

Wild boar diet and its implications on agriculture and biodiversity in Brazilian forest–grassland ecoregions

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Abstract

Wild boar diet and its implications on agriculture and biodiversity in Brazilian forest–grassland ecoregions. We aimed to describe the composition of *Sus scrofa* diet in three Brazilian ecoregions characterized by a mosaic of forests and grasslands: Pampa, Araucaria Forest and Pantanal. We evaluated the possible risks that the species may represent for agriculture and conservation of biodiversity by analyzing the stomach content of 118 boars. We examined dietary patterns in each ecoregion using PCA (principal component analysis) and verified how diet varies according to individual attributes through redundancy analysis. We visualized the composition of macronutrients in a multidimensional space by means of RMT (right–angled mixture triangle). The wild boars presented a diverse diet, influenced by season, time of day, and local availability of resources. Cultivated grains and herbs were the most commonly consumed items, leading to a high carbohydrate intake. Damage to agriculture is potentially high given the large consumption of cultivated grains. Population growth and expansion may be limited by the low availability of protein in the ecoregions.

Key words: Invasive species, *Sus scrofa*, Biodiversity, Agriculture

Resumen

La dieta del jabalí y sus implicaciones en la agricultura y la biodiversidad de las ecorregiones de bosques y pastizales del Brasil. En este artículo tratamos de describir la composición de la dieta de *Sus scrofa* en tres ecorregiones brasileñas caracterizadas por un mosaico de bosques y pastizales: la pampa, el bosque de araucaria y el pantanal. Evaluamos los riesgos que la especie puede representar para la agricultura y la conservación de la biodiversidad analizando el contenido estomacal de 118 jabalíes. Analizamos sus hábitos alimentarios en cada ecorregión utilizando el análisis de componentes principales y comprobamos que la dieta varía en función de las características de cada individuo mediante un análisis de la redundancia. Representamos la composición de macronutrientes en un espacio multidimensional mediante un diagrama triangular rectangular. El jabalí presentó una dieta diversa, influida por la estación, el momento del día y la disponibilidad local de recursos. Los cereales y hierbas cultivados fueron los productos consumidos más habitualmente, lo que apunta a una ingesta elevada de carbohidratos. Los daños provocados a la agricultura podrían ser elevados dado el gran consumo de cereales cultivados. El crecimiento y la expansión de la población pueden verse limitados por la escasa disponibilidad de proteína en las ecorregiones.

Palabras clave: Especie invasiva, *Sus scrofa*, Biodiversidad, Agricultura

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Introduction

The introduction of organisms by humans in the last 200 years, either accidentally or intentionally, overcame the dispersion by natural forces in previous periods of Earth's history (Mack et al., 2000; Lockwood et al., 2013). The wild boar *Sus scrofa* L. is one of worst invasive species at a global level (Lowe et al., 2000). Wild boar damage agricultural crops (Nunley, 1999; Schley and Roper, 2003; Deberdt and Scherer, 2007), attack domestic animals (Nunley, 1999; Deberdt and Scherer, 2007), serve as reservoirs of diseases (Nunley, 1999; Deberdt and Scherer, 2007), threaten native species by predation or competition (Wood and Roark, 1980), alter ecosystem processes (Wilcox and Van Vuren, 2009), and favor other exotic species. Wild boar of different lineages have been found in the wild in Brazil since they were accidentally introduced in the late nineteenth century. Later, as of 1960, they were being deliberately introduced for hunting and commercial purposes. Populations also expanded as they invaded over borders from nearby countries (Deberdt and Scherer, 2007; García et al., 2011; Pedrosa et al., 2015).

The dietary niche and the feeding habits are fundamental to our understanding of how species and individuals behave adaptively and what damage they can cause once introduced (Senior et al., 2016). The feeding habits of wild boar explain much of the unwanted ecological and economic effects (Zeman et al., 2018); the active rooting and foraging (Jones et al., 1994; Crooks, 2002) and their generalist diet (Hahn and Eisfeld, 1998; Schley and Roper, 2003; Morelle and Lejeune, 2015) explain their ability to exploit a wide range of resources and to maintain large populations. Agricultural crops are not only damaged in their search for food but also contribute to the establishment and expansion of wild boars (Keiter and Beasley, 2017). Moreover, wild boar may endanger wild species by predation, competition or habitat alteration (Bevins et al., 2014). In South Brazil, for example, preliminary assessments suggest that wild boar consume large amounts of *Araucaria angustifolia* (Deberdt and Scherer, 2007), a key resource for several vertebrate species in winter (Deberdt and Scherer, 2007; Zanin Hegel and Angelo Marini, 2013). They also predate toads, eggs and nestlings of ground nesting birds, and lambs (Chimera et al., 1995; Deberdt and Scherer, 2007). Their diet is influenced by a number of factors, including habitat, season, circadian activity, and individual traits (Keuling et al., 2008). It has been reported, for example, that roots of plants appear to be consumed more often in the winter and green parts in the spring (Ballari and Barrios-García, 2014), and that diet and movements are influenced by seasonal availability of agricultural crops (Hahn and Eisfeld, 1998; Schley and Roper, 2003; Morelle and Lejeune, 2015) and hunting pressure (Keuling et al., 2008). The moment and methods of capture may introduce bias in dietary analysis (Scillitani et al., 2010), since behavior, including diet, changes throughout the day and some control techniques include baiting.

Diet is determined by the breadth of the dietary niche of a species, or its degree of generalism, which

involves at least three interrelated dimensions (Westoby, 1978; Machovsky-Capuska et al., 2016). These are the range of physical attributes of food resources (food composition niche), the nutritional compositions of these resources (food exploitation niche), and the range of macronutrient diet composition (macronutrient niche). The degree of generalism of a species with regard to macronutrients and food composition may help reveal a population's suitability to a new environment, allowing the assessment of its colonization potential and geographical expansion (Hutchinson, 1957). The wild boar is known as a generalist regarding food exploitation and composition and has a broad macronutrient niche (Senior et al., 2016).

