAMA 2019
São João do Pau d'Alho	-51,673	-21,223	2018	IBAMA 2019
São Joaquim da Barra	-47,939	-20,551	2016	Rosa et al 2020
São José da Bela Vista	-47,627	-20,588	2014	IBAMA 2019
São José do Rio Pardo	-46,880	-21,604	2015	Pedrosa et al 2015
São José do Rio Preto	-49,358	-20,797	2013	IBAMA 2019
São José dos Campos	-45,929	-23,091	2016	IBAMA 2019
São Luiz do Paraitinga	-45,254	-23,240	2018	SAA-SP 2018
São Manuel	-48,540	-22,682	2014	Pedrosa et al 2015
São Miguel Arcanjo	-47,993	-23,914	2018	IBAMA 2019
São Pedro	-47,925	-22,558	2013	Pedrosa et al 2015
São Sebastião	-45,607	-23,754	2015	Pedrosa et al 2015
São Sebastião da Grama	-46,753	-21,754	2019	IBAMA 2019
São Simão	-47,568	-21,462	2015	BRASIL - PAN Javali 2017
Sarapuí	-47,786	-23,664	2016	IBAMA 2019
Sebastianópolis do Sul	-49,916	-20,629	2016	IBAMA 2019

Serra Azul	-47,550	-21,316	2015	Rosa et al 2020
Serra Negra	-46,687	-22,589	2016	IBAMA 2019
Serrana	-47,612	-21,217	2018	SAA-SP 2018
Sertãozinho	-48,009	-21,123	2015	Rosa et al 2020
Sete Barras	-47,934	-24,274	2013	Rosa et al 2020
Severínia	-48,794	-20,793	2013	Pedrosa et al 2015
Socorro	-46,524	-22,611	2015	Pedrosa et al 2015
Sud Mennucci	-50,901	-20,668	2017	IBAMA 2019
Suzanápolis	-51,076	-20,473	2018	SAA-SP 2018
Tabapuã	-49,029	-20,932	2015	Pedrosa et al 2015
Tabatinga	-48,629	-21,713	2015	Pedrosa et al 2015
Taiaçu	-48,530	-21,132	2016	IBAMA 2019
Taiúva	-48,428	-21,133	2016	IBAMA 2019
Tambaú	-47,239	-21,602	2015	Rosa et al 2020
Tanabi	-49,646	-20,531	2016	IBAMA 2019
Taquaritinga	-48,538	-21,426	2015	Pedrosa et al 2015
Taquarituba	-49,235	-23,530	2013	Pedrosa et al 2015
Taquarivaí	-48,688	-23,943	2015	Pedrosa et al 2015
Tatuí	-47,870	-23,362	2007	Deberdt and Scherer 2007
Taubaté	-45,502	-23,087	2013	Pedrosa et al 2015
Tejupá	-49,307	-23,343	2016	IBAMA 2019
Teodoro Sampaio	-52,374	-22,417	2003	Rosa et al 2020
Terra Roxa	-48,346	-20,779	2013	IBAMA 2019
Tietê	-47,708	-23,049	2018	SAA-SP 2018
Torrinha	-48,164	-22,445	2013	Pedrosa et al 2015
Trabiju	-48,345	-22,032	2019	IBAMA 2019
Tremembé	-45,604	-22,941	2014	IBAMA 2019
Três Fronteiras	-50,870	-20,274	2015	Rosa et al 2020
Tuiuti	-46,688	-22,830	2015	Pedrosa et al 2015
Tupã	-50,535	-21,947	2016	IBAMA 2019
Tupi Paulista	-51,587	-21,390	2015	IBAMA 2019

	Turiúba	-50,111	-20,940	2018	IBAMA 2019
	Turmalina	-50,457	-20,084	2015	Pedrosa et al 2015
	Uchoa	-49,158	-20,937	2016	IBAMA 2019
	Urânia	-50,653	-20,209	2013	Pedrosa et al 2015
	Urupês	-49,265	-21,205	2019	IBAMA 2019
	Valentim Gentil	-50,102	-20,421	2015	Pedrosa et al 2015
	Valparaíso	-50,924	-21,203	2008	Rosa et al 2020
	Vargem	-46,414	-22,890	2016	IBAMA 2019
	Vargem Grande do Sul	-46,899	-21,861	2015	Pedrosa et al 2015
	Viradouro	-48,310	-20,884	2013	Pedrosa et al 2015
	Vista Alegre do Alto	-48,649	-21,177	2016	IBAMA 2019
	Vitória Brasil	-50,485	-20,198	2018	IBAMA 2019
	Votorantim	-47,407	-23,580	2015	Rosa et al 2020
	Votuporanga	-49,989	-20,458	2015	Pedrosa et al 2015
	Zacarias	-50,049	-21,125	2015	IBAMA 2019
TO	Almas	-47,210	-11,429	2019	IBAMA 2019
	Lizarda	-46,939	-9,525	2002	Rosa et al 2020
	Natividade	-47,649	-11,798	2019	IBAMA 2019

Supplementary material 2. Five routes of dispersion for invasion wild pigs in Brazil: South-Midwest-North (RSMN), South-Midwest-Northeast (RSMNE), South-Southeast-Northeast (RSSNE), South-West (RSW) and South-West-North (RSWN).

Routes	Track	Initial Municipality	Final Municipality	Starting Year	Final Year	Distance (km)	Dispersion Rate (km/year)
RSMN	1	Jaguarão	Nova Prata	1989	2004	439.73	29.32
	2	Nova Prata	Esmeralda do Sul	2004	2008	91.30	22.83
	3	Esmeralda do Sul	Trindade do Sul	2008	2015	180.53	25.79
	4	Trindade do Sul	Nonoai	2015	2019	18.12	4.53
	5	Nonoai	Chapecó	2019	2005	34.25	2.45
	6	Chapecó	Passos Maia	2005	2007	83.21	41.60
	7	Passos Maia	Papanduva	2007	2009	180.35	90.18
	8	Papanduva	Três Barras	2009	2010	37.81	37.81
	9	Três Barras	Curitiba	2010	1995	123.91	8.26
	10	Curitiba	Fênix	1995	1996	329.12	329.12
	11	Fênix	Sertaneja	1996	2015	160.20	8.43
	12	Sertaneja	Teodoro Sampaio	2015	2003	165.23	13.77
	13	Teodoro Sampaio	Inoncência	2003	2013	310.83	31.08
	14	Inoncência	Costa Rica	2013	2015	178.31	89.16
	15	Costa Rica	Mineiros	2015	2002	109.78	8.44
	16	Mineiros	Luizâna	2002	2014	525.93	43.83
	17	Luizâna	Formosa	2014	2015	152.48	152.48
	18	Formosa	São João d'Aliança	2015	2019	92.91	23.23
	19	São João d'Aliança	Lizarda	2019	2002	551.49	32.44
	20	Lizarda	Soure	2002	2005	1023.39	341.13
					Total	**4788.89**	**66.79**
RSWN	1	Jaguarão	Nova Prata	1989	2004	439.733	29.316
	2	Nova Prata	Esmeralda do Sul	2004	2008	91.303	22.826
	3	Esmeralda do Sul	Trindade do Sul	2008	2015	180.531	25.790
	4	Trindade do Sul	Nonoai	2015	2019	18.122	4.530
	5	Nonoai	Chapecó	2019	2005	34.254	2.447
	6	Chapecó	Passos Maia	2005	2007	83.205	41.603
	7	Passos Maia	Papanduva	2007	2009	180.355	90.177
	8	Papanduva	Três Barras	2009	2010	37.809	37.809
	9	Três Barras	Curitiba	2010	1995	123.910	8.261
	10	Curitiba	Fênix	1995	1996	329.115	329.115
	11	Fênix	Sertaneja	1996	2015	160.201	8.432
	12	Sertaneja	Teodoro Sampaio	2015	2003	165.234	13.770
	13	Teodoro Sampaio	Rio Verde de Mato Grosso	2003	2007	491.355	122.839
	14	Rio Verde de Mato Grosso	Sonora	2007	2015	146.093	18.262
	15	Sonora	Porto Esperidião	2015	2001	529.963	37.854
	16	Porto Esperidião	Barra do Bugres	2001	2015	185.943	13.282
	17	Barra do Bugres	Paranaíta	2015	2016	626.220	626.220
	18	Paranaíta	Oriximiná	2016	2010	1113.768	185.628
					Total	**4937.11**	**89.90**

RSW	1	Jaguarão	Nova Prata	1989	2004	439.733	29.316
	2	Nova Prata	Esmeralda do Sul	2004	2008	91.303	22.826
	3	Esmeralda do Sul	Trindade do Sul	2008	2015	180.531	25.790
	4	Trindade do Sul	Nonoai	2015	2019	18.122	4.530
	5	Nonoai	Chapecó	2019	2005	34.254	2.447
	6	Chapecó	Passos Maia	2005	2007	83.205	41.603
	7	Passos Maia	Papanduva	2007	2009	180.355	90.177
	8	Papanduva	Três Barras	2009	2010	37.809	37.809
	9	Três Barras	Curitiba	2010	1995	123.910	8.261
	10	Curitiba	Fênix	1995	1996	329.115	329.115
	11	Fênix	Sertaneja	1996	2015	160.201	8.432
	12	Sertaneja	Teodoro Sampaio	2015	2003	165.234	13.770
	13	Teodoro Sampaio	Rio Verde de Mato Grosso	2003	2007	491.509	122.877
	14	Rio Verde de Mato Grosso	Sonora	2007	2015	146.176	18.272
	15	Sonora	Porto Esperidião	2015	2001	530.665	37.905
	16	Porto Esperidião	Barra do Bugres	2001	2015	185.964	13.283
	17	Barra do Bugres	Porto Velho	2015	2013	1020.082	510.041
					Total	**4218.17**	**77.44**
RSMNE	1	Jaguarão	Nova Prata	1989	2004	439.733	29.316
	2	Nova Prata	Esmeralda do Sul	2004	2008	91.303	22.826
	3	Esmeralda do Sul	Trindade do Sul	2008	2015	180.531	25.790
	4	Trindade do Sul	Nonoai	2015	2019	18.122	4.530
	5	Nonoai	Chapecó	2019	2005	34.254	2.447
	6	Chapecó	Passos Maia	2005	2007	83.205	41.603
	7	Passos Maia	Papanduva	2007	2009	180.355	90.177
	8	Papanduva	Três Barras	2009	2010	37.809	37.809
	9	Três Barras	Curitiba	2010	1995	123.910	8.261
	10	Curitiba	Fênix	1995	1996	329.115	329.115
	11	Fênix	Sertaneja	1996	2015	160.201	8.432
	12	Sertaneja	Teodoro Sampaio	2015	2003	165.234	13.770
	13	Teodoro Sampaio	Olímpia	2003	2007	402.729	100.682
	14	Olímpia	Ouroeste	2007	2013	174.217	29.036
	15	Ouroeste	Populina	2013	2015	12.144	6.072
	16	Populina	Buritis	2015	2007	645.327	80.666
	17	Buritis	Chapada Gaúcha	2007	2019	122.856	10.238
	18	Chapada Gaúcha	Barra da Estiva	2019	2000	511.361	26.914
	19	Barra da Estiva	Barra	2000	2019	380.748	20.039
	20	Barra	Caracol	2019	2015	214.964	53.741
	21	Caracol	Caldeirão Grande do Piauí	2015	2019	359.396	89.849
	22	Caldeirão Grande do Piauí	Bacabeira	2019	2013	636.985	106.164
	23	Bacabeira	Barreirinhas	2013	2019	161.328	26.888
					Total	**5465.83**	**50.62**
RSSNE	1	Jaguarão	Nova Prata	1989	2004	439.733	29.316
	2	Nova Prata	Esmeralda do Sul	2004	2008	91.303	22.826
	3	Esmeralda do Sul	Trindade do Sul	2008	2015	180.531	25.790

4	Trindade do Sul	Nonoai	2015	2019	18.122	4.530
5	Nonoai	Chapecó	2019	2005	34.254	2.447
6	Chapecó	Passos Maia	2005	2007	83.205	41.603
7	Passos Maia	Papanduva	2007	2009	180.355	90.177
8	Papanduva	Três Barras	2009	2010	37.809	37.809
9	Três Barras	Curitiba	2010	1995	123.910	8.261
10	Curitiba	Fênix	1995	1996	329.115	329.115
11	Fênix	Sertaneja	1996	2015	160.201	8.432
12	Sertaneja	Teodoro Sampaio	2015	2003	165.234	13.770
13	Teodoro Sampaio	Guaratinguetá	2003	2007	737.388	184.347
14	Guaratinguetá	São Gonçalo	2007	2010	229.477	76.492
15	São Gonçalo	Varre-sai	2010	2015	245.812	49.162
16	Varre-sai	Linhares	2015	2017	252.227	126.113
17	Linhares	Montanha	2017	2019	140.975	70.487
18	Montanha	Caravelas	2019	1992	81.467	3.017
19	Caravelas	Barra da Estiva	1992	2000	469.768	58.721
20	Barra da Estiva	Barra	2000	2019	380.737	20.039
21	Barra	Santa Quitéria	2019	2011	826.730	103.341
				Total	**5208.35**	**62.18**

Do cranium and mandible reflect the wild pig's geographic variation in South America?

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ABSTRACT

Our goal was to investigate if the wild pigs (*Sus scrofa* L.) cranium and mandible shape and size vary geographically in southern South America. We tested the hypotheses that the geographic variation of wild pigs is reflected in the species' morphological differences along the latitudinal gradient. We photographed the dorsal and lateral views of the cranium and the dorsal view of the mandible to verify variation within and among geographic groups in spatial and environmental aspects. We compared approximately 300 crania and mandibles of wild pigs from four different geographic groups in southern South America using geometric morphometrics. We applied 19 bioclimatic layers, one elevation layer, and one glob cover to analyze whether geographic variation could result from environmental variables. Our results showed a geographic differences in the size of cranium and mandible among some geographic groups. All geographic groups presented geographic differentiation along the latitudinal gradient for shape. Despite the statistical significance, the environment is not the main factor in wild pigs' shape and size variation. Our results indicate that geographic variation may respond to wild pigs' local adaptation to the environment (phenotypic plasticity). However, it also corroborates Bergmann's rule, with larger wild pigs in colder climates and distant southern regions in higher latitudes.

Keywords: Wild boar, Invasive Species, Geometric morphometrics, Skull variation, *Sus scrofa*

Introduction

Widely distributed mammals may show geographic variation in morphology because of variation in the latitudinal gradient or some ecological factors that vary with latitude (Bergmann's rule - Bergmann 1847; Rensch 1938); the phenotypic plasticity of the species concerning climatic and environmental conditions (Bradshaw 1965; Turcotte and Levine 2016, or 3) and the abundance and availability of resources in the environment (Resource's rule – McNab 2010). Thus, there may be a gradual differentiation of certain morphological characters of a species in geographically distant populations, giving individuals a better adaptation to different environments and a process of geographical differentiation (Salomon 2002). Currently, wild pigs (*Sus scrofa* L.) have wide geographic distribution (Barrios-García and Ballari 2012), and the geographic variation is probably reflected in a morphological differentiation of the species (Albarella et al. 2009). Furthermore, wild pigs also have ample ecological plasticity to use space and exploit the resources available in an area (Mayer and Brisbin 2009), and this may also reflect on morphology. Therefore, wild pigs are a suitable species for comparative morphometric studies in different latitudinal gradients.

In this sense, researchers worldwide have been utilizing morphology to explain the causes of the variations and differences in shape and the size of the wild boars and wild pigs (Endo et al. 2000; Albarella et al. 2009; Ježek et al. 2011). These global efforts help to show the processes by which wild pigs threaten ecosystems and how they are acclimating and adapting to the environmental differences found in the areas that they are introduced. Similarities in environmental effects of latitude and altitude on the size and shape of the mandible in wild pigs (Endo et al. 2000, 2002; Kyomi et al. 2002) as well as environmental conditions and biogeographic variation influence the size and physical development of wild boars (Albarella et al. 2009; Ježek et al. 2011). Also, hybridization that occurs with domestic or native pigs resulted in differentiation in the morphology of the skulls in wild pigs (Owen et al. 2014).

Crania and mandibles are important body structures to assess the effect of geographic variation in the morphology of the species. Investigating the differences in the shape and size of a species' cranium and mandibles means understanding the many functions that are associated with them (Thorpe 1976). Such as, for example, the size and protection of the brain associated with the sensory responses, or the dentition and musculature aspect related to the environmental conditions in which the individual is inserted (Maestri et al. 2016; Borges et al.

2017). Further, differences in the shape of the cranium and mandible are associated with diet (Antonucci et al. 2009; Nogueira et al. 2009; Maestri et al. 2016; Segall et al. 2020). These variations in size and shape reflect aspects of the morphological evolution of a species and are associated with historical and ecological factors (Schluter 2000; Viguier 2002). Thus, exploring differences in the morphology of wild pigs' crania and mandibles can help us understand how the species uses space and the environment and whether this is reflected along the latitudinal gradient of its geographic distribution.

Although native to Eurasia and North Africa, wild pigs have been introduced worldwide (Barrios-García and Ballari 2012). In South America, the introduction is recent and began in the southern countries of Argentina and Uruguay in the early 20th century (Navas 1987; Oliver 1993; García et al. 2011). Decades later, the introduction spread to other countries, including Brazil (Deberdt and Scherer 2007). The introduction of the wild pigs in southern South America and its short period geographic expansion to the north of Brazil may reflect a geographical variation in the morphology of the species to the new continent. Thus, our goal was to check if the shape and size of the cranium and mandible of the wild pigs follow their geographic variation in southern South America. To answer this question, we tested two hypotheses: 1) the geographic variation of the wild pigs is reflected in the species' morphological differences along the latitudinal gradient. We expected wild pigs of colder climates and at higher latitudes to have larger sizes (Bergmann's rule), and 2) that environmental components may influence the shape and size of skull differentiation. We expected that the morphological differences of the crania and mandibles would respond to those different environmental conditions.

Methods

Data collection

We used 294 specimens to measure the dorsal view of the cranium (184 males and 110 females) and 254 specimens for the lateral view of the cranium (164 males and 90 females). For the dorsal view of the mandible, we used 300 specimens (188 males and 112 females) (Table 1). Specimens were from collectios in Brazil – Museu do Suíno in Rio Grande do Sul state, Mastozoology Collection of the Universidade Federal de Santa Catarina (UFSC) in Santa Catarina state, and Museu Nacional do Rio de Janeiro (MNRJ) in Rio de Janeiro state;

in Uruguay – Museo Nacional de Historia Natural (MNHN) Montediveo; and in Argentina – Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Museo de La Plata (MPL), and the Mastozoology Collection of Universidad Nacional del Noroeste de la Provincia de Buenos Aires (UNNOBA). We also examined samples from private collections of wild pigs' hunters and specimens collected from hunting authorized by IBAMA in Brazil. When possible, the material was transported, prepared, and registered in the Scientific Collection of Mammals of the Universidade de Brasília (UnB), Brazil, and in the Scientific Collection of Mammals Museu Zoobotânico Augusto Ruschi da Universidade de Passo Fundo (UPF), Brazil.

We separated wild pigs into four groups according to geographic proximity to compare the data based on the specimens' origin records. Group A contemplated wild pigs from central Argentina provinces (La Pampa, Buenos Aires, San Luis, Neuquén and Río Negro), in latitudes between -41° at -35°. Group B covered specimens from the Argentine provinces of Entre Ríos on the Uruguay frontier, Misiones on the Brazilian frontier, and Formosa on the Paraguay frontier; in addition to specimens from the provinces of Soriano, Rocha, Paysandú, and Río Negro in Uruguay, in latitudes between -34° at -31° (except a female registered at latitude 25° in the Iguaçu National Park on the border between Argentina and Brazil). Group C comprised wild pigs from the Rio Grande do Sul and Santa Catarina in southern Brazil, in latitudes between -30° at -26°. Moreover, Group D with specimens from the most central states of Brazil (Minas Gerais, Goiás, Mato Grosso, and Mato Grosso do Sul) in latitudes between -19° at -15° (Figure 1).

Table 1. Wild pigs' cranium and mandibles numbers distributed among the four geographic groups in southern South America by sex and views of the cranium and mandible.

Geographic Group	Cranium dorsal	Cranium lateral	Mandible dorsal
Group A	52 ♂ / 24 ♀	41 ♂ / 24 ♀	33 ♂ / 25 ♀
Group B	25 ♂ / 39 ♀	25 ♂ / 32 ♀	27 ♂ /37 ♀
Group C	31 ♂ / 22 ♀	27 ♂ / 15 ♀	38 ♂ / 19 ♀
Group D	76 ♂ / 25 ♀	71 ♂ / 19 ♀	90 ♂ / 31 ♀
Total for sex	184 ♂ / 110♀	164 ♂ / 90 ♀	188 ♂ / 112 ♀
Total for view	294	254	300

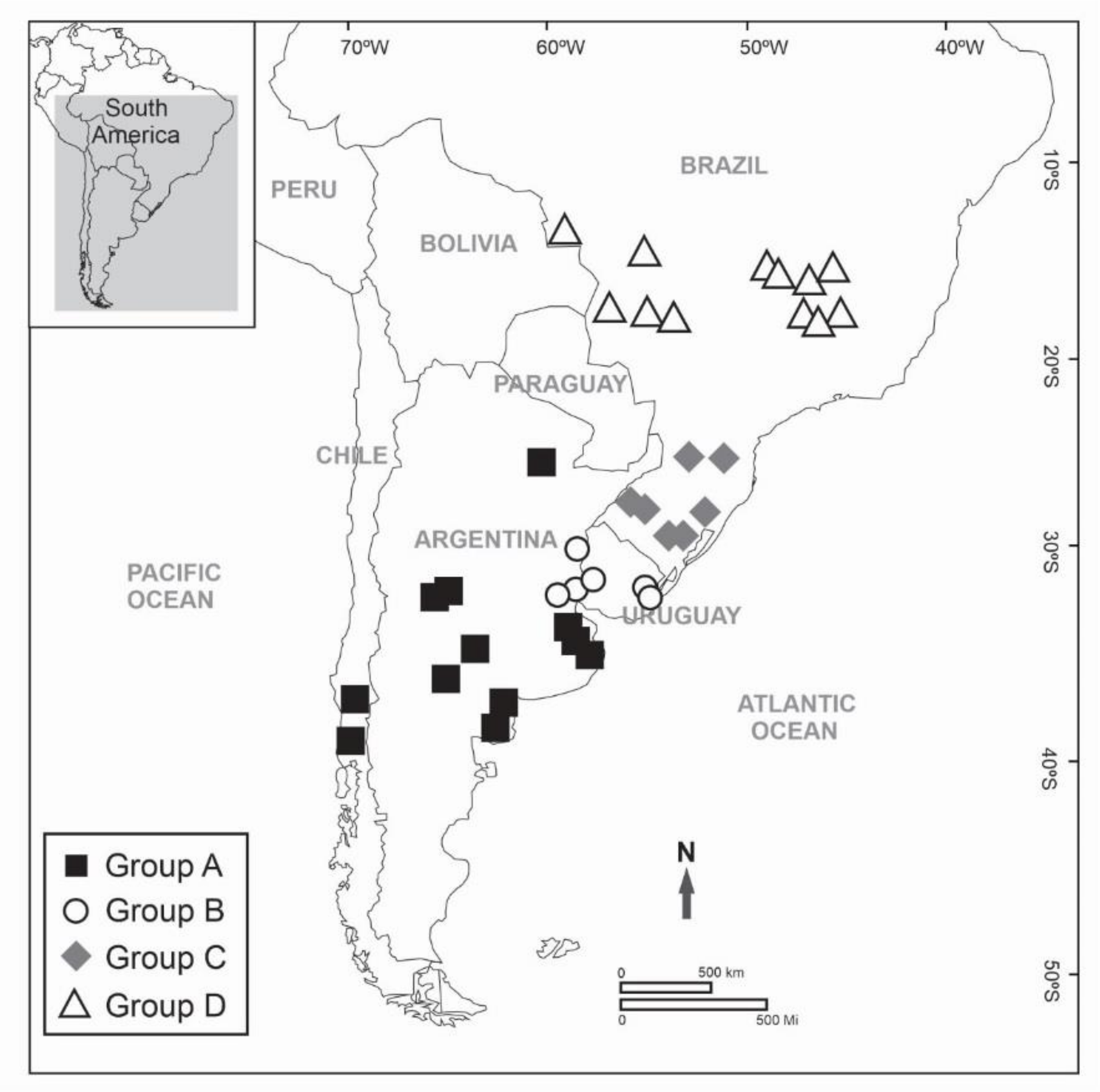


Figure 1. Geographical distribution of wild pigs according to geographic groups (A, B, C e D) in South America. The political map of South America was derived from http://www.diva-gis.org/

Geometric Morphometric Approach and Shape and Size Analysis

We photographed the crania in the dorsal and left lateral views and the mandibles in the dorsal view. The photos were taken with a digital camera with a resolution of 20 megapixels and a standardized focal length of 45 cm in height using camera support. We used only adults and subadults, males and females, based on the ridge height in the eminent canine bone, position, and total eruption of the canines (Herring 1972; Mayer and Brisbin 1988).

The digital photographs were organized in the program TpsUtil version 1.64 (Rohlf 2013). Homologous anatomical landmarks were better selected to represent the morphology of the cranium and mandible. These anatomical landmarks were digitized with the program TpsDig version 2.19 (Rohlf 2015). In total, we used 31 homologous anatomical landmarks in the dorsal view of the cranium, 20 landmarks in the left lateral view of the cranium, and 16 landmarks for the dorsal view of the mandible (Figure 2; Table 2).

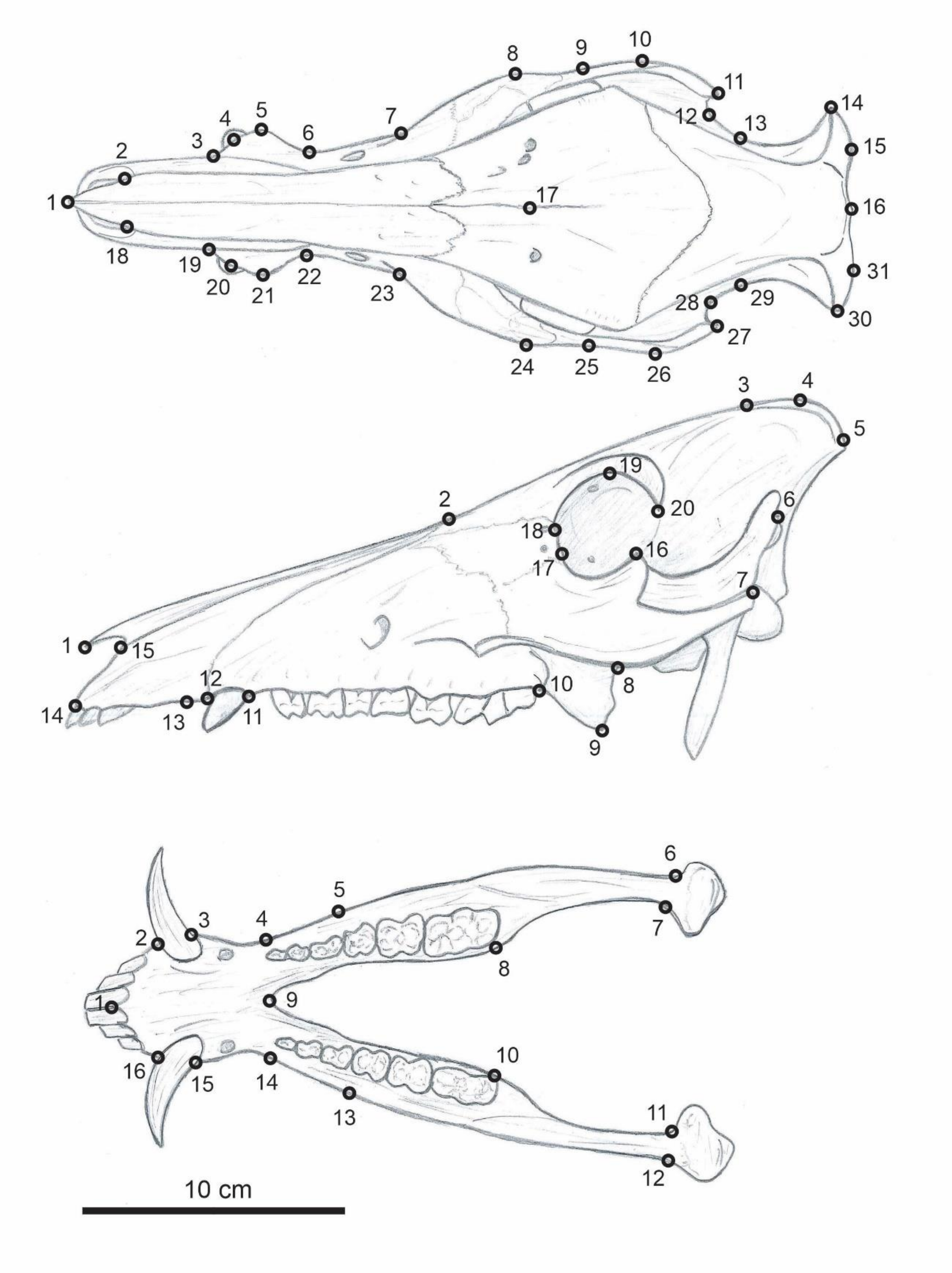


Figure 2. Anatomical landmarks on the skull of wild pigs (*Sus scrofa*) for dorsal and left lateral views of the cranium and on the dorsal view of the mandible.

Table 2. Descripton of the anatomical landmarks for cranium and mandible of wild pigs (*Sus scrofa*). See Figure 2.

