

**University of São Paulo
“Luiz de Queiroz” College of Agriculture
Center for Nuclear Energy in Agriculture**

**The armadillos: from ecosystem services and online opinions to land use in
agricultural landscapes**

Thiago Ferreira Rodrigues

Thesis presented to obtain the degree of Doctor
in Science. Area: Applied Ecology

**Piracicaba
2019**

Thiago Ferreira Rodrigues
Bachelor degree in Biological Sciences

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To Aline and Chica, my parents and sister,
and all of my past professors.
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EPIGRAPH

*“Tá tudo diferente
mata tu não vê
ab, meta tua”*

*Tô cabreiro
de tocaia a espiar
um ato capaz de mudar.”*

—Thiago F. Rodrigues - Agosto 2017

*“You can’t always get what you want
But if you try sometimes you just might find
You get what you need.”*

—Mick Jagger and Keith Richards

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RESUMO

Os tatus: de serviços ecossistêmicos e opiniões online ao uso da terra em paisagens agrícolas

Esta tese gira em torno da ideia de que os tatus representam um importante grupo de mamíferos que desempenham funções ecológicas essenciais, mas que ao longo dos anos tem recebido pouca atenção tanto pelos cientistas quanto pelo público em geral, o que aumenta a preocupação em relação ao status de conservação deste grupo. Ao longo dos cinco capítulos que compõem esta tese, utilizando os tatus como modelo de estudo, demonstro sua importância para o ecossistema terrestre, acesso as percepções do público geral, desenvolvo uma ferramenta computacional para viabilizar um aumento no número de pesquisas e busco entender como paisagens modificadas pelo homem podem influenciar este grupo. Para tanto, procurei utilizar uma abordagem multidisciplinar. No *Capítulo 1*, identifico quais são as contribuições ecológicas fornecidas pelos tatus diretamente relacionadas ao homem, levando em consideração aspectos sociais, econômicos, culturais, ambientais e biológicos. No *Capítulo 2*, reconheço por meio de comentários na mídia social que o público geral possui um grande apreço pelo grupo, mas desconhecem a maioria das espécies e correspondentes funções ecológicas. No *Capítulo 3*, desenvolvo uma ferramenta cujo objetivo é viabilizar o uso de tocas como um método não invasivo de baixo custo para a identificação de quatro espécies de tatus. No *Capítulo 4*, elucido que florestas nativas dentro e fora de Unidades de Conservação são essenciais para a manutenção de uma espécie de tatu, o tatu-galinha, em paisagens agrícolas, com implicações relacionadas à importância do Código Florestal Brasileiro. Finalmente, no *Capítulo 5*, ao mostrar como duas espécies pouco conhecidas de tatus (*Cabassons* sp.) respondem à um cenário predominantemente dominado por cana-de-açúcar, avanço na compreensão das ainda pouco estudadas consequências deste tipo de paisagem agrícola sobre a biodiversidade. Em conclusão, esta tese contribui para o entendimento da importância dos tatus de maneira ampla, bem como no oferecimento de alternativas para melhorar o status de conservação desse importante grupo.

Palavras-chave: Armadilha fotográfica; Aprendizado de máquina; Conservação; Mídia social; Paisagem agrícola; Serviço ecossistêmico.

ABSTRACT

The armadillos: from ecosystem services and online opinions to land use in agricultural landscapes

This thesis revolves around the idea that armadillos represent an important group of mammals that perform essential ecological functions; however, over the years have received little attention from both scientists and the general public, which raises a concern about the conservation status of this group. Over the five chapters of this thesis, using armadillos as a study model, I demonstrate their importance for the terrestrial ecosystem, access the perceptions of the general public, develop a computational tool to enable an increase in research and seek to understand how human-modified landscapes can influence this group. For that, I use a multidisciplinary approach. In *Chapter 1*, I identify the ecological contributions provided by armadillos directly related to humans, including social, economic, cultural, environmental, and biological aspects. In *Chapter 2*, I recognize through comments on social media that the general public has aroused great interest for this group, but they are unaware of most species and their corresponding ecological functions. In *Chapter 3*, I develop a tool that aims to enable the use of burrows as a low-cost non-invasive method to identify four species of armadillos. In *Chapter 4*, I elucidate that native forests inside and outside protected areas are essential for maintaining a species of armadillo, the nine-banded armadillo, in agricultural landscapes, with implications regarding the importance of the Brazilian Forest Code. Finally, *Chapter 5* advances in the understanding of the underexplored consequences of human-modified landscapes on biodiversity, by showing how two poorly known armadillo species (*Cabassous* sp.) respond to a scenario predominantly dominated by sugarcane. Altogether, this results contribute to broadening our understanding of the importance of armadillos, as well as offer ways to improve the conservation status of this important group.

Keywords: Camera-trap; Machine learning; Conservation; Social media; Agricultural landscape; Ecosystem service.

1. INTRODUCTION

Conservation is an interdisciplinary and applied field aiming to conserve biological diversity globally, including tackling complex and dynamic socio-ecological challenges (McShane *et al.*, 2011; Elliott, Ryan, & Wyborn, 2018). To address this complexity, conservation is becoming more integrative, interactive, and inclusive (Colloff *et al.*, 2017; Elliott *et al.*, 2018), with trends towards social awareness (Bennett *et al.*, 2017) and a greater consideration of social, political and economic trade-offs associated with conservation actions (McShane *et al.*, 2011; Díaz *et al.*, 2018). At the same time, the last decade has witnessed a rapid emergence of tools that facilitate widespread participation in generating scientific knowledge (Hampton *et al.*, 2013; Allan *et al.*, 2018). Conservationists now are faced with the challenge of developing new approaches to rapidly and robustly analyze these increasingly large datasets and to integrate different forms of data into practicable approaches to conservational problems (Di Minin, Tenkanen, & Toivonen, 2015; Elliott *et al.*, 2018).

1.1. Ecosystem services and the human well-being

Human needs have been, and continue to be, satisfied at the expense of altered land use, climate, biogeochemical cycles, biotic invasions, and species distributions (Millennium Ecosystem Assessment, 2005). The mark of humanity on the biosphere is now so profound and widespread that many consider Earth to have entered a new geological epoch, the *Anthropocene* (Waters *et al.*, 2016). As a result, wild populations and the places they live are declining faster now than at rates found in the fossil record (Barnosky *et al.*, 2012), raising concerns about the consequences of such loss for ecosystem functioning and human well-being (Millennium Ecosystem Assessment, 2005).

Nowadays, researchers, land managers, politicians, and the general public all have vested interests in better understanding the importance of biodiversity as a source of ecosystem services (Cardinale *et al.*, 2012). The concept of *ecosystem services* (currently known as *nature's contributions to people*) have been increasingly used to describe the supply of benefits from ecosystems to society that support human life and well-being (Millennium Ecosystem Assessment, 2005; Díaz *et al.*, 2018). By identifying the role of biodiversity in the provision of services with demonstrable value to people, conservation arguments no longer relies solely on the notion of biodiversity for biodiversity's sake, or for the *intrinsic value* of species (the spiritual or ethical consideration of a right of species to exist independent of their use by people). If we can identify linkages between people, biodiversity, and ecosystems and quantify their value, we can argue more effectively for

the protection of ecosystems and the species within them, and so influence public opinion and policy decisions (Daily *et al.*, 2009).

1.2. Culturomics towards conservation

One of the major conservation objectives has been to understand what drives the societal attention and interest regarding the natural world (Bennett *et al.*, 2017). As human activities are the main drivers of the ongoing biodiversity declines (Dirzo *et al.*, 2014), there is an urgent need to further the understanding of the public interest towards nature's conservation (Chan *et al.*, 2016). Culturomics is an emerging field that focuses on the study of human perception or behavior through the quantitative analysis of digital data, increasingly applied toward conservation (Ladle *et al.*, 2016; Toivonen *et al.*, 2019). Information gathered from culturomics studies provide, for instance, new approaches to studying public interest in the environment (Hausmann *et al.*, 2018) and species (Roberge, 2014; Hausmann *et al.*, 2019), trends in wildlife trade (Di Minin *et al.*, 2019), hunting (Bizri *et al.*, 2015) and fishing (Sbragaglia *et al.*, 2019), patterns in public visitation of protected areas (Tenkanen *et al.*, 2017) and cultural ecosystem services (Richards & Friess, 2015; Gliozzo, Pettoelli, & Haklay, 2016), impacts of conservation campaigns (Kerhoas *et al.*, 2019), among others insights. Culturomics is becoming increasingly feasible for analyzing video and audio files (Sherren *et al.*, 2017; Toivonen *et al.*, 2019), including sentiments (Lennox *et al.*, 2019). By engaging with new and powerful online data resources, the emerging field of conservation culturomics provides unprecedented opportunities to understand the human culture and its interaction with the natural world (Ladle *et al.*, 2016).

1.3. Technoecology and the use of machine-learning-based methods

Evaluating how wildlife and humans interact in the same environment can be often not an easy task, particularly for low-density, elusive and not well-known species, most of which are threatened (Schipper *et al.*, 2008). In recent years, the rapid advance of novel technologies and their widespread availability for research purposes has been successfully applied in ecology. Methods including camera-trapping, remote sensing and GIS, high-precision GPS, bio-loggers, and even drones are increasingly being developed to improve the access on wild populations (Allan *et al.*, 2018). For instance, camera trap methodology now encompasses a wide range of equipment and ecological applications which provide a unique advantage by recording the undisturbed behaviors of animals within their environment (*Fig. 1*). This has resulted in the discovery of surprising community structures, ecological interactions, and social dynamics, among other insights (Burton *et al.*, 2015).



Figure 1. Camera-trap positioned inside a forest fragment in Cerrado of southeastern Brazil.

On the other hand, improved *technoecology* has brought ecology into the realm of *big data* (generation of large data volumes), increasing up the challenges associated with the statistical framework (Hampton *et al.*, 2013; Cao, 2016; Allan *et al.*, 2018). A handful of ecologists have begun using statistical modeling not solely based on theory-driven (hypothesis-testing) but also based on data-driven (information-searching) due to the great amount of available information (Thessen, 2016). A high profile example is the current uses of deep learning systems (artificial intelligence) for species and animal individual identification from large datasets provided by camera traps (Norouzzadeh *et al.*, 2018). The advantage of machine-learning-based methods over traditional statistical techniques is the ability to model highly dimensional and non-linear data with complex interactions and missing values (Thessen, 2016). As ecological data specifically are known to be very intricate, ecologists and conservationists are particularly well positioned to take advantage of these methods.

1.4. Ecological research in agricultural landscapes

Biodiversity-ecosystem relationships can be even more complex in altered landscapes (Tschardt *et al.*, 2005; Fahrig *et al.*, 2011). Globally, forest conversion to agricultural lands

together with intensified land use in agriculture and forestry are irrefutably the main causes of global change on Earth (Tschardtke *et al.*, 2005; Foley *et al.*, 2005). These *human-modified landscapes* range widely in their degree of spatial and temporal heterogeneity which can influence both positively and negatively a variety of ecological responses (Tschardtke *et al.*, 2005; Fahrig *et al.*, 2011). By spatial heterogeneity, such landscapes can show different composition (types and proportions of different forms of land covers) and/or different spatial configuration (spatial arrangement of a given land use/land cover) (Fahrig *et al.*, 2011; *Fig. 2*). Changes in landscape composition and configuration not only alter patterns of local diversity (α) but also the structure of remaining assemblages, potentially altering the species turnover (β -diversity) and the whole ecosystem functioning (Carrara *et al.*, 2015; Beca *et al.*, 2017).