In this work, we characterize and compare the wild boar dietary niche in three neotropical ecoregions in Brazil where the species is established and currently expanding over wild and agricultural land (Pedrosa et al., 2015). Specifically, according to patterns in other regions invaded by wild boars, we expect that: 1) the diet varies between sexes, with females ingesting more protein than males, but not between ages, due to the gregarious feeding behavior, nor concerning the time of the day, due to behavioral plasticity; 2) since the wild boar is a generalist in food composition and exploitation, we expect the range of food resources to be broad and to vary regionally and seasonally; and 3) cultivated grains, when available, will play an important role in the diet, due to their high nutritional value and ease of access. We also expect the dietary niche of wild boar in Brazil to fall within the macronutrient niche space established by Senior et al. (2016).

Material and methods

Study area

We collected samples from three ecoregions (fig. 1) corresponding to three biogeographical provinces (Morrone, 2014): Pantanal Ecoregion (Pantanal Province), Uruguayan Savannas (Pampa Province) and Brazilian *Araucaria* Forest (*Araucaria angustifolia* Forest Province). In Brazil, wild boar invasion is particularly widespread in these three ecoregions (Pedrosa et al., 2015). All three ecoregions consist of mosaics of forests, shrublands and grasslands. The climate in the *Araucaria* Forest is temperate and humid, with an average annual temperature of 17°C. The total annual precipitation is 1,500–2,000 mm (Cfb) (Overbeck et al., 2009; Suertegray and da Silva, 2009). The climate in the Pampa is subtropical, with a mean annual temperature of 18°C and total annual rainfall of 1,500 mm (Cfa) (Moreno, 1961; IBGE, 2012). In these two ecoregions the critical season for vegetation growth is the winter, but droughts can occur in summer months. The climate in the Pantanal is tropical, with an average annual temperature of 26°C and total annual rainfall of 1,600 mm, alternating a wet season from November to April and a dry season from May to October (Aw) (Cadavid Garcia, 1984). The Pantanal is a lowland Savanna subjected to annual flooding in the wet season, extending from

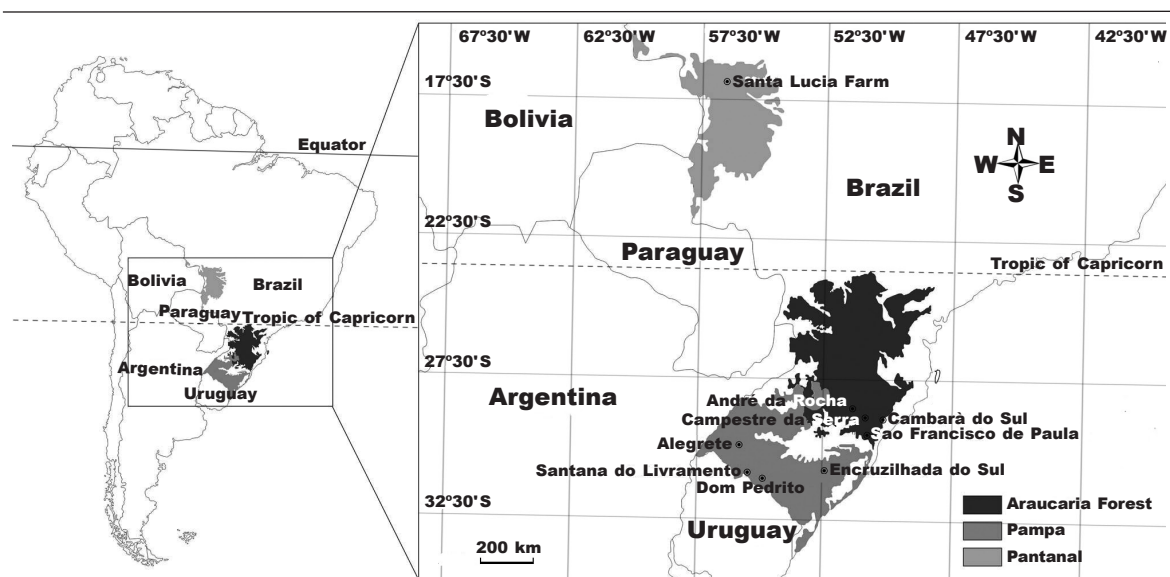


Fig. 1. Map of the three ecoregions studied: Araucaria Forest, Pampa and Pantanal, with the respective sampling sites of stomach contents of wild boar in 2015 and 2016.

Fig. 1. Mapa de las tres ecorregiones estudiadas: el bosque de araucaria, la pampa y el pantanal, con los respectivos sitios donde se recogieron las muestras de contenido estomacal de jabalíes entre 2015 y 2016.

four to nine months and covering up to 90% of the area (Cordeiro, 2004; Pott and Pott, 2004). About 33% to 50% of the Pantanal area is flooded annually (Apollonio et al., 1988; Silva et al., 2000).

Diet analysis

We obtained the stomach content of wild boar from individual hunters officially authorized to conduct wild boar control under Brazilian regulations. We obtained 45 samples from the Pampa between June 2015 and October 2016, 15 samples from the Araucaria Forest from September to October 2015, and 58 samples from the Pantanal, 31 of which were collected in September and October 2015 (flooding season) and 27 in June 2016 (dry season). All animals were culled with firearms in active boar beats (Araucaria and Pantanal) or attracted to stands of blinds with baiting. Each animal was obtained from a separate beat. Immediately after culling, we incised the stomach and collected samples of 500 ml from the centre of its content, stored them in vials containing a solution of 90% alcohol 70%, 5% formalin and 5% acetic acid (Skewes et al., 2007). These procedures were carried out in the field with assistance from the hunters. We were unable to weigh the carcasses. Each sample was washed in a 1.7 mm sieve (Wood and Roark, 1980). We determined the food items under stereoscopic lens, classifying them into eight categories: herbs and leaves, cultivated grains, wild seeds, fruits, roots, wood (parts of tree trunks and bark), invertebrates,

and vertebrates. Baiting with corn used by some hunters was not included in the food items of the animals captured using this technique. We calculated and recorded the percentage by volume of each food item by displacing the water in a volumetric beaker, according to Skewes et al. (2007). For each animal we recorded the sex (male or female), age (juvenile or adult, based on body size and tusk development), the method of capture (hunting with dogs, trapping, nocturnal hunting with searchlights) and the time of capture (morning, afternoon or night). We looked carefully at the stomach contents for remains of species considered particularly vulnerable to predation by wild boar (ground nesting birds, toads, bulbous perennial herbs, and seeds of *Araucaria angustifolia*).