Dorsal Cranium	
Landmark	**Description**
1	Anterior extremity of rostral process of nasal bone
2 - 18	End of the curvature of the base of the rostral process of nasal bone
3 - 19	Anterior extremity of the eminentia canina
4 -20	Lateral extremity of the anterior curvature of the eminentia canina
5 – 21	Lateral extremity of the posterior curvature of the eminentia canina
6 - 22	Posterior extremity of the eminentia canina
7 - 23	Anteriormost point of the root of zygomatic arch
8 - 24	Most lateral point in the curvatura of zygomatic arch perpendicular to the beginning of the orbital cavity
9 -25	Most lateral point in the curvature of zygomatic arch perpendicular to the end of the orbital cavity
10 – 26	Most curvature point in the posterior portion of the zygomatic arche
11 – 27	Tip of posterior process of jugal
12 - 28	Posteriormost point of the root of zygomatic arch
13 – 29	Lateral point of the squamous bar straight
14 - 30	Most lateral point of the extremity of paraoccipital apophysis
15 - 31	End of curvature of paraoccipital apophysis
16	End point of the nuchal crest
Lateral Cranium	
Landmark	**Description**
1	Anterior extremity of rostral process of nasal bone
2	Uppermost point in the nasal bone perpendicular to the root of the zygomatic arch
3	Midpoint of the temporal line
4	Point of greatest curvature of the temporal line
5	Most posterior point of the temporal line
6	Most posterior point of curvature of the ascending ramus of the zygomatic processo of the jugal bone
7	End point of the posterior jugal process
8	Midpoint of the lower curvature of the zygomatic arch
9	Posterior end of the pterygoid process
10	Posterior extremity of III molar alveolus
11	Posterior point of the canine alveolus in th eminentia canina
12	Anterior point of the canine alveolus in th eminentia canina
13	Posterior point of the III incisive alveolus
14	Anterior extremity of the premaxilla bone
15	Anteriormost point of the suture between nasal and premaxillar
16	Extremity of superior jugal process

17	Posterior suture point between jugal and lacrimal at the edge of the orbital cavity
18	Posterior suture point between lacrimal and frontal at the edge of the orbital cavity
19	Highest point on the edge of the orbital cavity
20	Tip of the post-orbital process of the frontal bone
Dorsal Mandible	
Landmark	**Description**
1	Most anterior point of the mandibular symphysis
2 -16	Anterior point of the canine alveolus
3 – 15	Most lateral point of the labial portion of the canine alveolus
4 – 14	Outermost point on the labial portion perpendicular to the beginning of the II premolar
5 – 13	Outermost point on the labial portion perpendicular to the beginning of the I molar
8 – 10	Outermost point on the labial lingual perpendicular to the beginning of the I molar
6 – 12	Point of contact between the ascending ramus and the mandibular condyle in the labial portion
7 – 11	Point of contact between the ascending ramus and the mandibular condyle in the lingual portion
9	Most posterior point of the mandibular symphysis

We superimposed the coordinates of the anatomical landmarks with the Generalized Procrustes Analysis (GPA) (Dryden and Mardia 1998). The GPA method removes differences unrelated to the shape in which scale, position, and orientation (Adams et al. 2004) result in new shape variables, shape residuals, or Procrustes residuals. We estimated the size of each cranium and mandible using its centroid size, that is, the square root of the sum of the squares of the distances from each anatomical landmark to the centroid of the configuration (Bookstein 1991).

After GPA, the dorsal views of the cranium and mandible, which presented a pattern of bilateral symmetry and avoided asymmetry, had the coordinates of the anatomical landmarks on the right and left sides symmetrized, and we used only the symmetric component. We made a Shapiro test to evaluate data normality. We tested the allometry (shape and size covariation) to evaluate how much of the shape (Procrustes residuals) was predicted by the size (centroid size) variation.

We made a t-test to compare the centroid sizes of males and females of wild pigs for size sexual dimorphism. We used an Analysis of Variance (one-way ANOVA) for size comparisons among South American locations. followed by the Tukey test for multiple comparisons. We also use a two-way ANOVA to test the interaction between the two factors, sex, and geographic groups.

The shape residuals generated by the GPA were used in the Principal Component Analysis (PCA), where the main components (PCs) were used as new shape variables to reduce the dimensionality of the data set, as well as working with independent variables (Cordeiro-Estrela et al. 2006). We calculated the proportion of classification with each combination of PCs to be included in for Linear Discriminant Analysis (LDA) (Baylac and Friess 2005), and we selected the subset of PCs with the highest overall correct classification percentage. We used a cross-validation procedure for evaluating the performance of classification by LDA (Ripley 1996; Baylac and Friess 2005). We used a Canonical Variate Analysis (CVA) to generate discriminant graphics that maximize the variation between geographic groups by canonical variables (CVs). The shape variation was visualized through deformation grids projected along with the PCs and CVs. To test the multiple factors that can cause differences in shape, we use Multivariate Analysis of Variance (MANOVA) with Wilks' test for sex, geographic groups, and the interaction between the factors. Finally, we used a pairwise MANOVA to check for differences among geographic groups. We used the Bonferroni correction for multiple comparisons of significant statistical differences (Wright 1992).

All analysis were performed in Program R version 4.0.3. (R Core Team 2020), in packtages “Geomorph” (Adams and Otárola-Castillo 2013); “Morpho” (Schlager 2017); “ape” (Paradis et al. 2004); “MASS” (Ripley et al. 2013); “Rvcg” (Schlager and Schlager 2014); “stats” (R Development Core Team 2021); and “vegan” (Oksanen et al. 2013).

Geographic and Environmental Data

We used 19 bioclimatic layers for the analysis of environmental variables (WorldClim version 1.4 - www.worldclim.org), one elevation layer (www.fao.org) with a resolution of 30 arc-seconds, and one of glob cover (due. esrin.esa.int) with a resolution of 300 meters (Table 3). The cut of the layers for the countries with a sampling of wild pigs’ individuals used in this analysis was performed with the program Quantum Gis (QGis) version 2.18.13.

The values of the environmental variables of each layer were extracted for each point of occurrence through the geographical location of each individual (Figure 1). With the matrix of environmental values, the relationship between size, shape, and environmental variables was tested for the dorsal and lateral view of the cranium and dorsal view of the mandible. We used Procrustes ANOVA that a regression analysis for Procrustes shape variables available in the Geomorph package. The analysis quantified the relative variation attributable to one or more factors in the linear model (Anderson 2001).

Table 3. Description of environmental variables used for Procrustes ANOVA for shape data.

Variables	Description
Bio1	Annual Mean Temperature
Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
Bio3	Isothermality (BIO2/BIO7) (* 100)
Bio4	Temperature Seasonality (standard deviation *100)
Bio5	Max Temperature of Warmest Month
Bio6	Min Temperature of Coldest Month
Bio7	Temperature Annual Range (BIO5-BIO6)
Bio8	Mean Temperature of Wettest Quarter
Bio9	Mean Temperature of Driest Quarter
Bio10	Mean Temperature of Warmest Quarter
Bio11	Mean Temperature of Coldest Quarter
Bio12	Annual Precipitation
Bio13	Precipitation of Wettest Month
Bio14	Precipitation of Driest Month
Bio15	Precipitation Seasonality (Coefficient of Variation)
Bio16	Precipitation of Wettest Quarter
Bio17	Precipitation of Driest Quarter
Bio18	Precipitation of Warmest Quarter
Bio19	Precipitation of Coldest Quarter
Elevation	Median elevation (meters)
Cover Land	Global Land Cover Map

Results

Skull size

Allometry was significant for all views (dorsal cranium: $r^2 = 0.06$, $p < 0.01$; lateral cranium: $r^2 = 0.02$, $p < 0.01$; dorsal mandible: $r^2 = 0.13$, $p < 0.01$) showing that between 2 and 13% of shape variation is predicted by size. We found significant sexual dimorphism in size for the dorsal view of the cranium (t = -7.958, df = 228.91, $p < 0.01$) and the lateral view of the cranium (t = -8.069, df = 202.06, $p < 0.01$), and in the dorsal view of the mandible (t = -9.9161, df = 258.15, $p < 0.01$), with males being on average larger than females (Figure 3).

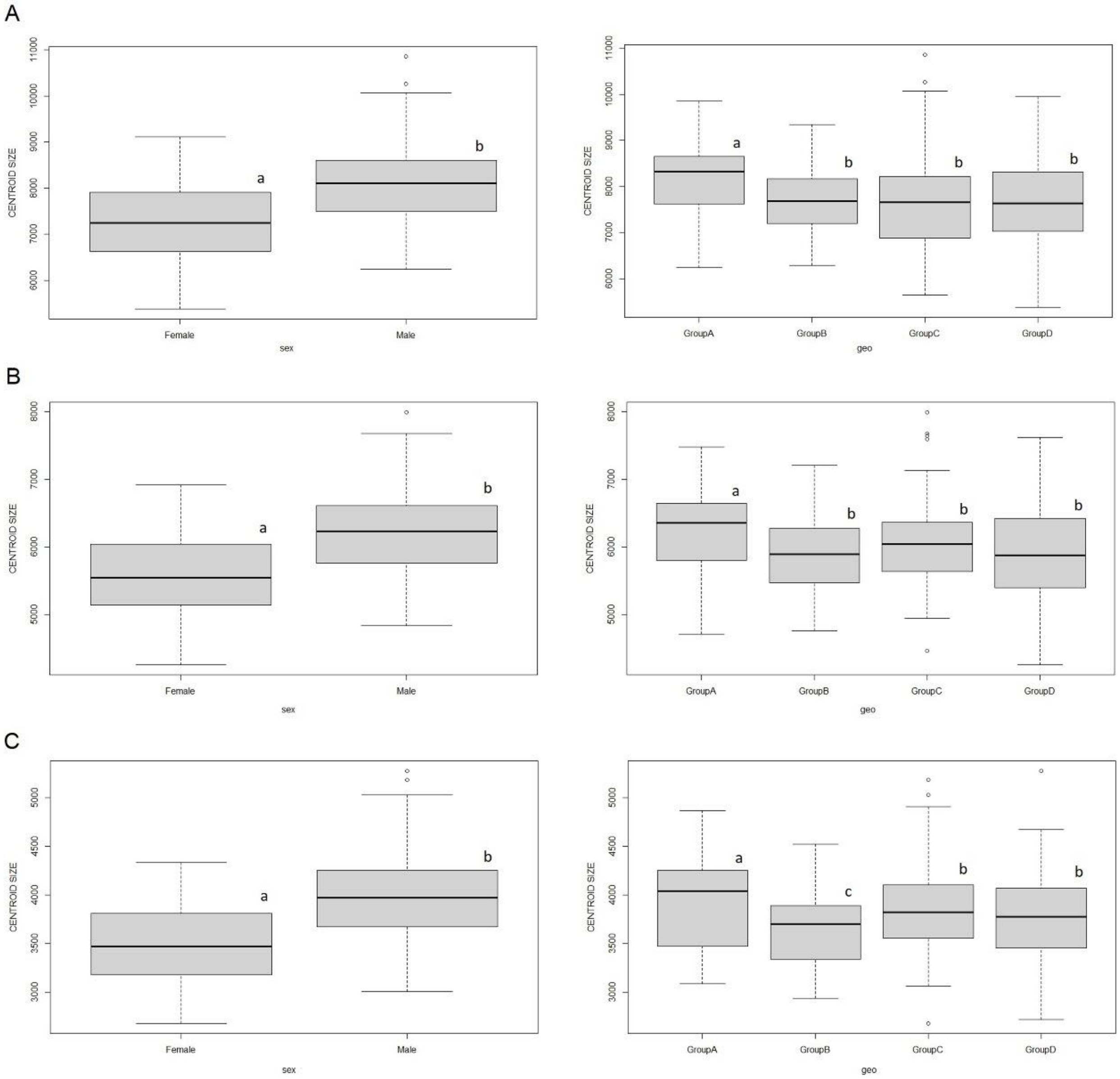


Figure 3. Box plots of centroid size variability for cranium and mandible of *Sus scrofa* between males and females and four geographic groups in southern South America. Different letters above boxes stand for significant differences among different groups for Tukey´s multiple comparison tests at the 5% level. In A: comparisons in dorsal view of the cranium; B: comparisons in lateral view of the cranium; C: comparisons in dorsal view of the mandible.

Regarding the differences in size among geographic groups, in ANOVA we found significant differences for cranium and mandible (dorsal view of the cranium (F = 4.959, df = 3, $p < 0.01$), lateral view of the cranium (F = 2.914, df = 3, $p < 0.01$), and dorsal view of the mandible (F = 5.027, df = 3, $p < 0.01$). However, when we analyze this difference between the pairs of geographic groups, we see that not all groups differ (Figure 3). In the dorsal and lateral views of the cranium, only Group A and Group B differ. For the dorsal view of the mandible, Group A and Group B differ from Group B and Group C. This means that the further south, the larger the crania and mandibles sizes of wild pigs are compared to other groups more north, especially wild pigs from the southern part of Argentina. Still, when we analyze the interaction of factors (sex and geographic groups) concerning size, we do not obtain significant statistical interaction ($p > 0.05$).

Skull shape

In the shape analyses, the first two principal components (PC) of the PCA show no structuring among the four geographic groups for cranium and mandible views (See Supplementary material 2).

For LDA, the cranium views showed at least more than 70% of correct classification for each geographic group (Table 4). For the mandible, the percentages of correct classification were, on average lower than cranium views (Table 4).

Table 4. Percentage of correct classification for four geographic groups of *Sus scrofa* in southern South America using linear discriminant analysis (LDA) for dorsal and lateral views of the cranium and dorsal view of the mandible.

Skull View	**Geographic Group**			
	Group A	Group B	Group C	Group D
Cranium - Dorsal	77.631	93.750	79.245	89.108
Cranium - Lateral	72.307	84.210	83.333	91.111
Mandible - Dorsal	41.379	71.875	50.877	85.123

For the MANOVA test, we found significant differences for all factors, sex, geographic groups, and their interaction (Table 5). Despite the significant interaction and the strong sexual dimorphism in *Sus scrofa*, all paired comparisons among the four geographic groups were statistically significant for the shape of the cranium and mandible.

Table 5. Results of MANOVA with interaction for dorsal and lateral views of the cranium and dorsal view of the mandible.

	Df	**Wilks'λ**	**F**	***P***
Dorsal Cranium				
Sex	1	0.24729	69.755	< 0.001
Geo	3	0.19316	16.820	< 0.001
Sex × Geo	3	0.71316	2.738	< 0.001
Residuals	286			
Lateral Cranium				
Sex	1	0.68778	6.1417	< 0.001
Geo	3	0.59383	2.5716	< 0.001
Sex × Geo	3	0.66252	1.9936	< 0.001
Residuals	246			
Dorsal Mandible				
Sex	1	0.79473	6.0484	< 0.001
Geo	3	0.64775	3.6545	< 0.001
Sex × Geo	3	0.78856	1.9324	< 0.001
Residuals	292			

The CVA analysis distinctly plotted four groups of wild pigs with a slight overlap of groups by the morphology of cranium and mandible (Groups A and B, and Groups C and D are more similar in shape). However, the pairwise comparison analyses, showed significant differences between all groups. This shows a geographic structure of specimens from southern South America along the latitudinal gradient. The 1st canonical axes of the dorsal view of the cranium indicate that groups A and B, located further south, have a proportionally more elongated and narrower cranium, mainly the rostrum region, than the C and D northernmost groups (Figure 4). For 1st canonical axes of the lateral view of the cranium, southern groups A and B showed a more elongated cranium with a straighter profile than northernmost groups C and D (Figure 5). For the mandible, the scatterplot of CVA in the 1st canonical axes showed that the A and B southern groups have a proportionally more elongated and narrow mandible than the C and D northern groups (Figure 6) (Figures 4, 5, and 6).

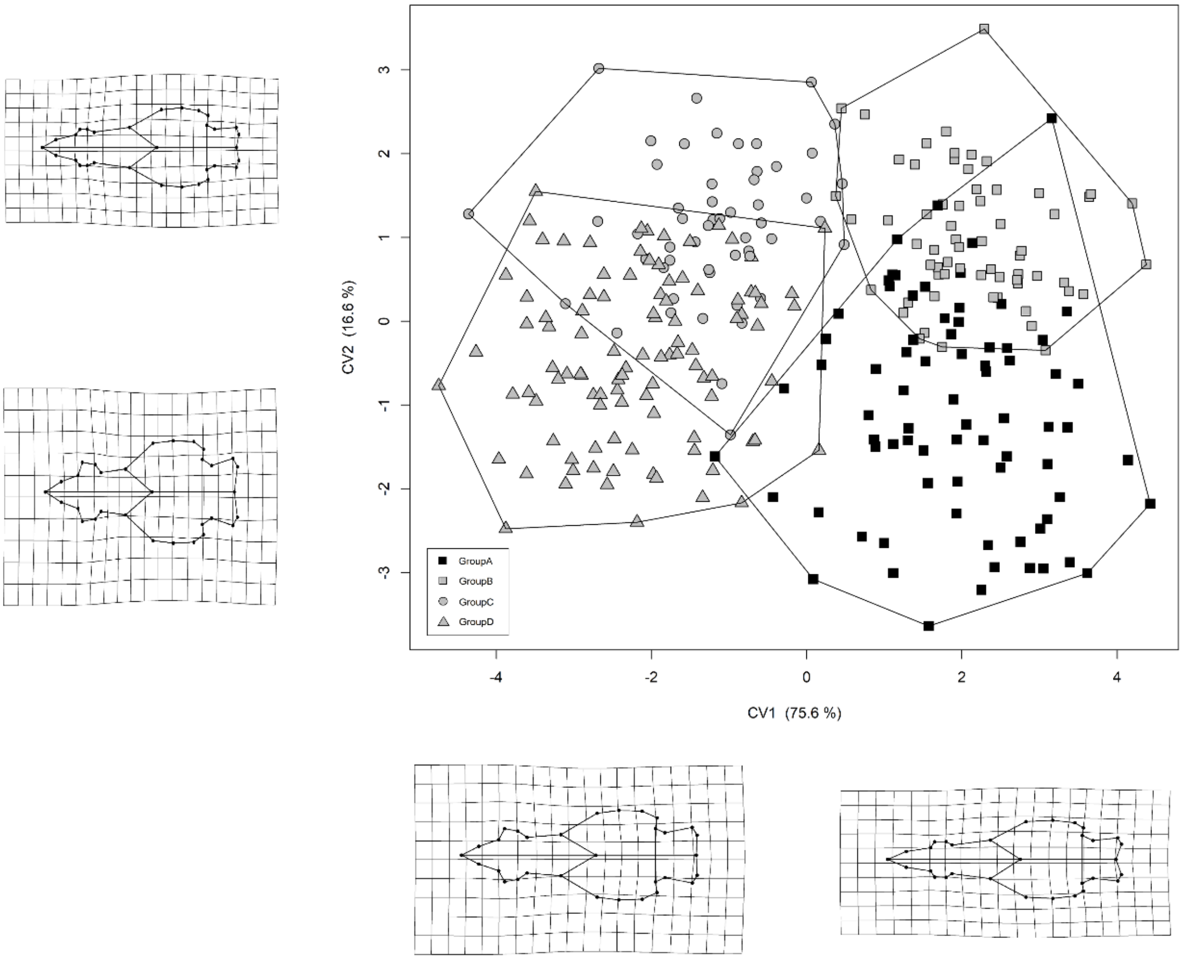


Figure 4. Scatterplot of canonical variate analysis (CVA) show the two first canonical axis for the cranium shape in dorsal view, for four geographic groups of wild pigs in southern South America. The grids represent differences for landmark configuration along the first and second CVs representing the extreme negative and positive scores. Variance percentages for CV1 and CV2 are given in parenthesis.

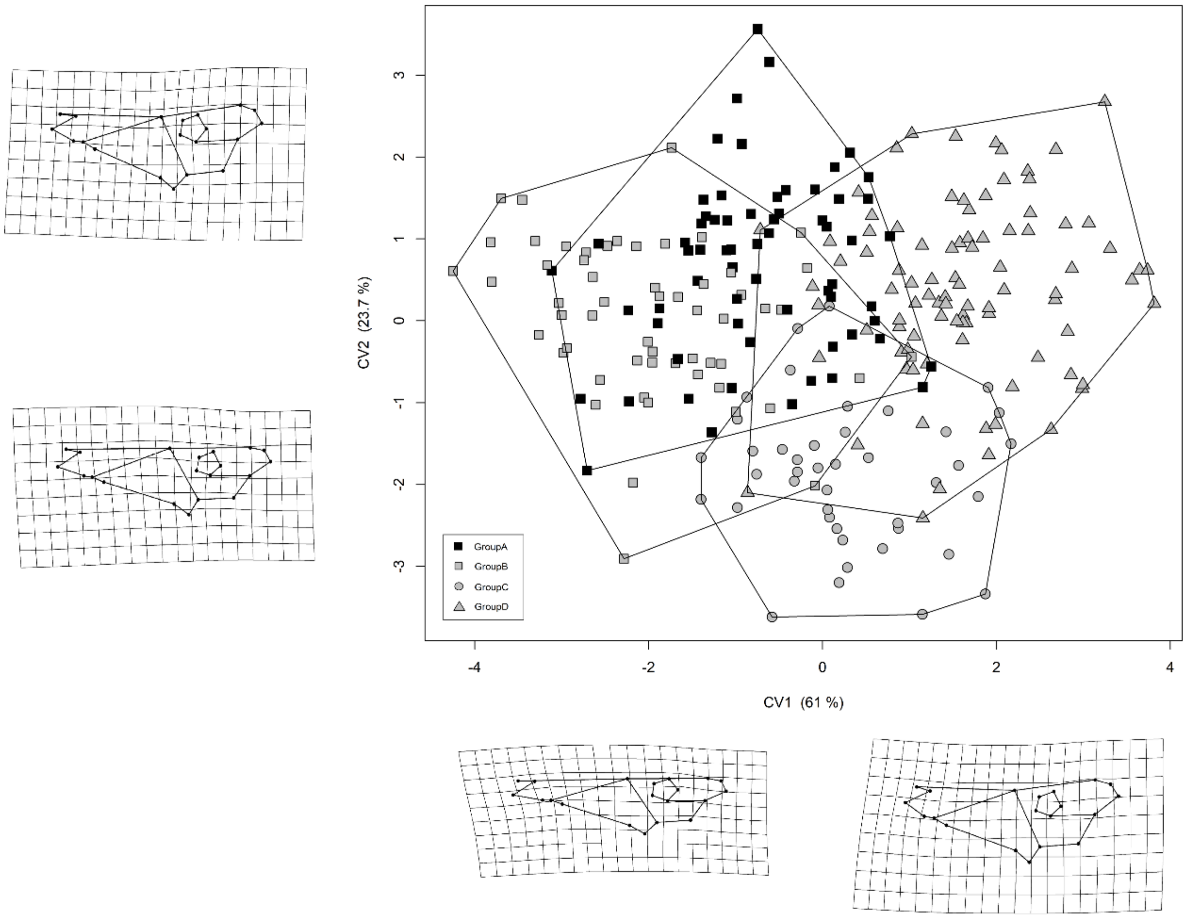


Figure 5. Scatterplot of canonical variate analysis (CVA) show the two first canonical axis for the cranium shape in lateral view, for four geographic groups of wild pigs in southern South America. The grids represent differences for landmark configuration along the first and second CVs representing the extreme negative and positive scores. Variance percentages for CV1 and CV2 are given in parenthesis.

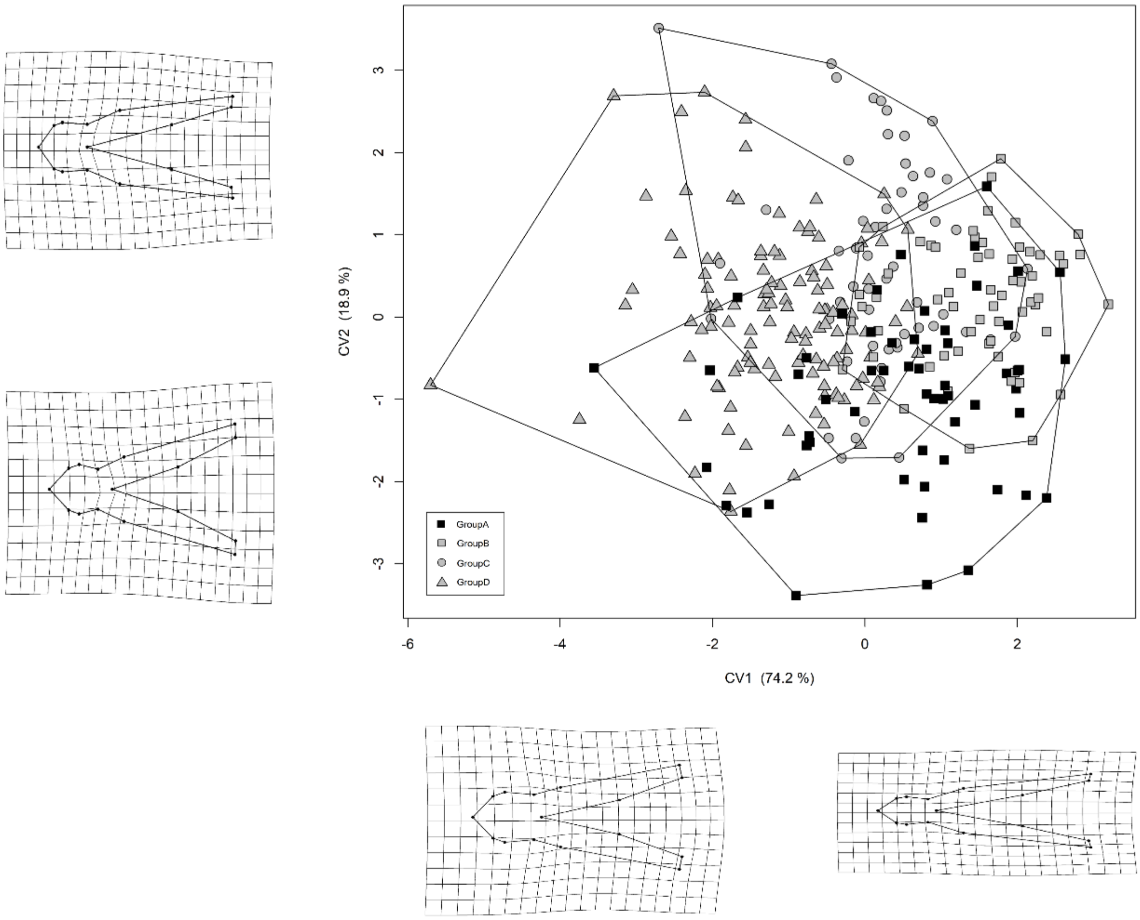


Figure 6. Scatterplot of canonical variate analysis (CVA) show the two first canonical axis for the mandible shape in dorsal view, for four geographic groups of wild pigs in southern South America. The grids represent differences for landmark configuration along the first and second CVs representing the extreme negative and positive scores. Variance percentages for CV1 and CV2 are given in parenthesis.

Geographic and Environmental Analysis

The analysis of the influence of environmental variables on the variation in the shape and size of the wild pigs' skull showed an influence in all the views analyzed with $p < 0.05$. However, the values of the coefficient of determination R^2 were not very high (Table 6).

Table 6. Results of Procrustes ANOVA for shape data for the cranium and mandible views of the wild pigs. Both for the size and shape of the cranium and mandible in relation to environmental variables.

	Dorsal Cranium		**Lateral Cranium**		**Dorsal Mandible**	
	R^2	*p*	R^2	*p*	R^2	*p*
Shape x environmental variables	0.382	0.001	0.302	0.001	0.318	0.001
Size x environmental variables	0.253	0.001	0.081	0.001	0.057	0.002

Discussion

Our goal was to check if the shape and size of the cranium and mandible of the wild pigs have geographic differentiation in southern South America. We confirmed there is a geographic variation in shape and size of the skulls of wild pigs in the regions of South America. The variation is mainly on the nasal and parietal bones shortening or elongation and widening or narrowing the frontal and jugal bones. Thus, our results corroborate Eurasian studies. In Japan wild pigs showed geographic variation in size and shape, with the mandibles from northern localities being larger than those from southern localities (Endo et al. 2000). Furthermore, osteological characters in the mandibles of the Taiwanese population have been affected by north latitude and geographical and climatic fac (Kyomi et al. 2002).

Allometry refers to variation in shape that is related to variation in size (Thorpe 1976). Allometry is not the cause but the consequence in wild pigs of our study. Every group's size range implies a systematic shape alteration, resulting in phenotypic differences along evolutionary lineages (Gould 1966; Thorpe 1976). Adaptive advantages of size increase in the phylogeny (metabolic and isolating efficiencies of large forms) result from differences in physiological proportions between large and small forms, while advantages (as attack and defense) result from differences in morphological proportions (Gould 1966).

Regarding size, we showed in our results that the further south, the larger the crania and mandibles of the wild pigs, with a difference between group A and the other three groups. According to Mayr (1963), animals with large body sizes have an advantage in colder climates because their smaller surface-to-volume ratio limits heat loss and metabolism per gram of body mass. Therefore, the bigger they are less heat they need to create. However, the relationship between wild pigs' body size and temperature may not directly affect thermoregulatory mechanisms but rather a consequence of the indirect effect of temperature on food availability (Dayan et al. 1991). The tendency of mammals to increase or decrease body size also depends on the availability, abundance, and size of resources. According to McNab (2010), resource availability controls body mass and energy expenditure considering factors with to geography, including latitude (Bergmann's rule), desert existence, or life on oceanic islands (Island rule), seasonal anticipation of winter (Dehnel's phenomenon) and a tendency for some lineages to increase in mass through time (Cope's rule). This is the Resource rule. In wild pigs, food availability directly affects reproductive success and body size (Pepin et al. 1986; Servanty et al. 2009).