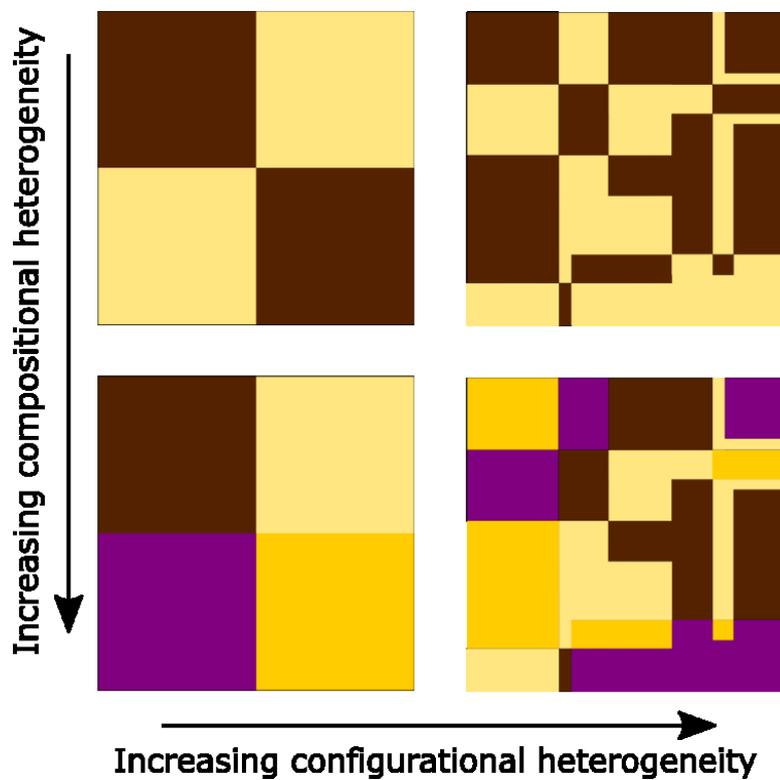


Figure 2. Illustration of the two major axes of spatial heterogeneity: compositional and configurational heterogeneity. Each large square is a landscape and different colours represent different cover types within landscapes. Compositional heterogeneity increases with increasing number and/or evenness of cover types. Configurational heterogeneity increases with increasing complexity of the spatial pattern. Source: Fahrig *et al.* (2011).

Understanding how wildlife responds to these human-modified habitats remains a key challenge. Furthermore, species often shows multi-scale responses to specific habitat feature (Miguet *et al.*, 2016). As we usually do not know the best scale for a given environmental variable and biological response, a common goal for landscape ecologists has been to relate a biological

response at a given location (e.g. species occupancy) to environmental factors in the surrounding area (e.g. spatial heterogeneity), considering multiple spatial scales (Miguet *et al.*, 2016). To identify the optimal *scale of effect* researchers compare the effect of landscape structure on the species response using a multiscale study design (Jackson & Fahrig, 2015). This approach has improved our knowledge of how landscape context shape wildlife-habitat-ecosystem relationships thus offering a great opportunity of research.

1.5. The amazing armadillos

Among the vertebrate orders, terrestrial mammals are highly negatively influenced by agricultural habitat disturbance, partly due to their overall dependence on forest ecosystems (Dirzo *et al.*, 2014; Bogoni *et al.*, 2018). In virtually all environments worldwide, mammals are severely threatened by population declines (Dirzo *et al.*, 2014). In terrestrial system, mammals play crucial ecological roles including as top-down regulators of prey populations, primary consumers, seed dispersal and bioturbation agents, and several other non-redundant ecosystem services (Davidson, Detling, & Brown, 2012; Fleming *et al.*, 2014). Notably, an interesting group, the armadillos (*Fig. 3*), mediate several of these key ecological processes while facing anthropogenically landscapes, but have long been neglected by the scientific community and usually does not reach a wide audience (Superina, Pagnutti, & Abba, 2014; Loughry *et al.*, 2015).



Figure 3. *Dasypos novemcinctus*, the nine-banded armadillo. Photograph: Mariella Superina.

To meet our objectives, this thesis has been organized into five chapters, each one to address a specific issue above commented. Briefly, we start this work by systematically reviewing the literature to identify ecological functions provided by armadillos with direct consequences for ecosystem services and human well-being; Then, we assess the online opinions towards armadillos on social media to get insights for their conservation; and, we present an automatic burrow identification analysis (based on machine learning approach) for four species of armadillos allowing ecologists to use a non-invasive low-cost method to study them; Finally, we investigate how agricultural and silvicultural landscapes affect a species of armadillo, the nine-banded armadillo, and how sugarcane dominated landscapes within private lands affect two poorly known armadillo species (*Cabassous* sp.) in a broader geographic area. We conclude this thesis with general considerations of our results and their implications based on these five chapters. The main objectives of each chapter are detailed below:

- Chapter 1.* We summarize current knowledge about ecosystem services provided by armadillos, clarify the importance of their services and suggest directions for future research. We highlight ecosystem services that are unique to armadillos, particularly those that represent powerful arguments to justify their conservation.
- Chapter 2.* We use online data from YouTube to assess attitudes towards armadillos whether positive or negative and to gain insights through comments about armadillos online.
- Chapter 3.* We target the following question: is it possible to identify similar body-sized armadillos based on their burrows?
- Chapter 4.* We evaluate how agricultural and silvicultural landscapes affect nine-banded armadillos with occupancy modeling using camera trap data from three highly modified landscapes in southeastern Brazil. Specifically, we assessed the relative effects of landscape composition (native forest, sugar cane, and managed forest plantation) and configuration (edge density), as well as anthropogenic impacts (distance from human residences), degree of protection (government protected areas) and natural features (terrain slope and distance from watercourses) as potential predictors of landscape occupancy.

Chapter 5. We evaluate how composition and configuration landscape variables affect naked-tailed armadillos (*Cabassous* sp.) occurrence in sugarcane dominated landscapes.



As a last remark, if the reader got here I suppose the text aroused some curiosity about these awesome species and their ecology. I hope that the organization of the chapters as such will make sense to the reader and that it be an enjoyable reading experience as far as possible. Although the chapters generally follow the structure of a scientific manuscript, I made some small adjustments thinking of the comfort of reading, such as the addition of some photos and the insertion of figures and tables in the body of the text. Finally, I would like to register that I really enjoyed doing a Ph.D. and I had great moments during the last three and a half years.

To those who will read this thesis, I hope it is a pleasant reading.

To those who will leaf through it, I hope you like some of the figures and you are lucky to find one or other information that you find interesting.



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2. ECOSYSTEM SERVICES PROVIDED BY ARMADILLOS

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Abstract

Awareness of the natural ecological processes provided by organisms that benefit human well-being has significantly progressed towards the goal of making conservation a mainstream value. Identifying different services and the species that provide them is a vital first step for the management and maintenance of these so-called ecosystem services. Herein, we specifically address the armadillos, which play key functional roles in terrestrial ecosystems, including as ecosystem engineers, predators, and vectors of invertebrates and nutrients, although these roles have often been overlooked. Armadillos can control pests, disperse seeds, and be effective sentinels of potential disease outbreaks or bioindicators of environmental contaminants. They also supply important material (meat, medicines) and non-material (learning, inspiration) contributions all over the Americas. We identify key gaps in the understanding of ecosystem services provided by armadillos and areas for future research required to clarify their functional role in terrestrial ecosystems and the services they supply. Such information will produce powerful arguments for armadillo conservation.

Keywords: biodiversity, Cingulata, conservation, ecological function, ecosystem services, interactions, mammal, nature's contribution to people, sustainability, Xenarthra.

2.1. Introduction

Over the past few decades, knowledge about the relationships between biodiversity and ecosystem function has gained importance allowing more effective arguments for the protection

of ecosystems and the species that inhabit them, and influencing public opinion and policy decisions (Daily *et al.*, 2009). In an era of ongoing biodiversity declines (Dirzo *et al.*, 2014; Young *et al.*, 2016), there is an urgent need to further the understanding of which ecosystem services (natural ecological processes that benefit human society) are provided by species that interact with a broad range of other species directly or indirectly, for example as keystone species or ecosystem engineers (Caro & Girling, 2010), and to establish methodologies for quantifying their value (Wenny *et al.*, 2011; Green & Elmberg, 2014). In terrestrial systems, mammals play important roles in diverse ecological processes such as nutrient cycling, seed dispersal and bioturbation (Fleming *et al.*, 2014), and armadillos mediate several of these processes.

Armadillos (Xenarthra, Cingulata) are semi-fossorial mammals that are widely distributed in Central and South America; only one species currently reaches North America (Wetzel, 1985). There are 20 extant armadillo species that vary in size (15–150 cm body length) and mass (adult body mass: 0.1–40 kg) (McDonough & Loughry, 2018; Superina & Abba, 2018). Half of the living species have an unknown population trend but at least six species are declining (Abba & Superina, 2010; IUCN, 2019). They are the only mammals bearing a carapace that consists of osteoderms covered by epidermal scales (Engelmann, 1985). In addition to their conspicuous carapace, they have relatively low metabolic rates (McNab, 1985), which may contribute to their relatively poor thermoregulatory abilities. Diets emphasize invertebrate prey (Redford, 1985), and all species dig burrows (Eisenberg & Redford, 1999; Attias *et al.*, 2016). By so doing, armadillos can create new habitats or modify ecosystem features. For example, their burrowing activity alters vegetation, promotes sediment movement and increases nutrient availability, which, in turn, affects forest dynamics and regeneration (Mazía *et al.*, 2010; Sawyer *et al.*, 2012). Moreover, their burrows act as a refuge and form suitable habitats for vertebrates and invertebrates (Taber, 1945; Clark, 1951; Leite-Pitman, 2004; Desbiez & Kluyber, 2013; Aya-Cuero, Rodríguez-Bolaños & Superina, 2017). Armadillos act as key prey for top and mesocarnivores (Foster *et al.*, 2010; Giordano *et al.*, 2018; Miranda *et al.*, 2018), as sentinel species (Bagagli *et al.*, 2003; Jarvis *et al.*, 2013; Rossi *et al.*, 2016), and have cultural importance in many parts of America (Bovey, 2003; Alves *et al.*, 2012b; Valle *et al.*, 2015). Thus, they are an ideal group to examine ecosystem services. Surprisingly, however, there is virtually no research about ecosystem services provided by armadillos. In fact, armadillo research is plagued by several knowledge gaps and usually does not reach a wide audience (Superina, Pagnutti & Abba, 2014; Loughry *et al.*, 2015), which increases the importance of explicitly considering the role armadillos play as subsidies in terrestrial ecosystems.

The ecosystem services (ES) approach emphasizes the relationships among ecosystems, biodiversity, and their contributions to people (Millennium Ecosystem Assessment, 2005; Díaz *et al.*, 2018), including social, environmental, economic, and cultural aspects (Wenny *et al.*, 2011; Green & Elmberg, 2014). The ES approach recognizes the multiple values of ecosystems, as it helps to build meaningful relationships between nature and humans (i.e. relational values), provides individual utility and economic development (i.e. instrumental value), and places value on the ecosystems themselves (i.e. intrinsic values) (Chan *et al.*, 2016). Identifying such values is key not only to environmental stewardship but also to achieving social–ecological relationships that yield fulfilling lives for present and future generations. Here we summarize current knowledge about ecosystem services provided by armadillos, clarify the importance of their services and suggest directions for future research. We highlight ecosystem services that are unique to armadillos, particularly those that represent powerful arguments to justify their conservation.