Data analysis

We checked sample sufficiency through rarefaction. We used principal component analysis (PCA) to explore the dietary patterns in each ecoregion and redundancy analysis (RDA) to explore how the diet varies according to ecoregions, sex, age and the capture method, time of the day and season. In these ordinations, cultivated grains and wild seeds were pooled in order to evaluate the importance and variation of grain consumption. The data were previously standardized by Hellinger's transformation. We analyzed the significance of the RDA through the permutation test. These multidimensional techniques are suitable to obtain an overview of the data and to

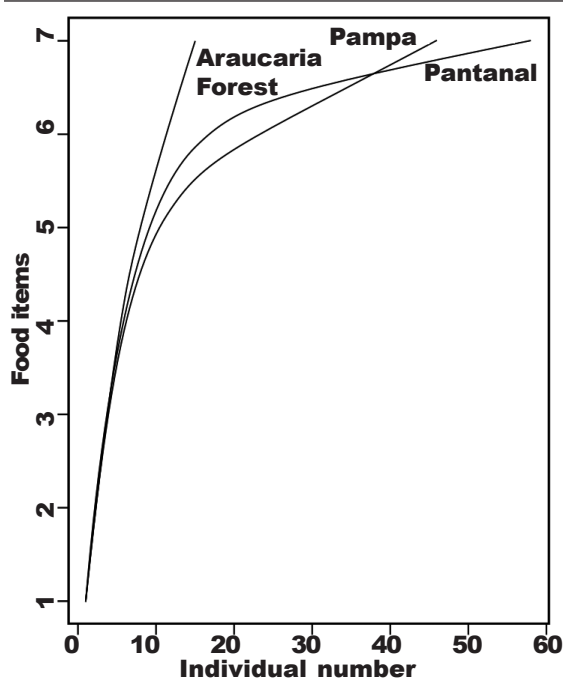


Fig. 2. Rarefaction curve using samples of stomach contents of wild boar from the Araucaria Forest, Pampa and Pantanal.

Fig. 2. Curva de rarefacción utilizando muestras de contenido estomacal de jabalíes del bosque de araucaria, la pampa y el pantanal.

orient further hypothesis testing. We employed the vegan package (Oksanen et al., 2017) of the software R (R Core Team, 2017) to perform these analyses.

We calculated the standardized Levin's index (Feinsinger et al., 1981) to estimate the breadth of the food composition niche within ecoregions and the Pianka index to estimate the food composition niche overlap between ecoregions (Colwell and Futuyma, 1971). For both indexes we used the proportion of each food item in each ecoregion, pooling the data of all stomach contents. These indexes vary from a minimum breadth or overlap of 0 to a maximum of 1. We calculated the index in the LibreOffice Calc spreadsheet (LibreOffice, 2018).

We analyzed the food and macronutrient composition through the RMT (right-angled mixture triangles) technique used to visualize the distribution of macronutrients in a multidimensional space (Machovsky-Capuska et al., 2016). In order to evaluate the percentage of each macronutrient in the diet, we first estimated the percentage of contribution of each food in grams to the total diet of each ecoregion. We then estimated the percentage of carbohydrates, lipids and proteins of each food from published data (appendix 1). Finally, we transformed them into energy content, taking carbohydrates and proteins as

equivalent to 17 KJ/g and lipids to 37 KJ/g (Raubenheimer and Rothman, 2013). The primary axes X and Y represent carbohydrates and proteins, respectively, while the implicit Z axis represents lipids. Each point represents the percentage participation in KJ of proteins (P), lipids (L) and carbohydrates (C) found in a food item. Segments of lines joining the points of the graph in a minimum convex polygon demarcate the nutrient space potentially accessible to wild boars in each ecoregion or season (Coogan et al., 2014). This nutrient space defines the fundamental niche of macronutrients, the space of the RMT in which the population may persist (Machovsky-Capuska, 2016). We calculated and designed the RMT in the LibreOffice Calc spreadsheet (LibreOffice, 2018).

Results

Rarefaction curves indicated that the number of samples was sufficient to characterize the diet in the Pantanal and Pampa, but insufficient to characterize those in the Araucaria Forest (see fig. 2). Consumption of herbs and leaves, cultivated grains, wild seeds, fruits, roots and vertebrates varied greatly across ecoregions and seasons, as is evident in the PCA. The first two axes of the PCA cumulatively explained 68.4 % of the variations in the proportion of food items among the individuals in the three ecoregions (see fig. 3). The diet showed a common pattern across ecoregions (as shown in table 1). In summary, herbs/leaves and roots were the items consumed in highest volume (respectively 11.4 to 44.1 % and 19.3 to 28.7 %) and frequency (33.3 to 65.5 % and 46.7 to 53.4 %) in all three ecoregions; cultivated grains were an important part of the diet in the two ecoregions characterized by agricultural matrix (Pampa and Araucaria Forest; above 40 % in frequency and volume); vertebrates, invertebrates and fruits were consumed in lower volume and frequency. Crops found in the stomachs were oats, sorghum, ryegrass, corn, rice and soybean. The consumption of vertebrates was frequent in the Pantanal (24.1 %, mainly amphibians) and in the Pampa (30.4 %, mainly sheep and armadillos *Dasypus* sp.). Fruits were frequent (15.5 %) in the Pantanal, with bocaiúva *Acrocomia aculeata* (Jacq.) Lodd. Mart. being the most consumed item in this category. We found baiting with corn in three samples, two from the Araucaria Forest (13 %) and one from the Pampa (2%). Corn baiting was identified by the pink color of seeds treated with fungicides.