In other studies, the more accepted explanation for the differences in size and shape of skulls, mandibles, or molar teeth has been the Bergmann Rule (Genov 1999; Albarella et al. 2009; Evin et al. 2015). Bergmann's rule (Bergmann 1847; Rensch 1938) predicts a relationship between body size and climate, where a species geographically distributed in different climate regions tends to have generally larger individuals in colder regions and smaller individuals in regions hotter. Albarella et al. (2009) and Evin et al. (2015) found South-North and West-East clines, with an increase in size along a South-North cline and an increase in size along a West-East cline. Differences in shape and size in the cranium and molars were also found by Genov (1999), where eastern populations had larger cranial structures than western populations; and a reduction in size in the East-West direction. We found an increase in the size and robustness of the shape of wild pigs’ crania and mandibles in the North-South clinal direction. Our results corroborate the abovementioned studies, and wild pigs from southern South America are under Bergmann's rule events.

However, environmental factors are the primary determinants of the size and weight of wild pigs (Marsan and Mattioli 2013). We suppose that the overlapping of the environmental and land use matrix did not demonstrate to have an apparent effect on the variation of the shape and size of the craniums and mandibles of the wild pigs of South America. Our results on the influence of environmental variables on the wild pigs' skull showed that despite the statistically significant value, the environment does not appear to be the main factor in shape and size variation in wild pigs. This finding leads us to suppose that wild animals' adaptations are local (geographic groups) and influenced by local factors and natural selection leads to acclimatization and future incorporation of these morphological characteristics in wild pigs. Thus, we suggest that differences in size and shape of crania and mandibles are attributed to the phenotypic plasticity of the species concerning adaptation to environmental factors.

Marsan and Mattioli (2013) reported that individuals in the Mediterranean regions of Europe are up to 50% smaller than individuals in the most productive areas of Eastern Europe and are even smaller than individuals in Western and Central Europe. The size difference is because wild pigs that live in arid areas with low productivity tend to reach smaller sizes than wild pigs that live in areas with abundant food and water (Marsan and Mattioli 2013). Consequently, spatial and environmental variations naturally cause changes in species morphology, within and between populations, genetic diversity, natural selection, reproductive isolation, and other factors, characterizing evolutionary adaptations in species along the latitudinal gradient (Dos Reis et al. 2002).

We showed that the shape of the crania and mandibles differed among all groups, which the availability of local resources may influence (e.g. Are wild pigs eating in a particular region that might influence the muscles involved in chewing?). Wild pigs are opportunistic omnivores, and their diet is determined by the availability of different food types (herbaceous plants, seeds, fruits, invertebrates, carcasses of animals, and vertebrates), according to seasonal, geographical, and human-caused changes (Schley et al. 2003; Herrero et al. 2006; Hegel and Marini 2013; Cervo and Guadagnin 2020). Therefore, these morphological differences found in our results may be associated with the different diets of wild pigs of each geographic group. According to their geographic variation, their diet may vary from maize to native plants and invertebrates or vertebrates' animals (Cuevas et al. 2013; Ballari and Barrios-García 2014).

Other studies with mammals indicate that species with larger, more robust craniums and mandibles have a more potent bite force, while species with elongated, smaller craniums and mandibles can include certain foods for weaker bites in their diet. Those pigs would not be able to break or masticate (Nogueira et al. 2009; Maestri et al. 2016). Neaux et al. (2021) associated wild pigs with controlled mobility and diet showed craniofacial shape changes (more concave and mediolaterally larger cranium with more robust zygomatic arches and a greater angle between the parietal and the occipital). In captivity, carnivorous mammalian species with a limited diet exhibited the most consistent changes associated with skull enlargement, while mammals with a more generalized diet showed fewer morphological changes (Siciliano-Martina et al. 2021). Environmental conditions and available food resources can cause changes in the size and shape of crania and wild pigs mandibles and deserve to be further investigated.

Concluding, we found no differences in size among all groups; however, all groups varied concerning shape (only group A differed from the others). We found a weak allometric relationship in the wild pigs because size and shape did not show the same pattern. This may be occurring along with the effect of availability and variability in each group's diet, in addition to climatic and environmental conditions. Moreover, we also consider the already proven effect of Bergmann's rule, Resource's rule, and phenotypic plasticity acting on the species. Therefore, our study showed a geographical, morphological variation among the groups, which is probably an effect of the latitudinal gradient (Bergmann's rule), of the species phenotypic plasticity to different environments and the resources in the environment (Resource's rule).

References

Adams D.C, Rohlf F.J., Slice D.E. (2004). Geometric morphometrics: ten years of progress following the ‘revolution’. *Italian Journal of Zoology*, 71:5-16.

Adams D.C., Otárola-Castillo E. (2013). Geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, 4(4):393-399.

Albarella U., Dobney K., Rowley-Conwy P. (2009). Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environmental Archaeology*, 14:103–136.

Anderson M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26:32-46.

Antonucci F., Costa C., Aguzzi J., Cataudella S. (2009). Ecomorphology of morpho-functional relationships in the family of sparidae: A quantitative statistic approach. *Journal of Morphology*, 270(7):843-855.

Ballari S.A., Barrios-García M.N. (2014). A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mammal Review*, 44(2):124-134.

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

Baylac M., Friess M. (2005). Fourier descriptors, Procrustes superimposition and data dimensionality: An example of cranial shape analysis. In: Slice DE (ed) *Modern Morphometrics in Physical Anthropology*. Springer-Verlag, New York, pp 145-166.

Bergmann C. (1847). Ober die Verhaltnisse der Warmeokonomie der Thiere zu ihrer Grosse. *Gottinger Studien*, 3:595-708.

Bookstein F.L. (1991). *Morphometric Tools of Landmark Data: Geometry and Biology*. London, United Kingdom. Cambridge University Press. 435p.

Borges L.R., Maestri R., Kubiak B.B., Galiano D., Fornel R., et al. (2017). The role of soil features in shaping the bite force and related skull and mandible morphology in the subterranean rodents of genus Ctenomys (Hystricognathi: Ctenomyidae). *Journal of Zoology*, 301(2):108-117.

Bradshaw A.D. (1965). Evolutionary significance of phenotypic plasticity in plants. In *Advances in genetics* (Vol. 13, pp. 115-155). Academic Press.

Cervo I. B., Guadagnin D.L. (2020). Wild boar diet and its implications on agriculture and biodiversity in Brazilian forest–grassland ecoregions. *Animal Biodiversity and Conservation*, 43(1):123-136.

Cordeiro-Estrela P., Baylac M., Denys C., Marinho-Filho, J. (2006). Interspecific patterns of skull variation between sympatric Brazilian vesper mice: geometric morphometrics assessment. *Journal of Mammalogy*, 87:1270–1279.

Cuevas M.F., Ojeda R.A., Dacar M.A., Jaksic F.M. (2013). Seasonal variation in feeding habits and diet selection by wild boars in a semi-arid environment of Argentina. *Acta Theriologica*, 58(1):63-72.

Dayan T., Simberloff D., Tchernov E., Yom-Tov Y. (1991). Calibrating the paleothermometer; climate, communities, and the evolution of size. *Paleobiology*, 17(2):189–99.

Deberdt A.J., Scherer S.B. (2007). O javali asselvajado: ocorrência e manejo da espécie no Brasil. *Natureza & Conservação*, 5:31-44.

Dos Reis S.F., Duarte L.C., Monteiro L.R., Von Zuben F.J. (2002). Geographic variation in cranial morphology in *Thrichomys apereoides* (Rodentia: Echimyidae). I. geometric descriptors and patterns of variation in shape. *Journal of Mammalogy*, 83:333-344.

Dryden I.L., Mardia K.V. (1998). *Statistical shape analysis*. New York, NY: John Wiley & Sons, Inc. 376p.

Endo H., Hayashi Y., Sasaki M., Kurosawa Y., Tanaka K., et al. (2000). Geographical variation of mandible size and shape in the Japanese wild pig (*Sus scrofa leucomystax*). *Journal of Veterinary Medical Science*, 62(8):815-820.

Endo H., Hayashi Y., Yamazaki K., Motokawa M., Pei J.-C.K., et al. (2002). Geographical Variation of Mandible Size and Shape in the Wild Pig (*Sus scrofa*) from Taiwan and Japan. *Zoological Studies*, 41:452-460.

Evin A., Dobney K., Schafberg R., Owen J., Vidarsdottir U.S., et al. (2015). Phenotype and animal domestication: A study of dental variation between domestic, wild, captive, hybrid and insular *Sus scrofa*. *BMC Evolutionary Biology*, 15(1):1-16.

García G., Vergara J., Lombardi R. (2011). Genetic characterization and phylogeography of the wild boar *Sus scrofa* introduced into Uruguay. *Genetics and Molecular Biology*, 34(2):329-37.

Genov P.V. (1999). A review of the cranial characteristics of the Wild Boar (Susscrofa Linnaeus 1758), with systematic conclusions. *Mammal Review,* 29(4):205-234.

Gould S.J. (1966). Allometry and size in ontogeny and phylogeny. *Biological Reviews*, 41(4):587-638.

Hegel C.G.Z., Marini M.Â. (2013). Impact of the wild pigs, *Sus scrofa*, on a fragment of Brazilian Atlantic Forest. Neotropical Biology and Conservation 8:17–24.

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

Herring S.W. (1972). The role of canine morphology in the evolutionary divergence of pigs and peccaries. *Journal of Mammalogy,* 53(3):500-512.

Ježek M., Štípek K., Kušta T., Červený J., Vícha, J. (2011). Reproductive and morphometric characteristics of wild boar (*Sus scrofa*) in the Czech Republic. *Journal of Forest Science,* 57:285–292.

Kyomi M.M., Kurtis P.J., Liang-Kong L., Cheng-Han C., Tatsuo O. (2002). Geographical variation of mandible size and shape in the wild pig (*Sus scrofa*) from Taiwan and Japan. *Zoological studies,* 41(4):452-60.

Maestri R., Patterson B.D., Fornel R., Monteiro L.R., De Freitas T.R.O. (2016). Diet, bite force and skull morphology in the generalist rodent morphotype. *Journal of Evolutionary Biology*, 29(11):2191-2204.

Marsan A.; Mattioli S. (2013). Il Cinghiale (in Italian). *Il Piviere (collana Fauna selvatica. Biologia e gestione).*

Mayr E. (1963). *Populations, Species, and Evolution.* Belknap Press, Cambridge, Massachusetts, USA.

Mayer J.J., Brisbin I.L. (1988). Sex identification of *Sus scrofa* based on canine morphology. *Journal of Mammalogy,* 69(2):408-412.

Mayer J., Brisbin I. (2009). *Wild boars: biology, damage control techniques and management.* Savannah River National Laboratory, University of Georgia, U.S. Forest Service, Georgia.

McNab B.K. (2010). Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia,* 164(1):13-23.

Navas J.R. (1987). Los vertebrados exóticos introducidos en la Argentina. *Revista del Museum Argentino de Ciências Naturales Zoologia,* 2:7–37.

Neaux D., Blanc B., Ortiz K., Locatelli Y., Laurens F., et al. (2021). How changes in functional demands associated with captivity affect the skull shape of a wild boar (*Sus scrofa*). *Evolutionary Biology,* 48(1):27-40.

Nogueira M.R., Peracchi A.L. Monteiro L.R. (2009). Morphological correlates of bite force and diet in the skull and mandible of phyllostomid bats. *Functional Ecology,* 23:715–723.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., et al. (2013). Package ‘vegan’. *Community ecology package*, 2(9):1-295.

Oliver W.L. (Ed.). (1993). *Pigs, peccaries and hippos: status survey and conservation action plan.* Island Pr.

Owen J., Dobney K., Evin A., Cucchi T., Larson G., et al. (2014). The zooarchaeological application of quantifying cranial shape differences in wild boar and domestic pigs (*Sus scrofa*) using 3D geometric morphometrics**.** *Journal of Archaeological Science*, 43:159–67.

Paradis E., Claude J., Strimmer K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics,* 20(2):289-290.

Pepin D., Spitz F., Janeau G. Valet G. (1986). Dynamics of reproduction and development of weight in the wild boar (*Sus scrofa*) in south-west France. *Mammalian Biology,* 52:21–30.

R Core Team (2013). *R: A language and environment for statistical computing*. Available at: https://www.R-project.org/. Accessed in 22 February 2021.

Rensch B. (1938). Some problems of geographical variation and species-formation. In: *Proceedings of the Linnean Society of London,* 150(4):275-285.

Ripley B.D. (1996). *Pattern Recognition and Neural Networks.* Cambridge University Press.

Ripley B., Venables B., Bates D.M., Hornik K., Gebhardt A., et al. (2013). Package ‘mass’. *Cran r,* 538:113-120.

Rohlf F.J. (2013). *tpsUtil, file utility program, version 1.64.* Department of Ecology and Evolution, State University of New York at Stony Brook.

Rohlf F.J. (2015). *tpsDig, digitize landmarks and outlines, version 2.19.* Department of Ecology and Evolution, State University of New York at Stony Brook.

Salomon, M. (2002). A revised cline theory that can be used for quantified analyses of evolutionary processes without parapatric speciation. *Journal of Biogeography,* 29(4):509-517.

Schlager S. (2017). Morpho and Rvcg–Shape Analysis in R: R-Packages for geometric morphometrics, shape analysis and surface manipulations. In *Statistical shape and deformation analysis* (pp. 217-256). Academic Press.

Schlager S., Schlager M.S. (2014). *Package ‘Rvcg’.*

Schley L., Roper T.J. (2003). Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review,* 33:43-56.

Schluter D. (2000). *The ecology of adaptive radiation*. Oxford: Oxford University Press.

Segall M., Cornette R., Godoy-Diana R., Herrel A. (2020). Exploring the functional meaning of head shape disparity in aquatic snakes. *Ecology and evolution,* 10(14):6993-7005.

Servanty S., Gaillard J.-M., Togo C., Brandt S., Baubet E. (2009). Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *Journal of Animal Ecology,* 78:1278–1290.

Siciliano-Martina L., Light J.E., Lawing A.M. (2021). Cranial morphology of captive mammals: a meta-analysis. *Frontiers in zoology*, 18(1):1-13.

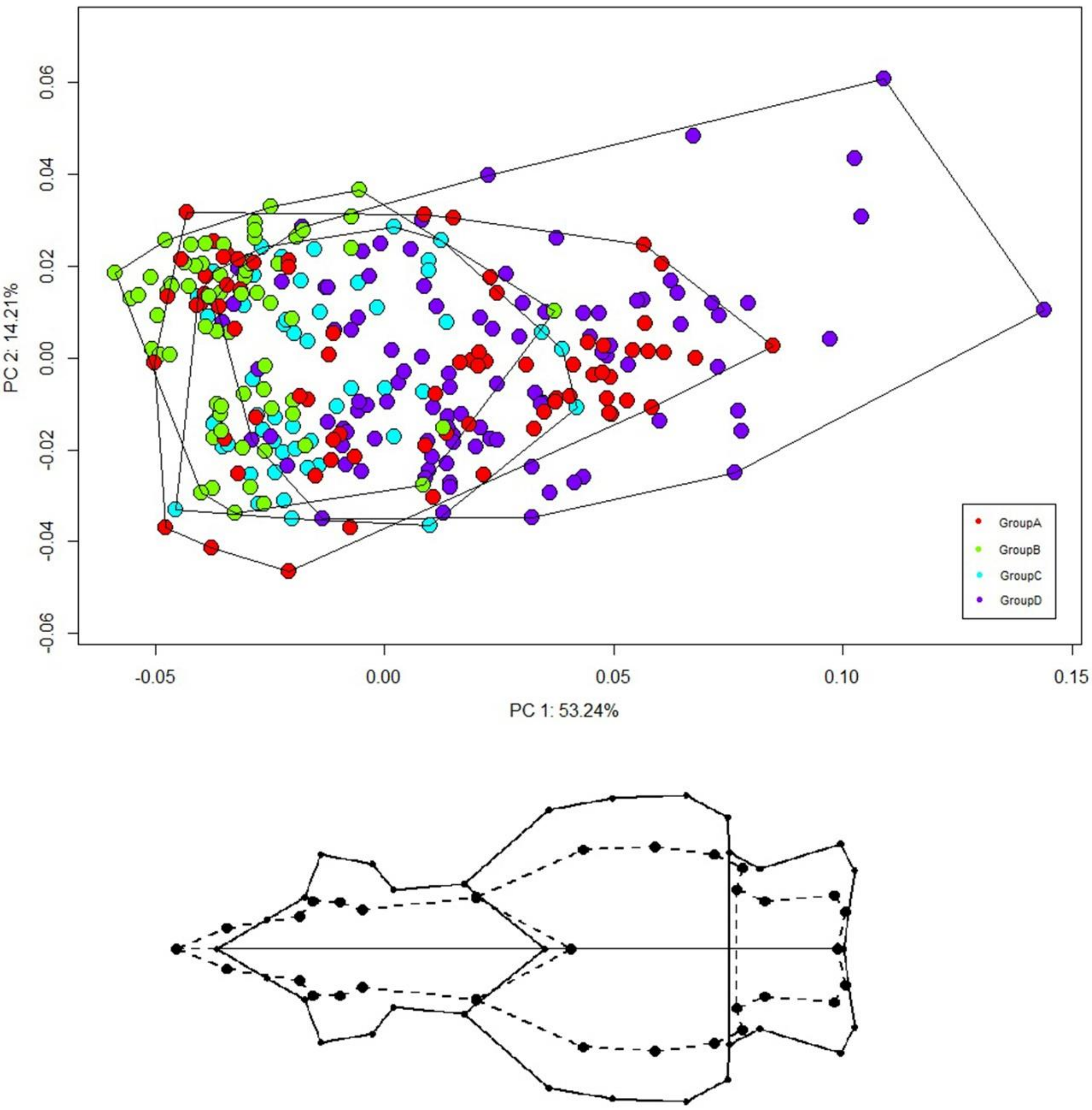
Thorpe R.S. (1976). Biometric analysis of geographic variation and racial affinities. *Biological Reviews*, 51:407–452.

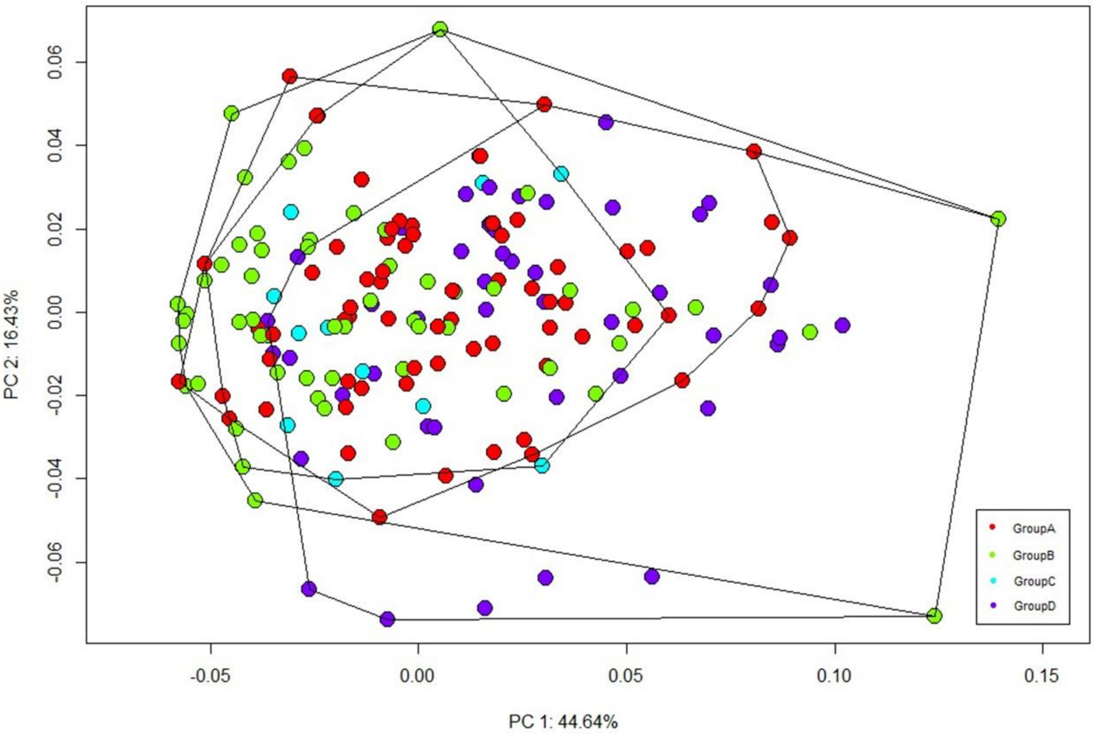
Turcotte M.M., Levine J.M. (2016). Phenotypic plasticity and species coexistence. *Trends in Ecology & Evolution*, 31:803–813.

Viguier B. (2002). Is the morphological disparity of lemur skulls (Primates) controlled by phylogeny and/or environmental constraints? *Biological Journal of the Linnean Society*, 76:577–590.

Wright S.P. (1992). Adjusted P-values for simultaneous inference. *Biometrics*, 48:1005–1013.

Supplementary material 1. Results of PCA analysis for dorsal and left lateral views of the cranium, and on the dorsal view of the mandible.




0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
PC 2: 16.43%
-0.05
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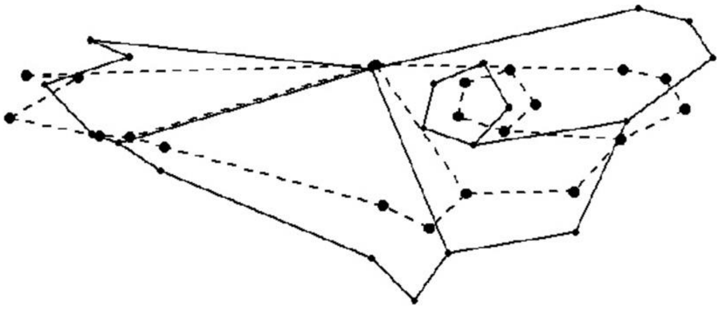
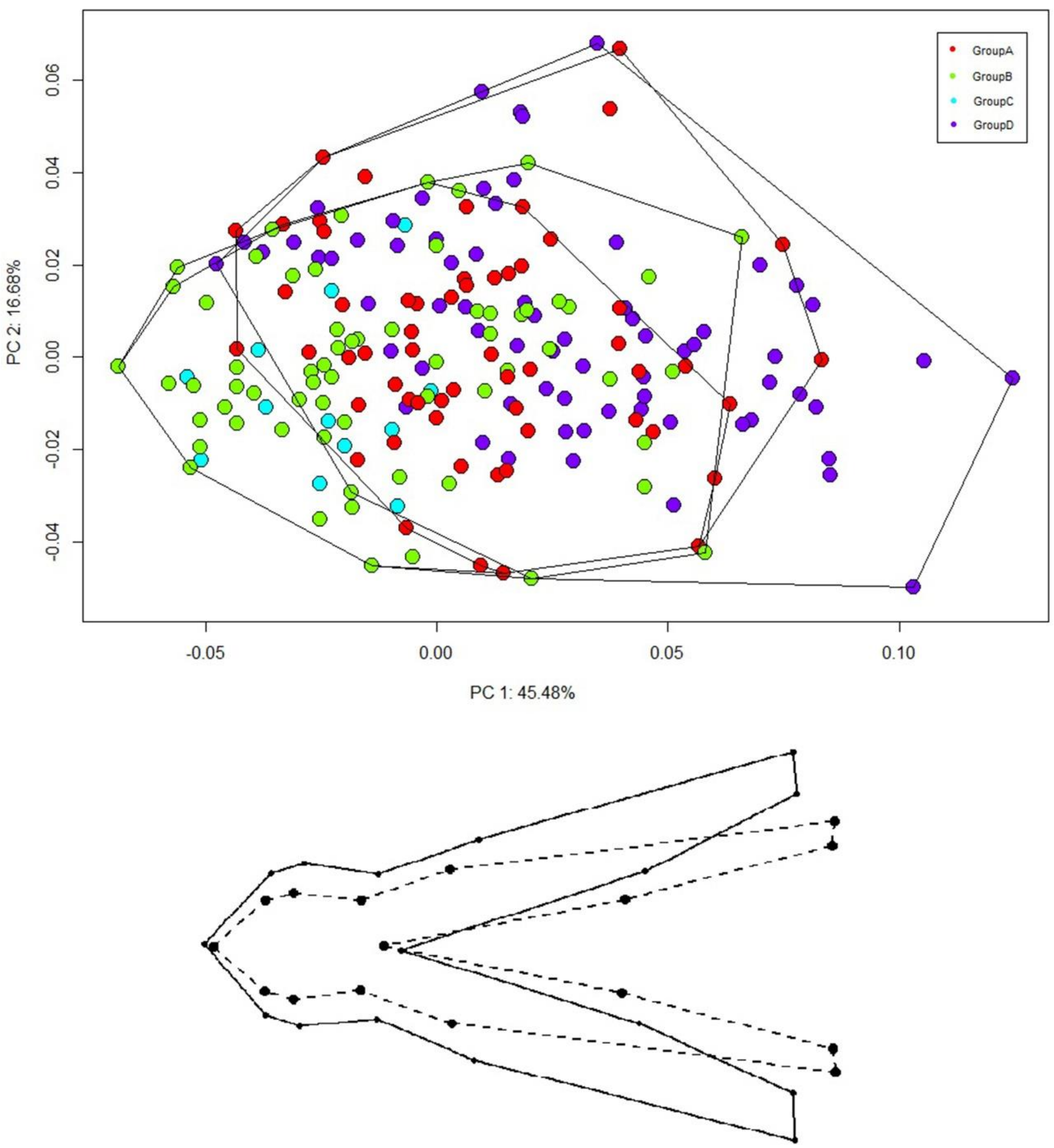
0.05
0.10
0.15
PC 1: 44.64%
GroupA
GroupB
GroupC
GroupD




GroupA
GroupB
GroupC
GroupD
PC 2: 16.68%
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.05
0.00
0.05
0.10
PC 1: 45.48%

Is there differentiation in the morphology of the skull of wild pigs (*Sus scrofa* L.) structured between native and introduced areas?

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ABSTRACT

Sus scrofa (L.) is found worldwide and is considered a very successful invasive species. However, morphological changes can occur in invasive species to better adapt to new and different introduced areas. Our goal was to verify if wild pigs present morphological differences in the cranial structure in introduced areas or keep the same characteristics of wild boars in native areas. We used geometric morphometrics for comparisons of shape and size of the crania and mandibles of wild boars and wild pigs from different collections. We separated the sample into seven groups based on the place of origin of the specimens and the following geographic location. In total, we photographed 407 individuals in the dorsal view of the cranium, 359 individuals in the left lateral view of the cranium, and 425 individuals in the dorsal view of the mandible. We found that all groups present a significant difference in size, resulting in sexual dimorphism in the species within groups. Comparison among groups showed that some *S. scrofa* present differences in size between introduced and native areas. The groups also present differences in shape. Wild pigs from Argentina and Southern Brazil groups maintained morphological characteristics similar in size and shape to European wild boars. North American wild pigs were the most different in size and shape, probably because captivity or island life. We conclude that there is morphological differentiation in *S. scrofa* in some groups introduced areas compared to native areas, while some groups maintain similar size or shape. However, genetic studies are needed to assess better the effects of geographic differentiation and environmental conditions on the species.

Keywords: Wild boars, Wild pigs, Invasive Species, Geometric Morphometrics, Skull variation

Introduction

Across the world, different organisms have been intentionally or accidentally introduced in environments other than their original distribution (Vitousek et al. 1996). The similarities in physical characteristics between the native environment of the species and the place of introduction may favor the adaptation/acclimatization of the non-native to have a successful invasion (Delariva and Agostinho 1999; Clout and Russell 2008). During the biological invasion process, many introduced populations change their morphology due to geographic, environmental, and temporal factors (Mooney and Cleland 2001). Mammals of the family Artiodactyla, such as *Sus scrofa*, appear to be successful invaders (Clout and Russell 2008) and show morphological variability in response to new environmental conditions (Albarella et al. 2009).

The wild boars (*Sus scrofa* L.) have one of the broadest geographical distributions of all terrestrial mammals (Barrios-García and Ballari 2012). Its natural range covers Europe, Asia, and North Africa (Oliver and Brisbin 1993). However, human action has widely expanded wild boars' distribution, which nowadays occurs on all continents except in Antarctica (Barrios-García and Ballari 2012). During this process of geographic expansion due to introduction into new areas, wild boars and their lineages derived from crosses with domestic pigs established naturalized populations in the Americas, Australia, and Oceania (Oliver and Brisbin 1993). These mixed populations are called wild pigs and occupy a wide range of habitats from sub-Antarctic to tropical and desert (Meijaard et al. 2011). Crossing between wild boars and domestic pigs may be a probable explanation for the invasive potential of wild pigs' population (García et al. 2011).

Cytogenetically wild boars have 36 chromosomes, while domestic pigs have 38, regardless of their origin and breed (Darré et al. 1992). Both belong to the same species and crossing these subspecies results in mixed lineages with distinct phenotypic characteristics of parental species (Grossi et al. 2006). Due to their varied ancestry, several wild pigs vary widely in physical appearance and morphometry (Šprem et al. 2011), which often makes identification at the subspecies level difficult. Phenotypes and morphological variations in size and shape led the *Sus scrofa* species to describe several subspecies (Groves 1981, 2007). Currently, at least sixteen *Sus scrofa* subspecies are recognized based on morphology (Groves 1981, 2007) and supported by genetic markers (Larson et al. 2005) worldwide.