2.2. Methods

Our literature search was based on *Web of Science* and *Scopus* using all available years and a combination of the following key words: ‘*armadillo**’ OR ‘*dasypus*’ OR ‘*dasypos**’ OR ‘*euphract**’ OR ‘*priodont**’ OR ‘*tolypeut**’ OR ‘*chaetophract**’ OR ‘*zaedyus*’ OR ‘*cabassous*’ OR ‘*calyptophract**’ OR ‘*chlamyphorus*’ AND (‘*ecosystem**’ OR ‘*service**’ OR ‘*ecolog**’ OR ‘*conservat**’ OR ‘*manag**’ OR ‘*agricultur**’ OR ‘*zoolog**’ OR ‘*geomorpholog**’ OR ‘*cultur**’). We also conducted haphazard searching in *Google Scholar* using some of the key words listed above and by conducting an additional search using the key words in Portuguese and Spanish. We based our review on structured literature using the preferred reporting items for systematic reviews and meta-analyses, PRISMA (Moher *et al.*, 2009; Nakagawa *et al.*, 2017; see online Supporting Information, *Fig. S1*), but did not conduct a formal meta-analysis. The online database search was last performed on 2 December 2018 on titles, abstracts and key words in all databases, except on *Google Scholar*. From the list of studies obtained, we used their titles to identify studies of interest and scanned their abstracts searching for information on ecosystem services provided by armadillos. In order to be included in this review, the study had directly or indirectly to provide information towards an ecosystem service provided by armadillo species. When this information was found, we consulted the main text and classified it within the generalizing perspective of the ‘*nature’s contribution to people*’ (NCP) framework (Díaz *et al.*, 2018). The NCP framework evolved from the ES concept popularized by the Millennium Ecosystem Assessment (2005) and is the current framework adopted by the Intergovernmental Science–Policy Platform on Biodiversity and Ecosystem Services (IPBES)

(Díaz *et al.*, 2018). The NCP framework encompasses 18 categories from three main groups of ecosystem services or, as they put it, contributions: regulating, material, and non-material (see *Fig. S3* and *Table S1* in Díaz *et al.*, 2018). Ecosystem services and ‘contributions’ (short for nature’s contributions to people) are treated here as synonyms. We also searched the references (backward search) and citation record (forward search) of the selected studies for other studies that could provide additional data (see *Table S1* and *Fig. S1*). This procedure was last performed on 5 April 2019.

2.3. Results

Ecosystem services provided by armadillos were mentioned directly or indirectly 355 times in 289 studies (*Table 1*, see *Table S1* for full details). Studies were not evenly distributed among ecosystem services, with some services receiving more attention (e.g. interaction with other taxa) than others (e.g. nutrient cycling, *Table 1*) or addressing fewer armadillo species. Overall, armadillos provided many positive effects on ecosystem services, but the majority of studies lacked direct measurement of those effects and their benefits.

Table 1. Summary of the number of relevant studies and the number of armadillo species reported for each ecosystem service found in the literature search.

NCP category	Ecosystem service	Studies	Species
Regulating	1. Bioturbation	32	14
Regulating	2. Ecosystem engineering	21	7
Regulating	3. Nutrient cycling	5	7
Regulating	4. Seed dispersal	31	13
Regulating	5. Sentinel species for contaminants	7	2
Regulating	6. Disease surveillance	47	13
Regulating	7. Interaction with other taxa	45	9
Regulating	8. Pest control	21	11
Material	9. Meat	74	15
Material	10. Medicine	31	13
Material	11. Other material contributions	27	13
Non-material	12. Conservation flagship	2	6
Non-material	13. Other non-material contributions	12	10
Total^a		355	

^a Note that a study may be included in more than one category, hence the sum of the studies in the 13 functions exceeds the total number of studies.

2.3.1. Regulating contributions

Regulating contributions are functional and structural aspects of organisms and ecosystems that modify environmental conditions experienced by people and/or regulate the generation of material and non-material contributions (Díaz *et al.*, 2018). Here we include armadillos as important drivers of bioturbation, ecosystem engineering, nutrient cycling, seed dispersal, as sentinel species, and how armadillos affect food webs and help regulate pests/invasers.

(a) Bioturbation

Bioturbation is the supporting service that refers to the displacement and mixing of soils and sediments by animals (Meysman, Middelburg & Heip, 2006). Armadillos play a role in bioturbation by moving large quantities of earth to the soil surface through their burrowing activity (Simkin & Michener, 2005; Aya-Cuero *et al.*, 2017; Haussmann, 2017; *Fig. 1*). While this burrowing activity is generally assumed to generate small-scale disturbances (Platt, Rainwater & Brewer, 2004; Simkin & Michener, 2005; Mazía *et al.*, 2010; Frontini & Escosteguy, 2012; Sawyer *et al.*, 2012), these effects have rarely been assessed empirically. For instance, *Euphractus sexcinctus* and *Chaetophractus villosus* were identified as taphonomic agents that move different archaeological materials during their burrowing activity (Araujo & Marcelino, 2003; Frontini & Escosteguy, 2012). However, the mixing of cultural soil horizons was the only attribute mentioned that strictly refers to bioturbation (Araujo & Marcelino, 2003; Frontini & Escosteguy, 2012). In fact, only a single study has measured the volume of soil moved in 187 burrows excavated by *Dasylops novemcinctus* (Sawyer *et al.*, 2012). One experimental study highlighted the overall negative impact on tree recruitment and the increased light level and soil nitrogen availability in armadillo-like diggings (Mazía *et al.*, 2010).

Given the scant data on the amount of soil excavated by armadillos, we tentatively calculated a conservative volume (m^3/burrow) using data on burrow morphometrics available for a few species (*Table 2*). We used the average length of the burrow (reported value or, when absent, body length of the species) and mean width and height of the burrow's entrance (*Table 2*). A single study found 157 burrows constructed by *Priodontes maximus* in an area of 307 km^2 (Aya-Cuero *et al.*, 2017), which would result in 99.3 m^3 mixing of soils and sediments (a conservative value). It is important to mention, however, that there are many ways in which armadillos may provide bioturbation services (Schaeztl & Anderson, 2005). Importantly, as some armadillos are able to dig many burrows in short periods of time, and not all of them return to the same burrow every night (e.g. Greigor, 1985), their potential as bioturbation agents is likely to be much higher.

We therefore highlight that our understanding of the bioturbation role of armadillos remains very limited. Furthermore, we found no studies that assessed the impact of burrowing activity on soil structural properties and/or the subsequent impacts on plant productivity or on biodiversity. There were no studies, either, that empirically measured the relative effects of soil compaction, aeration, nitrogen mobilization on plant growth, and water infiltration, even though the importance of armadillo burrows for water infiltration is culturally recognized by rural workers (Tamburini, 2016).



Figure 1. Burrow entrance (with soil mound below) constructed by *Prionodontes maximus*. Photograph: Carlos Aya-Cuero.

Table 2. Measurements of burrows constructed by armadillos and the amount of soil excavated.

Species	Mean entrance height/width (cm)	Mean burrow length (cm)	Volume (m ³ /burrow)	Reference
<i>C. tatouay</i>	18.1/17.7	Not given	0.063 ^a	Anacleto (2006)
<i>C. tatouay</i>	15.0/20.0	Not given	0.059 ^a	Carter & Encarnação (1983)
<i>C. truncatus</i>	6.5/6.5	Not given	0.002 ^a	Minoprio (1945)
<i>C. truncatus</i>	6.4/6.4	250	0.032	Melchor <i>et al.</i> (2012)
<i>C. unicinctus</i>	12.4/12.1	Not given	0.027 ^a	Anacleto (2006)
<i>C. unicinctus</i>	12.4/12.1	Not given	0.027 ^a	Anacleto & Diniz-Filho (2008)
<i>C. unicinctus</i>	16.0/17.5	Not given	0.050 ^a	Carter & Encarnação (1983)
<i>C. unicinctus</i>	13.0/13.0	Not given	0.030 ^a	Trovati (2009)
<i>C. unicinctus</i>	10.0/10.0	Not given	0.018 ^a	Desbiez <i>et al.</i> (2018)
<i>C. vellerosus</i>	10.0/10.0	Not given	0.010 ^a	Gregor (1985)
<i>C. vellerosus</i>	13.1/13.1	Not given	0.018 ^a	Crespo (1944)
<i>C. villosus</i>	19.5/20.7	131.0	0.166	Abba <i>et al.</i> (2005)
<i>D. hybridus</i>	15.3/15.3	118.8	0.087	González <i>et al.</i> (2001)
<i>D. novemcinctus</i>	20.3/18.0	Not given	0.099 ^a	Anacleto (2006)
<i>D. novemcinctus</i>	11.2/11.2	126.5	0.050	Clark (1951)
<i>D. novemcinctus</i>	15.4/20.0	56.0	0.054	McDonough <i>et al.</i> (2000) – USA
<i>D. novemcinctus</i>	13.1/16.8	58.9	0.041	McDonough <i>et al.</i> (2000) – Brazil
<i>D. novemcinctus</i>	13.6/18.8	Not given	0.069 ^a	Platt <i>et al.</i> (2004)
<i>D. novemcinctus</i>	20.4/25.7	142.5	0.235	Sawyer <i>et al.</i> (2012)
<i>D. novemcinctus</i>	17.8/20.3	426.7	0.484	Talmage & Buchanan (1954)
<i>D. novemcinctus</i>	19.8/21.9	Not given	0.117 ^a	Zimmerman (1990)
<i>D. septemcinctus</i>	11.5/11.5	Not given	0.017 ^a	Anacleto (2006)
<i>E. sexcinctus</i>	17.2/17.6	Not given	0.055 ^a	Anacleto (2006)
<i>E. sexcinctus</i>	19.0/21.0	Not given	0.073 ^a	Carter & Encarnação (1983)
<i>E. sexcinctus</i>	15.5/19.4	150.0	0.055	Medri (2008)
<i>E. sexcinctus</i>	14.5/19.9	Not given	0.053 ^a	Trovati (2009)
<i>P. maximus</i>	39.5/39.6	Not given	0.304 ^a	Anacleto (2006)
<i>P. maximus</i>	35.0/42.0	Not given	0.633 ^a	Aya-Cuero <i>et al.</i> (2017)
<i>P. maximus</i>	30.8/41.3	Not given	0.547 ^a	Carter (1983)
<i>P. maximus</i>	32.0/45.0	Not given	0.620 ^a	Carter & Encarnação (1983)
<i>P. maximus</i>	36.0/43.0	Not given	0.666 ^a	Ceresoli & Fernandez-Duque (2012)
<i>T. matacus</i>	11.0/12.8	35.0	0.015	Attias <i>et al.</i> (2016)
<i>T. tricinctus</i>	10.5/14.0	43.5	0.020	Attias <i>et al.</i> (2016)
<i>Z. pichiy</i>	8.0/15.0	150	0.057	Superina & Abba (2014)

^a volume calculated based on armadillo body length.