The first two axes of the PCA in dry and flooding seasons in the Pantanal explained 80 % of the variation (see fig. 4). The wild boar diet in the Pantanal was composed mainly of roots in the flooding season (77.6 % in volume), and herbs/leaves in the dry season (56.7 % in volume), also including fruits and roots, as shown in table 2.

The major items in the diet of males and females were the same across ecoregions: cultivated grains (25.2 % and 26.5 %, respectively), herbs/leaves (24.3 % and 38.1 %) and roots (26.1 % and 22.7 %), although males ate almost four times more wild seeds

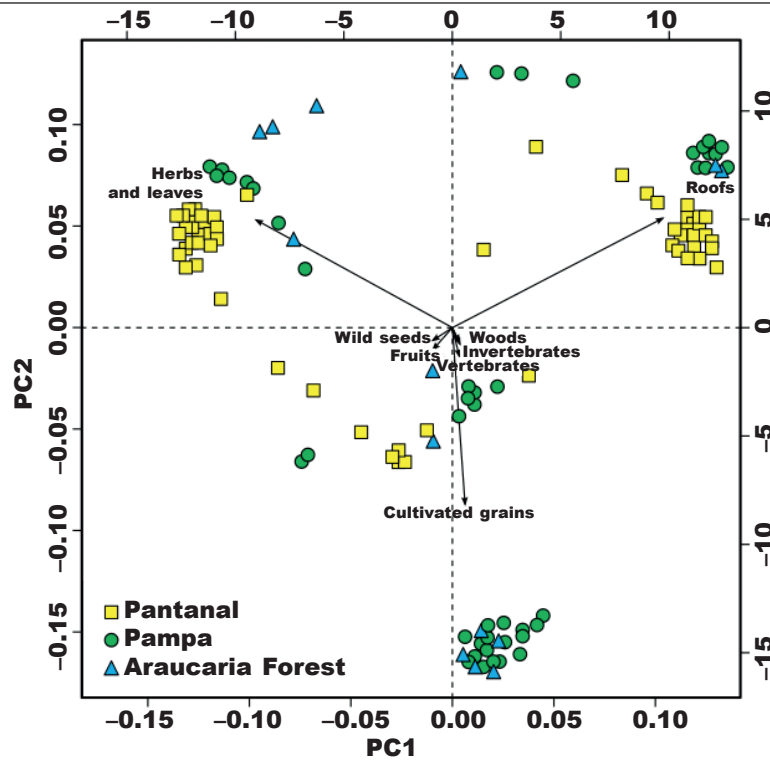


Fig. 3. Principal component analysis (PCA) depicting variations in the proportions of food items (cultivated grains, woods, invertebrates, vertebrates, fruits, wild seeds, roots and herbs/leaves) among individual wild boar in three Brazilian ecoregions: Pantanal, Pampa and Araucaria Forest.

Fig. 3. Análisis de componentes principales en el que se muestra la variación de la proporción de productos alimenticios (cereales cultivados, maderas, invertebrados, vertebrados, frutas, semillas silvestres, raíces e hierbas u hojas) en los individuos de jabalí en las tres ecorregiones del Brasil: el pantanal, la pampa y el bosque de araucaria.

Table 1. Percentage of volume and frequency of occurrence of food items in the stomachs of boar in three Brazilian ecoregions in 2015 and 2016.

Tabla 1. Porcentaje del volumen y la frecuencia de la presencia de productos alimenticios en el estómago de los jabalíes en tres ecorregiones del Brasil en 2015 y 2016.

	Pantanal (58 samples)		Pampa (45 samples)		Araucaria Forest (15 samples)	
	Volume	Frequency	Volume	Frequency	Volume	Frequency
Herbs and leaves	44.1	65.5	11.4	34.8	20.9	33.3
Cultivated grains	0.0	0.0	48.1	43.5	44.4	40.0
Fruits	7.0	15.5	0.2	6.5	0.0	0.0
Roots	28.7	53.4	28.5	47.8	19.3	46.7
Wild seeds	15.9	56.9	0.0	0.0	12.6	6.7
Vertebrates	0.4	24.1	9.4	30.4	1.7	13.3
Invertebrates	3.8	39.6	2.3	50.0	0.1	13.3
Woods	0.1	5.2	0.1	4.3	0.8	13.3

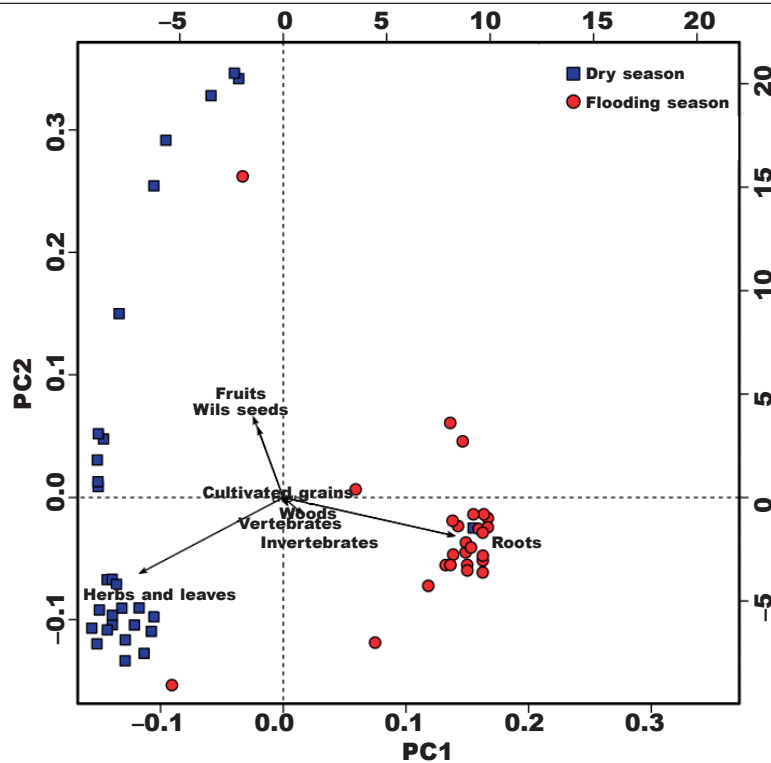


Fig. 4. Principal component analysis (PCA) depicting variations in the proportions of food items (cultivated grains, woods, invertebrates, vertebrates, fruits, wild seeds, roots and herbs/leaves) among individual wild boar in the dry and flooding seasons in the Pantanal ecoregion.