Body measurements and size and shape of cranial bones are recognized as one of the important ways to classify *Sus scrofa*, whether from wild boars, domestic pigs, or wild pigs (Groves 1981, 2007; Genov 1999; Mayer and Brisbin 2008; Albarella et al. 2009; Owen et al. 2014; Iqbal et al. 2020). Wild boars present narrow cranium with narrow nasal bone, straight, and long cranium; domestic pigs, on the other hand, have a shorter, wider, and rounded cranium and wild pigs are a mixture of these characteristics (Brisbin et al. 1977; Genov 1999). Geographic location and environmental conditions can also affect the size and shape of the cranial structure of these animals (Albarella et al. 2009; Evin et al. 2015). Thus, size and shape analyses play an essential role in biological studies, as they indicate the different functional roles played in responding to selective pressures on species (Zelditch et al. 2004), in native or introduced areas. In this context, our goal was to verify if wild pigs present morphological differences in the cranial structure in introduced areas or keep the same characteristics of wild boars in native areas. We expected to find morphological differences between specimens from native areas and introduced areas.

Methods

Data collection

We used crania and mandibles of the specimens of *S. scrofa* from North and South America, Europe and Asia. In Brazil (BR), we used samples from the collections of the Museu do Suíno in Rio Grande do Sul state; from the Mastozoology Collection of the Universidade Federal de Santa Catarina (UFSC) in Santa Catarina state, and Museu Nacional do Rio de Janeiro (MNRJ) in Rio de Janeiro state. In addition, we photographed samples from private collections hunters and collected specimens from hunting authorized by IBAMA in Brazil. Specimens from hunting were transported, prepared, and registered in the Scientific Collection of Mammals of the University of Brasília (UnB) and in the Scientific Collection of Mammals Augusto Ruschi Zoobotanical Museum of the University of Passo Fundo (UPF).

We also used specimens from the mastozoology collections of collections from different countries, Argentina (AR), Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN); Museum of La Plata (MPL), and the Mastozoology Collection Universidad Nacional del Noroeste de la Provincia de Buenos Aires (UNNOBA). From Uruguay (UR) Museo Nacional de Historia Natural (MNHN). And United States (USA), Field Museum of Natural History, Chicago, Illinois; and American Museum of Natural History, New York.

We considered for the analyzes only specimens with the place of origin and with complete bone structures, or that could be underestimated based on their other symmetric view. We consider all wild specimens of *Sus scrofa*, regardless of subspecies. Domestic specimens (*S. scrofa domesticus*) were disregarded. We photographed the dorsal and left lateral views of the cranium and the dorsal view of the mandibles. The photos were taken with a digital camera with a resolution of 20 megapixels and a standardized focal length of 45 cm in height with support. We used only skulls of males and females, adults and subadults to avoid classification errors regarding sex. This sex classification was based on the position and total eruption of the canine and on the ridge height in the eminent canine bone, according to Herring (1972) Mayer and Brisbin (1988). Males have an exclusive rostral structure adjacent to the upper canine, and the lower tusks are larger than those in females (Herring 1972). We photographed 407 specimens for dorsal and 359 for lateral views of the cranium and 425 specimens for the dorsal view of the mandible.

To compare the data, we separated the sample into seven groups of wild boars and wild pigs according to geographic distribution, based on the place of origin of the specimens. Thus, the groups of specimens were as follows: Group A: from central Argentina provinces La Pampa, Buenos Aires, San Luis, Neuquén, and Río Negro; Group B: from the Argentine provinces of Entre Ríos on the Uruguay frontier, Misiones on the Brazilian frontier, Formosa on the Paraguay frontier, and provinces of Soriano, Rocha, Paysandú, and Río Negro in Uruguay; Group C: from the states of Rio Grande do Sul and Santa Catarina in southern Brazil; Group D: from the most central states of Brazil (Minas Gerais, Goiás, Mato Grosso, and Mato Grosso do Sul); Group E: from the USA; Group F: from Europe; and Group G: from the Asia (Table 1; Figure 1).

Table 1. Number of individuals and total of *Sus scrofa* specimens analyzed with the sample size for each group in North America (Group E) and South America (Group A, Group B, Group C, and Group D), Europe (Group F) and Asia (Group G), by sex and view of the cranium and mandible.

Geographic Group	Cranium dorsal	Cranium lateral	Mandible dorsal
Group A	52 ♂ / 24 ♀	41 ♂ / 24 ♀	33 ♂ / 25 ♀
Group B	25 ♂ / 39 ♀	25 ♂ / 32 ♀	27 ♂ /37 ♀
Group C	31 ♂ / 22 ♀	27 ♂ / 15 ♀	38 ♂ / 19 ♀
Group D	76 ♂ / 25 ♀	71 ♂ / 19 ♀	90 ♂ / 31 ♀
Group E	18 ♂ / 9 ♀	17 ♂ / 7 ♀	17 ♂ / 9 ♀
Group F	7 ♂ / 5 ♀	6 ♂ / 4 ♀	8 ♂ / 6 ♀
Group G	34 ♂ / 40 ♀	35 ♂ / 36 ♀	41 ♂ / 44 ♀
Total for sex	243 ♂ / 164 ♀	222 ♂ / 137 ♀	254 ♂ / 171 ♀
Total for view	407	359	425

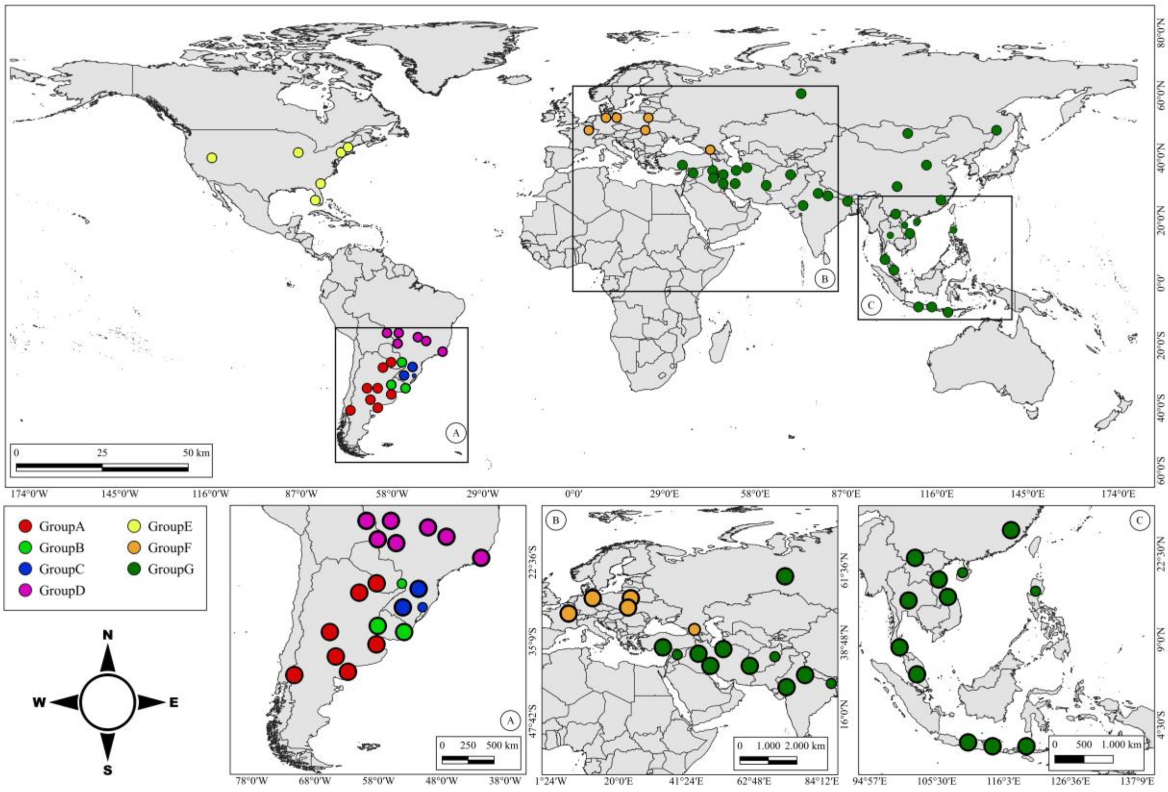

Figure 1. World geographical distribution of wild pigs and wild boars used in this study and the seven groups we identified.

Geometric Morphometric Procedures and Skull Shape and Size Analysis

The photographs were organized in the program TpsUtil version 1.64 (Rohlf 2013). After, we selected homologous anatomical landmarks to represent best the size and shape of the skull and mandibles. For this, we used 31 homologous anatomical landmarks in the dorsal view of the cranium, 20 landmarks in the left lateral view of the cranium, and 16 landmarks in the dorsal view of the mandible (Supplementary material 1). These anatomical landmarks were digitized with the TpsDig version 2.19 program (Rohlf 2015) (Supplementary material 1) by the same person (CGZH).

The coordinates of the anatomical landmarks were superimposed with the method of the Generalized Procrustes Analysis (GPA) (Dryden and Mardia 1998) to remove differences in scale, position, and orientation unrelated to the shape (Adams et al. 2004). The size of each cranium and mandible was estimated using its centroid size (Bookstein 1991). The views with the pattern of bilateral symmetry (dorsal cranium and dorsal mandible) had the coordinates of the anatomical landmarks on the right and left sides. To avoid redundancy in the data, we symmetrized both sides. To evaluate data normality, we made a Shapiro test. The allometry (shape and size covariation) was tested to evaluate how much of the shape (Procrustes residuals) was predicted by the size (centroid size) variation.

We used a t-test for size sexual dimorphism to compare centroid sizes of males and females of wild pigs and wild boars, in size analysis. We used an Analysis of Variance (one-way ANOVA) followed by the Tukey test, for size multiple comparisons among geographic groups of the native areas and groups of the invasive areas. We also use a two-way ANOVA to test the interaction between factors sex and groups.

For the shape analysis, we made a Principal Component Analysis (PCA) an exploratory analysis, and we used a Canonical Variate Analysis (CVA) to generate discriminant graphics for sex and groups in the different areas. The shape variation was visualized through deformation grids projected along with the PCs and CVs. We used a Linear Discriminant Analysis (LDA) to obtain the highest percentage overall correct classification and a cross-validation procedure for evaluating the performance of classification by LDA (Ripley 1996; Baylac and Friess 2005). To test the multiple factors that can cause differences in shape, we use Multivariate Analysis of Variance (MANOVA) with Wilks'λ test, for sex, for groups, and to test the interaction between the factors. Finally, we used a pairwise MANOVA to check for differences among groups of native areas and invasive areas. In the case of significant differences, we use the Bonferroni correction for multiple comparisons (Wright 1992).

We did all analyses in Program R. version 4.0.3. (R Core Team 2020), using the packages “Geomorph” (Adams and Otárola-Castillo 2013); “Morpho” (Schlager 2017); “ape” (Paradis et al. 2004); “MASS” (Ripley et al. 2013); “Rvcg” (Schlager and Schlager 2014); “stats” (R Development Core Team 2021); and “vegan” (Oksanen et al. 2013).

Results

Skull size

Allometry test was significant for all views (dorsal cranium: $r^2 = 0.07$, $p < 0.01$; lateral cranium: $r^2 = 0.03$, $p < 0.01$; dorsal mandible: $r^2 = 0.13$, $p < 0.01$) showing that between 3 and 13% of shape variation is predicted by size. Already expected for the species, we found size sexual dimorphism in all views (dorsal cranium $t = -9.8809$, $df = 326.9$, $p < 0.01$; lateral cranium $t = -9.0237$, $df = 286.2$, $p < 0.01$; and dorsal mandible $t = -10.4$, $df = 387.64$, $p < 0.01$). The males on average are larger than females in all geographic groups (Figure 2).

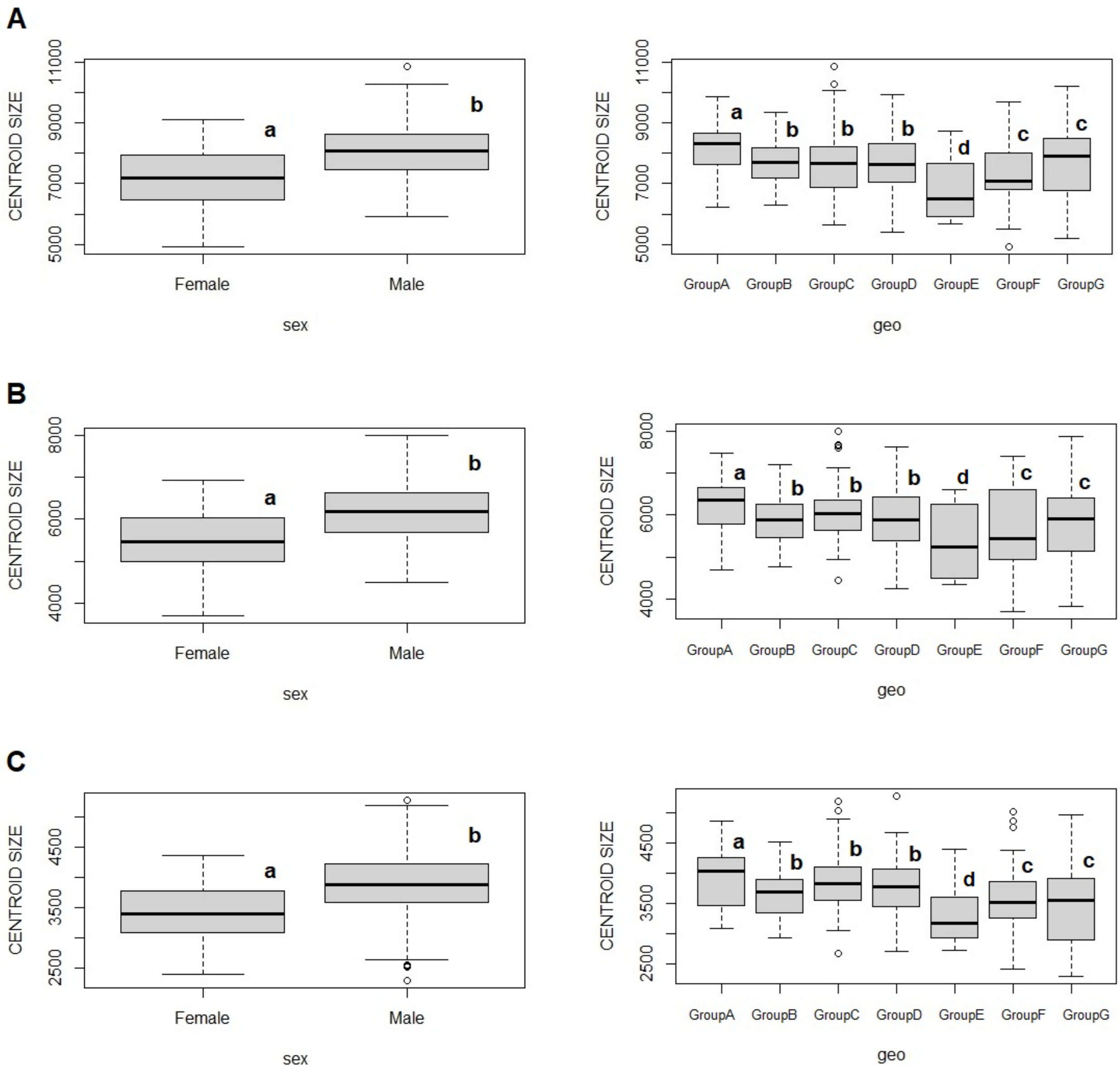

Figure 2. Sexual dimorphism in skull size (centroid size) in wild boars and wild pigs, and differences in size among geographic groups in native areas and invasive areas. Different letters above boxes represent significant differences among different groups for Tukey´s multiple comparison tests at the 5% level. In A: comparisions in dorsal view of the cranium; B: comparisions in lateral view of the cranium; C: comparisions in dorsal view of the mandible.

We found significant differences in size among geographic groups for in all views (dorsal cranium (F = 6.396, df = 6, $p < 0.01$), lateral cranium (F = 7.032, df = 6, $p < 0.01$), and dorsal mandible (F = 10.87, df = 6, $p < 0.01$). However, not all geographic groups differ. In paired comparisons, the dorsal view of the cranium, the difference is in Group A and Group E compared to the other groups. Group A differs from Group B, Group D, Group E, and Group G but does not differ significantly from Group C and Group F. All groups differ significantly only from Group E. In the lateral view of the cranium, Group A differs from Group E and Group G but does not differ significantly from Group B, Group C, Group D, or Group F. Also, all groups differ significantly from Group E. In the dorsal mandible view, Group A differs from Group B, Group E, and Group G; Group C and Group D differ from Group E and Group G, and Group F differs from Group E and Group G (Figure 2). Analyses with the interaction of factors, we do not see significant interaction between sex and geographic groups for size ($p > 0.05$) for none of the cranium and mandible views. Thus, differences in size are attributed specially to sex and not as geographic groups.

Skull shape

There was no structuring among the seven geographic groups in PCA analysis. The first two principal components (PCs) explained more than 57% of the variation in the shape of the cranial structure of *Sus scrofa* in three views (See Supplementary material 2).

For LDA the cranium views showed at least more than 50% of correct classification for each geographic group, and for the mandible, the percentages of correct classification were on average lower than cranium views (Table 2).

Table 2. Percentage of correct classification for seven gographic groups of *Sus scrofa* using linear discriminant analysis (LDA), for dorsal and lateral views of the cranium and dorsal view of the mandible.

Skull View	**Geographic Group**						
	Group A	Group B	Group C	Group D	Group E	Group F	Group G
Dorsal Cranium	72.368	85.937	79.245	86.138	88.888	50.000	82.432
Lateral Cranium	70.769	82.456	76.190	86.666	70.833	50.000	91.549
Dorsal Mandible	39.655	73.437	47.368	78.512	50.000	21.428	78.823

The MANOVA test with the interaction between sex and group was significant for all views, and we confirmed that the shape of the cranial structure of groups is affected by sex (Table 3). However, the paired test was not significant for all groups. In the dorsal view of the cranium, Group B and Group C no differ from Group F, and Group F no differ from Group G. In the lateral view of the cranium, Group A and Group C no differ from Group F. And in the dorsal view of the mandible, Group A and Group C no differ from Group F. This means that the southeast most groups in South America (Group A, Group B, and Group C) maintain very similar characteristics in the morphology of the cranial structure with native wild boars of Europe, which may be a reflection of past introductions into these regions (Table 4). These wild pigs and boars feature more elongated and narrower skull and mandibles, with a slight curvature in the frontal bone. Group F and Group G also show similar shapes, not significantly different in the cranium's dorsal view. Possibly, this is a result of the crossing between European and Asian lineages during the domestication process in Eurasia, which gave rise to the mixed lineages and known subspecies.

Table 3. Results of MANOVA with interaction for dorsal and lateral views of the cranium and dorsal view of the mandible.

	Dorsal Cranium			
	Df	**Wilks'λ**	**F**	***P***
Sex	1	0.24807	96.489	< 0.001
Geo	6	0.11242	14.310	< 0.001
Sex × Geo	6	0.71214	1.864	< 0.001
Residuals	393			
	Lateral Cranium			
Sex	1	0.81218	4.4753	< 0.001
Geo	6	0.52605	2.2013	< 0.001
Sex × Geo	6	0.61555	1.6398	< 0.001
Residuals	345			
	Dorsal Mandible			
Sex	1	0.88205	4.4574	< 0.001
Geo	6	0.65892	2.4151	< 0.001
Sex × Geo	6	0.73832	1.7379	< 0.001
Residuals	411			

Table 4. Pairwise distances between means of the seven geographic groups in relation for shape, for dorsal and lateral views of the cranium and dorsal view of the mandible. In bold, *p* values that were not significant.

Dorsal Cranium				
	d	**UCL (95%)**	**Z**	**Pr > d**
GroupA:GroupB	0.03921190	0.01429641	4.1589612	0.001
GroupA:GroupC	0.02749534	0.01510836	3.0882702	0.001
GroupA:GroupD	0.02211796	0.01253338	3.0748905	0.001
GroupA:GroupE	0.05544848	0.01916741	3.8496020	0.001
GroupA:GroupF	0.03297959	0.02596497	2.2834933	0.009
GroupA:GroupG	0.02481544	0.01373987	2.9479126	0.002
GroupB:GroupC	0.02422008	0.01582609	2.6143641	0.004
GroupB:GroupD	0.05633905	0.01373218	4.7998207	0.001
GroupB:GroupE	0.08783218	0.01985914	5.1192980	0.001
GroupB:GroupF	0.02253409	0.02633888	1.2006623	**0.123**
GroupB:GroupG	0.02236110	0.01490979	2.5355974	0.002
GroupC:GroupD	0.03927134	0.01398453	4.0368428	0.001
GroupC:GroupE	0.07673892	0.01959890	4.2714905	0.001
GroupC:GroupF	0.02082985	0.02634461	0.9273262	**0.183**
GroupC:GroupG	0.01979400	0.01529059	2.2896796	0.009
GroupD:GroupE	0.04614138	0.01821564	3.8870632	0.001
GroupD:GroupF	0.04974574	0.02580399	3.1685046	0.001
GroupD:GroupG	0.03966143	0.01279565	4.4605918	0.001
GroupE:GroupF	0.08213391	0.03020801	3.5580651	0.001
GroupE:GroupG	0.07373011	0.01938153	4.2111713	0.001
GroupF:GroupG	0.02232155	0.02586527	1.1943711	**0.114**
Lateral Cranium				
GroupA:GroupB	0.03572618	0.01691192	3.5402914	0.001
GroupA:GroupC	0.02069002	0.01888869	1.9020247	0.026
GroupA:GroupD	0.02680645	0.01548952	3.2008413	0.001
GroupA:GroupE	0.04760164	0.02267862	3.6529069	0.001
GroupA:GroupF	0.02576440	0.03130777	1.0417564	**0.153**
GroupA:GroupG	0.03660794	0.01586718	4.1649731	0.001
GroupB:GroupC	0.02441038	0.01945017	2.2998716	0.009
GroupB:GroupD	0.05865743	0.01568299	4.7472270	0.001
GroupB:GroupE	0.07932492	0.02313478	4.3086251	0.001
GroupB:GroupF	0.03581097	0.03230734	2.0017577	0.020
GroupB:GroupG	0.03638060	0.01599989	4.0367031	0.001
GroupC:GroupD	0.03852015	0.01846162	3.3650690	0.001
GroupC:GroupE	0.06228257	0.02414208	4.0358705	0.001
GroupC:GroupF	0.02547426	0.03330941	0.8540055	**0.199**
GroupC:GroupG	0.03587738	0.01909829	3.3688852	0.001
GroupD:GroupE	0.03375369	0.02089032	2.9948360	0.001
GroupD:GroupF	0.03816913	0.03105428	2.3037568	0.011
GroupD:GroupG	0.05444628	0.01468455	5.1215025	0.001
GroupE:GroupF	0.05572634	0.03512230	3.1368045	0.001
GroupE:GroupG	0.06961157	0.02198802	5.1263563	0.001

GroupF:GroupG	0.03702047	0.03144660	2.2041589	0.015
Dorsal Mandible				
GroupA:GroupB	0.02885424	0.01599326	3.48814224	0.001
GroupA:GroupC	0.02392801	0.01635885	2.82937947	0.004
GroupA:GroupD	0.02680911	0.01381042	3.79277892	0.001
GroupA:GroupE	0.06038077	0.01980820	4.77567992	0.001
GroupA:GroupF	0.01486113	0.02541522	-0.03969972	**0.531**
GroupA:GroupG	0.02329150	0.01540547	2.88032380	0.004
GroupB:GroupC	0.01854847	0.01612058	2.07415279	0.024
GroupB:GroupD	0.04775459	0.01353446	5.36591221	0.001
GroupB:GroupE	0.08334696	0.01975995	6.34039796	0.001
GroupB:GroupF	0.02774281	0.02592676	1.89203240	0.033
GroupB:GroupG	0.03860351	0.01442101	4.75991680	0.001
GroupC:GroupD	0.03596919	0.01401255	4.29511009	0.001
GroupC:GroupE	0.07654431	0.02000245	6.00729664	0.001
GroupC:GroupF	0.02143695	0.02589077	1.08035618	**0.140**
GroupC:GroupG	0.03847843	0.01540885	4.48737282	0.001
GroupD:GroupE	0.04317052	0.01820623	4.48559151	0.001
GroupD:GroupF	0.03389448	0.02399002	2.69568125	0.004
GroupD:GroupG	0.03770115	0.01251886	4.77968365	0.001
GroupE:GroupF	0.06885511	0.02908624	4.58276550	0.001
GroupE:GroupG	0.06271552	0.01917473	5.47434339	0.001
GroupF:GroupG	0.02902770	0.02512956	2.08880058	0.016

The CVA analysis distinctly was not classified the seven *Sus scrofa* by the morphology of crania and mandibles. There is a partial overlap of groups of both introduced and native areas, of both native groups, and of introduced groups. However, the pairwise comparison analyzes showed that there are significant morphological differences for almost all groups of the *Sus scrofa* concerning the shape, in native and introduced areas. Groups A and C in introduced areas were more like Group F in native areas, with a more elongated and narrower skull, mainly the rostrum region, indicating that certain morphological characters are maintained in the species (Figures 3, 4, and 5). Group D and Group E had less overlap with the other groups, and both are composed of wild pigs in introduced areas. Group D are those wild pigs found in the central region of Brazil. Group E is composed of animals from North America. The wild pigs of both groups possess shorter, more robust crania and mandibles (Figure 3).

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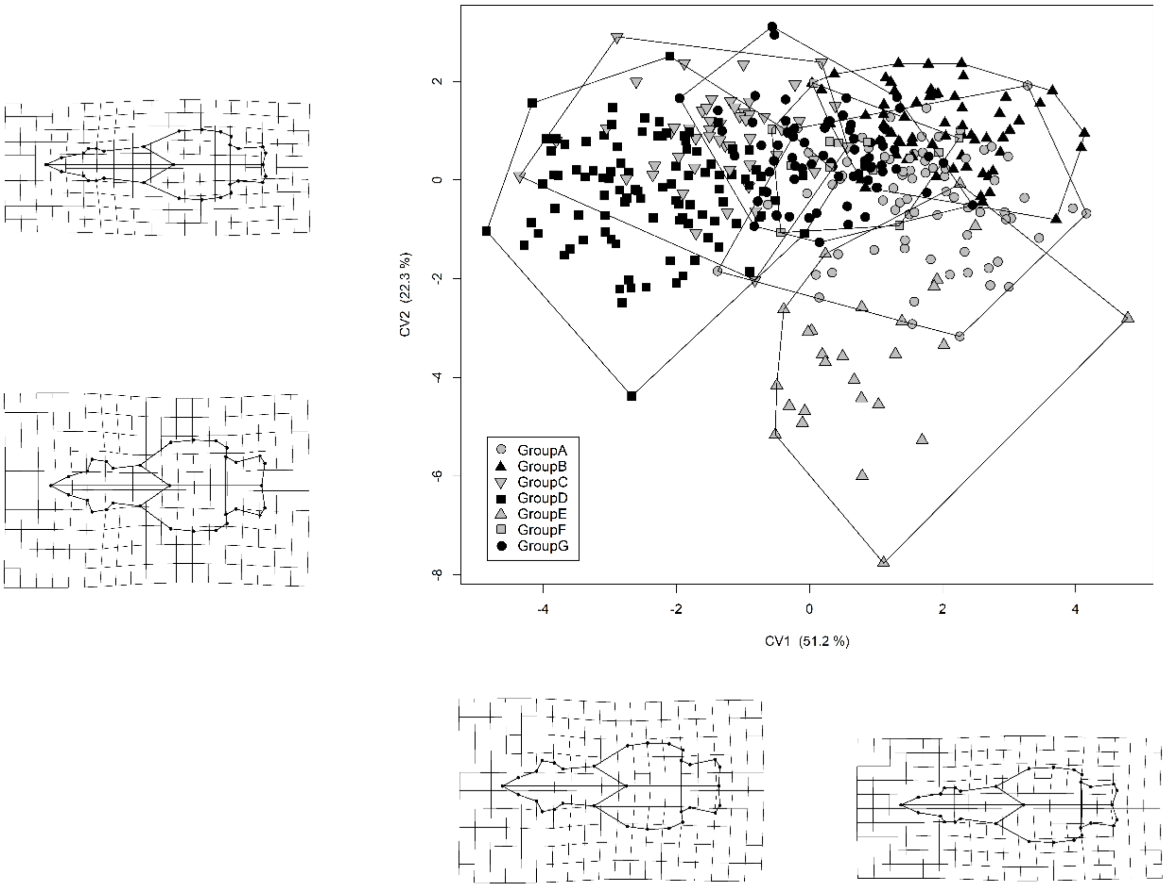


Figure 3. Scatterplot of canonical variate analysis (CVA) show the two first canonical axis for the cranium shape in dorsal view, for seven geographic groups of *Sus scrofa*. The grids represent differences for landmark configuration along the first and second CVs representing the extreme negative and positive scores. Variance percentages for CV1 and CV2 are given in parenthesis.