(b) Ecosystem engineering

Ecosystem engineering is a supporting service provided by armadillos that involves the creation of new habitats or modification of ecosystem features (e.g. burrow construction; Romero *et al.*, 2015; Coggan, Hayward & Gibb, 2018) that are later used by other organisms. Many animals, including insects like beetles and social wasps, lizards, snakes, frogs, and even

mammals use armadillo burrows (Taber, 1945; Clark, 1951; Vitt & Caldwell, 1993; Dias-Lima *et al.*, 2003; Leite-Pitman, 2004; Platt *et al.*, 2004; Desbiez & Kluwyber, 2013; Aya-Cuero *et al.*, 2017).

Armadillo burrows vary greatly in their usefulness to other organisms. For example, the soil mound in front of the burrows of *P. maximus* is used by different animals (e.g. *Tayassu pecari*, *Sus scrofa*, and *Pecari tajacu*) to wallow, rest, and cool down (Desbiez & Kluwyber, 2013; Noss *et al.*, 2013; Aya-Cuero *et al.*, 2017). Many species search for their prey either in the soil mound or at the entrance of the burrow (Desbiez & Kluwyber, 2013; Aya-Cuero *et al.*, 2017). Other species use the burrow itself as a refuge against predators or to avoid/mitigate temperature extremes (both high and low), or for foraging (Desbiez & Kluwyber, 2013; Aya-Cuero *et al.*, 2017). Nevertheless, although well documented for *P. maximus*, ecosystem-engineer research associated with other armadillos is lacking. Burrows constructed by *Dasypus* sp., *Cabassous unicinctus*, and *E. sexcinctus* are used by small rodents to facilitate their movement inside their own galleries (Bueno *et al.*, 2004), by birds as protection against predation, for thermal regulation, and for feeding (Kanegae & Reis, 2011), by hoary-fox (*Lycalopex vetulus*) for reproduction and care of the young (Dalponte, 2009; F.G. Lemos, personal communication); and burrows of *C. villosus* are used by owls as nesting sites (Machicote, Branch & Villarreal, 2004). Furthermore, insects and arachnids (Clark, 1951; Barreto, Barreto & D'Alessandro, 1985; Dias-Lima *et al.*, 2003), reptiles (Timmerman, 1995; Martin & Means, 2000; Ealy, Fleet & Rudolph, 2004; Platt *et al.*, 2004), birds (Taber, 1945), and mammals (Taber, 1945; Clark, 1951; Hunt, 1959; Thomas, 1974; Zimmerman, 1990; Silveira & Cademartori, 2017) were found inhabiting *D. novemcinctus* burrows, and may also inhabit burrows constructed by other similar-sized armadillo species.

Besides offering thermal and wildfire refuge (Vitt & Caldwell, 1993; Platt *et al.*, 2004; Noss *et al.*, 2013) and providing habitat for a variety of taxa (Taber, 1945; Clark, 1951), armadillo burrows also contribute to the structural complexity of the habitats. Such features may locally increase the abundance and/or the richness of invertebrates and vertebrates, which, in turn, may influence the whole community (Romero *et al.*, 2015; Coggan *et al.*, 2018). To summarize, the role of armadillos as physical ecosystem engineers has largely been ignored and is in need of additional research effort.

(c) Nutrient cycling

The role animals play in modulating nutrient cycling has been recognized as an important influence on both community structure and ecosystem function (Vanni *et al.*, 2002; Estes *et al.*, 2011; Atkinson *et al.*, 2017). Animals translocate nutrients by consuming them at one point and excreting them or dying at another location (Wolf, Doughty & Malhi, 2013; Atkinson *et*

al., 2017). In addition, regions of animal concentration impact nutrient accumulation and the rate of nutrient cycling in ecosystems (Hutchinson, 1950). Armadillos contribute to nutrient cycling in two different ways: by their burrowing activity and their feeding behaviour (Fig. 2).

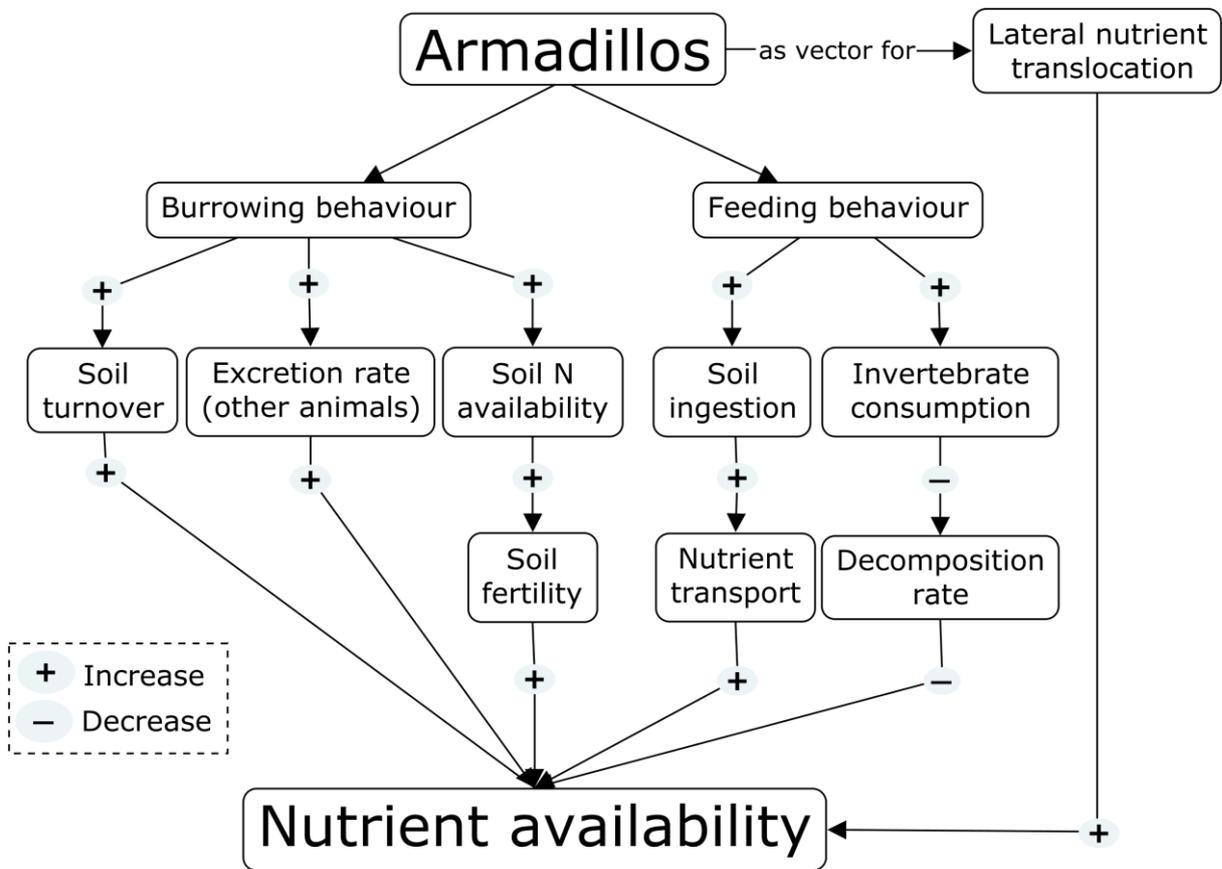


Figure 2. Schematic diagram of the roles of armadillos in nutrient cycling.

While foraging or digging, armadillos cause soil turnover that brings deep soils and their nutrients to the surface, increasing the nutrients' availability for different species (e.g. Whitford & Kay, 1999; Fleming *et al.*, 2014). Furthermore, since armadillo burrows are generally used by a variety of taxa (see Section 2.3.1*b*), the amount of urine and dung excreted might locally be higher. At high densities of burrows, those excretions, which are generally nitrogen-rich, may affect heterogeneity in nutrient availability, or even dominate nutrient cycling (Vanni *et al.*, 2002; Bakker *et al.*, 2004). We found, however, only a single study in a nutrient-cycling context that highlighted the increase of soil nitrogen availability (especially NO_3^-) from armadillo-like burrows, thus enhancing soil fertility (Mazía *et al.*, 2010). We therefore argue that armadillo burrows potentially act as important nutrient pools in soil, while also influencing nutrient flux and primary production rates (e.g. Bakker *et al.*, 2004; Clark *et al.*, 2005).

Armadillo feeding behaviour also influences nutrient cycling. Because of the large amount of soil commonly ingested by armadillos (Greggor, 1980; Beyer, Connor & Gerould, 1994; Bolković, Caziani & Protomastro, 1995; Anacleto, 2007), they may translocate nutrients across environments through their faeces. Likewise, they probably play an important role as a vector for nutrients crossing the boundary between water and terrestrial realms, i.e. mediating lateral diffusion of nutrients (Wolf *et al.*, 2013). For instance, *D. novemcinctus* and *P. maximus* have been shown to feed primarily on land in riparian habitats (McBee & Baker, 1982; Carter, Superina & Leslie, 2016; Aya-Cuero *et al.*, 2017), but to excrete and move in or close to freshwater (Clark, 1951; Civita, 1970; McBee & Baker, 1982; Carter *et al.*, 2016; Aya-Cuero *et al.*, 2017), potentially creating a nutrient flux into the water. Furthermore, the high consumption of invertebrates by armadillos may affect important drivers of ecosystem processes, such as decomposition rates (Yang & Gratton, 2014). However, we found no studies related to the influence of armadillo diet on nutrient transportation or on the invertebrate community, except for a single study that showed no significant changes of *D. novemcinctus* feeding habits on abundances of their prey species over three decades (Whitaker, Ruckdeschel & Bakken, 2012). Our understanding of the role of armadillos as mediators of nutrient cycling is thus incipient but offers great opportunities for research.

(d) Seed dispersal

Seed dispersal is a supporting service that influences key processes in the dynamics of natural vegetation and has large effects on ecosystems (Nathan & Muller-Landau, 2000; Wang & Smith, 2002). Although armadillos are considered predominantly (and, in some cases, exclusively) insectivorous, some species also consume fruit and seeds (Greggor, 1980; Redford, 1985; Dalponte & Tavares-Filho, 2004; Superina *et al.*, 2009a; Wallace & Painter, 2013). Nevertheless, the role of armadillos as seed-dispersal agents has received little attention.

Besides being relatively limited in number, and not providing precise identification of the plant matter being ingested, the majority of diet studies suggest that armadillos consume a great variety of fruit and seeds (*Table 3*). At least eight species of armadillos eat fruit to some extent and stand out as potential seed-dispersing agents, including many plant species of direct value to humans for timber, medicine, food, or other uses (*Table 3*). Apparently, *Chaetophractus vellerosus* and *E. sexcinctus* depend heavily on plant material (Greggor, 1980; Schaller, 1983; Dalponte & Tavares-Filho, 2004; Soibelzon *et al.*, 2007), potentially making them the top agents, among armadillos, regarding potential for seed-dispersal. Plants of about 29 families and 37 genera have already been reported as part of the diet of armadillos (*Table 3*). Fruits consumed by

armadillos vary highly in virtually all characteristics. They range in size from small (e.g. *Celtis pallida*: 8 mm) to large (e.g. *Reinealmia alpinia*: 35 mm). Colours vary from green and white, to yellow and blue, to red and black. Some fruits are very fragrant, whereas others are much less so (to human olfactory senses). Some contain a single seed or ‘stone’ (e.g. *Prunus*) and others several dozen (e.g. *Vaccinium*).