Fig. 4. Análisis de componentes principales en el que se muestra la proporción de productos alimenticios (cereales cultivados, maderas, invertebrados, vertebrados, frutas, semillas silvestres, raíces e hierbas u hojas) en los individuos de jabalí en la estación seca y la estación de las inundaciones en la ecorregión del pantanal.

Table 2. Percentage of volume and frequency of occurrence of food items in stomachs of boar for the flooding and dry seasons in the Pantanal ecoregion in 2015 and 2016.

Tabla 2. Porcentaje del volumen y la frecuencia de la presencia de productos alimenticios en el estómago de los jabalíes en la estación de las inundaciones y la estación seca en la ecorregión del pantanal en 2015 y 2016.

	Pantanal (15 samples)			
	Flooding season		Dry season	
	Volume	Frequency	Volume	Frequency
Herbs and leaves	6.4	40.7	56.7	90.3
Cultivated grains	0.0	0.0	0.0	0.0
Fruits	4.2	7.4	20.6	80.6
Roots	77.6	96.3	0.8	16.1
Wild seeds	1.9	29.6	20.6	80.6
Vertebrates	0.0	0.0	0.6	45.2
Invertebrates	9.8	70.4	0.6	12.9
Woods	0.0	0.0	0.1	9.7

Table 3. Percentage of volume of food items in stomachs of male and female boar in the three Brazilian ecoregions in 2015 and 2016.

Tabla 3. Porcentaje del volumen de los productos alimenticios encontrados en el estómago de machos y hembras de jabalíes en las tres ecorregiones del Brasil en 2015 y 2016.

	Pantanal (58 samples)		Pampa (45 samples)		Araucaria Forest (15 samples)		Total	
	Females	Males	Females	Males	Females	Males	Females	Males
Herbs and leaves	62.6	26.6	12.4	8.2	37.9	8.5	38.1	24.3
Cultivated grains	0.0	0.0	53.3	69.8	31.7	54.6	26.5	25.2
Fruits	7.0	20.1	0.5	0.0	0.0	0.1	3.5	8.9
Roots	20.0	30.0	23.9	14.5	30.4	23.8	22.7	26.1
Wild seeds	4.8	20.3	0.0	0.0	0.0	0.0	2.2	8.6
Vertebrates	0.3	0.4	6.4	4.8	0.0	10.6	3.0	4.0
Invertebrates	5.1	2.5	3.1	0.2	0.0	2.2	3.7	2.8
Woods	0.1	0.1	0.3	2.5	0.0	0.0	0.2	0.1

than females (8.6% in volume for males, 2.2% for females), as shown in table 3. The RDA showed that dietary differences were highly variable among individuals, being related to the spatial and temporal distribution of the samples ($F = 2.325$, $p < 0.001$), as shown in table 4. The first two axes of the RDA cumulatively explained 15.7% of dietary differences between individuals in relation to the time of year, the ecoregion, and the method and period of the hunting. Cultivated grains were consumed in a greater proportion in the Pampa, during the night, and when hunting with dogs. Roots and invertebrates were consumed more often during times of less abundance of resources, in the Pantanal, and in the morning or afternoon. Herbs/leaves were more consumed in the Araucaria Forest or in trapping (fig. 5, table 4).

The niche breadth measured by the standardized Levins index was 0.34 in the Araucaria Forest, 0.28 in the Pampa and 0.32 in the Pantanal. In the Pantanal, this index was 0.09 in the dry season and 0.15 in the flooding season. The niche overlap was low when the three studied ecoregions were compared (Pianka index = 0.15), being higher among the Pampa and Araucaria Forest and smaller between these and the Pantanal, as shown in table 5. The overlap was also low between flooding and dry seasons (Pianka Index = 0.10).

The analysis of the composition of macronutrients through RMT (fig. 6) indicated that the wild boar diet in the three ecoregions is on the margin of the macronutrient niche space established by Senior et al. (2016), especially due to the low intake of proteins. The diet was mainly composed of carbohydrates in all ecoregions. The proportion of carbohydrates in the diet was lower in Pantanal. In all cases the energy from proteins was below 20%, close to the lowest values found in other countries (Machovsky–Capuska

et al., 2016). Protein intake was relatively higher in the Pampa, mainly due to the contribution of vertebrates. Lipid intake in Pantanal (48%) was high, compared to that in other ecoregions studied. The lipid intake in this region was mainly due to the contribution of palm fruits. The diet in the flooding and dry seasons in the Pantanal was predominantly composed of carbohydrates (fig. 7). However, in the flooding season, carbohydrates corresponded to almost 90% of the diet due to the higher intake of grasses and roots, while in the dry season they corresponded to about 50%.

Discussion

We found that wild boars introduced in the Araucaria Forest, Pampa and Pantanal, three Brazilian ecoregions characterized by mosaics of grasslands and forests, have a diverse diet that is influenced by season, capture method and differences in local availability of resources, but not by individual traits. The consumption of cultivated grains, when available, was found in most samples, demonstrating the importance of these food items. The availability of cultivated grains (in our case oats, sorghum, rye, corn, rice and soybean), either used as supplementary feeding or for baiting, is related to the wild boar population and impact increase in Europe (Ballari et al., 2015; Miloš et al., 2016). In all ecoregions, the diet was located at the fringe of the ideal target that maximizes fitness, as proposed by Senior et al. (2016), and the supply of proteins was generally critical.