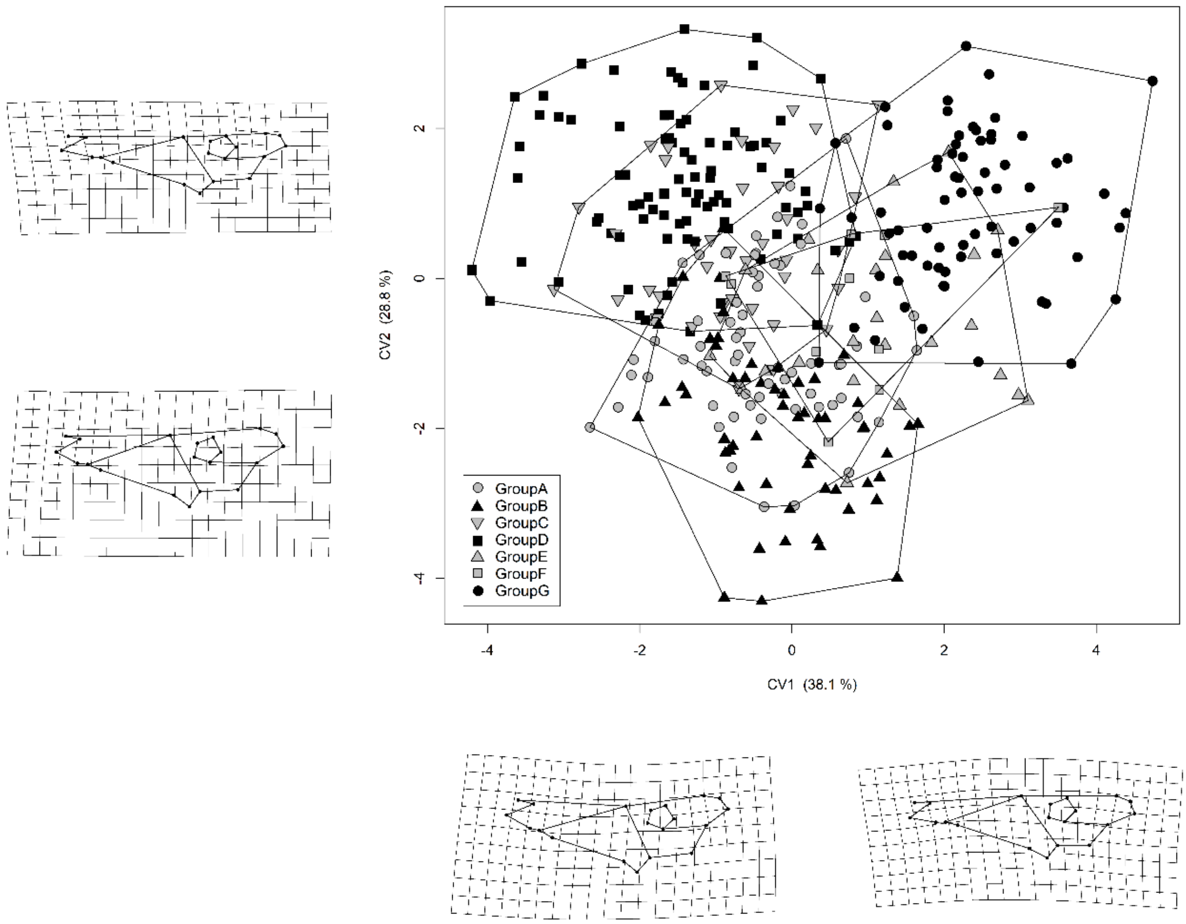


Figure 4. Scatterplot of canonical variate analysis (CVA) show the two first canonical axis for the cranium shape in lateral view, for seven geographic groups of *Sus scrofa*. The grids represent differences for landmark configuration along the first and second CVs representing the extreme negative and positive scores. Variance percentages for CV1 and CV2 are given in parenthesis.

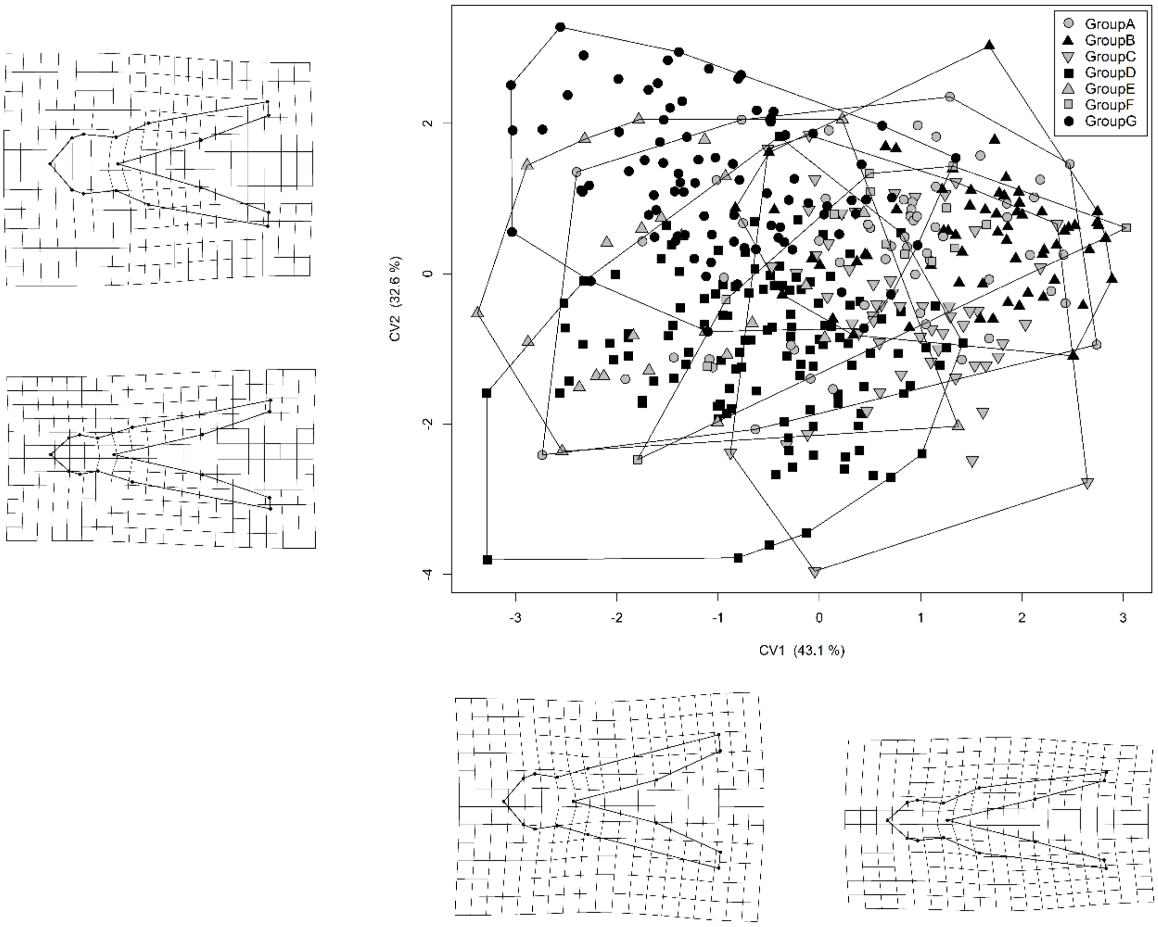


Figure 5. Scatterplot of canonical variate analysis (CVA) show the two first canonical axis for the mandible shape in dorsal view, for seven geographic groups of *Sus scrofa*. The grids represent differences for landmark configuration along the first and second CVs representing the extreme negative and positive scores. Variance percentages for CV1 and CV2 are given in parenthesis.

Discussion

Our goal was to verify if wild pigs presented morphological differences in the skulls in introduced areas or kept the same characteristics of wild boars in native areas. Our hypothesis was partially corroborated because only a few groups of wild pigs showed morphological differences in size or in shape between native and introduced areas. Even knowing the effect of sexual dimorphism in these animals, we discuss the implications of geographic aspects of phenotypic variation in space.

Sexual dimorphism is well known for wild pigs in the literature (Parés-Casanova 2013; Tack 2018; Susol et al. 2021). We showed that males in all groups were larger than females, as was expected for the species. Wild pigs are sexually dimorphic, being the males larger in various measures of the crania and mandibles (Mayer and Brisbin 2008). In this sense, we can attribute size variations to sex, this was significant in all groups in our study. However, geographic variation can also be attributed to differences in size and shape in wild boars and wild pigs, as suggested by other studies. The size, shape, and allometry of wild boars' molars appear to be strongly affected by geographic location (Evin et al. 2015). Wild boars exhibit significant morphological differentiation in size and shape (Albarella et al. 2009). Western European specimens are smaller than Eastern European specimens, Russian specimens have the largest teeth, and specimens from North Africa (Algeria and Morocco) are the smallest (Evin et al. 2015). Wild pigs also show morphological differences in size and shape influenced by geographic variation in introduced areas (see Chapter 2). Wild pigs in Argentina have bigger, longer, and narrower skull and mandibles than wild pigs from central Brazil, which have shorter skull and mandibles, tall, broad, and robust (unpublished data - see Chapter 2). The differentiation seem to be related not to the fact that the species is native or introduced in a particular area but to environmental conditions and the introduction and hybridization processes through which it went along time.

European and Asian wild boars evolved independently from a common ancestor and later from the domestication process 10,000 years ago (Larson et al. 2005; Ottoni et al. 2013). With the intensification of the swine industry from the 18th and 19th centuries, these populations were artificially hybridized, resulting in various breeds (Larson et al. 2005; Ottoni et al. 2013; Bosse et al. 2014). UK boars were hybridized with Asian boars and subsequently, due to superior production characteristics, became founders of several modern commercial pig breeds (Bosse et al. 2014). European boars (which were better adapted to the selective pressure of the transition from forested areas to more urban environments) were crossed with Asian boars as they seemed to perform better in these relatively new environments (White 2011). During this period, exchanges of boars were intensified for crossbreeding and experimental breeding, giving rise to the first modern breeds of pigs with mixed English and Asian origins (Larson et al. 2005; White 2011; Bosse et al. 2014). Currently, phylogenetic studies show Asian strains, European strains, and mixed strains (with Asian and European genes) in nature (Larson et al. 2005; Albarella et al. 2009; White 2011; Ottoni et al. 2013; Bosse et al. 2014). Evin et al. (2015) found two main groups of Eurasian wild boars based on the molar form: 1) one that includes populations from Eastern Western Eurasia (Turkey, Syria, Iran, Iraq, and Russia) that likely correspond to a mixture of *S. scrofa scrofa*, *S. scrofa attila*, and *S. scrofa lybicus*; 2) a second including Western specimens divided into two subgroups: those of North African origin (Morocco and Algeria) that correspond to the subspecies *S. scrofa algira*, and those of European origin (France, Germany, Poland, Switzerland) that correspond to the subspecies *S. scrofa scrofa*. Thus, these historical crosses between European and Asian wild boars could explain the overlapping of native geographic groups found in our analyses. Group F and Group G presented similarities in the shape of the cranium. Possibly, this is a result of the crossing between European and Asian lineages during the domestication process in Eurasia, which gave rise to the mixed lineages and known subspecies.

They can also explain the overlapping of wild boars with groups from introduced areas (wild pigs), as both European lineages and Asian lineages were introduced to the new continent. The first introduction of wild pigs in the United States took place in the 16th century by European explorers, and later in the early 20th century, new introductions occurred for hunting purposes (Taylor 1993). Currently, populations in the United States have resulted from a mixture of Eurasian wild boars, domestic pigs and from crossing these two forms (Sweeney et al. 2003; Hernández et al. 2018; Delgado-Acevedo et al. 2021). Argentinians and Uruguayan wild pigs' populations also have phylogenetic traits of European and Asian lineages (García et al. 2011; Sagua et al. 2018; Acosta et al. 2019). In Argentina, wild pigs' populations in Buenos Aires Province, presented a genetic origin from wild boars from Europe and Caucasus (eastern Europe and western Asia) with the low frequency of individuals of Asian origin (Acosta et al. 2019), while the population from El Palmar National Park was of Asian origin (Sagua et al. 2018). Genetic diversity in Argentina populations is lower than populations in Europe and Uruguay, which means that wild boars in Argentina still retains a reservoir of original wild boars genetic variability introduced in the early 20th century (Sagua et al. 2018). In Uruguay, wild pigs' populations have a marked mixture of European and Asian lineages (García et al. 2011; Sagua et al. 2018). According to García et al. (2011), two different introduction events are related to genetic lineages in Uruguayan wild pig populations: 1) Historical introduction of European wild boars in the Colony Department in 1920, and its spread through localities in southern, central, and northeastern Uruguay across basins the Rio Santa Lucía and the Río Negro; and 2) In southeastern Uruguay near the Cebollatí River in the Merin lagoon basin (border between Uruguay and Brazil - may have been raised to the deliberate introduction of Asian hybrids from southern Brazil). Thus, our morphometric results corroborate with phylogenetics studies by García et al. (2011), Sagua et al. (2018), and Acosta et al. (2019), who found genes from European and Asian lineages in wild pigs in Argentina and Uruguay. This could explain why both the size and shape of the crania and mandibles of Group A differ more about the other groups in our study, while group B with specimens from Uruguay did not differ about the size of the Brazilian groups (Group C and Group D). The differences in shape can be attributed to the diet (see discussion in Chapter 2), although diets do not vary significantly among wild pigs and wild boars' populations (Ballari and Barrios-García 2014).

Although we have not explored the effect of domestication in this study, we can make small comparisons between different morphologies that we found and with characters resulting from domestication. As already mentioned, bone growth is directly affected by the environment (Ehrlich and Lanyon 2002). Domesticated animals concerning wild-type ancestors show a reduction in the upper and lower mandible, reduction in the nasal bone (snout) and zygomatic bones, reduction in tooth size, more rounded and flatter faces, enlargement of molars and craniofacial bones (Darwin 1868; Kusatman 1991; Kruska 2005). Brain size is also reduced in most domesticated animals. In the case of domestic pigs, it is 35% smaller than expected for wild boars of the same size (Kruska 2005). Domestic pigs decreased by 20–30% dental and postcranial size over five millennia a timeframe, suggesting that wild boar might have been somewhat larger in the past than today (Price and Evin 2019). We found all these characteristics mainly in Groups D, and E. Group D is found in a region with warmer temperatures in Brazil, without regular rainfall throughout the year (except for the states of Mato Grosso and Mato Grosso do Sul), in the Cerrado and Pantanal Biomes. In the past, introductions of domestic pigs in Pantanal region (see Chapter 1), migth have influenced the current morphological characteristics of wild pigs. Knackfuss et al. (2013), attributed the low genetic differentiation and the small genetic distance to wild pigs in this region in relation to domestic specimens, by the recent process of wild pigs' feralization in the Pantanal. Group E presented animals in zoos, game reserves, or islands as St Cathelines in the USA, in different periods between the late 1800s and the 1970s. Therefore, Group E can be an effect of captivity or isolation of islands in the sample. Wild pigs on islands have different morphological characteristics than wild pigs on continents (Albarella et al. 2009). Our study has samples limited to free-living wild pigs from North America, so animals from this region need to be better evaluated compared to other groups.

Our study has a sample limitation, and one of the main reasons is the absence of invasive species in scientific collections. In Brazil, the number of specimens is so low that we had to create a collection of crania and mandibles of the wild pigs (contacting hunters, preparing the material, and depositing them in scientific collections). Another limiting factor in our study was that most samples of wild boars and wild pigs' crania and mandibles come from hunting, which affects the integrity of the structure. This led us to discard about 40% of the collected specimens because they had missing parts. Despite the sampling limitations, this is the first work that used geometric morphometrics to compare cranial structures of *Sus scrofa* from Eurasia with the wild pigs in Americas, and this has merit. We showed here that certain characteristics were maintained over time and across geographic regions (native and introduced), while others differed significantly, reflecting phenotypic plasticity in species morphology in introduced environments. Furthermore, our morphological results corroborate with the phylogenetic data found by renowned researchers, mencionated in our manuscript. We strongly recommend developing a phylogenetic and morphometric approach to confirm or refute our assertion that wild pigs' morphological differences and similarities are also related to genetics and not only to the phenotypic plasticity in the morphology of the species on the new continent.

References

Acosta D.B., Figueroa C.E., Fernández G.P., Carpinetti B.N., Merino M.L. (2019). Genetic diversity and phylogenetic relationships in feral pig populations from Argentina. *Mammalian Biology*, 99(1):27-36.

Adams D.C, Rohlf F.J., Slice D.E. (2004). Geometric morphometrics: ten years of progress following the ‘revolution’. *Italian Journal of Zoology*, 71:5-16.

Adams D.C., Otárola-Castillo E. (2013). Geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, 4(4):393-399.

Albarella U., Dobney K., Rowley-Conwy P. (2009). Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environmental Archaeology*, 14:103–136.

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

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

Baylac M., Friess M. (2005). Fourier descriptors, Procrustes superimposition and data dimensionality: An example of cranial shape analysis. In: Slice DE (ed) *Modern Morphometrics in Physical Anthropology*. Springer-Verlag, New York, pp 145-166.

Bookstein F.L. (1991). *Morphometric Tools of Landmark Data: Geometry and Biology.* London, United Kingdom. Cambridge University Press. 435p.

Bosse M., Megens H.J., Madsen O., Frantz L.A., Paudel Y., et. Al. (2014). Untangling the hybrid nature of modern pig genomes: a mosaic derived from biogeographically distinct and highly divergent *Sus scrofa* populations. *Molecular Ecology*, 23(16):4089-4102.

Brisbin I.JR., Geiger R., Graves H., Pinder J.E.III, Sweeney J.M., et al. (1977). Morphological comparisons of two populations of feral swine. *Acta Theriologica*, 22:75-85.

Clout M.N., Russell J.C. (2008). The invasion ecology of mammals: a global perspective. *Wildlife Research*, 35:180–184.

Darré R., Berlandh M., Goustat A. (1992). Statut chromosomique des populations de sangliers sauvages et d'élevages en France. *Revue de Médecine Vétérinaire*, 143:225-232.

Darwin C. (1868). *The Variation in Animals and Plants under Domestication*. John Murray, London.

Delariva L., Agostinho A. (1999). Introdução de espécies: uma síntese comentada. *Acta Scientiarum*, 21(2):255-262.

Delgado-Acevedo J., Zamorano A., DeYoung R.W., Campbell T.A. (2021). Genetic Population Structure of Wild Pigs in Southern Texas. *Animals*, 11(1): 168.

Dryden I.L., Mardia K.V. (1998). *Statistical shape analysis.* New York, NY: John Wiley & Sons, Inc. 376p.

Ehrlich P.J., Lanyon L.E. (2002). Mechanical strain and bone cell function: A review. *Osteoporosis Internation*, 13:688–700.

Evin A., Dobney K., Schafberg R., Owen J., Vidarsdottir U.S., et al. (2015). Phenotype and animal domestication: A study of dental variation between domestic, wild, captive, hybrid and insular *Sus scrofa*. *BMC Evolutionary Biology*, 15(1):1-16.

García G., Vergara J., Lombardi R. (2011). Genetic characterization and phylogeography of the wild boar *Sus scrofa* introduced into Uruguay. *Genetics and Molecular Biology*, 34(2):329-337.

Genov P.V. (1999). A review of the cranial characteristics of the Wild Boar (*Sus scrofa* Linnaeus 1758), with systematic conclusions. *Mammal Review*, 29(4):205-234.

Grossi S.F., Lui J.F., Garcia J.E., Meirelles F.V. (2006). Genetic diversity in wild (*Sus scrofa scrofa*) and domestic (*Sus scrofa domestica*) pigs and their hybrids based on polymorphism of a fragment of Dloop region in the mitochondrial DNA. *Genetics and Molecular Research*, 5(4):564-568.

Groves C. (1981). Ancestors for the pigs; taxonomy and phylogeny of the genus Sus. Department of Prehistory, Research School of Pacific Studies. *Australian Natural University Technical Bulletin*, 3:1-96.

Groves C.P. (2007). Current views on taxonomy and zoogeography of the genus Sus. *Pigs and humans*, 10:15-29.

Hernández F.A., Parker B.M., Pylant C.L., Smyser T.J., Piaggio A.J., et al. (2018). Invasion ecology of wild pigs (*Sus scrofa*) in Florida, USA: The role of humans in the expansion and colonization of an invasive wild ungulate. *Biological Invasions*, 20:1865–1880.

Herring S.W. (1972). The role of canine morphology in the evolutionary divergence of pigs and peccaries. *Journal of Mammalogy*, 53(3):500-512.

Iqbal A., Sarwar G., Khan A.M., Waseem M.T., Ahmad R.M., et al. (2020). Craniometrical Analysis of Wild Boar (*Sus scrofa*) from Northern Punjab, Pakistan. *Punjab University Journal of Zoology*, 35(1):157-165.

Knackfuss F.B., Paes R.D.C., de Menezes A.N., Herrera H.M., Piovezan U., et al. (2014). Análise filogenética entre Suínos Asselvajados no Pantanal e comerciais (*Sus scrofa*, Artiodactyla: Suidae). *Embrapa Pantanal-Artigo em periódico indexado (ALICE).*

Kusatman B. (1991). *The origins of pig domestication with particular reference to the near east*. PhD Dissertation, University College London.

Kruska D.C.T. (2005). On the evolutionary significance of encephalization in some Eutherian mammals: effects of adaptive radiation, domestication, and feralization. *Brain, Behavior and Evolution*, 65:73–108.

Larson G., Dobney K., Albarella U., Fang M., Matisoo-Smith E., et al. (2005). Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science*, 307(5715):1618-1621.

Marsan, A., Mattioli S. (2013). Il Cinghiale (in Italian). *Il Piviere (collana Fauna selvatica. Biologia e gestione).* ISBN 978-88-96348-178.

Mayer J.J., Brisbin I.L. (1988). Sex identification of *Sus scrofa* based on canine morphology. *Journal of Mammalogy*, 69(2):408-412.

Mayer J.J, Brisbin I.L. (2008). *Wild pigs in the United States: Their history, comparitive morphology, and current status*. (University of Georgia Press, 2008).

Meijaard E., d'Huart J., Oliver W.L.R. (2011). Family Suidae (Pigs). In book: *Handbook of the Mammals of the World,* Volume 2. Edition: Barcelona, Publisher: Lynx Edicions, Editors: Wilson, Mittermeier, pp. 248-291.

Mooney H.A., Cleland, E.E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, 98(10):5446-5451.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., et al. (2013). Package ‘vegan’. *Community ecology package,* 2(9):1-295.

Oliver W.L.R., Brisbin I.L. (1993) Introduced and feral pigs: problems, policy and priorities. In: Oliver WLR (ed) *Status survey and conservation action plan: pigs, peccaries and hippos*. IUCN, gland, pp 179–191.

Ottoni C., Girdland Flink L., Evin A., Geörg C., De Cupere B., et al. (2013). Pig domestication and human-mediated dispersal in western Eurasia revealed through ancient DNA and geometric morphometrics. *Molecular Biology and Evolution*, 30(4):824-832.

Owen J., Dobney K., Evin A., Cucchi T., Larson G., et al. (2014). The zooarchaeological application of quantifying cranial shape differences in wild boar and domestic pigs (*Sus scrofa*) using 3D geometric morphometrics**.** *Journal of Archaeological Science*, 43:159–67.

Paradis E., Claude J., Strimmer K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20(2):289-290.

Parés-Casanova P.M. (2013). Sexual size dimorphism in swine denies Rensch" s rule. *Asian Journal of Agriculture and Food Sciences (AJAFS)*, 1(4):112-118.

Price M.D., Evin A. (2019). Long-term morphological changes and evolving human-pig relations in the northern Fertile Crescent from 11,000 to 2000 cal. BC. *Archaeological and Anthropological Sciences*, 11(1):237-251.

R Core Team (2020). *R: A language and environment for statistical computing.* (2013). Available at: https://www.R-project.org/. Accessed in 22 February 2021.

Ripley B. D. (1996). *Pattern Recognition and Neural Networks.* Cambridge University Press.

Ripley B., Venables B., Bates D.M., Hornik K., Gebhardt A., et al. (2013). Package ‘mass’. *Cran r,* 538:113-120.

Rohlf F.J. (2013). *tpsUtil, file utility program, version 1.64.* Department of Ecology and Evolution, State University of New York at Stony Brook.

Rohlf F.J. (2015). *tpsDig, digitize landmarks and outlines, version 2.19.* Department of Ecology and Evolution, State University of New York at Stony Brook.

Sagua M.I., Figueroa C.E., Acosta D.B., Fernández G.P., Carpinetti B.N., et al. (2018). Inferring the origin and genetic diversity of the introduced wild boar (*Sus scrofa*) populations in Argentina: an approach from mitochondrial markers. *Mammal Research*, 63(4):467-476.

Schlager S., Schlager M.S. (2014). *Package ‘Rvcg’*.

Schlager S. (2017). Morpho and Rvcg–Shape Analysis in R: R-Packages for geometric morphometrics, shape analysis and surface manipulations. In *Statistical shape and deformation analysis* (pp. 217-256). Academic Press.

Šprem N., Piria M., Florijančić T., Antunović B., Dumić T., et al. (2011). Morphometrical analysis of reproduction traits for the wild boar (*Sus scrofa* L.) in Croatia. *Agriculturae Conspectus Scientificus (ACS)*, 76(3):263-265.

Susol R., Garmatyuk K., Tatsiy O. (2021). The phenomenon of sexual dimorphism in the context of rearing pigs of modern commercial breeds under conditions of the south of

Ukraine. *Scientific Papers-Animal Science Series: Lucrări Ştiinţifice - Seria Zootehnie,* 75:307-312.

Sweeney J.R., Sweeney J.M., Sweeney S.W. (2003). Feral hog. In *Wild Mammals of North. America*; Feldhamer, G., Thomson, B., Chapman, J., Eds.; Johns Hopkins University Press: Baltimore, MD, USA, pp. 1164–1179.

Tack J. (2018). *Wild Boar (Sus scrofa) populations in Europe: a scientific review of population trends and implications for management.* European Landowners' Organization, Brussels, 56 pp.

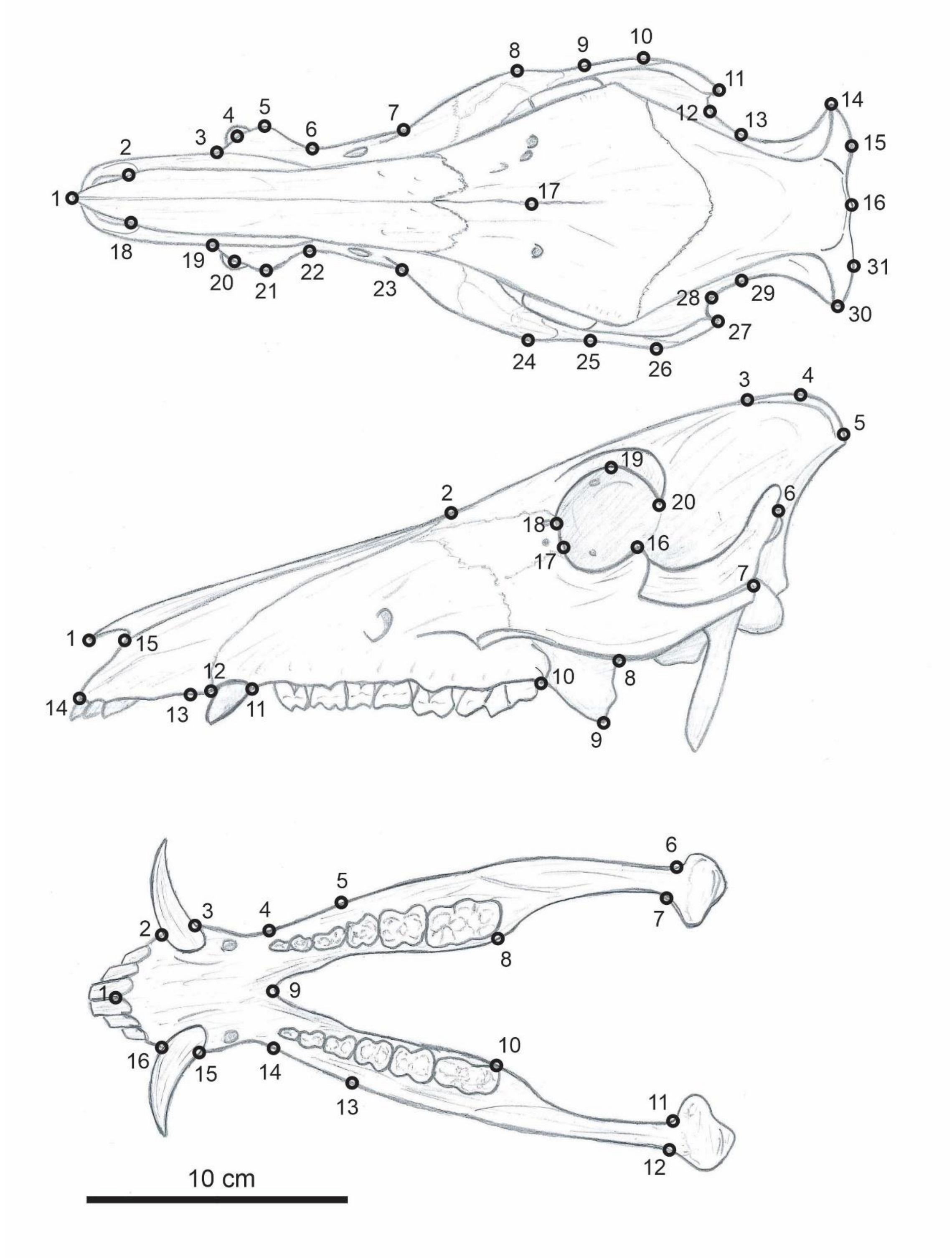
Taylor R.B. (1993). Feral hogs: history and distribution in Texas. Pages 17-27 in C.W. Hanselka and J.F. Cadenhead, eds. *Feral swine: a compendium for resource managers.* Texas Agric. Ext. Service, College Station, Texas.

Vitousek P.M., D'Antonio C.M., Loope L.L., Westbrooks R. (1996). Biological invasions as global environmental change. *American Scientist*, 84:468–478.

Zelditch M.L., Swiderski D.L., Sheets H.D., Fink W.L. (2004). *Geometric Morphometrics for Biologists: a Primer.* Elsevier Academic Press, San Diego, California, USA.

Wright S.P. (1992). Adjusted P-values for simultaneous inference. *Biometrics*, 48:1005–1013.

Supplementary material 1. Anatomical and descripton of the landmarks in the dorsal and in the left lateral view of the cranium, and in the dorsal view of the mandible.