Although fruit consumers sometimes destroy seeds, seed predation seems to be rare among armadillos (e.g. Bolković *et al.*, 1995; Arriagada *et al.*, 2017). For instance, *Dasybus*, *Cabassous*, *Tolypeutes*, and *Priodontes* species rarely chew their food, i.e. they swallow it whole and undamaged (Redford, 1985), suggesting that their capacity to destroy seeds will be low. Likewise, the morphology of some armadillos’ teeth is not adapted to destroy seeds (McBee & Baker, 1982). In fact, up to 300 seeds of an unidentified plant species were found in *P. maximus* stomach contents (Barreto *et al.*, 1985). Some studies were able to identify the seeds, although no information was reported on whether these seeds were intact (Hamilton, 1946; Fitch, Goodrum & Newman, 1952; Superina *et al.*, 2009a; Whitaker *et al.*, 2012; Wallace & Painter, 2013; Arriagada *et al.*, 2017). A single study found a considerable number of well-preserved seeds from *Tolypeutes matacus* stomach contents (Bolković *et al.*, 1995). Furthermore, the passage of seeds through the gastrointestinal tract might be important to allow seed germination. While no study has attempted to elucidate the anatomical adaptations of the armadillo digestive system that potentially affect seed degradation, intact seeds were found in their faeces (Bolković *et al.*, 1995; Anacleto & Marinho-Filho, 2001; Whitaker *et al.*, 2012) and based on observations in captive *Zaedyus pichiy*, *Prosimops* seeds that were ingested by the armadillos indeed germinated (M. Superina, personal communication).

Armadillos such as *D. novemcinctus* and *Z. pichiy* can defecate inside their burrows (Taber, 1945; Superina, Carreño & Jahn, 2009b; Loughry & McDonough, 2013) or may cover their faeces with soil when they do so above ground (Loughry & McDonough, 2013; M. Superina, personal communication). Likewise, as *C. unicinctus* spend most of their time underground (Desbiez *et al.*, 2018), this species may also defecate inside its burrows. Nobody has tested germination rates of such seeds, but it is likely that at least some of them, particularly those in shallow burrows, would have some chance of germination. In addition, since some armadillos are wide-ranging (e.g. the omnivore *E. sexcinctus* has home ranges of up to 190 ha; Medri, 2008) and have medium body sizes, they may carry numerous seeds in their gastrointestinal tract over considerable distances. Armadillos might therefore have an important ecosystem function as seed-dispersal agents, and there is a need for more research efforts about such services.

Table 3 (continued).

Plant genus, by family	Armadillo species							
	1	2	3	4	5	6	7	8
<i>Pinus</i>				E				
Poaceae				V	V			
<i>Zea</i>		A			N			
<i>Oryza</i>					N			
<i>Saccharum</i>					N			
<i>Setaria</i>							K	
<i>Festuca</i>								Z
<i>Pappostipa</i>		Z						Z
Rhamnaceae								
<i>Zyzyphus</i>							K	
Rosaceae								
<i>Rubus</i>				B,C,E				
<i>Prunus</i>				B,L				
Rutaceae								
<i>Citrus</i>					N			
Smilacaceae								
<i>Smilax</i>				L				
Vitaceae					V			
<i>Vitis</i>				E,G,I,L,U				
<i>Nekemias</i>				U				
Zingiberaceae								
<i>Renalmia</i>				S				

References: A, Hudson (1922); B, Kalmbach (1943); C, Baker (1943); D, Hamilton (1946); E, Fitch *et al.* (1952); F, Greeger (1980); G, Zimmerman (1982); H, Redford (1985); I, Brece & Dusi (1985); J, Sikes *et al.* (1990); K, Bolković *et al.* (1995); L, Osborn *et al.* (2000); M, Anacleto & Marinho-Filho (2001); N, Dalponte & Tavares-Filho (2004); O, Azurduy *et al.* (2005); P, Superina (2008); Q, Superina *et al.* (2009a); R, Cavalcanti *et al.* (2009); S, García-Robledo & Kuprewicz (2009); T, Golin *et al.* (2011); U, Whitaker *et al.* (2012); V, Vaz *et al.* (2012); X, Wallace & Painter (2013); Z, Arriagada *et al.* (2017).

(e) Sentinel species for contaminants monitoring

Over recent years, native sentinel organisms have become a new tool for studying the interactions between organisms and contaminants, and for monitoring the potential biological effects of xenobiotics, with many species being identified as suitable candidates (Poletta *et al.*, 2008; Zhou *et al.*, 2008; Thomason *et al.*, 2016). When species are used as bioindicators, they can provide a low-cost shortcut for monitoring (Zhou *et al.*, 2008). Armadillos can be used as sentinel species for environmental biomonitoring of genotoxic chemicals and of metal contamination in terrestrial systems, but there have been virtually no toxicological or biomonitoring studies involving them (e.g. Jarvis *et al.*, 2013; Rossi *et al.*, 2016; Luaces *et al.*, 2017).

Among mammals, some armadillo species possess attributes that make them ideal sentinels for terrestrial biomonitoring. They have a broad geographic distribution and can occupy a wide range of terrestrial habitats (Abba & Superina, 2010; Taulman & Robbins, 2014; Feng & Papes, 2015). Notably, some seem quite tolerant of human disturbance and can be found even in highly altered sites (McDonough *et al.*, 2000; Rodrigues & Chiarello, 2018). In the laboratory, they are relatively easy to handle with some precautions (Storrs, 1971; Balaña *et al.*, 1985; Vijayaraghavan, 2009; Rossi *et al.*, 2016). Their behaviour further contributes to their potential utility as sentinels of environmental contamination in terrestrial systems. They are in constant contact with soils both during burrowing and foraging activity. Further, armadillos ingest large quantities of soil either incidentally or intentionally (Gregor, 1980; Beyer *et al.*, 1994; Bolković *et al.*, 1995; Anacleto, 2007). Armadillos would therefore seem likely to experience high exposure to any soil-borne contaminants, either directly from their foraging activities and burrowing, or indirectly *via* consumption of their soil-dwelling prey (e.g. Jarvis *et al.*, 2013).

Despite attributes that potentially make armadillos useful species to examine environmental contamination in terrestrial systems, knowledge about the effects of contaminants and accumulation in these animals remains limited to few studies and species. Studies are mostly based on two species, *D. novemcinctus* and *C. villosus* (Wheeler *et al.*, 1975, 1977; Herbst *et al.*, 1989; Jarvis *et al.*, 2013; Rossi *et al.*, 2016; Luaces *et al.*, 2017). The presence of pesticides and their metabolites in the stomach contents of armadillos was first reported by Wheeler *et al.* (1975) as a consequence of their consumption of insects exposed to the contaminant. However, these authors did not examine the pesticide effects or their accumulation in *D. novemcinctus* tissues. A single study reported pesticide accumulation at high levels in various tissues of *D. novemcinctus* (Wheeler *et al.*, 1977), while another reported metal accumulation in liver tissue (Jarvis *et al.*, 2013). In addition, relatively low plasma cholinesterase activity was found (Herbst *et al.*, 1989), which might make them more sensitive to organophosphate-based (anti-cholinesterase) pesticides (M. Superina, personal communication). Thus, as *D. novemcinctus* can accumulate contaminants and is sensitive to herbicides or insecticides, it might represent a useful sentinel species for monitoring contaminants in terrestrial ecosystems. Likewise, other species of armadillos might present similar characteristics and successfully provide this ecosystem service (Rossi *et al.*, 2016, 2018; Luaces *et al.*, 2017). More research is needed to clarify under what circumstances armadillos are reliable bioindicators, and how much they can contribute to the improvement of biomonitoring while providing a low-cost ecosystem service shortcut.

(f) *Disease surveillance*

Armadillos are natural reservoir hosts for a wide range of parasites and pathogens, some of which are specific for Cingulata, whereas others may also affect other vertebrates, including humans (e.g. Diniz, Costa & Oliveira, 1997; Bagagli *et al.*, 2003; Silva *et al.*, 2018). Host–pathogen systems can be used to monitor pathogens, and armadillos could aid in determining pathogen distribution and understanding disease ecology. Ecosystem changes can modify the distribution and abundance of pathogens that can affect humans, and monitoring the prevalence of these pathogens in armadillo populations over time could help to predict the risk of disease outbreaks in humans. For instance, armadillos play an important role in the sylvatic transmission cycle of *Trypanosoma cruzi*, the causative agent of Chagas disease, and have been used to determine the origin of *T. cruzi* subtypes in South America (Yeo *et al.*, 2005). Armadillos are wild reservoir hosts of this pathogen and have been identified as an important food source for triatomine bugs that can transmit *T. cruzi* (Sarquis *et al.*, 2010; Georgieva, Gordon & Weirauch, 2017). Moreover, *D. novemcinctus* can be used to address spatial patterns of *Mycobacterium leprae* (Hansen’s disease; Loughry *et al.*, 2009; Truman *et al.*, 2011; Silva *et al.*, 2018) or other pathogens (e.g. Richini-Pereira *et al.*, 2009), which are useful to make inferences about the geographical spread of diseases (Loughry *et al.*, 2009).

As armadillos are known hosts for a number of fungal, bacterial and parasitic pathogens, including *Histoplasma*, *Coccidioides*, *Mycobacterium*, *Trypanosoma*, *Toxoplasma*, *Sarcocystis*, *Leptospira*, *Sporothrix*, *Leishmania* and *Paracoccidioides* (e.g. Convit & Pinardi, 1974; Arias *et al.*, 1982; Kaplan, Broderick & Pacific, 1982; Bogado *et al.*, 1983; Naiff *et al.*, 1986, 1991; Diniz *et al.*, 1997; Bagagli *et al.*, 1998, 2003; Corredor *et al.*, 1999; Sharma *et al.*, 2013), they can also be used as models to study the role of genetic and biological factors in disease susceptibility (e.g. Walsh *et al.*, 1999; Misch *et al.*, 2010; Sharma *et al.*, 2013). Many of these pathogens have serious social and economic costs. Chagas disease, for instance, affects 8 million people in 21 Latin American countries (WHO, 2012), and it is responsible for nearly \$750 million/year (Brazil) and \$900 million/year (USA) in treatment costs alone (Moncayo & Silveira, 2009; WHO, 2012). Understanding the effectiveness of new therapies using armadillos as a model may also provide information on the pathogenic mechanisms involved in those diseases, thus improving their prevention or reducing the costs of treatment (e.g. Sharma *et al.*, 2013).

(g) *Interaction with other taxa*

Armadillos directly interact with other taxa through mutualistic (e.g. commensalism) or antagonistic (e.g. predator–prey system) ecological processes which, in turn, can have both

positive and negative effects on terrestrial biodiversity. For example, birds have been reported following armadillos to catch insects near the ground that are flushed by their movements (Levey, 1999; Komar & Hanks, 2002; Di Giacomo & Di Giacomo, 2006). This interaction benefits the commensal foraging efficiency of insectivorous birds (Levey, 1999), positively influencing them locally and even at regional scales.