It is known that the wild boar is an opportunistic animal, feeding on any available food resource, although there are preferences (Schley and Roper, 2003). Seasonal differences in habitat use may also be related to changes in food availability (Oja et al.,

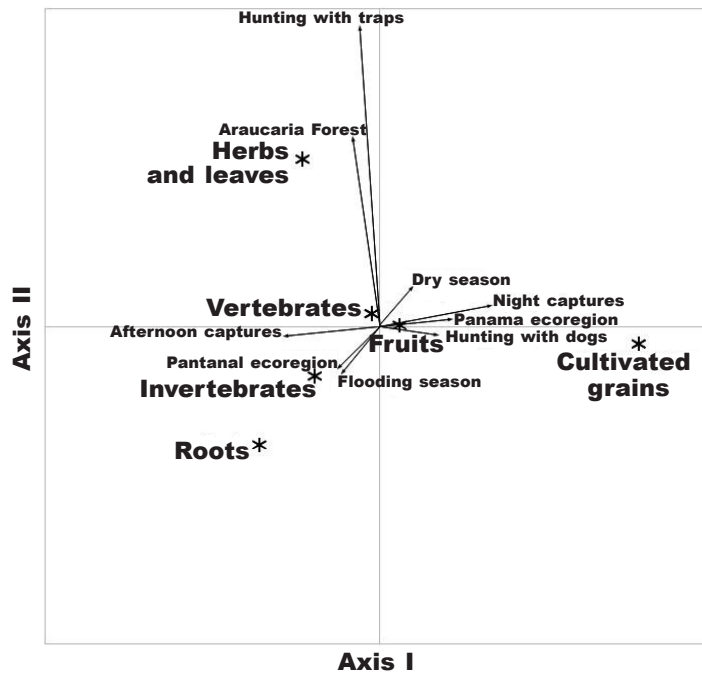


Fig. 5. Redundancy analysis (RDA) depicting the relationship of differences in the diet of wild boar according to the spatial and temporal distribution of the samples in the Pantanal, Pampa and Araucaria Forest.

Fig. 5. Análisis de la redundancia en el que se muestra la relación de las diferencias en la dieta del jabalí según la distribución espacial y temporal de las muestras en el pantanal, la pampa y el bosque de araucaria.

Table 4. Significance of the association of attributes of the wild boars and the spatial and temporal distribution of the samples (redundancy analysis axes) with the differences in the proportion of food items in the stomach contents of wild boar in three Brazilian ecoregions in 2015 and 2016.

Tabla 4. Significación de la asociación de las características de los jabalíes en la distribución espacial y temporal de las muestras (ejes del análisis de la redundancia) con las diferencias en la proporción de los productos alimenticios encontrados en el contenido estomacal del jabalí en tres ecorregiones del Brasil en 2015 y 2016.

Factor	Variance	F	P
Capture shift	0.043	4.161	0.001
Capture method	0.024	2.343	0.017
Period of the year	0.015	2.827	0.037
Ecoregion	0.023	2.261	0.025
Age strata	0.005	0.996	0.37
Sex	0.002	0	0.747
Residual	0.504		

2015). Herbs/leaves and roots formed the basis of the diet in the three ecoregions, perhaps because they are the most abundant and most widely available items everywhere (Chimera et al., 1995; Ballari and Barrios-García, 2014). Moreover, since pigs have difficulty extracting energy from fresh herbage (Wie-

Table 5. Food niche overlap (Pianka index, PI) of wild boar captured in the Pantanal, Pampa and Araucaria Forest ecoregions in 2015 and 2016.

Tabla 5. Solapamiento del nicho alimentario (índice de Pianka, PI) de los jabalíes capturados en las ecorregiones del pantanal, la pampa y el bosque de araucaria en 2015 y 2016.

	PI
Pantanal, Pampa and Araucaria Forest	0.15
Pantanal and Araucaria Forest	0.41
Pantanal and Pampa	0.55
Pampa and Araucaria Forest	0.94
Flooding and dry season	0.1

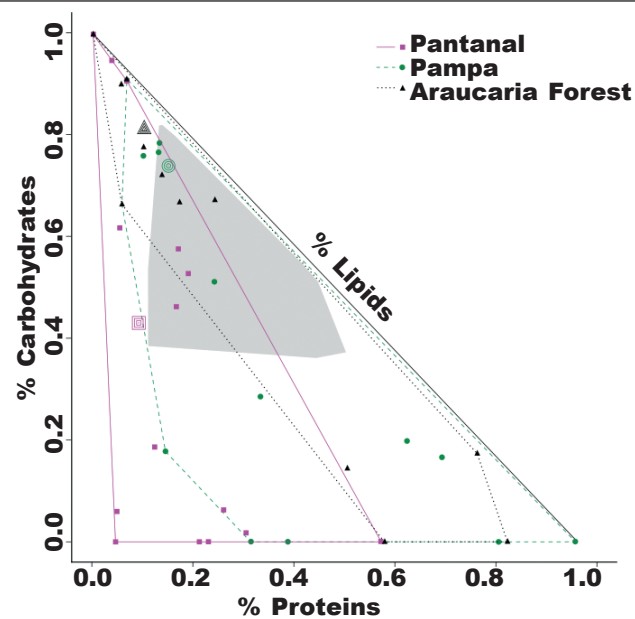


Fig. 6. Right-angled mixture triangle (RMT) of the three ecoregions studied in 2015 and 2016: Pantanal, Pampa and Araucaria Forest. The smaller symbols are the composition of macronutrients (carbohydrates, proteins and lipids) as a percentage of each food eaten by boar in each ecoregion. The larger symbols (diets) are the proportion of energy carbohydrates, proteins and lipids that the food set found in the diet provides the boar in each ecoregion. The gray area represents an estimate of the fundamental macronutrient niche found in the work of Senior et al. (2016), corresponding to the convex polygon formed by all diets. The areas surrounded by pink, green and black lines represent, respectively, the estimation of the fundamental macronutrient niche of the Pantanal, Pampa and Araucaria Forest.