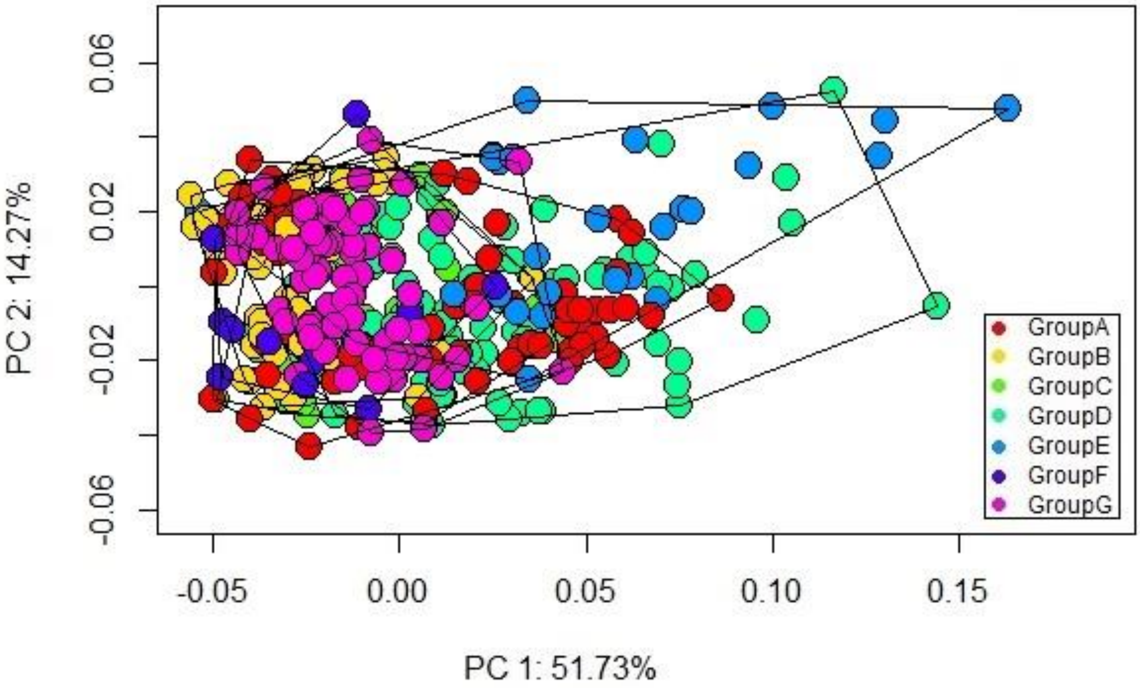


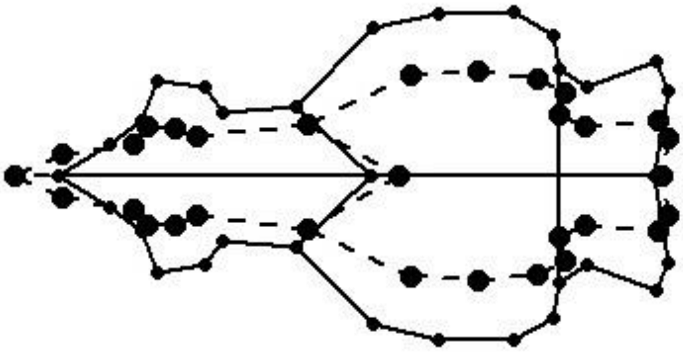
Dorsal Cranium	
Landmark	**Description**
1	Anterior extremity of rostral process of nasal bone
2 – 18	End of the curvature of the base of the rostral process of nasal bone
3 – 19	Anterior extremity of the eminentia canina
4 – 20	Lateral extremity of the anterior curvature of the eminentia canina
5 – 21	Lateral extremity of the posterior curvature of the eminentia canina
6 – 22	Posterior extremity of the eminentia canina
7 – 23	Anteriormost point of the root of zygomatic arch
8 – 24	Most lateral point in the curvatura of zygomatic arch perpendicular to the beginning of the orbital cavity
9 – 25	Most lateral point in the curvature of zygomatic arch perpendicular to the end of the orbital cavity
10 – 26	Most curvature point in the posterior portion of the zygomatic arche
11 – 27	Tip of posterior process of jugal
12 – 28	Posteriormost point of the root of zygomatic arch
13 – 29	Lateral point of the squamous bar straight
14 – 30	Most lateral point of the extremity of paraoccipital apophysis
15 – 31	End of curvature of paraoccipital apophysis
16	End point of the nuchal crest

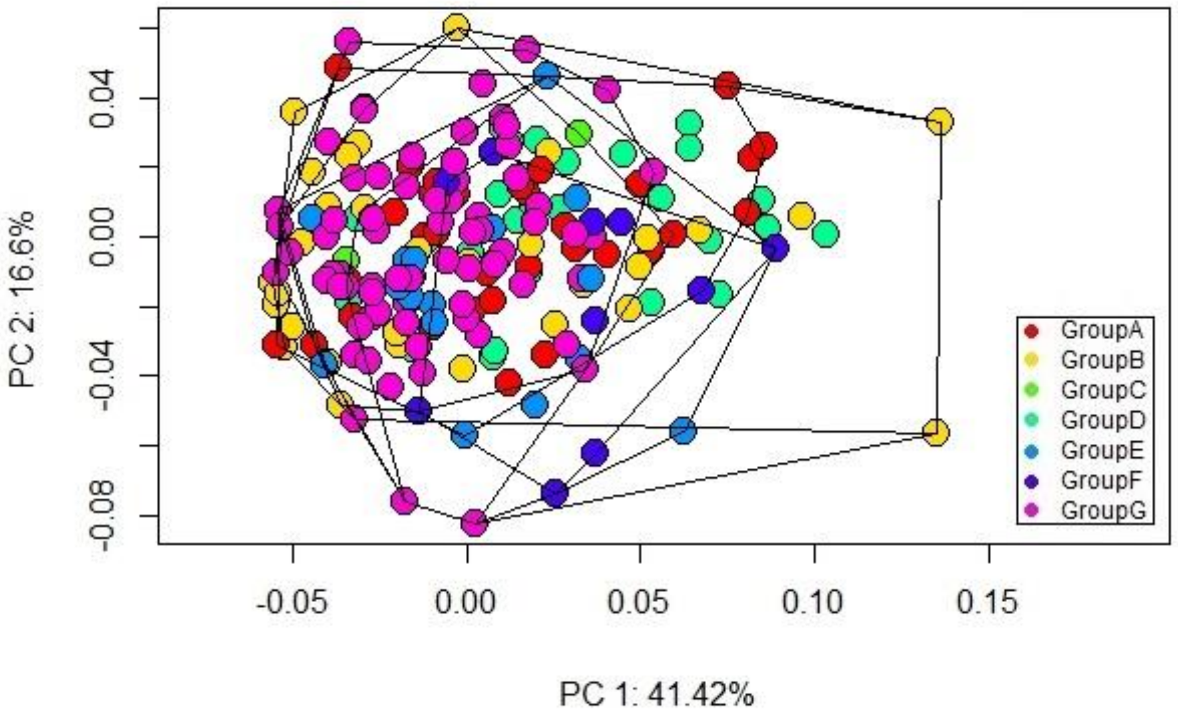
Lateral Cranium	
Landmark	**Description**
1	Anterior extremity of rostral process of nasal bone
2	Uppermost point in the nasal bone perpendicular to the root of the zygomatic arch
3	Midpoint of the temporal line
4	Point of greatest curvature of the temporal line
5	Most posterior point of the temporal line
6	Most posterior point of curvature of the ascending ramus of the zygomatic processo of the jugal bone
7	End point of the posterior jugal process
8	Midpoint of the lower curvature of the zygomatic arch
9	Posterior end of the pterygoid process
10	Posterior extremity of III molar alveolus
11	Posterior point of the canine alveolus in th eminentia canina
12	Anterior point of the canine alveolus in th eminentia canina
13	Posterior point of the III incisive alveolus
14	Anterior extremity of the premaxilla bone
15	Anteriormost point of the suture between nasal and premaxillar
16	Extremity of superior jugal process
17	Posterior suture point between jugal and lacrimal at the edge of the orbital cavity
18	Posterior suture point between lacrimal and frontal at the edge of the orbital cavity
19	Highest point on the edge of the orbital cavity
20	Tip of the post-orbital process of the frontal bone

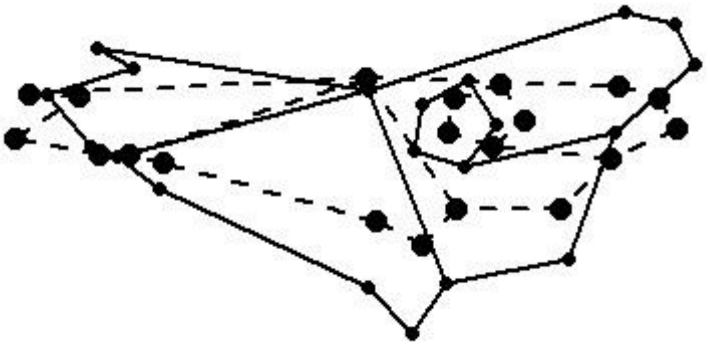
Dorsal Mandible	
Landmark	**Description**
1	Most anterior point of the mandibular symphysis
2 – 16	Anterior point of the canine alveolus
3 – 15	Most lateral point of the labial portion of the canine alveolus
4 – 14	Outermost point on the labial portion perpendicular to the beginning of the II premolar
5 – 13	Outermost point on the labial portion perpendicular to the beginning of the I molar
8 – 10	Outermost point on the labial lingual perpendicular to the beginning of the I molar
6 – 12	Point of contact between the ascending ramus and the mandibular condyle in the labial portion
7 – 11	Point of contact between the ascending ramus and the mandibular condyle in the lingual portion
9	Most posterior point of the mandibular symphysis

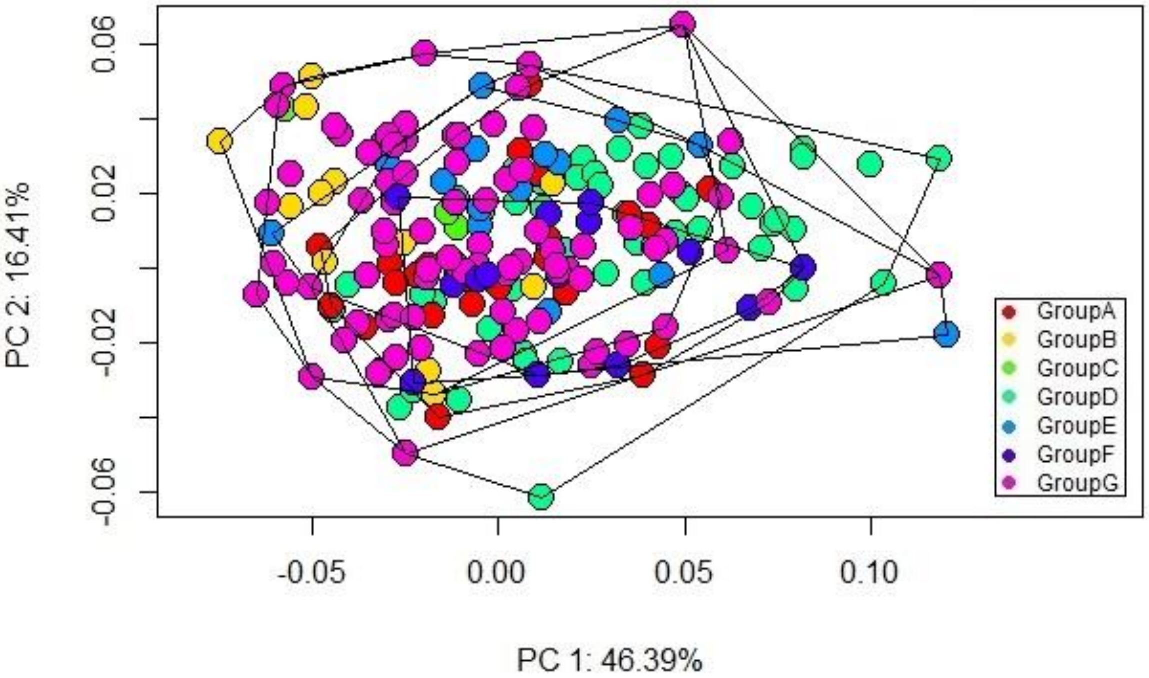
Supplementary material 2. PCA Analysis of the dorsal and in the left lateral view of the cranium, and of the dorsal view of the mandible, respectively.

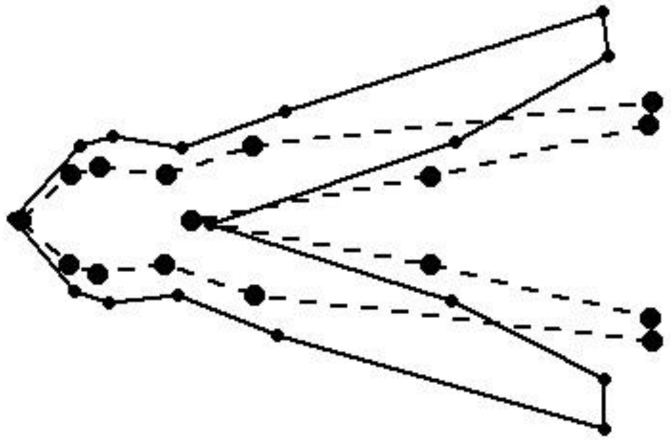





PC 2: 16.6%
0.04
0.00
-0.04
-0.08
-0.05
0.00
0.05
0.10
0.15
PC 1: 41.42%
GroupA
GroupB
GroupC
GroupD
GroupE
GroupF
GroupG




PC 2: 16.41%
0.06
0.02
-0.02
-0.06
-0.05
0.00
0.05
0.10
PC 1: 46.39%
GroupA
GroupB
GroupC
GroupD
GroupE
GroupF
GroupG



Terminators of the future: Controlling population growth of the wild pigs (*Sus scrofa* L.)

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ABSTRACT

The control and eradication of invasive species population represent a major ecological concern. In Brazil, wild pigs have negative environmental and economic impacts. We aimed to develop models of sex-based hunting scenarios using population viability analysis (PVA) to support the planning of long-term wild pigs' population reduction. Based on biological data gathered in a literature review, we created models for future scenarios focused on the hunting of each sex in which hunting pressure was increased by 5%, 10%, 30%, 50%, or 70%. Current (baseline) and male-based hunting models did not affect long-term population trends. Increased hunting pressure on females was shown to reduce the population growth of wild pigs over time significantly. The dramatic effect of hunting females on wild pigs' population control may reflect the species' reproductive biology. In conclusion, current and male-biased hunting strategies are not expected to achieve effective wild pigs' population control, whereas management directed at the hunting of females can yield efficient wild pigs population control in Brazil. These findings provide a novel perspective on wild pigs' management.

Keywords: Artiodactyla, Brazil, feral pigs, invasive species, population viability analysis (PVA), Neotropics, wild boar, wildlife management.

Introduction

Invasive species represent a major conservation threat and have caused the extinction of many native species (Simberloff 2009). Biological invasions occur when nonnative species are introduced accidentally or intentionally for economic, scientific, and social reasons (Simberloff 2010). Hence, a significant concern for wildlife conservation is the control and eradication of alien's populations (Simberloff et al. 2013). The consequences for local environments of such invasions are frequently unknown (Mack et al. 2000). An introduced species may have insignificant effects on native species and ecosystems in one region but a devastating impact elsewhere (Simberloff 2010).

Shooting and trapping are methods commonly used to manage invasive animal species, although they are controversial (see Simberloff 2002; Orueta 2003; Simberloff et al. 2005; Rosa et al. 2018; Carvalho et al. 2019). In some countries, controlled hunting has been applied as a wildlife management tool to control invasive species population (Bieber and Ruf 2005; Rosa et al. 2018) and consequently, ultimately, can enhance threatened wildlife populations (Heffelfinger et al. 2013). For example, live-trapping (e.g., with box and corral traps) has been used to complement wild pigs hunting for population control and is considered adequate (Rosa et al. 2018).

The wild pigs (*Sus scrofa* L.), produced by breeding of wild boars (*Sus scrofa* L.) with domestic pigs (*Sus scrofa domesticus* Erxleben), is an ecologically crucial invasive suid that has been introduced in many regions (Keiter et al. 2016; Melletti and Meijaard 2017). The wild pigs are habit generalists (Mayer and Brisbin 2009; West et al. 2009) who adapt efficiently to new environments (Sales et al. 2017). Nowadays, it can be found worldwide (Barrios-García and Ballari 2012) and is considered one of the 100 most invasive species (Lowe et al. 2000; IUCN 2019). Wild pigs can cause negative impacts on ecosystems and their ecological processes by affecting negatively native species and causing economic damage, such as loss of crops and domestic animals (Oliver and Brisbin 1993; Massei and Genov 2004; Barrios-García and Ballari 2012; Hegel and Marini 2013; Myrphy et al. 2014; Hegel et al. 2019a, 2019b). Furthermore, wild pigs can also carry and transmit diseases to other animals (Rosell et al. 2001).

Currently, wild pigs live throughout most of Brazil (Pedrosa et al. 2015). Hegel and Marini (2013) verified that they undertake intense herbivory, rooting, and soil turning in the

Atlantic Forest, where they exhibit a random pattern of the landscape occupation (Hegel et al. 2019a). They also have adverse effects on the detection and occupancy of native mammalian species (Hegel et al. 2019b). Wild pigs' population is controlled, to some extent, through the predation of piglets and juveniles by pumas (*Puma concolor*) and possibly jaguars (*Panthera onca*) (Hegel and Marini 2018). However, both species are threatened in Brazil indicating a small population where they are still occurring (Jędrzejewski et al. 2018) in low densities (see Finnegan et al. 2021). Another method of control applied is through hunting permitted by the Brazilian government (IBAMA 201, 2019). However, wild pigs' population densities in Brazil are not well known, with estimates ranging widely from 0.22 to 22.3 individuals/km² in the South and Southeastern regions of the country (Oliveira 2012; Puertas 2015). Nevertheless, the increase of the wild pigs' population is evident in Brazil, indicating that current control techniques are insufficient. Information on the biology and behavior of the wild pigs in introduced areas is mainly lacking. There has been inadequate attention given to the long-term conservation and maintenance of the population of native species in wild pigs invaded areas.

Population viability analysis (PVA) scenarios have been used to guide strategies to maintain viable populations, and thus preventing extinction, of a species of interest over time (Gilpin and Soulé 1986; Thompson 1991; Lacy 1993, 2000; Beissinger and McCullough 2002). In PVA, the likelihood of future events is predicted based on currently available data, containing some uncertainty (Shaffer 1990). Traditionally, PVA results are used to develop potential management scenarios and action plans for conserving native species (Beissinger and McCullough 2002). However, in invasive species, the method can be applied for an alternate aim of conservation wherein extinction is a desirable outcome to solve an invasion problem (Andersen 2005). The wild pigs are an excellent model for such an analysis.

The present study aimed to develop models of sex-based hunting scenarios using population viability analysis (PVA) for supporting the planning of long-term wild pigs' population reduction. Based on the reproductive biology of the wild pigs, we expect that a female-focused hunting strategy may improve the effects of population control measures. By increasing hunting pressure on particular groups, we hope to achieve a future scenario projection wherein it is feasible to stabilize the population growth of wild pigs in Brazil.

Methods

Study area

Brazil is the largest country in South America with 8,510,346 km² and has six biomes: Amazon, Atlantic Forest, Cerrado, Caatinga, Pampa, and Pantanal (IBGE 2021). It is limited to the east by the Atlantic Ocean and land frontiers with Uruguay to the south; Argentina and Paraguay to the southwest; Bolivia and Peru to the west; Colombia to the northwest and Venezuela, Suriname, Guyana, and French Guiana to the north. According to the climatic classification of Köppen-Geiger, Brazil is found in equatorial, tropical, semiarid, tropical altitude, temperate and subtropical distributed according to the relief of the region (Peel et al. 2007). In these regions, tropical forests to the most desert and driest areas can be found, such as the Caatinga (Morrone 2014). Temperatures in Brazil range from 30 °C to below 0 °C depending on climatic region, and rainfall is plentiful, except in central Brazil, where they are seasonal.

Data collection

For constructing the baseline population model, we gathered biological data on wild pigs from the literature. We focused our data collection on literature related to invasive wild pigs in the Neotropical region so that our PVA would represent the circumstances in Brazil. We used North American and European literature when information for South America was absent. Nevertheless, wild pigs' life history information is scarce, therefore we employed population dynamics parameters based on the life history of native wild boars (Table 1). The only data available on wild pigs' mortality rates are those provided by IBAMA-regulated hunters, who submit reports periodically with the numbers of harvested individuals and the sex, age, size, and location of capture of each hunted animal. However, the actual mortality rate of the species is likely to be much higher because of illegal poaching and the fact that some hunters (personal communication) neglect to report all captured animals to avoid bureaucratic requirements.

Table 1. Life history and input parameters used to model the viability of the Brazilian population of wild pigs.

Parameters		Base value	Source
Reproductive system		Polygynous	Rosell et al. 2001
Age of first offspring (female)		1	Barrett 1978, Rosell et al. 2001
Age of first offspring (male)		2	Barrett 1978, Rosell et al. 2001
Maximum lifespan (years)		13	Rosell et al. 2001
Maximum age of female reproduction		13	Rosell et al. 2001
Maximum age of male reproduction		13	Rosell et al. 2001
Maximum number of broods per year		2	Gethoffer et al. 2007, Mendina-Filho et al. 2015
Maximum number of progenies per brood		7	Barrett 1978, Mendina-Filho et al. 2015
Sex ratio at birth		1:1	Gerard et al. 1991, Rosell et al. 2001
% Adult females breeding	**< = 2 years**	50	Gethoffer et al. 2007
	> 2 years	75	Gethoffer et al. 2007
% Males in breeding pool		50	Rosell et al. 2001

We could not use harvesting information from Brazil due to the absence of other population dynamics data, such as population size, to estimate the mortality rate. We used mortality data from a PVA work published by Gonzalez-Crespo et al. (2018) to construct scenarios and mortality parameters (Table 2). Then we defined hypothetical population thresholds to establish carrying capacities (K value). Because the species adapts easily to new areas, can achieve high reproductive rates, and has low mortality in the absence of natural predators (West et al. 2009; Heise-Pavlov et al. 2009), we believe that each wild pig population will tend to approach its carrying capacity, being limited only by environmental and hunting factors, until an equilibrium is reached. Due to the scarcity of population research examining wild pigs in Brazil, their population demographic rates have not been established. Therefore, we created scenarios to simulate population trends over time, with the same initial number of individuals in the same threshold carrying capacities (K value) under the different capacity of harvest pressures in males and females. The parameters and sources used are presented in Table 1.

Table 2. Mortality parameter values inputted for each scenario in the PVA of the wild pigs' population in Brazil (sd =10).

Parameter	**Age**	**Model**										
		Baseline	**Female 5%**	**Female 10%**	**Female 30%**	**Female 50%**	**Female 70%**	**Male 5%**	**Male 10%**	**Male 30%**	**Male 15%**	**Male 70%**
Mortality of females as %	< 1 year	29	29	29	29	29	29	29	29	29	29	29
	1–2 years	35	35	35	35	35	35	35	35	35	35	35
	> 2 years	39	41	43	51	59	66	39	39	39	39	39
Mortality of males as %	< 1 year	30	30	30	30	30	30	30	30	30	30	30
	1–2 years	43	43	43	43	43	43	43	43	43	43	43
	> 2 years	35	35	35	35	35	35	37	39	46	53	60

Description of the history life

Wild pigs presented a polygynous reproductive system (Rosell et al. 2001) with a matriarchal social organization formed by an alpha female, other related females, and young males (Dardallion 1988; Mendina-Filho et al. 2015). Females generally start their reproductive age in the first year of life, while males start at two years (Barrett 1978; Bieber and Ruf 2005). However, in introduced areas, wild pigs' reproduction begins at 6 months for females and 10 months for males (Mendina-Filho et al. 2015). In wild condition they can survive from 10 to 13 years, as well as reproduce up to this maximum lifespan (Massei 1996; Rosell et al. 2001; Marsan and Mattioli 2013; Mendina-Filho et al. 2015). Thus, all juvenile and adult females in the flock are capable of reproducing, however, only 50 to 75% reproduce in a breeding season (Bieber and Ruf 2005; Gethoffer et al. 2007). The younger females (up to 1 year and half) and older adult females (from 7 or 8 years old) may not reproduce, and they help in the care of the offspring of other females' increasing reproductive success (Jezierski 1977; Massei et al. 1996). Females can breed up to 2 times per year (Taylor et al. 1998, Mendina-Filho et al. 2015), and unlike in native areas, wild pigs can have up to 12 to 14 offspring in a single litter (Taylor et al. 1998; Bieber and Ruf 2005; Mendina-Filho et al. 2015). The reproductive success and the size of the litter are dependent on the conditions of the environment and food resources (Rosell et al. 2001). As for males, only the alpha male reproduces with the females of the group. The alpha male usually has solitary habits and return to their pack in the reproductive period (Dardallion 1988). Young males leave the group around two years old to form their groups (Rosell et al. 2001, Bieber and Ruf 2005, Gethoffer et al. 2007, Mendina-Filho et al. 2015). Mortality rates are higher in piglets and are highly dependent on environmental factors, usually related to hypothermia, disease, and predation (Jezierski 1977, Massei et al. 1997, Rossel et al. 2001). Juveniles and adults have minor mortality rates, mainly due to hunting (Jezierski 1977, Mendina-Filho et al. 2015).

Sensitivity Analysis

Initially, we did a Sensitivity Analysis to evaluate the impact of the parameters on the models based on different harvest pressures in males and females. For this, we tested the following parameters for sensitivity: 1) number of reproductive females, 2) the number of offspring per gestation, and 3) male mortality rate and female mortality rate. We used estimated minimum and maximum for 200 years projection (Table 3).

Table 3. Parameters used to Sensitivity Analysis to evaluate the impact on the models.

Parameters	Minimum	Maximum	Source
Number of reproductive females (%)	50	100	Bieber and Ruf 2005, Gethoffer et al. 2007
Number of offspring per gestation	3	12	Taylor et al. 1998, Bieber and Ruf 2005, Mendina-Filho et al. 2015
Female mortality rate (%)	25	50	IBAMA (2018), SIMAF/IBAMA (2020)
Male mortality rate (%)	27	72	IBAMA (2018), SIMAF/IBAMA (2020)

Population Viability Analysis

We simulated the wild pigs' extinction risk in VORTEX software (version 10.3.6.0, Lacy and Pollak 2015). We set the duration of each simulation to 200 years and obtained two main results for each model: genetic diversity and probability of extinction. To assess the effort required, we modeled scenarios following a hypothetical population of 3000 individuals of the wild pigs in the threshold carrying capacities (K value) of 3000 individuals, under different capacity harvest pressures in males and females.

We made five models for scenarios to determine the impact of different harvest rates (an increase in harvesting on 5%, 10%, 30%, 50%, and 70%) on each target sex and the baseline model, yielding 11 models (Table 2). We present all biological data obtained from the literature for the baseline scenario and then extrapolated values for subsequent scenarios in Table 5.

Results

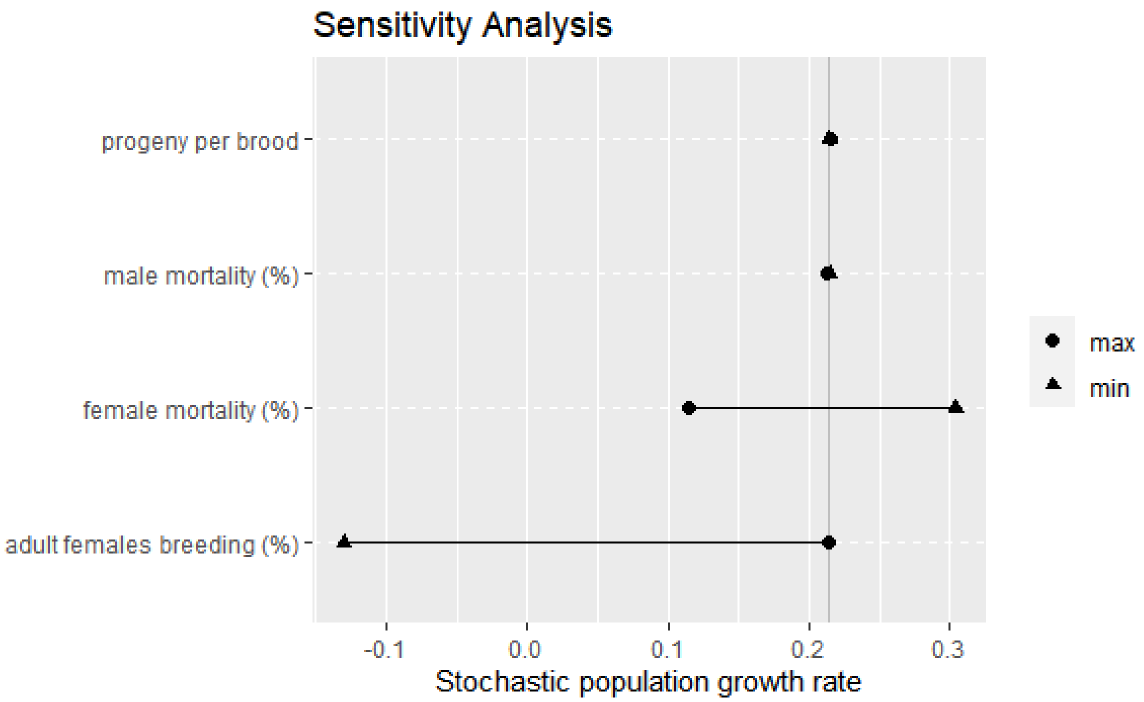
Sensitivity Analysis

Sensitivity analysis helped explore uncertainties in estimating parameters and showed that the parameters 'number of reproductive females' and 'female mortality rate' were sensitive to the models. The parameters 'number of offspring per gestation', and 'male mortality rate' were not sensitive to the models (Table 4, Figure 1)**.**

Table 4. Results of Sensitivity Analysis. Abbreviations: Det-r, deterministic growth rate; Stoch-r, stochastic growth rate; PE, probability of extinction; N-extant, mean ending population size of interactions that do not go extinct; N-all, total number of individuals in the population; GeneDiv, genetic diversity.