Armadillos can also play an important role in maintaining the integrity of food webs, as they may act as a food resource for top and mesocarnivores (e.g. Gómez-Ortiz & Monroy-Vilchis, 2013; Giordano *et al.*, 2018; Miranda *et al.*, 2018). For instance, armadillos have been recorded in the diet of coyote (*Canis latrans*) (Cherry *et al.*, 2016), black bear (*Ursus americanus floridanus*) (Maehr & Brady, 1984), maned wolf (*Chrysocyon brachyurus*) (Motta-Junior *et al.*, 1996; Aragona & Setz, 2001; Juarez & Marinho-Filho, 2002; Santos, Setz & Gobbi, 2003; Bueno & Motta-Junior, 2004, 2009; Jácomo, Silveira & Diniz-Filho, 2004; Queirolo & Motta-Junior, 2007), South American gray fox (*Lycalopex griseus*) (Zapata, Travaini & Delibes, 1998), crab-eating raccoon (*Procyon cancrivorus*) (Gatti *et al.*, 2006; Quintela, Iob & Artioli, 2014), ocelot (*Leopardus pardalis*) (Martins, Quadros & Mazzolli, 2008; Bianchi, Mendes & Marco-Júnior, 2010; Giordano *et al.*, 2018), puma (*Puma concolor*) and jaguar (*Panthera onca*) (Rabinowitz & Nottingham, 1986; Aranda, 1994; Aranda & Sánchez-Cordero, 1996; Taber *et al.*, 1997; Chinchilla, 1997; Núñez, Miller & Lindzey, 2000; Garla, Setz & Gobbi, 2001; Scognamillo *et al.*, 2003; Novack *et al.*, 2005; Moreno, Kays & Samudio, 2006; Weckel, Giuliano & Silver, 2006; Monroy-Vilchis *et al.*, 2009; Foster *et al.*, 2010, 2016; Gómez-Ortiz *et al.*, 2011; Gómez-Ortiz & Monroy-Vilchis, 2013; Soria-Díaz, Fowler & Monroy-Vilchis, 2017; Soria-Díaz *et al.*, 2018; Giordano *et al.*, 2018; Miranda *et al.*, 2018), black-chested buzzard eagle (*Geranoaetus melanoleucus*) (Saggese & De Lucca, 2004), and crowned eagle (*Urubitinga coronata*) (Sarasola, Santillán & Galmes, 2010; Berkunsky *et al.*, 2012) in different countries. At least 43 studies reported armadillos as a food item in the diet of carnivores, and at least 16 (37%) reported them as the main food resource, either by preference, by biomass importance, or both. Considering the ongoing defaunation process (Dirzo *et al.*, 2014; Young *et al.*, 2016) and the apparently high ecological flexibility of some armadillo species (Feng & Papes, 2015; Bilenca *et al.*, 2017; Rodrigues & Chiarello, 2018), it is not at all unlikely that armadillos play a key role in sustaining predator populations. Although this service has not yet been measured accordingly, it potentially represents an important ecosystem function provided by armadillos which, in turn, may exert strong bottom-up effects on food webs.

(b) Pest control

Biocontrol is the use of organisms to reduce the abundance of pest populations and thus decrease pest damage. Armadillos might control crop-feeding invertebrates through the destruction of their nests or direct predation (Fitch *et al.*, 1952; Elizalde & Superina, 2019). Nevertheless, the role of armadillos as agents of pest control and their effectiveness in reducing the costs of pest damage has been overlooked.

Armadillos have been reported to destroy nests of social wasps, *Vespula* spp. (Clark, 1951), and of leaf-cutting ants, *Atta* spp. and *Acromyrmex* spp. (Link, Moreira-Link & Moreira-Link, 1998; Elizalde & Superina, 2019). Although there has been little research to date, nest destruction activity by *C. villosus* and *Z. pichiy* contributes to the suppression of leaf-cutting ants (Elizalde & Superina, 2019), while *Dasyops hybridus* is able to destroy up to 30% of nests of *Acromyrmex* spp. (Link *et al.*, 1998). On the other hand, by consuming predominantly invertebrate prey, predation by armadillos potentially contributes to population regulation of agricultural pests such as fall armyworm (*Spodoptera frugiperda*), Surinam cockroach (*Pycnoscelus surinamensis*) (Nesbitt *et al.*, 1977), wireworm beetles (Elateridae) (Fitch *et al.*, 1952; Szeplaki, Ochoa & Clavijo, 1988; Osborn, Nelson & Warren, 2000; Whitaker *et al.*, 2012; Gallo, Fasola & Abba, 2019), cane beetles (*Dermolepida albobirtum*) (Fitch *et al.*, 1952), May/June beetles (Fitch *et al.*, 1952; Sikes, Heidt & Elrod, 1990; Tyler, Molinaro & Messina, 1996; Osborn *et al.*, 2000; Whitaker *et al.*, 2012), leaf-cutting ants, *Atta* spp. (Barreto *et al.*, 1985; Szeplaki *et al.*, 1988; Anacleto & Marinho-Filho, 2001) and *Acromyrmex* spp. (Bolković *et al.*, 1995), fire ants, *Solenopsis* spp. (Bolković *et al.*, 1995; Superina *et al.*, 2009a) and *Wasmannia* spp. (Bolković *et al.*, 1995), and termites, *Syntermes* spp., *Heterotermes* spp. (Anacleto & Marinho-Filho, 2001) and *Cornitermes* spp. (Anacleto & Marinho-Filho, 2001; Anacleto, 2007). Nevertheless, we are not aware of any studies quantifying the influence that armadillos may have on the abundance of these or other pest species. We suspect this might be substantial, especially if we consider their indirect effects through damage to nests (e.g. Elizalde & Superina, 2019) and that 245 fall armyworms were found in a single stomach of *D. novemcinctus* in Florida (Nesbitt *et al.*, 1977) while important pest arthropods reach values close to or greater than 50% of the diet of another five armadillo species (*D. hybridus*, *C. vellerosus*, *C. villosus*, *T. matacus*, and *Z. pichiy*) (Gallo *et al.*, 2019).

It is important to highlight that the pest species potentially consumed by armadillos cause serious economic problems. For instance, the economic impact of a single pest species (fire ants) in the U.S. alone was estimated to be between \$5.6 and \$6.3 billion/year (Lard *et al.*, 2006). Likewise, termites are responsible for approximately \$2 billion/year of damage (Su & Scheffrahn,

1990). In Brazil, fall armyworms caused economic losses exceeding \$600 million/year (Ferreira-Filho *et al.*, 2010).

2.3.2. Material contributions

Material contributions are substances, objects, or other material elements from ecosystems that directly sustain people's physical existence and material assets (Díaz *et al.*, 2018). Humans use armadillos as products for food, medicine, and ornaments. Here, we focus on those services produced directly by them.

(a) Meat

Armadillos are harvested for human consumption in many regions of the Americas (Abba & Superina, 2010). In Brazil, armadillos are one of the most, if not the most, harvested wild species in Amazon (Bonaudo *et al.*, 2005; Cajaiba, Silva & Piovesan, 2015; Rocha, Silva & Nascimento, 2016; Mesquita, Rodríguez-Teijeiro & Barreto, 2018), Atlantic Forest (Cullen, Bodmer & Pádua, 2000; Hanazaki, Alves & Begossi, 2009; Pereira & Schiavetti, 2010; Dantas-Aguiar *et al.*, 2011; Castilho *et al.*, 2017; Sousa & Srbeek-Araujo, 2017), and Brazilian semiarid region (Mourão, Araujo & Almeida, 2006; Barboza *et al.*, 2011; Oliveira *et al.*, 2017). Armadillos also represent the most important species hunted for food in Mexico (Naranjo *et al.*, 2004; Lorenzo *et al.*, 2007; Tlapaya & Gallina, 2010; Ávila-Nájera *et al.*, 2011; Valle *et al.*, 2015; Reyes, Ramirez Bravo & Talancón, 2017; González-Marín *et al.*, 2017), and one of the most harvested species in Argentine Chaco (Zuleta & Bolkovic, 1994; Altrichter, 2006; Camino *et al.*, 2018). Other countries including Paraguay, Bolivia, Peru, Colombia, Ecuador, Guatemala, Venezuela, and Panama also use armadillos as a food supply (Noss, Cuéllar & Cuéllar, 2008; *Fig. 3*).

Among the 20 extant species of armadillo, *D. novemcinctus* stands out as the most frequently harvested species for human consumption (e.g. Noss, 1998; Rumiz *et al.*, 2001; Smith, 2005; Tlapaya & Gallina, 2010; Mesquita *et al.*, 2018), although *E. sexcinctus* is also important in the Brazilian semiarid region (Mourão *et al.*, 2006; Barboza *et al.*, 2011; Oliveira *et al.*, 2017) and *T. matacus* for the Chaco region (Bolkovic, 1999; Noss, Cuéllar & Cuéllar, 2003; Altrichter, 2006). In some places, *D. novemcinctus* corresponds to at least twice the biomass of any other hunted mammal (e.g. Hill *et al.*, 1997; Tlapaya & Gallina, 2010; Mesquita *et al.*, 2018). Indigenous and rural communities that use *D. novemcinctus* prefer this species because it is commonly found and easy to catch, abundant, and has tasty meat (Mourão *et al.*, 2006; Barboza *et al.*, 2011; Dantas-Aguiar *et al.*, 2011). In fact, these characteristics confer high market value to *D. novemcinctus*, one of the most prized game species in the Brazilian semiarid and Cerrado (El-Bizri *et al.*, 2015; Alves

et al., 2016a). Nevertheless, it is important to highlight that the species is a natural reservoir host for the etiological agents of several potentially zoonotic diseases (see Section 2.3.1f). While subsistence harvest is still the main way of acquiring high-protein foods in many small isolated or poor communities in Neotropical areas (Novaro, Redford & Bodmer, 2000), armadillos, especially *D. novemcinctus*, act as an important food supply for traditional and rural communities. There may be a potential market exploring *D. novemcinctus* meat as exotic food.



Figure 3. Piece of armadillo (*Dasypus* sp.) used as food resource and armadillo blood used as traditional medicine against asthma by rural communities in Colombia. Photograph: Fernando Trujillo.

(b) Medicine

According to the World Health Organization, in many developing countries traditional medicine is still the main way to cover primary healthcare needs, and sometimes the only source of care for human populations (WHO, 2013). Latin-American indigenous and rural communities frequently harvest armadillos for medicinal purposes (e.g. Alves & Alves, 2011; Alonso-Castro, 2014). While the population uses traditional medicine due to its relatively low cost and difficulty in accessing modern health facilities, or even due to the cultural acceptability of such practices (Alves & Alves, 2011), armadillos provide raw materials for remedies used to treat different diseases, thus increasing their cultural value (e.g. Valle *et al.*, 2015).

At least 11 species of armadillos have been reported in use for medicinal purposes in at least 19 countries (Noss *et al.*, 2008; Alves & Alves, 2011; Trujillo & Superina, 2013). Several parts of the animals are usually used including their carapace, tail, skin, meat, fat, and blood to treat diseases such as dermatitis, insect and snake bites, inflammation, asthma, pain and swelling, sore throat, cough, wounds, tuberculosis, skin infection, ear pain, deafness, sinusitis, pneumonia, dysentery, stomach-ache, ‘evil eye’, varicose veins, and to accelerate parturition (e.g. Vázquez *et al.*, 2006; Alves & Rosa, 2007b; Noss *et al.*, 2008; Cardona-Castro *et al.*, 2009; Alves & Alves, 2011; Trujillo & Superina, 2013). Nevertheless, despite their zootherapeutic importance, the therapeutic uses of armadillos and their body parts have been poorly explored scientifically. A single study showed that the oil fat provided by *E. sexcinctus* does have a topical anti-inflammatory activity (Ferreira *et al.*, 2014). By contrast, no relevant antibacterial activity against *Escherichia coli* and *Staphylococcus aureus* was found (Ferreira *et al.*, 2018). Hence, as armadillos can provide important raw materials for medicines, it is important to integrate the cultural and biological aspects of their traditional uses into a broader practice encompassing public health policies, cooperative management, conservation and sustainability, and biological prospection and patents (e.g. Alves & Rosa, 2005).