Fig. 6. Diagrama triangular rectangular de la composición de la dieta de las tres ecorregiones estudiadas en 2015 y 2016: el pantanal, la pampa y el bosque de araucaria. Los símbolos pequeños representan la composición de macronutrientes (hidratos de carbono, proteínas y lípidos), expresada en porcentaje, de cada alimento consumido por el jabalí en cada ecorregión. Los símbolos grandes (dietas) representan la proporción de la energía que procede de los carbohidratos, las proteínas y los lípidos respecto de toda la energía que el conjunto de alimentos encontrados en la dieta proporciona a los jabalíes en cada región. El área gris representa una estimación del nicho fundamental relativo a los macronutrientes encontrado en el trabajo de Senior et al. (2016), que corresponde al polígono convexo formado por todas las dietas. Las áreas delimitadas por líneas rosas, verdes y negras representan, respectivamente, la estimación del nicho de macronutrientes fundamentales del pantanal, la pampa y el bosque de araucaria.

ren, 2000; Edwards, 2003; Massei and Genov, 2004), they need to feed themselves abundantly with herbs and leaves in order to extract enough energy for their survival. Rooting is also considered a signal of scarcity of preferred above ground resources (Zeman et al., 2018). The intake of cultivated grains in the Pampa and Araucaria Forest and fruits and wild seeds in the Pantanal was high in the seasons where these items were available, suggesting that these are preferred items, known to have high energy value (Caley, 1993). The lipid intake in Pantanal in the dry season was among the highest reported globally (Senior et al., 2016). Roots and invertebrates are important foods in the Pantanal, especially in the dry season. The niche overlap between peccaries and wild boars increases in the flooding season, when both species increase the consumption of fresh plants and fruits and reduce rooting (Sicuro and Oliveira, 2002).

The differences in stomach content as a function of hunting time and method probably reflect a habitat and feeding shift for refuges rather than biases due to collection method. Hunting influences wild boar behavior (Scillitani et al., 2010) and feeding patterns. Each mode of hunting occurs in a specific place and period of the day, and the stomach contents reflect the most recent feeding activity. Our results from stomach content analysis suggest that wild boar tend to move either to cultivated or open areas more frequently at night.

Sex and age group had negligible influences on the variation between individuals regarding stomach content. Although wild boar nutritional needs were reported to vary with age (Dardaillon, 1986), sex, and reproduction (Wilcox and Van Vuren, 2009), not all studies have found significant differences (Wood and Roark, 1980; Loggins et al., 2002; Adkins and

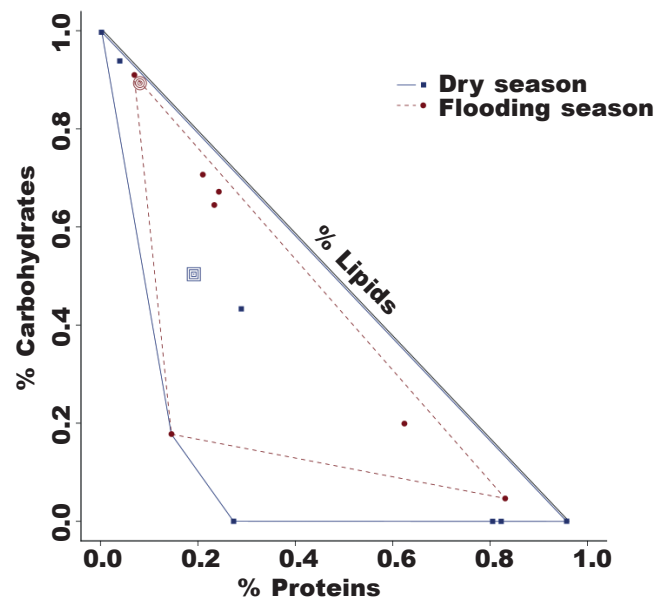


Fig. 7. Right-angled mixture triangle (RMT) of the Pantanal ecoregion in the flooding and dry seasons in 2015 and 2016. The smaller symbols represent the composition of macronutrients (carbohydrates, proteins and lipids) in percentage of each food ingested by the boars in each period. The larger symbols (diets) are the proportion of energy carbohydrates, proteins and lipids that the food set found in the diet provides to the boar in each period. The areas surrounded by the blue and red lines represent, respectively, the estimation of the fundamental macronutrient niche of the Pantanal in the flooding season and in the dry season.

Fig. 7. Diagrama triangular rectangular de la composición de la dieta de la ecorregión del pantanal en la estación seca y la estación de las inundaciones en 2015 y 2016. Los símbolos pequeños representan la composición de macronutrientes (hidratos de carbono, proteínas y lípidos), expresada en porcentaje, de cada alimento consumido por los jabalíes en cada período. Los símbolos grandes (dietas) representan la proporción de la energía que procede de los carbohidratos, las proteínas y los lípidos respecto de toda la energía que el conjunto de alimentos encontrados en la dieta proporciona a los jabalíes en cada período. Las áreas delimitadas por líneas azules y rojas representan, respectivamente, la estimación del nicho de macronutrientes fundamentales del pantanal en estación de las inundaciones y la estación seca.

Harveson, 2006). We interpret this as a consequence of the difficulty in adjusting the diet under the limiting conditions of wild environments. It is also possible that differences are undetected because hunted animals do not represent the complete age structure of the population. The gregarious habit could also minimize differences in the food content of animals of the same group, but the individuals we collected were always independent sampling units.

In our data, the consumption of native fauna was sporadic. We recorded a few samples of amphibians in the Pantanal and armadillos *Dasyus* sp. in the Pampa and bird feather in the Araucaria Forest. We did not record the egg intake found in the Pantanal by Desbiez et al. (2009), nor did we record the intake of fauna and flora of special conservation concern.