Scenario	Det-r	Stoch-r	PE	N-extant	N-all	GeneDiv
Baseline	0.2339	0.2139	0	2964.43	2964.43	0.9676
offspring_min	0.2339	0.2143	0	2957.9	2957.9	0.9671
offspring_max	0.2339	0.2161	0	2954.3	2954.3	0.9675
reproductive_min	-0.107	-0.1342	1	0	0	0
reproductive_max	0.2339	0.2139	0	2964.43	2964.43	0.9676
Male_mortality_min	0.2339	0.2155	0	2978.28	2978.28	0.9703
Male_mortality_max	0.2339	0.212	0	2958.28	2958.28	0.9576
Female_ mortality_min	0.3194	0.304	0	2992.07	2992.07	0.966
Female_mortality_max	0.1417	0.1145	0	2762.57	2762.57	0.9673

Figure 1. Sensitivity Analysis of the parameters: number of reproductive females, the number of offspring per gestation, and male mortality rate and female mortality rate; on the models for 50 years.



Models

According to the models (Table 5, Figure 2) there is a positive growth control of the wild pigs' population as expected for the biological potential of species. Compared to the stochastic growth rates calculated for our baseline and male-targeting models (both model types, rstoch = 0.22) the female removal models predicted stochastic growth rates that were reduced for all models. The female models with 50% and 70% of increase yielded negative stochastic growth rates (respectively, rstoch =-0.01 and rstoch =-0.11) which was lower than 5% (rstoch = 0.20), 10% (rstoch = 0.19) and 30% (rstoch = 0.11). The male-targeting and baseline models yielded equal deterministic growth rates (rdet = 0.23), whereas the female-targeting models had a markedly lower deterministic growth rate for the 5% (rdet = 0.22), 10% (rdet = 0.20), 30% (rdet = 0.13), 50% (rdet = 0.03) and 70% (rdet = -0.12) harvest scenario (Table 5).

Females selective harvesting resulted in controlled population growth in our projection models with a baseline population of 3000 individuals (Figure 2). Our results indicated that the predicted final population sizes above 50% increase in female mortality were the ideal for controlling the invasion. However, the final population size with 5%, 10%, and 30% of female-harvesting does not reach extinction probability. The final population size was smaller than was achieved with male harvesting and baseline models. Final population sizes were shown to be reduced in our female harvesting models (Figure 2). The 200-years population growth results were nearly identical for the baseline and male-based models, with values near the K value in each model (Table 5). Only the models in which female mortality was increased by 50% and 70% showed a probability of wild pigs' extinction (respectively 4% and 100%) (Table 5).

Table 5. Results of population viability for the wild pigs in Brazil. Values with considerable reductions in population size and PE in each model are in bold. Abbreviations: Det-r, deterministic growth rate; Stoch-r, stochastic growth rate; PE, probability of extinction; N-extant, mean ending population size of interactions that do not go extinct; N-all, total number of individuals in the population; GeneDiv, genetic diversity.

Scenario	Det-r	Stoch-r	PE	N-extant	N-all	GeneDiv
Baseline	0.2339	0.2163	0	2968.27	2968.27	0.9686
Female 5%	0.2193	0.2004	0	2967.67	2967.67	0.9684
Female 10%	0.2039	0.1834	0	2914.56	2914.56	0.9677
Female 30%	0.1315	0.1068	0	2784.57	2784.57	0.968
Female 50%	**0.0275**	**-0.0058**	**0.45**	**1001.07**	**550.6**	**0.8473**
Female 70%	**-0.1193**	**-0.1097**	**1**	**0**	**0**	**0**
Male 5%	0.2339	0.2158	0	2965.21	2965.21	0.9659
Male 10%	0.2339	0.2158	0	2965.94	2965.94	0.9661
Male 30%	0.2339	0.2157	0	2954.04	2954.04	0.9642
Male 50%	0.2339	0.2173	0	2971.84	2971.84	0.9623
Male 70%	0.2339	0.2151	0	2929.57	2929.57	0.9599

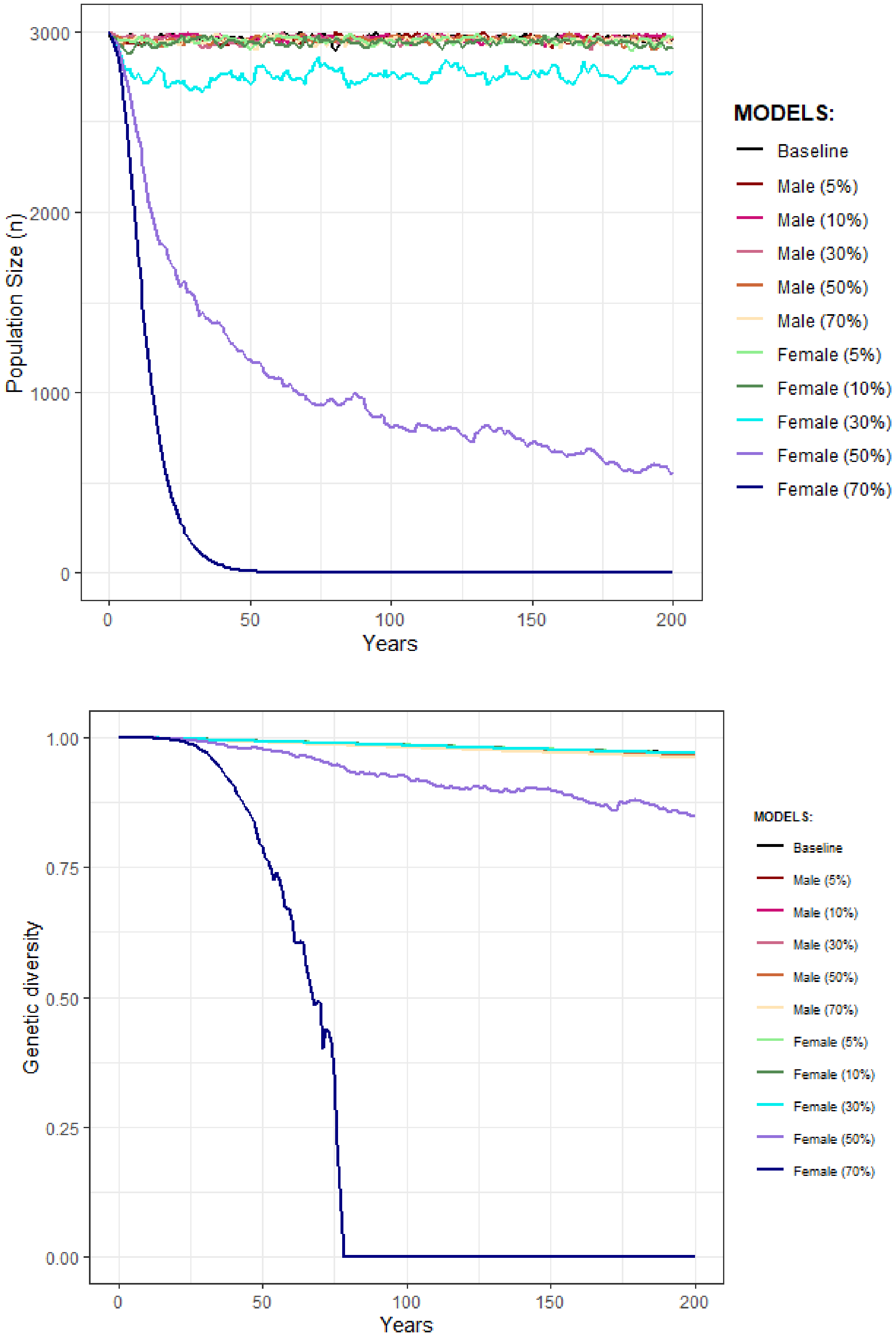


Figure 2. Projections of 200-years wild pig population size and genetic diversity trends in scenarios of sex-based harvesting of population control without inbreeding depression.

Discussion

We present a new approach for effective wild pigs' population control planning based on PVA. We found that increasing harvesting pressure on male wild pigs is ineffective as controlling strategy in the assumption scenarios analyzed. Conversely, our simulations indicated that more significant harvesting pressure on females could be used to at least stabilize the population and perhaps, ultimately, lead to extinction over time in some models. Our results corroborate the findings of other studies indicating that adult female mortality-based models reduce population growth rates, including the findings of Bieber and Ruf (2005), who examined increased harvesting pressure on female wild pigs. Also, in California, modeling showed that population control of wild pigs would require that >70% of individuals be harvested annually, with the targeting of juveniles and adult females (at least 50%) being the most effective interventions (White and Kunkel 2016). In Europe, selective removal of juveniles (<1 year) and yearlings (1–2 years) was reported to be an effective wild boars' population control strategy, particularly with the removal of females given that they have high fecundity across a broad age range (Gonzalez-Crespo et al. 2018).

Compared to other ungulates, wild pigs have a relatively high female fecundity (Fernandez-Llario and Mateos-Quesada 1998). Although post-pubescent males can reproduce with many females, females have the most substantial impact on population growth. Considering that mature female can be expected to produce two litters each year of 6–10 piglets per litter (Long 2003; Taylor et al. 1998), each female can be estimated to produce 12–20 new offspring each year. Assuming a 1:1 sex ratio (Gerard et al. 1991; Rosell et al. 2001), we would have each of 3–5 new females in each successive breeding generation generating 12–20 new offspring per year for up to 13 years, with the potential to produce some 156-260 progeny each over a lifetime. Given the high reproductive potential of the species (Heise-Pavlov et al. 2009), in which up to 90% of adult female wild pigs may reproduce within a single reproductive season (Massei et al. 1996), female reproduction and juvenile survival can be considered significant determinants of wild pigs' population growth (Pepin et al. 2017; Tabak et al. 2018).

Although some juvenile mortality can be expected (~3.5 piglets/female, up to 85%) due to hypothermia, disease, predation, and harvesting (Saunders 1993; Rosell et al. 2001), young females provide piglet care support to breeding females, increasing the piglets' chances of survival (Barrett 1978). Wild pigs have a matriarchal organization centered around adult female groups and their offspring. Males leave their maternal groups at 2-3 years of age, while females either remain with their mothers or relatives for life or establish new territories nearby (Kaminski et al. 2005; Marsan and Mattioli 2013). Sub-adult males and solitary adult males join and return to a group when females enter heat (Barrett 1978; West et al. 2009; Mendina-Filho et al. 2015). When they leave a group, males and females tend to form new groups close to their birthplace; thus, reproduction among related individuals is common for wild pigs (Truvé and Lemel 2003; Poteaux et al. 2009).

The reproductive behavior of wild pigs among relatives can lead to inbreeding depression. The effects of inbreeding vary among species and in populations within species (Thornhill 1993). Although Brazilian pigs' breeds exhibit genetic variability (Sollero et al. 2009), the genetic structure of wild pigs' population in Brazil is unknown, and inbreeding depression must be considered. Inbreeding depression was detected in a specific region containing genes associated with litter size in isolated populations of Guadyerbas Iberian pigs (Saura et al. 2015). In two populations of Austrian pigs, inbreeding was found to have a significant adverse effect on reproductive traits, whereas litter inbreeding reduced the number of total piglets produced and the number of live-borne piglets (Köck et al. 2009). In another study, the formation of regions of homozygosity was influenced mainly by past demographic events and local recombination rates, implying the occurrence of inbreeding and an influence on the fitness of individuals in populations (Bosse et al. 2012). Therefore, considering the inbreeding depression of wild pigs, the application of our harvest scenarios may provide a good strategy for solving wild pig problems in Brazil. Specifically, our results indicate that increasing female wild pigs' harvesting can reduce population growth rates, reduce genetic diversity due to inbreeding, and increase the probability of extinction due to intensifications in the expression of mutations and deleterious recessive alleles in the population (Kristensen and Sorensen 2005). Furthermore, our 200-year simulation from a 70% increase in female hunting pressure. An assumption of an otherwise stable wild pigs' population showed that inbreeding depression could help bring the wild pigs' population to extinction.

Harvesting is an important wild pigs' management and control tool in many countries (Nores et al. 2008; Tsachalidis and Hadjisterkotis 2008; Acevedo et al. 2009; Heffelfinger et al. 2013; Massei et al. 2015; Rosa et al. 2018). However, the intensity of the harvesting pressure needed to be applied for effectiveness is location dependent. In the Brazilian Pantanal, the current traditional harvest levels appear insufficient to regulate the wild pigs' population. However, when the wild pigs' harvest rate increases beyond 35%, declines in population growth may be achieved, leading to extinction if there is no recolonization from neighboring populations (Desbiez et al. 2009). Similarly, annual wild pigs culling intensities in the range of 20–60% have been reported to lead to a population decline of ~20% over four years; without immigration, 50–100% declines were observed over four years (Pepin et al. 2017). Similar previous analyses of hunter harvest data in Queensland, Australia (open to immigration) showed that sustained 20% annual harvest rates could reduce abundance by 30% over four years (Gentle and Pople 2013).

Incentivizing harvesting can be controversial and polarizing (Carvalho et al. 2019). A combined species management and population control method can be used for pest species, as outlined in the National Wild Pig Control Plan (PAN Wild Pig) (Brasil 2017). However, the success of control programs depends on the enactment of rigorous monitoring programs alongside management to enable resource allocation and strategy planning to be responsive to population reductions (Cruz et al. 2005; McCann and Garcelon 2008). Thus, to achieve wild pigs' population control, enforcement agencies must be involved with harvesting groups to prevent the recreational harvesting of native wildlife (Carvalho et al. 2019).

Male wild pigs have been a primary harvesting target (a "trophy") owing to their solitary behavior and their large body size and tusks (personal communication with hunters). According to the latest wild pigs' control informative bulletin in Brazil, 72% of harvested animals were male, and only 28% were reported to be female (SIMAF/IBAMA 2020). However, this strategy is inefficient for reducing the population. Our PVA findings indicate that current harvesting practices cannot achieve wild pigs' population control and can provide essential information to guide hunters. Our findings offer a novel perspective on wild pigs' management. Specifically, our findings indicate that effective management of wild pigs will require targeted harvesting of females, which increases by at least 5%. Dialogue between hunters and government agencies, such as IBAMA will be essential to achieving population control objectives while minimizing the harvesting of native species. A form of incentive to hunters for the targeted control of females could be to facilitate the renewal of the hunting license with the government agencies when a large number harvesting of females.

Management implications

Our study has several limitations, related mainly to the lack of population density and local population biology data. Extrapolations of densities may vary among regions and do not reflect the actual numbers of existing wild pigs. Likewise, the mortality data used in our models were reported by hunters and unlikely to correspond entirely with reality. These limitations notwithstanding, this study is the first wild pigs' PVA study in Brazil in which harvesting was targeted based on sex, and the results can be considered a reliable application. We would recommend a wild pigs population control program that applies the results of our models by considering female-focused harvesting to stabilize and suppress the wild pigs' population in Brazil as soon as possible. Future research based on annual data from new harvesting and population density reports may extend this study, updating the panorama of the country's wild pigs' problem. New research on the biological attributes of local species may contribute to estimates more accurate.

References

Acevedo P., Vicente J., Alzaga V., Gortázar C. (2009). Wild boar abundance and hunting effectiveness in Atlantic Spain: environmental constraints. *Galemys*, 21:13-29.

Andersen M.C. (2005). Potential applications of population viability analysis to risk assessment for invasive species. *Human and Ecological Risk Assessment*, 11:1083-1095.

Barrett R.H. (1978). The feral hog at Dye Creek ranch, California. *Hilgardia*, 46:283-355.

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

Beissinger S.R., McCullough D.R. (2002). *Population Viability Analysis.* Chicago, IL: University of Chicago Press.

Bieber C., Ruf T. (2005). Population dynamics in wild boar *Sus scrofa:* ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology*, 42:1203–1213.

Bosse M., Megens H.J., Madsen O., Paudel Y., Frantz L.A., et al. (2012). Regions of homozygosity in the porcine genome: consequence of demography and the recombination landscape. *PLoS genetics*, 8(11):e1003100.

Brasil. (2017). *Plano Nacional de Prevenção, Controle e Monitoramento do Javali (Sus scrofa) no Brasil.* Ministério do Meio Ambiente (MMA) & Ministério da Agricultura, Pecuária e Abastecimento (MAPA). Brasília, Brasil.

Carvalho W.D., Mustin K., Paulino J.S., Adania C.H., Rosalino L.M. (2019). Recreational hunting and the use of non-selective traps for population control of feral pigs in Brazil. *Biodiversity and Conservation*, 28:1-6.

Cruz F., Donlan C.J., Campbell K., Carrion V. (2005). Conservation action in the Galapagos: feral pig (*Sus scrofa*) eradication from Santiago Island. *Biological Conservation*, 121:473–478.

Dardallion M. (1988). Wild boar social groupings and their seasonal changes in the Camargue, southern France. *Zeitschrift Fur Säugetierkunde,* 53:22–30.

Desbiez A.L.J., Keuroghlian A., Piovezan U., Bodmer R.E. (2009). *Population ecology of feral pigs in the Brazilian Pantanal.* Corumbá: Embrapa Pantanal. 106:44p.

Fernandez-Llario P., Mateos-Quesada P. (2003). Population structure of the wild boar (*Sus scrofa*) in two Mediterranean habitats in the western Iberian Peninsula. *Folia Zoologica – Praha*, 52:143-148.

Finnega, S.P., Galvez-Bravo L., Silveira L., Tôrres N.M., Jácomo A.A., et al. (2021). Reserve size, dispersal and population viability in wide ranging carnivores: the case of jaguars in Emas National Park, Brazil. *Animal Conservation*, 24(1):3-14.

Gentle M., Pople A. (2013). Effectiveness of commercial harvesting in controlling feral-pig populations. *Wildlife Research*, 40:459–469.

Gerard J.F., Cargnelutti B., Spitz F., Valet G., Sardin T. (1991). Habitat use of wild boar in a French agroecosystem from late winter to early summer. Acta *Theriologica*, 36:119-129.

Gethoffer F., Sodekeit G., Pohlmayer K. (2007). Reproductive parameters of wild boar (*Sus scrofa*) in three different parts of Germany. *European Journal of Wildlife Research*, 53:287–297.

Gilpin M.E., Soulé M.E. (1986). Minimum viable populations: processes of species extinction. Pages 125-139 *in Conservation biology: the science of scarcity and diversity*. Soulé, M.E. (Ed.). Massachusetts: Sinauer, Sunderland.

González-Crespo C., Serrano E., Cahill S., Castillo-Contreras R., Cabañeros L., et al. (2018). Stochastic assessment of management strategies for a Mediterranean peri-urban wild boar population. *PloS one*, 13(8):e0202289.

Heffelfinger J.R., Geist V., Wishart W. (2013). The role of hunting in North American wildlife conservation. *International Journal of Environmental Studies*, 70:399-413.

Hegel C.G.Z, Marini M.Â. (2013). Impact of the wild boar, *Sus scrofa*, on a fragment of Brazilian Atlantic Forest. *Neotropical Biology* and *Conservation,* 8:17–24.

Hegel C.G.Z, Marini M.Â. (2018). Large felids as predators of wild boar in the Atlantic Forest: reconciling Verdade et al. and Rosa et al. *Animal Conservation*, 21:363–364.

Hegel C.G.Z., Santos L.R., Pichorim M., Marini M.Â. (2019a). Wild pig (*Sus scrofa* L.) occupancy patterns in the Brazilian Atlantic forest. *Biota Neotropica,* 19: e20180719.

Hegel C.G.Z., Santos L.R., Marinho J.R., Marini M.Â. (2019b). Is the wild pig the real "big bad wolf"? Negative effects of wild pig on Atlantic Forest mammals. *Biological Invasions,* 21:3561-3574.

Heinsohn R., Olah G., Webb M., Peakall R., Stojanovic D. (2019). Sex ratio bias and shared paternity reduce individual fitness and population viability in a critically endangered parrot. *Journal of Animal Ecology*, 88:502-510.

Heise-Pavlov P.M., Heise-Pavlov S.R., Nelson J.E. (2009). *Sus scrofa*: Population structure, reproduction and condition in tropical north-eastern Australia. *Acta Silvatica et Lignaria Hungarica*, 5:179–188.

IBAMA. (2013). *Instrução Normativa Ibama Nº 03 de 31 de janeiro de 2013 do Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (IBAMA).* Brasília: Ministério do Meio Ambiente (MMA). Available at: http://www.ibama.gov.br/component/legislacao/?view=legislacao&legislacao=129393http://www.ibama.gov.br/component/legislacao/?view=legislacao&legislacao=129393. Accessed 15 July 2019.

IBAMA. (2018). *Relatório Técnico de Gestão do Manejo de Javalis no Brasil de 2013 a 2016 do Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (IBAMA).* Brasília: Ministério do Meio Ambiente (MMA). Available at: https://www.gov.br/ibama/pt-br/centrais-de-conteudo/ibama-relatorio-javali-2013-a-2016-final-pdf. Accessed 15 July 2019.

IBAMA. (2019). *Instrução Normativa Ibama Nº 12 de 25 de março de 2019 do Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (IBAMA).* Brasília: Ministério do Meio Ambiente (MMA). Available at: http://www.ibama.gov.br/component/legislacao/?view=legislacao&force=1&legislacao=138381. Accessed 15 July 2019.

IBGE. (2021). *Diário Oficial da União nº 41, de 03 de março de 2021, conforme Portaria nº 47, de 01 de março de 2021 do Instituto Brasieleiro de Geografia e Estatística.* Available at: https://www.ibge.gov.br/geociencias/organizacao-do-territorio/estrutura-territorial/15761-areas-dos-municipios.html?=&t=o-que-e. Accessed 16 Ago 2021.

IUCN - International Union for Conservation of Nature. (2019). The IUCN red list of threatened species. Available at: http://www.iucnredlist.org/search/details. Accessed 15 July 2019.

Jędrzejewski W., Robinson H.S, Abarca M., Zeller K.A., Velasquez G., et al. (2018). Estimating large carnivore populations at global scale based on spatial predictions of density and distribution – Application to the jaguar (*Panthera onca*). *PLoS One*, 13:e0194719.

Jezierski W. (1977). Longevity and Mortality Rate in a Population of Wild Boar. *Acta Theriologica*, 22(24):337–348.

Kaminski G., Brandt S., Baubet E., Baudoin C. (2005). Life-history patterns in female wild boars (*Sus scrofa*): mother–daughter postweaning associations. *Canadian Journal of Zoology*, 83:474-480.

Keiter D.A., Mayer J.J., Beasley J.C. (2016). What is in a “common” name? A call for consistent terminology for nonnative *Sus scrofa*. *Wildlife Society Bulletin,* 40:384-387.

Köck A., Fürst-Waltl B., Baumung R. (2009). Effects of inbreeding on number of piglets born total, born alive and weaned in Austrian Large White and Landrace pigs. *Archives Animal Breeding*, 52:51-64.

Kristensen T.N., Sorensen A. C. (2005). Inbreeding—Lessons from animal breeding, evolutionary biology and conservation genetics. *Animal Science*, 80:121–133.

Lacy R.C. (1993). Vortex: a computer simulation model for population viability analysis. *Wildlife Research*, 20:45-65.

Lacy R.C. (2000). Structure of the Vortex simulation model for population viability analysis. *Ecological Bulletins*, 48:191-203.

Lacy R.C., Pollock J.P. (2015). *VORTEX: a stochastic simulation of the extinction process. Version 10.0.8.* Brookfiled, IL: Chicago Zoological Society.

Long J.L. (2003). *Introduced mammals of the world: their history distribution and influence.* Collingwood: CSIRO Publishing.

Lowe S., Browne M., Boudjelas S., De Poorter M. (2000). *100 of the world's worst invasive alien species: a selection from the global invasive species database.* 12nd edn. Auckland, New Zealand: Invasive Species Specialist Group.

Mack R.N., Simberloff D., Lonsdale W.M., Evans H., Clout M, et al. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, 10:689–710.

Marsan A., Mattioli S. (2013). Il Cinghiale (in Italian). *Il Piviere (collana Fauna selvatica. Biologia e gestione).*

Massei G., Genov P.V. (2004). The environmental impact of wild boar. *Galemys*, 16:135-145.

Massei G., Genov P.V., Staines B.W. (1996). Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. *Acta Theriologica*, 41:307–320.

Massei G., Genov P.V., Staines B.W., Gorman M.L. (1997). Mortality of wild boar, *Sus scrofa*, in a Mediterranean area in relation to sex and age. *Journal of Zoology*, 242(2):394-400.

Massei G., Kindberg J., Licoppe A., Gačić D., Šprem N., et al. (2015). Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Management Science*, 71:492–500.

Mayer J.J., Brisbin I.L.Jr.. (2009). *Wild pigs: Biology, damage, control techniques and management.* Aiken, SC: Savannah River National Laboratory.

McCann B.E., Garcelon D.K. (2008). Eradication of feral pigs from Pinnacles National Monument. *Journal of Wildlife Management*, 72:1287–1295.

Melletti M., Meijaard E. (2017). Ecology, *Conservation and Management of Wild Pigs and Peccaries.* Cambridge: Cambridge University Press.

Mendina Filho L.H., Wallau M.O., Dos Reis T.X. (2015). *O Javali no Pampa: contexto, biologia e manejo.* Santana do Livramento: Pallotti.

Morrone J.J. (2014). Biogeographical regionalisation of the Neotropical region. *Zootaxa*, 3782(1):1-110.

Myrphy M.J., Inman-Narahari F., Ostertag R., Litton C.M. (2014). Invasive feral pigs impact native tree ferns and woody seedlings in Hawaiian forest. *Biological Invasions*, 16:63-71.

Nores C., Llaneza L., Alvarez A. (2008). Wild boar *Sus scrofa* mortality by hunting and wolf *Canis lupus* predation: an example in northern Spain. *Wildlife Biology*, 14:44–51.

Oliveira C.H.S. (2012). *Ecologia e manejo de javali (Sus scrofa L.) na América do Sul*. Thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil. [In Portuguese.]

Oliver W.L.R., Brisbin I.L. (1993). Introduced and feral pigs: Problems, policy and priorities. Pages 159-191 *in Status Survey and Conservation Action Plan. Pigs, Peccaries and Hippos*. Oliver, W.L.R. (ed). IUCN.

Orueta J.F. (2003). *Manual práctico para el manejo de vertebrados invasores en islas de España y Portugal*. Espanha: Gobierno de las Islas Baleares y Gobierno de Canarias.

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

Peel M.C., Finlayson B.L, McMahon T.A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology Earth System Sciences*, 11:1633-1644.

Pepin K.M., Davis A.J., Cunningham F.L., VerCauteren K.C., Eckery D.C. (2017). Potential effects of incorporating fertility control into typical culling regimes in wild pig populations. *PloS one*, 12:e0183441.

Poteaux C., Baubet E., Kaminski G., Brandt S., Dobson F.S., et al. (2009). Socio-genetic structure and mating system of a wild boar population. *Journal of Zoology*, 278:116-125.

Puertas F.H.G. (2015). *A invasão do javali na Serra da Mantiqueira: aspectos populacionais, uso do habitat e sua relação com o homem*. Thesis, University Federal de Lavras, Lavras, Minas Gerais, Brazil. [In Portuguese] Avaiable at: http://repositorio.ufla.br/bitstream/1/9779/1/DISSERTACAO_A invasão do javali na serra da mantiqueira Aspectos populacionais, uso do habitat e sua relação com o Homem.pdf Acessed 19 July 2019.

Rosa C.A., Wallau M.O., Pedrosa F. (2018). Hunting as the main technique used to control wild pigs in Brazil. *Wildlife Society Bulletin*, 42:111-118.

Rosell C., Fernández-Llario P., Herrero J. (2001). El jabalí (*Sus scrofa* Linnaeus, 1758). *Galemys*, 13:1–25.

Sales L.P., Ribeiro B.R., Hayward M.W., Paglia A., Passamani M., et al. (2017). Niche conservatism and the invasive potential of the wild boar. *Journal of Animal Ecology*, 86:1214-1223.

Saunders G. (1993). The demography of feral pigs (*Sus scrofa*) in Kosciusko National Park, New South Wales. *Wildlife Research*, 20:559-569.

Saura M., Fernández A., Varona L., Fernández A.I., de Cara M.Á.R., et al. (2015). Detecting inbreeding depression for reproductive traits in Iberian pigs using genome-wide data. *Genetics Seletion Evolution*, 47:1.

Shaffer M.L. (1990). Population Viability Analysis. *Conservation Biology*, 4:39–40.

SIMAF/IBAMA (Sistema De Monitoramento De Fauna/IBAMA). (2020). *Boletim Informativo Nº 04 de 01 de junho de 2020 do Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (IBAMA).* Brasília: Ministério do Meio Ambiente (MMA).

Simberloff D., Martin J.L., Genovesi P., Maris V., Wardle D.A., et al. (2013). Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, 28(1):58-66.

Simberloff D. (2010). Invasive species. Pages 131-152 i*n Conservation biology for all*. Sodhi, N.S., & Ehrlich, P. R. (Eds.). Oxford: Oxford University Press.

Simberloff D., Parker I.M., Windle P.N. (2005). Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment*, 3:12-20.