(c) *Other material contributions*

Armadillos provide many common ornamental resources. For many years, entrepreneurs sold armadillo shells as decorative baskets and wall ornaments in Texas, U.S. (Doughty & Smith, 1981; Smith & Doughty, 1984). In fact, over a 70-year period the ‘*Apelt Armadillo Company*’ sold baskets, lampshades, wall hangings, purses, and other ornaments fashioned from the shells of *D. novemcinctus* (Doughty & Smith, 1981; Smith & Doughty, 1984). In South and Central America, armadillos such as *D. novemcinctus*, *P. maximus*, *C. unicinctus*, *E. sexcinctus*, *T. matacus*, *C. vellerosus*, *Dasypus kappleri* and *Dasypus sabanicola* also have been used as ornamental resources. For example, the carapaces of armadillos are used to make wallets, purses, shoes, cradles, pots, suitcases, adornments, for crafting musical instruments called *charangos*, and to build the so-called *matracas* used in traditional dances, alongside their use in amulets and as souvenirs (Yensen, Tarifa & Anderson, 1994; Altrichter, 2006; Romero-Muñoz & Pérez-Zubieta, 2008; Richard, Zapata & Contreras, 2010; Trujillo & Superina, 2013; Fig. 4). Whole stuffed animals are used as decorative objects or to make ritual masks (Trujillo & Superina, 2013; Alves *et al.*, 2016a). Armadillo tails are used to make decorative knife handles, artisanal megaphones and handicrafts, and their claws are used as a tool for cleaning crops (Sampaio, Castro & Silva, 2009; Trujillo & Superina, 2013). Armadillos have been used as pets. In the Argentine Chaco, *P.*

maximus are highly valued as pets or as hunting trophies (Quiroga *et al.*, 2017). In Brazil, *D. novemcinctus* and *E. sexcinctus* are often kept in captivity and fattened for later consumption (Alves *et al.*, 2016a). In Colombia and Paraguay, they are popular pets (Smith, 2012; Rodríguez-Durán *et al.*, 2018). In fact, *T. matacus* is also exported to zoos and for the pet trade, although at the cost of a high rate of mortality during the export process (Abba & Superina, 2010). We highlight, however, that some armadillo species are threatened with extinction or have declining populations. In order to maintain these ecosystem services, it is therefore key to monitor their populations and ensure that their harvest and use are sustainable (Noss *et al.*, 2008; Abba *et al.*, 2015).



Figure 4. Basket fashioned from an armadillo (*Dasypus* sp.) carapace. Photograph: Fernando Trujillo.

2.3.3. Non-material contributions

Non-material contributions are nature's effects on subjective or psychological aspects underpinning people's quality of life, both individually and collectively (Díaz *et al.*, 2018). Armadillos provide many of these benefits, as they are spiritually and aesthetically valued in some regions. However, the value of such services is not easily quantifiable because cultural attitudes

vary widely among individuals and communities. Here, we briefly describe some non-material contributions.

(a) *Conservation flagship*

A flagship species is one that can be used to anchor a conservation campaign because it arouses public interest and sympathy. At least some species of armadillos can be used as conservation flagships. A recent high-profile example was the appropriation by the *Fédération Internationale de Football Association* (FIFA) of the Brazilian three-banded armadillo (*Tolypeutes tricinctus*) to serve as the mascot for the 2014 World Cup in an attempt to increase environmental awareness of species conservation issues. One of the measurable results, although only thanks to lobbying by Brazilian scientists (Melo *et al.*, 2014), was the establishment of the *Poti Canyon State Park* that encompasses 6872 hectares (Anonymous, 2017). This example illustrates the potential of armadillos as flagship species for conservation practices, and thus their valuable cultural service. Indeed, the *Armadillo Conservation Programme* in Colombia, which is a pioneering multidisciplinary initiative for the conservation and management of armadillos in the eastern floodplains of Colombia, has shown that even conservation programmes targeted at inconspicuous and poorly known species can stimulate public interest and be successful when using them as flagship species (Superina, Cortés Duarte & Trujillo, 2019). The giant armadillo (*P. maximus*) is also an important flagship species. For instance, in Brazil, the *Giant Armadillo Project* (<https://www.giantarmadillo.org.br/>), which is the first long-term ecological study of giant armadillos in the Brazilian Pantanal wetland, has contributed to filling important knowledge gaps and increased education and public awareness about this armadillo and its habitat.

(b) *Other non-material contributions*

Recreational services are those that provide opportunities for recreational activities (e.g. outdoor activities, nature viewing), and armadillos also fulfil this role. For instance, in Texas, USA, *D. novemcinctus* provides such services through armadillo races (Doughty & Smith, 1981; Smith & Doughty, 1984). Each armadillo is handled by an owner–trainer who is allowed to run behind the armadillo to encourage it to move forward (Bovey, 2003). Furthermore, armadillos entertain and stimulate people. For example, *D. novemcinctus* had great importance in the culture of Texas during the 20th century, entertaining and inspiring many Americans, such as Jim Franklin ‘*the Michelangelo of armadillo art*’, and the ‘*Armadillo World Headquarters*’ (Doughty & Smith, 1981; Smith & Doughty, 1984; Bovey, 2003). *D. novemcinctus* is considered one of the official symbols of Texas (<https://statesymbolsusa.org/>). Besides that, armadillos are spiritually valuable (e.g. Alves

et al., 2012*b*; Trujillo & Superina, 2013) and have inspired many artistic expressions, modern art, music, architecture of religious temples, marketing campaigns, clothing, documentaries, and tattoos (Doughty & Smith, 1981; Smith & Doughty, 1984; Bovey, 2003; Alves *et al.*, 2012*b*). They were even featured on a banknote in Venezuela and a coin in Uruguay. These cultural services potentially increase the market value and demands for products that are inspired by armadillos and sold on the internet and/or markets. Many zoos use armadillos as ambassador species in their educational programs, allowing visitors to observe them while learning about their biology and importance (e.g. Meritt, 2006; Clark & Melfi, 2012; Cortés Duarte, Trujillo & Superina, 2016).

2.4. Discussion

We believe this review serves as a valuable first step towards a clearer understanding of the ecosystem services provided by armadillos. As shown in Section 2.3, armadillos provide links within and among ecosystems and can have large effects on biodiversity, thus increasing their value to humans. We still lack much basic information to connect the ecological functions of armadillos to consequences for ecosystem services but hope we have made progress here by identifying their currently known ecosystem services and important gaps for future research. We are still a long way from the full understanding of their behaviour and ecology necessary to allow us to formulate models of ecosystem valuation to estimate the economic importance of such services. Detailed research about all ecosystem services is essential before quantifying their value becomes possible.

Evaluating ecosystem functions is often not straightforward. The first step should be to identify the ecosystem services provided by the species, and by so doing we can begin to understand how to utilize, conserve, and manage armadillos effectively in an interdisciplinary fashion. The next step should be to increase our knowledge about these services (e.g. Elizalde & Superina, 2019) and quantify their economic values, for example to make a solid economic case to counter proposals for economic development with a harmful impact on ecosystems (e.g. Sparovek *et al.*, 2016). The concept of ‘*ecosystem services*’ is increasingly influential in public opinion and in policy decision-making, as it has increased the attention of stakeholders who have previously failed to recognize the value of ‘*nature*’ or seen it as an impediment to economic growth (e.g. Juniper, 2013). However, an ecosystem-service approach should be used in combination with traditional conservation strategies, as it does not necessarily advocate for the conservation of endangered species but may positively value non-endangered taxa (Luck *et al.*, 2009).

Armadillos have long been neglected by the scientific community (Superina *et al.*, 2014). For instance, according to the IUCN *Red List of Threatened Species*, 10 out of the 20 extant armadillo species have unknown population trends, whilst six are in decline. Five species are categorized as *Data Deficient*, two as *Vulnerable*, and five as *Near Threatened* (IUCN, 2019). This translates into a loss of their positive ecosystem services, such that the declining status of armadillos is likely to have important negative consequences for terrestrial ecosystems. It is therefore urgent to identify and quantify the services provided by armadillo populations that are declining or have an unknown trend. Another key question for research is how much functional redundancy there is in the provision of services by different species. This is currently difficult to determine because the existing information on armadillos is heavily biased towards a small number of species (Superina *et al.*, 2014). If different armadillo species provide unique services over space and time, this might increase the impact of disturbance on the service.

2.4.1. Ecosystem disservices provided by armadillos

In addition to positive ecosystem services provided by armadillos such as pest control and ecosystem engineering, ecosystem disservices (i.e. effects that are harmful to human well-being) should be mentioned. For instance, *D. novemcinctus* are considered a nuisance in some urban and suburban areas in the USA (Chamberlain, 1980; Ober *et al.*, 2011; Whitaker *et al.*, 2012; Hohbein & Mengak, 2018). Their foraging and burrowing activity can cause damage in flower and vegetable gardens, nurseries, lawns, golf courses, sports fields, cemeteries, building structures, and to crops (Fitch *et al.*, 1952; Chamberlain, 1980; Whitaker *et al.*, 2012; Pérez & Pacheco, 2014). Furthermore, armadillos have been accused of plundering wild turkey (*Meleagris gallopavo*) and quail (*Colinus virginianus*) eggs from nests (Fitch *et al.*, 1952; Chamberlain, 1980; Staller *et al.*, 2005; Whitaker *et al.*, 2012). Some species, such as *C. villosus*, *C. vellerosus*, and *E. sexcinctus*, can damage and contaminate silo bags (e.g. Abba & Cassini, 2008; Zufiaurre, Abba & Bilenca, 2019) or act as direct consumers of crops, and their burrowing activity can seriously affect agricultural labour and represent a risk of fracture for cattle, horses, and rural workers (Dalponte & Tavares-Filho, 2004; Abba & Cassini, 2008). In fact, some species are locally considered agricultural pests (Abba & Superina, 2010). Nevertheless, virtually no research has been done to estimate the extent of these harmful impacts and their resulting economic costs. An exception to this is a study on *D. novemcinctus* in the southern USA reporting an estimated loss of \$20,000 over five years (between 1975 and 1979; Chamberlain, 1980). More research is needed to identify and understand the harmful effects of armadillos in novel ecosystems (e.g. urban areas or agricultural fields), and how to reduce the resulting damage.

2.4.2. Major research gaps

We identified important research gaps for each ecosystem service. Overall, there is a need for research on the relationships between armadillo biodiversity and function and links between ecosystem functions and services, as those factors have largely been neglected (Superina *et al.*, 2014; Loughry *et al.*, 2015). Studies should explicitly consider the ecosystem services provided by armadillos (e.g. Elizalde & Superina, 2019) through the identification of the socio-economical and ecological contexts where a given function is directly relevant to humans. Most of the studies we reviewed here are based on a specific ecological function provided by armadillos, but do not directly relate them to their consequences for ecosystem services, and thus give only limited, coarse-scale information. Furthermore, the majority of ecosystem services we identified here were provided by, or studied in, only a few species of armadillos (e.g. see Section 2.3.1e), with *D. novemcinctus* receiving the greatest attention (Superina *et al.*, 2014). Thus, it will be important to assess interspecific differences among armadillo species as not all of them are expected to provide the same ecosystem services, at least not in the same way or to the same extent across different socio-cultural, economic and environmental contexts. Finally, a variety of approaches should be used to determine how armadillo responses to anthropogenic threats affect ecosystem services.