The main economic effect of the presence of wild boar, based on the stomach contents, is the consumption of cultivated grains, whereas in the livestock sector, the damage appears to be sporadic or localized. Cultivated grains were found in most of the sample from the Pampa and Araucaria Forest. We recorded

a few stomachs with sheep meat and wool. Most of the vertebrate samples contained fly larvae, indicating that at least part of this consumption was of carcasses. This finding agrees with the opportunistic scavenger habit of wild boars in the Pampa ecoregion (Herrero and Fernández de Luco, 2003; Desbiez et al., 2009), as well as in its native range (Espadas et al., 2010). Alternatively, boars could be actively searching for alternative protein rich resources, which are scarce in the available plant material (Ballari and Barrios-García, 2014).

In the three ecoregions, the diet we recorded is at the margin of the ideal target that maximizes the fitness of wild boar according to Senior et al. (2016), mainly due to the low protein intake, suggesting an unbalanced diet. Potential consequences on reproduction and caring capacity are expected (Senior et al., 2016) and deserve further research. The domestic pig, under optimum conditions for fattening and reproduction, requires about 14.5% of protein in periods of growth and lactation (Zardo and Lima, 1999). Crude protein content in diet of feral pigs is optimal above

12% (Coblentz and Baber, 1987). These targets are higher than the amount we found in Pantanal (9.3%) and in the Araucaria Forest (10.3%), but not in the Pampa (15.2%). In the studied ecoregions, this may apply particularly in the Pampa and in the dry season in the Pantanal.

Comparing our RMT results with Senior et al. (2016), correspondence of the food niche with climate becomes evident. The food niche in the Pampa and Araucaria Forest resembles that found in Australia, in Italian Piedmont (Cfa) and in France (Cfb). None of the regions revised by Senior et al. (2016) have a tropical seasonal climate similar to that of the Pantanal (Tropical Savanna, Aw). Our data highlight the plasticity of the wild boar diet.

We recognize some limitations of our study. We obtained an unbalanced sample between the regions and seasons of the year, and the sampling in the Araucaria Forest ecoregion was insufficient to recover the whole set of potential foods. However, we were still able to characterize regional patterns and provide an overview of the wild boar food and macronutrient niches for these three regions where the species is already established and expanding. We segregated the items into general categories, which allowed us to provide information about regional differences in major items, the macronutrient share in the diets and relative niche breadth based on major food categories. We were unable to discriminate the intake at the species level, which precludes the identification of predation over species of special conservation concern, a central question about effects of invasive species. However, we adopted a standard and precise volumetric analysis (Zeman et al., 2016) and are confident that vertebrates and insects were predated only passively or opportunistically, at low levels. Moreover, we did not find remains of major plant families, including endangered species particularly vulnerable to wild boar feeding habits, such as Cactaceae, Amarillydaceae, Liliaceae and Amaranthaceae. Molecular techniques are best suited for recovering the presence of items consumed in low quantity (Robeson II et al., 2017) but can only provide frequency measures.

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Appendix 1. Values and sources of information regarding the percentage of carbohydrates, lipids and proteins for each food item according to macro-nutritional analyses.

Apéndice 1. Valores y fuentes de información relativa al porcentaje de carbohidratos, lípidos y proteínas de cada producto alimenticio según los análisis macronutricionales.

Item	Protein	Carbohydrate	Lipid	Source
Herbs and leaves	0.25	0.69	0.04	USDA/APHIS/WS (2010)
Bromeliads	0.04	0.95	0.01	USDA/APHIS/WS (2010)
Corn and oats	0.15	0.78	0.07	USDA/APHIS/WS (2010)
Legumes	0.0028	0.997	0.0002	USDA/APHIS/WS (2010)
Corn	0.11	0.83	0.06	USDA/APHIS/WS (2010)
Corn and sorghum	0.12	0.82	0.05	USDA/APHIS/WS (2010)
Salvinia	0.34	0.51	0.15	Henry-Silva and Camargo (2002)
Oats	0.19	0.73	0.08	USDA/APHIS/WS (2010)
Sorghum	0.14	0.81	0.05	USDA/APHIS/WS (2010)
Rice	0.14	0.82	0.04	USDA/APHIS/WS (2010)
Rice and soybeans	0.28	0.59	0.13	USDA/APHIS/WS (2010)
Soybeans	0.42	0.36	0.22	USDA/APHIS/WS (2010)
Rosaceae	0.11	0.82	0.07	USDA/APHIS/WS (2010)
Grass	0.22	0.74	0.04	USDA/APHIS/WS (2010)
Amphibians	0.98	0.00	0.02	Waibel et al. (1987)
Mammals	0.9	0.00	0.1	Waibel et al. (1987)
Sheep	0.58	0.00	0.42	Pinheiro et al. 2007
Armadillo	0.9	0.00	0.1	Waibel et al. (1987)
Vertebrates	0.91	0.00	0.09	Waibel et al. (1987)
Birds	0.75	0.00	0.25	Waibel et al. (1987)
Roots	0.07	0.92	0.01	USDA/APHIS/WS (2010)
Fruits	0.17	0.27	0.56	Coimbra and Jorge (2011)
Seeds	0.25	0.69	0.06	Coimbra and Jorge (2011)
Araucaria seed	0.06	0.92	0.02	NEPA (2011)
Bivalve mollusks	0.69	0.22	0.09	USDA/APHIS/WS (2010)
Ants and beetles	0.45	0.00	0.55	Bukkens (1997)
Crustaceans	0.89	0.05	0.06	USDA/APHIS/WS (2010)
Invertebrates	0.63	0.18	0.2	Bukkens (1997)
Earthworms	0.79	0.18	0.03	Tacon et al. (1983)
Fly larva	0.75	0.18	0.07	Bukkens (1997)
Beetle larva	0.62	0.00	0.38	Bukkens (1997)
Wood	0.07	0.78	0.16	USDA/APHIS/WS (2010)