Simberloff D. (2002). Why not eradication? Pages 541–548 in *Managing for healthy ecosystems*. Rapport, D.J., Lasley, W.L., Ralston, D.E., Nielsen, N.O., Qualset, C.O. & Damania, A.B. (Eds.). Boca Raton: CRC/ Lewis Press.

Simberloff D. (2009). The role of propagule pressure in biologicalninvasions. *Annual Review of Ecology, Evolution and Systematics*, 40:81-102.

Sollero B.P., Paiva S.R., Faria D.A., Guimarães S.E.F., Castro S.T.R., et al. (2009). Genetic diversity of Brazilian pig breeds evidenced by microsatellite markers. *Livestock Science*, 123(1):8-15.

Tabak M.A., Webb C.T., Miller R.S. (2018). Propagule size and structure, life history, and environmental conditions affect establishment success of an invasive species. *Scientific Reports*, 8:1-9.

Taylor R.B., Hellgren E.C., Gabor T.M., Ilse L.M. (1998). Reproduction of feral pigs in Southern Texas. *Journal of Mammalogy*, 79:1325-1331.

Thompson G.G. (1991). *Determining minimum viable populations under the Endangered Species Act.* Alaska: US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Resource Ecology and Fisheries Management Division.

Thornhill N.W. (1993). *Natural history of inbreeding and outbreeding*. Theoretical and empirical perspectives. Chicago: University of Chicago Press.

Truvé J., Lemel J. (2003). Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. *Wildlife Biology*, 9:51-58.

Tsachalidis E.P., Hadjisterkotis E. (2008). Wild boar hunting and socioeconomic trends in Northern Greece, 1993–2002. *European Journal of Wildlife Research*, 54:643-649.

West B.C., Cooper A.L., Armstrong J.B. (2009). Managing wild pigs: A technical guide. *Human-Wildlife Interactions Monograph,* 1:1-55.

White M.D., Kunkel K. (2016). Evaluating Feral Pig Management Strategies at Tejon Ranch, California. *Proceedings of the Vertebrate Pest Conference,* 27:128-132.

Conclusão geral

Pela história do processo de invasão e cálculo das taxas da dispersão do javali no Brasil, foi possível perceber que as introduções intencionais feitas pelo homem aceleraram o processo natural de distribuição da espécie. Em menos de quatro décadas, o javali é encontrado em boa parte do território brasileiro, e mantendo esse ritmo, estará encontrado em todos os munícipios, incluindo os da região Amazônica, onde ainda não foi registrado. Outro ponto importante para salientar, é que as introduções intencionais e atualmente ilegais, devem ser cessadas imediatamente para evitar a propagação da espécie para novas áreas. Além disso, os cruzamentos com indivíduos domésticos contribuíram para o aumento do sucesso da invasão do javali.

Entretanto, percebemos que as introduções intencionais não ocorreram apenas por aqui. Javalis estão amplamente distribuídos pelo mundo e foram cruzados com espécies domésticas com o intuito de melhorar os resultados na suinocultura. Essa hibridização com espécies domésticas e a ampla variação geográfica estão refletidas na genética e morfologia da espécie. Foi possível evidenciar a variação morfológica ao longo do gradiente latitudinal e que os diversos fatores históricos, ambientais e climáticos estão envolvidos nesse processo. O efeito da latitude (Regra de Bergmann), foi detectado nos javalis do Brasil e suas populações fundadoras da Argentina e do Uruguai confirmando que quanto mais ao sul e em climas mais frios, endotérmicos como os javalis tendem a ser maiores e possuir uma estrutura craniana alongada e estreita, enquanto os animais mais ao norte são menores e com uma estrutura craniana encurtada e robusta.

Caracteres morfológicos distintos foram sendo incorporados na morfologia dos javalis ao longo do tempo, porém algumas semelhanças entre indivíduos nativos e introduzidos foram mantidas, especialmente com relação ao tamanho na espécie. A forma da estrutura craniana dos javalis, apresentou maior diferença entre indivíduos de áreas nativas e áreas introduzidas, o que provavelmente está relacionado à dieta. Embora os javalis tenham hábito alimentar generalista, diferentes recursos estão disponíveis nos diferentes hábitats e climas onde eles estão presentes. Essa oferta e disponibilidade variada de recursos, e a ausência de predadores, têm consequências devastadoras nos ecossistemas naturais, devido à competição com espécies nativas. O javali é hoje considerado uma praga em todo o país e o método vigente de controle populacional não tem se mostrado eficaz.

Devido a constatação da ineficácia do controle do javali, construímos modelos de viabilidade populacional voltada para o controle populacional e apresentamos uma provável solução mitigadora para a problemática do javali no Brasil. Os cenários modelados indicaram que o controle direcional baseado na eliminação de fêmeas é capaz de reduzir as populações e até leva-las à extinção em longo prazo. Entretanto, manejar as populações não é uma tarefa simples, pois requer o envolvimento e comprometimento da sociedade, principalmente dos órgãos de fiscalização, dos controladores de javalis credenciados e das instituições de pesquisa. Atualmente, a caça no Brasil é autorizada apenas para o controle do javali, mas tem se mostrado polêmica e controversa, pois a falta de fiscalização eficiente e clareza sobre as condições para a caça abrem precedentes para a ilegalidade, atingindo a fauna silvestre.

Esses resultados trouxeram um panorama preocupante do ponto de vista econômico, ecológico e da conservação, reforçando a necessidade de um manejo e controle populacional do javali mais eficiente. O javali mostrou ser um invasor de sucesso, com alta plasticidade fenotípica e potencial adaptativo no Brasil, e seus danos provocados às culturas agrícolas e sobre os ambientes naturais geram prejuízos ecológicos para os ecossistemas naturais e para a conservação da fauna e flora, especialmente nas áreas em que a espécie foi introduzida.

Assim, a alternativa proposta para um controle populacional do javali direcionado para caça das fêmeas pode ser mais eficaz, imediato e de menor custo, sendo indispensável para a conservação dos ecossistemas e das espécies nativas. O controle do javali merece atenção especial dos órgãos ambientais fiscalizadores para que ocorra dentro dos trâmites legais previstos na legislação brasileira vigente. Sugerimos estudos de longo prazo sobre o controle direcional da caça do javali, e também estudos genéticos que forneçam um diagnóstico mais preciso sobre as relações filogenéticas das populações do Brasil, dos países vizinhos e dos países de origem.

Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
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Dados do titular

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Nome da Instituição : FUNDAÇÃO UNIVERSIDADE DE BRASÍLIA	CNPJ: 00.038.174/0001-43

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Transporte crânios de coleções	11/2017	03/2021

Observações e ressalvas

1	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
2	Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
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8	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade.

Locais onde as atividades de campo serão executadas

#	Município	UF	Descrição do local	Tipo
1	BRASILIA	DF	Universidade de Brasília	Fora de UC Federal

Atividades X Táxons

#	Atividade	Táxons
1	Coleta/transporte de amostras biológicas ex situ	Sus scrofa
2	Coleta/transporte de amostras biológicas in situ	Sus scrofa

Material e métodos

1	Amostras biológicas (Outros mamíferos)	Pêlo, Animal encontrado morto ou partes (carcaça)/osso/pele, Fragmento de tecido/órgão

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2	Método de captura/coleta (Outros mamíferos)	Outros métodos de captura/coleta

Destino do material biológico coletado

#	Nome local destino	Tipo Destino
1	FUNDAÇÃO UNIVERSIDADE DE BRASÍLIA	

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Registro de coleta imprevista de material biológico

De acordo com a Instrução Normativa nº 03/2014, a coleta imprevista de material biológico ou de substrato não contemplado na autorização ou na licença permanente deverá ser anotada na mesma, em campo específico, por ocasião da coleta, devendo esta coleta imprevista ser comunicada por meio do relatório de atividades. O transporte do material biológico ou do substrato deverá ser acompanhado da autorização ou da licença permanente com a devida anotação. O material biológico coletado de forma imprevista, deverá ser destinado à instituição científica e, depositado, preferencialmente, em coleção biológica científica registrada no Cadastro Nacional de Coleções Biológicas (CCBIO).

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Nome da Instituição : FUNDAÇÃO UNIVERSIDADE DE BRASÍLIA	CNPJ: 00.038.174/0001-43

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* Identificar o espécime no nível taxonômico possível.

Este documento (Autorização para atividades com finalidade científica) foi expedido com base na Instrução Normativa nº 03/2014. Através do código de autenticação abaixo, qualquer cidadão poderá verificar a autenticidade ou regularidade deste documento, por meio da página do Sisbio/ICMBio na Internet (www.icmbio.gov.br/sisbio).

Código de autenticação: 89589775

Ministério do Meio Ambiente - MMA

Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio

Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 60140-2	**Data da Emissão: 16/05/2019 10:55:16**	**Data da Revalidação*: 16/05/2020**
De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.		

Dados do titular

Nome: CARLA GRASIELE ZANIN HEGEL	CPF: 007.467.920-18
Nome da Instituição: Fundação Universidade de Brasília	CNPJ: 00.038.174/0001-43

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Transporte crânios de coleções	11/2017	03/2021

Observações e ressalvas

1	A autorização não eximirá o pesquisador da necessidade de obter outras anuências, como: I) do proprietário, arrendatário, posseiro ou morador quando as atividades forem realizadas em área de domínio privado ou dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso; II) da comunidade indígena envolvida, ouvido o órgão indigenista oficial, quando as atividades de pesquisa forem executadas em terra indígena; III) do Conselho de Defesa Nacional, quando as atividades de pesquisa forem executadas em área indispensável à segurança nacional; IV) da autoridade marítima, quando as atividades de pesquisa forem executadas em águas jurisdicionais brasileiras; V) do Departamento Nacional da Produção Mineral, quando a pesquisa visar a exploração de depósitos fossilíferos ou a extração de espécimes fósseis; VI) do órgão gestor da unidade de conservação estadual, distrital ou municipal, dentre outras.
2	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infraestrutura da unidade.
3	O titular de autorização ou de licença permanente, assim como os membros de sua equipe, quando da violação da legislação vigente, ou quando da inadequação, omissão ou falsa descrição de informações relevantes que subsidiaram a expedição do ato, poderá, mediante decisão motivada, ter a autorização ou licença suspensa ou revogada pelo ICMBio, nos termos da legislação brasileira em vigor.
4	Este documento somente poderá ser utilizado para os fins previstos na Instrução Normativa ICMBio n° 03/2014 ou na Instrução Normativa ICMBio n° 10/2010, no que especifica esta Autorização, não podendo ser utilizado para fins comerciais, industriais ou esportivos. O material biológico coletado deverá ser utilizado para atividades científicas ou didáticas no âmbito do ensino superior.
5	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
6	O titular de licença ou autorização e os membros da sua equipe deverão optar por métodos de coleta e instrumentos de captura direcionados, sempre que possível, ao grupo taxonômico de interesse, evitando a morte ou dano significativo a outros grupos; e empregar esforço de coleta ou captura que não comprometa a viabilidade de populações do grupo taxonômico de interesse em condição in situ.
7	Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
8	Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen.

Autorização para atividades com finalidade científica

Número: 60140-2	**Data da Emissão: 16/05/2019 10:55:16**	**Data da Revalidação*: 16/05/2020**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: CARLA GRASIELE ZANIN HEGEL	CPF: 007.467.920-18
Nome da Instituição: Fundação Universidade de Brasília	CNPJ: 00.038.174/0001-43

Outras ressalvas

1	Flona de Silvânia 01. Os créditos da pesquisa devem mencionar a Flona de Silvânia e o ICMBio. Flona de Silvânia 02. O pesquisador, ao utilizar a Flona, deverá respeitar as normas gerais da Unidade estabelecidas no Plano de Manejo. Flona de Silvânia 03. Quando possível, e em comum acordo com a gestão da UC, o pesquisador deverá apresentar o projeto de pesquisa e/ou os resultados, ao Conselho Consultivo da Flona de Silvânia.	FLONA Silvânia

Locais onde as atividades de campo serão executadas

#	**Descrição do local**	**Município-UF**	**Bioma**	**Caverna?**	**Tipo**
1	Floresta Nacional de Silvânia	GO	Cerrado	Não	Dentro de UC Federal
2	Universidade de Brasília	Brasília-DF	Cerrado	Não	Fora de UC Federal

Atividades X Táxons

#	**Atividade**	**Táxon**	**Qtde.**
1	Coleta/transporte de amostras biológicas in situ	Sus scrofa	-
2	Coleta/transporte de amostras biológicas ex situ	Sus scrofa	-

Materiais e Métodos

#	**Tipo de Método (Grupo taxonômico)**	**Materiais**
1	Amostras biológicas (Outros mamíferos)	Fragmento de tecido/órgão, Pêlo, Animal encontrado morto ou partes (carcaça)/osso/pele, Pêlo, Fragmento de tecido/órgão, Animal encontrado morto ou partes (carcaça)/osso/pele
2	Método de captura/coleta (Outros mamíferos)	Outros métodos de captura/coleta

Destino do material biológico coletado

#	**Nome local destino**	**Tipo destino**
1	Fundação Universidade de Brasília	Outro

Autorização para atividades com finalidade científica

Número: 60140-2	**Data da Emissão: 16/05/2019 10:55:16**	**Data da Revalidação*: 16/05/2020**
De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.		

Dados do titular

Nome: CARLA GRASIELE ZANIN HEGEL	CPF: 007.467.920-18
Nome da Instituição: Fundação Universidade de Brasília	CNPJ: 00.038.174/0001-43

Registro de coleta imprevista de material biológico

De acordo com a Instrução Normativa nº03/2014, a coleta imprevista de material biológico ou de substrato não contemplado na autorização ou na licença permanente deverá ser anotada na mesma, em campo específico, por ocasião da coleta, devendo esta coleta imprevista ser comunicada por meio do relatório de atividades. O transporte do material biológico ou do substrato deverá ser acompanhado da autorização ou da licença permanente com a devida anotação. O material biológico coletado de forma imprevista, deverá ser destinado à instituição científica e, depositado, preferencialmente, em coleção biológica científica registrada no Cadastro Nacional de Coleções Biológicas (CCBIO).

Táxon*	**Qtde.**	**Tipo de Amostra**	**Qtde.**	**Data**

* Identificar o espécime do nível taxonômico possível.

Este documento foi expedido com base na Instrução Normativa nÂº 03/2014. Através do código de autenticação abaixo, qualquer cidadão poderá verificar a autenticidade ou regularidade deste documento, por meio da página do Sisbio/ICMBio na Internet (www.icmbio.gov.br/sisbio).

Código de autenticação: 0601400220190516

Ministério do Meio Ambiente - MMA

Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio

Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 60140-3	**Data da Emissão: 07/01/2020 16:35:20**	**Data da Revalidação*: 16/05/2020**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: CARLA GRASIELE ZANIN HEGEL	CPF: 007.467.920-18
Título do Projeto: A MORFOMETRIA DO CRÂNIO DE JAVALIS (SUS SCROFA, ARTIODACTYLA, SUIDAE) REVELANDO ASPECTOS MACROGEOGRÁFICOS E AMBIENTAIS.	
Nome da Instituição: Fundação Universidade de Brasília	CNPJ: 00.038.174/0001-43

Cronograma de atividades

#	**Descrição da atividade**	**Início (mês/ano)**	**Fim (mês/ano)**
1	Transporte crânios de coleções	11/2017	03/2021

Observações e ressalvas

1	A autorização não eximirá o pesquisador da necessidade de obter outras anuências, como: I) do proprietário, arrendatário, posseiro ou morador quando as atividades forem realizadas em área de domínio privado ou dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso; II) da comunidade indígena envolvida, ouvido o órgão indigenista oficial, quando as atividades de pesquisa forem executadas em terra indígena; III) do Conselho de Defesa Nacional, quando as atividades de pesquisa forem executadas em área indispensável à segurança nacional; IV) da autoridade marítima, quando as atividades de pesquisa forem executadas em águas jurisdicionais brasileiras; V) do Departamento Nacional da Produção Mineral, quando a pesquisa visar a exploração de depósitos fossilíferos ou a extração de espécimes fósseis; VI) do órgão gestor da unidade de conservação estadual, distrital ou municipal, dentre outras.
2	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infraestrutura da unidade.
3	O titular de autorização ou de licença permanente, assim como os membros de sua equipe, quando da violação da legislação vigente, ou quando da inadequação, omissão ou falsa descrição de informações relevantes que subsidiaram a expedição do ato, poderá, mediante decisão motivada, ter a autorização ou licença suspensa ou revogada pelo ICMBio, nos termos da legislação brasileira em vigor.
4	Este documento somente poderá ser utilizado para os fins previstos na Instrução Normativa ICMBio n° 03/2014 ou na Instrução Normativa ICMBio n° 10/2010, no que especifica esta Autorização, não podendo ser utilizado para fins comerciais, industriais ou esportivos. O material biológico coletado deverá ser utilizado para atividades científicas ou didáticas no âmbito do ensino superior.
5	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
6	O titular de licença ou autorização e os membros da sua equipe deverão optar por métodos de coleta e instrumentos de captura direcionados, sempre que possível, ao grupo taxonômico de interesse, evitando a morte ou dano significativo a outros grupos; e empregar esforço de coleta ou captura que não comprometa a viabilidade de populações do grupo taxonômico de interesse em condição in situ.
7	Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
8	Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen.

Autorização para atividades com finalidade científica

Número: 60140-3	**Data da Emissão: 07/01/2020 16:35:20**	**Data da Revalidação*: 16/05/2020**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: CARLA GRASIELE ZANIN HEGEL	CPF: 007.467.920-18
Título do Projeto: A MORFOMETRIA DO CRÂNIO DE JAVALIS (SUS SCROFA, ARTIODACTYLA, SUIDAE) REVELANDO ASPECTOS MACROGEOGRÁFICOS E AMBIENTAIS.	
Nome da Instituição: Fundação Universidade de Brasília	CNPJ: 00.038.174/0001-43

Outras ressalvas

1	Flona de Silvânia 01. Os créditos da pesquisa devem mencionar a Flona de Silvânia e o ICMBio. Flona de Silvânia 02. O pesquisador, ao utilizar a Flona, deverá respeitar as normas gerais da Unidade estabelecidas no Plano de Manejo. Flona de Silvânia 03. Quando possível, e em comum acordo com a gestão da UC, o pesquisador deverá apresentar o projeto de pesquisa e/ou os resultados, ao Conselho Consultivo da Flona de Silvânia.	FLONA Silvânia

Locais onde as atividades de campo serão executadas

#	Descrição do local	Município-UF	Bioma	Caverna?	Tipo
1	Floresta Nacional de Silvânia	GO	Cerrado	Não	Dentro de UC Federal
2	Área de Proteção Ambiental Bacia Hidrográfica do Rio Paraíba do Sul	SP	Mata Atlântica	Não	Dentro de UC Federal
3	APA São Francisco Xavier	São José dos Campos-SP	Mata Atlântica	Não	Dentro de UC Estadual
4	interior	Uberaba-MG	Cerrado	Não	Fora de UC Federal
5	interior	Araxá-MG	Cerrado	Não	Fora de UC Federal
6	interior	Edéia-GO	Cerrado	Não	Fora de UC Federal
7	Universidade de Brasília	Brasília-DF	Cerrado	Não	Fora de UC Federal
8	interior	São Gabriel do Oeste-MS	Cerrado	Não	Fora de UC Federal
9	interior	Uruguaiana-RS	Mata Atlântica	Não	Fora de UC Federal
10	interior	Pinheiro Machado-RS	Mata Atlântica	Não	Fora de UC Federal

Atividades

#	Atividade	Grupo de Atividade
1	Coleta/transporte de amostras biológicas in situ	Dentro de UC Federal
2	Coleta/transporte de amostras biológicas in situ	Fora de UC Federal
3	Coleta/transporte de amostras biológicas ex situ	Atividades ex-situ (fora da natureza)

Atividades X Táxons

#	Atividade	Táxon	Qtde.
1	Coleta/transporte de amostras biológicas ex situ	Sus scrofa	-
2	Coleta/transporte de amostras biológicas in situ	Sus scrofa	-

Autorização para atividades com finalidade científica

Número: 60140-3	**Data da Emissão: 07/01/2020 16:35:20**	**Data da Revalidação*: 16/05/2020**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: CARLA GRASIELE ZANIN HEGEL	CPF: 007.467.920-18
Título do Projeto: A MORFOMETRIA DO CRÂNIO DE JAVALIS (SUS SCROFA, ARTIODACTYLA, SUIDAE) REVELANDO ASPECTOS MACROGEOGRÁFICOS E AMBIENTAIS.	
Nome da Instituição: Fundação Universidade de Brasília	CNPJ: 00.038.174/0001-43

Materiais e Métodos

#	Tipo de Método (Grupo taxonômico)	Materiais
1	Amostras biológicas (Outros mamíferos)	Fragmento de tecido/órgão, Pêlo, Animal encontrado morto ou partes (carcaça)/osso/pele, Pêlo, Fragmento de tecido/órgão, Animal encontrado morto ou partes (carcaça)/osso/pele
2	Método de captura/coleta (Outros mamíferos)	Outros métodos de captura/coleta

Destino do material biológico coletado

#	Nome local destino	Tipo destino
1	Fundação Universidade de Brasília	Outro

Ministério do Meio Ambiente - MMA

Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio

Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 60140-3	**Data da Emissão: 07/01/2020 16:35:20**	**Data da Revalidação*: 16/05/2020**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: CARLA GRASIELE ZANIN HEGEL	CPF: 007.467.920-18
Título do Projeto: A MORFOMETRIA DO CRÂNIO DE JAVALIS (SUS SCROFA, ARTIODACTYLA, SUIDAE) REVELANDO ASPECTOS MACROGEOGRÁFICOS E AMBIENTAIS.	
Nome da Instituição: Fundação Universidade de Brasília	CNPJ: 00.038.174/0001-43

Registro de coleta imprevista de material biológico

De acordo com a Instrução Normativa nº03/2014, a coleta imprevista de material biológico ou de substrato não contemplado na autorização ou na licença permanente deverá ser anotada na mesma, em campo específico, por ocasião da coleta, devendo esta coleta imprevista ser comunicada por meio do relatório de atividades. O transporte do material biológico ou do substrato deverá ser acompanhado da autorização ou da licença permanente com a devida anotação. O material biológico coletado de forma imprevista, deverá ser destinado à instituição científica e, depositado, preferencialmente, em coleção biológica científica registrada no Cadastro Nacional de Coleções Biológicas (CCBIO).

Táxon*	**Qtde.**	**Tipo de Amostra**	**Qtde.**	**Data**

* Identificar o espécime do nível taxonômico possível.

Autorização para atividades com finalidade científica

Número: 60140-4	**Data da Emissão: 22/06/2020 17:58:28**	**Data da Revalidação*: 01/05/2021**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: CARLA GRASIELE ZANIN HEGEL	CPF: 007.467.920-18
Título do Projeto: A MORFOMETRIA DO CRÂNIO DE JAVALIS (SUS SCROFA, ARTIODACTYLA, SUIDAE) REVELANDO ASPECTOS MACROGEOGRÁFICOS E AMBIENTAIS.	
Nome da Instituição: Fundação Universidade de Brasília	CNPJ: 00.038.174/0001-43

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Transporte crânios de coleções	11/2017	03/2021

Observações e ressalvas

1	A autorização não eximirá o pesquisador da necessidade de obter outras anuências, como: I) do proprietário, arrendatário, posseiro ou morador quando as atividades forem realizadas em área de domínio privado ou dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso; II) da comunidade indígena envolvida, ouvido o órgão indigenista oficial, quando as atividades de pesquisa forem executadas em terra indígena; III) do Conselho de Defesa Nacional, quando as atividades de pesquisa forem executadas em área indispensável à segurança nacional; IV) da autoridade marítima, quando as atividades de pesquisa forem executadas em águas jurisdicionais brasileiras; V) do Departamento Nacional da Produção Mineral, quando a pesquisa visar a exploração de depósitos fossilíferos ou a extração de espécimes fósseis; VI) do órgão gestor da unidade de conservação estadual, distrital ou municipal, dentre outras.
2	O pesquisador somente poderá realizar atividade de campo após o término do estado de emergência devido à COVID-19, assim declarado por ato da autoridade competente.
3	O titular de autorização ou de licença permanente, assim como os membros de sua equipe, quando da violação da legislação vigente, ou quando da inadequação, omissão ou falsa descrição de informações relevantes que subsidiaram a expedição do ato, poderá, mediante decisão motivada, ter a autorização ou licença suspensa ou revogada pelo ICMBio, nos termos da legislação brasileira em vigor.
4	Este documento somente poderá ser utilizado para os fins previstos na Instrução Normativa ICMBio n° 03/2014 ou na Instrução Normativa ICMBio n° 10/2010, no que especifica esta Autorização, não podendo ser utilizado para fins comerciais, industriais ou esportivos. O material biológico coletado deverá ser utilizado para atividades científicas ou didáticas no âmbito do ensino superior.
5	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
6	O titular de licença ou autorização e os membros da sua equipe deverão optar por métodos de coleta e instrumentos de captura direcionados, sempre que possível, ao grupo taxonômico de interesse, evitando a morte ou dano significativo a outros grupos; e empregar esforço de coleta ou captura que não comprometa a viabilidade de populações do grupo taxonômico de interesse em condição in situ.
7	Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
8	Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen.
9	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infraestrutura da unidade.

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Autorização para atividades com finalidade científica

Número: 60140-4	**Data da Emissão: 22/06/2020 17:58:28**	**Data da Revalidação*: 01/05/2021**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: CARLA GRASIELE ZANIN HEGEL	CPF: 007.467.920-18
Título do Projeto: A MORFOMETRIA DO CRÂNIO DE JAVALIS (SUS SCROFA, ARTIODACTYLA, SUIDAE) REVELANDO ASPECTOS MACROGEOGRÁFICOS E AMBIENTAIS.	
Nome da Instituição: Fundação Universidade de Brasília	CNPJ: 00.038.174/0001-43

Outras ressalvas

1	Flona de Silvânia 01. Os créditos da pesquisa devem mencionar a Flona de Silvânia e o ICMBio. Flona de Silvânia 02. O pesquisador, ao utilizar a Flona, deverá respeitar as normas gerais da Unidade estabelecidas no Plano de Manejo. Flona de Silvânia 03. Quando possível, e em comum acordo com a gestão da UC, o pesquisador deverá apresentar o projeto de pesquisa e/ou os resultados, ao Conselho Consultivo da Flona de Silvânia.	FLONA Silvânia

Locais onde as atividades de campo serão executadas

#	**Descrição do local**	**Município-UF**	**Bioma**	**Caverna?**	**Tipo**
1	interior	Pinheiro Machado-RS	Mata Atlântica	Não	Fora de UC Federal
2	interior	Uruguaiana-RS	Mata Atlântica	Não	Fora de UC Federal
3	Área de Proteção Ambiental Bacia Hidrográfica do Rio Paraíba do Sul	SP	Mata Atlântica	Não	Dentro de UC Federal
4	Floresta Nacional de Silvânia	GO	Cerrado	Não	Dentro de UC Federal
5	interior	São Gabriel do Oeste-MS	Cerrado	Não	Fora de UC Federal
6	Universidade de Brasília	Brasília-DF	Cerrado	Não	Fora de UC Federal
7	interior	Edéia-GO	Cerrado	Não	Fora de UC Federal
8	interior	Araxá-MG	Cerrado	Não	Fora de UC Federal
9	interior	Uberaba-MG	Cerrado	Não	Fora de UC Federal
10	APA São Francisco Xavier	São José dos Campos-SP	Mata Atlântica	Não	Dentro de UC Estadual

Atividades

#	**Atividade**	**Grupo de Atividade**
1	Coleta/transporte de amostras biológicas in situ	Fora de UC Federal
2	Coleta/transporte de amostras biológicas in situ	Dentro de UC Federal
3	Coleta/transporte de amostras biológicas ex situ	Atividades ex-situ (fora da natureza)

Atividades X Táxons

#	**Atividade**	**Táxon**	**Qtde.**
1	Coleta/transporte de amostras biológicas in situ	Sus scrofa	-
2	Coleta/transporte de amostras biológicas ex situ	Sus scrofa	-

Autorização para atividades com finalidade científica

<table>
<tr><td>Número: 60140-4</td><td>Data da Emissão: 22/06/2020 17:58:28</td><td>Data da Revalidação*: 01/05/2021</td></tr>
<tr><td colspan="3">De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.</td></tr>
</table>

Dados do titular

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</table>

Materiais e Métodos

#	Tipo de Método (Grupo taxonômico)	Materiais
1	Amostras biológicas (Outros mamíferos)	Fragmento de tecido/órgão, Pêlo, Animal encontrado morto ou partes (carcaça)/osso/pele, Pêlo, Fragmento de tecido/órgão, Animal encontrado morto ou partes (carcaça)/osso/pele
2	Método de captura/coleta (Outros mamíferos)	Outros métodos de captura/coleta

Destino do material biológico coletado

#	Nome local destino	Tipo destino
1	Fundação Universidade de Brasília	Outro

Autorização para atividades com finalidade científica

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Nome da Instituição: Fundação Universidade de Brasília	CNPJ: 00.038.174/0001-43

Registro de coleta imprevista de material biológico

De acordo com a Instrução Normativa nº03/2014, a coleta imprevista de material biológico ou de substrato não contemplado na autorização ou na licença permanente deverá ser anotada na mesma, em campo específico, por ocasião da coleta, devendo esta coleta imprevista ser comunicada por meio do relatório de atividades. O transporte do material biológico ou do substrato deverá ser acompanhado da autorização ou da licença permanente com a devida anotação. O material biológico coletado de forma imprevista, deverá ser destinado à instituição científica e, depositado, preferencialmente, em coleção biológica científica registrada no Cadastro Nacional de Coleções Biológicas (CCBIO).

Táxon*	Qtde.	Tipo de Amostra	Qtde.	Data

* Identificar o espécime do nível taxonômico possível.

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