2.4.3. Recommendations to scientists and other researchers

We encourage scientists to undertake research that quantifies the potential effects, whether positive or negative, of armadillos on ecosystem services. In addition, we encourage them to use an interdisciplinary approach, and thus to gather more empirical data on the linkages between armadillos and ecosystem services, management, and policy decisions (e.g. Rodrigues & Chiarello, 2018; Elizalde & Superina, 2019). In particular, we suggest framing ecological questions within an economic view, as this may provide a better understanding of the economic value of armadillo contributions to ecosystem services. To complement this, these questions could also be framed within a sociological view, which may improve both our understanding of the cultural value of armadillos and the implementation feasibility of conservation and management strategies by human populations that directly benefit from these services.

2.5. Conclusions

(1) Armadillos provide a range of important ecosystem services (*Table 1*). We summarize how armadillos affect ecosystem services including regulating, material, and non-material contributions that often are underappreciated. We identify significant knowledge gaps and future directions. Although little attention has been paid to ecosystem services provided by armadillos, this research subject has recently been receiving growing interest.

(2) To sustain nature's contribution to people, it is imperative to understand which organisms and mechanisms affect these contributions. We suggest that ecosystem services should be studied better and valued properly to ensure that humans continue to receive the benefits that armadillos provide.

(3) An ecosystem-service approach has great potential as a positive force for the management and conservation of armadillos. Armadillo ecologists should investigate the ecosystem services in more detail and use the results to inform the general public, decision-makers, and managers. Further research to understand the economic value of armadillos will improve management practices and policy, promote and justify armadillo conservation efforts, and ultimately demonstrate the vital connections between human well-being and the preservation of armadillo biodiversity.

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3. ATTITUDES TOWARDS ARMADILLOS AMONG PUBLIC ONLINE ON YOUTUBE – INSIGHTS FOR CONSERVATION

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Abstract

Understanding public attitudes toward wildlife are essential to ensure continued support for conservation efforts. Despite this, access to such data remains scarce at broader spatial scales mostly due to a lack of adequate methods for their assessment. The emergence of digital applications and social media platforms is providing exciting new opportunities to study the public visibility of wildlife and to produce valuable insights at an unprecedented scale. Here, we used a Bayesian multinomial model to investigate the public attitudes towards armadillos based on YouTube videos' comments, a popular social media website, to gain conservation insights. Our results indicate that the public online has a strong affection for individual armadillos that appeared on videos, demonstrating concern for the well-being of the animals, but they are unaware of most species and their corresponding ecological functions. We herein suggest that further increasing their popularity and visibility through social media, especially for poorly known species and/or threatened of extinction, can be an effective strategy for improving conservation practices involving them.

Keywords: culturomics, human dimension, social media, wildlife, Xenarthra.

3.1. Introduction

Conservation science has emerged in recognition of the need to include human dimensions to improve conservation policies, actions, and outcomes (Bennett *et al.*, 2017). As human activities are the main drivers of the ongoing biodiversity declines (Dirzo *et al.*, 2014; Young *et al.*, 2016), there is an urgent need to further the understanding of the public interest

towards nature's conservation (Chan *et al.*, 2016). At the same time, collecting information on human-nature interactions remains challenging as they usually are time-consuming and requires more resources than are usually available (Waldron *et al.*, 2013). User-generated data sourced from social media platforms (e.g. YouTube, Twitter, Facebook) represent new cost-efficient opportunities for measuring public interest regarding both the environment (Tenkanen *et al.*, 2017; Hausmann *et al.*, 2018; Retka *et al.*, 2019) and species (Roberge, 2014; Shiffman *et al.*, 2017; Adams *et al.*, 2018; Fidino, Herr, & Magle, 2018), thus providing relevant insights toward conservation (Di Minin, Tenkanen, & Toivonen, 2015; Wu *et al.*, 2018; Toivonen *et al.*, 2019).

Over recent years, there is increasing enthusiasm in using social media as a data source for wildlife conservation (Di Minin *et al.*, 2015). A few examples have demonstrated attitudes of hunters and non-hunters (Bizri *et al.*, 2015), public interest about particular species (Nekaris *et al.*, 2013; Roberge, 2014; Fidino *et al.*, 2018), impact of conservation campaigns (Kerhoas *et al.*, 2019), and potential changes in opinion following key media events such as the death of Cecil the Lion (Carpenter & Konisky, 2017). This type of knowledge is not only key for successful conservation, as public interest largely drives public policy, but also helps to identify potential biases relative to conservation needs (Di Minin *et al.*, 2015). On the other hand, the way the species and their contributions are perceived by, and attract attention from, humans may vary due to the non-randomness in human interests and affections (Batt, 2009; Gaston, 2010). For example, people are more interested in the well-being and prolonged persistence of animals which are cuter (Borgi *et al.*, 2014), larger (Gunnthorsdottir, 2001; Johnson *et al.*, 2010; Žmihorski *et al.*, 2013; Macdonald *et al.*, 2015), more brightly colored (Prokop & Fančovičová, 2013; Lišková, Landová, & Frynta, 2015), and phylogenetically close to us (Gunnthorsdottir, 2001; Batt, 2009). However, the extent to which low-density, elusive and not well-known species, even those with wide-ranging distribution, vary in their cultural importance or impact remains very poorly studied (Gaston, 2010).

Armadillos are usually less in the public eye when compared to the other groups of mammals, due to several knowledge gaps and the fact they are not charismatic species (Superina, Pagnutti, & Abba, 2014; Loughry *et al.*, 2015). They are semi-fossorial mammals with unusual appearance bearing a carapace that consists of osteoderms covered by epidermal scales (Engelmann, 1985). Despite there are 20 extant armadillo species that vary highly in size (15–150 cm body length) and mass (adult body mass: 0.1–40 kg) (McDonough & Loughry, 2018; Superina & Abba, 2018), a substantial taxonomic bias regarding *Dasybus novemcinctus*, the nine-banded armadillo, dominate the literature (Superina *et al.*, 2014; Loughry *et al.*, 2015). Some armadillo species are virtually unknown to science and so to the public – e.g. the greater fairy armadillo

(*Calyptophractus retusus*) and the northern naked-tailed armadillo (*Cabassous centralis*) (Superina *et al.*, 2014). As a result, the scientific knowledge of basic biological attributes of armadillos as a whole is much lower, and thus so is our ability to develop sound conservation practices (Abba & Superina, 2010). Most importantly, armadillos play key roles in terrestrial ecosystems (Rodrigues *et al.*, 2019). Assessing and understanding the public interest about armadillos can help to identify contributions provided by species from the public eye, and thus better frame strategies to increase the visibility of this group towards better research and conservation approaches, including online.

YouTube is a particularly important video-sharing platform that represents a worldwide dynamic system where more than one billion users interact in a participatory way (via comments, views, likes, shares) around video footage, resulting in billions of hours viewed each day (Arthurs, Drakopoulou, & Gandini, 2018; Burgess & Green, 2018). YouTube continues to expand rapidly due to increasingly greater worldwide access to ground-breaking technological advances on cameras and mobile phones (Arthurs *et al.*, 2018). Whilst it facilitates the rapid accumulation of data from shared recordings, YouTube has revealed a promising tool towards wildlife conservation (Nekaris *et al.*, 2013; Bizri *et al.*, 2015; Adams *et al.*, 2018; Toivonen *et al.*, 2019). Here, we use online data from YouTube to assess attitudes towards armadillos whether positive or negative and to gain insights through comments about armadillos online. To understand the public interest about armadillos, we address two specific research questions: (RQ1) what are the online attitudes toward armadillos as reported via comments on YouTube? (RQ2) what are the most commonly held words toward armadillos online as reported via comments on YouTube?

3.2. Methods

3.2.1. Collecting comments on social media

To identify relevant videos on YouTube we used the search feature from the site and queried videos using the keyword *armadillo*, filtering by the number of views. YouTube considers the number of views as the fundamental parameter of video popularity. We selected the top 15 most viewed videos on YouTube regarding armadillos, not including two videos about hunting them, as they might bias the viewer attitude (Fidino *et al.*, 2018). Because we could not guarantee a representative sample of the viewers and comments for the next videos, we limited our search to the top 15 (*Table S1*). Up to seven species of armadillos were mentioned, individually or not, on videos' content: nine-banded armadillo (*Dasypus novemcinctus*), yellow armadillo (*Euphractus*

sexcinctus), Brazilian three-banded armadillo (*Tolypeutes trincinctus*), southern three-banded armadillo (*Tolypeutes matacus*), giant armadillo (*Priodontes maximus*), screaming hairy armadillo (*Chaetophractus vellerosus*), and pink fairy armadillo (*Chlamyphorus truncatus*).

For each of the 15 videos in our data set viewer comments was collected (i.e., downloaded) using the YouTube Data Tools (Rieder, 2015) on 10 June 2019 approximately at 2 PM (*Table S1*). In total, 19,264 comments were collected, representing both comments and replies to comments. We included in our data set only comments in English, Spanish, and Portuguese and excluded repetitive comments posted by the same user ID. Comments made up in Spanish and Portuguese were translated to English, facilitating the text mining and all subsequent analysis. Finally, the viewer comments were cleaned before analysis. More specifically, noise-words, punctuation, and numbers were removed, and all words were lowercased. These procedures were performed using the *tm* package (Feinerer, Hornik, & Meyer, 2008) with version 3.5.1 of the R program (R Core Team, 2018).

3.2.2. Categorizing comments toward attitudes

Each comment was read and placed into one of the categories detailed in *Table 1*. To ensure that these categories represented distinct attitudes we used categories defined by Kellert that describe contrasting attitudes toward wildlife (Kellert, 1984). Such categories are still relevant for describing opinions held toward wildlife (George *et al.*, 2016; Fidino *et al.*, 2018). We did not use the esthetic category and, therefore, used eight of the nine Kellert categories (*Table 1*). Comments could also be placed into multiple categories if they covered varying topics. For example, the comment *their armor is actually to run through berry bushes so they can escape without getting cut and they can reach a top speed of mph* would fit into the *scientific* and *ecologicistic* categories because the comment focuses on the species' biology (*they can reach a top speed*) and its ecology (*their armor is actually to run through berry bushes... without getting cut*).

Table 1. Kellert categories used to assess online opinions toward armadillos. Definitions of Kellert categories were taken from Kellert (1984), while comments were taken from different videos that were collected.

Kellert category	Definition	Examples from YouTube comments
Naturalistic	Primary interest and affection for wildlife and the outdoors	<i>love armadillos are my favorite animal</i>
Ecologistic	Primary concern for the environment as a system, for interrelationships between wildlife species and natural habitats	<i>what if they are digging then an animal comes and attacks it?</i>
Humanistic	Primary interest in and strong affection for individual animals, principally pets	<i>so cute now want pet armadillo</i>
Moralistic	Primary concern for the right and wrong treatment of animals, with strong opposition to exploitation or cruelty toward animals	<i>first of all they are getting extinct and they are not pets like cat or dog they should be in the wild</i>
Scientistic	Primary interest in the physical attributes and biological functioning of animals	<i>armadillos can hold their breath for a long time</i>
Utilitarian	Primary concern for the practical and material value of animals.	<i>why don't you eat it?</i>
Dominionistic	Primary satisfactions derived from mastery and control over animals, typically in sporting situations	<i>shot one with a few days ago kill it with fire</i>
Negativistic	Primary orientation an active avoidance of animals due to dislike or fear	<i>I'm afraid to touch armadillos because they can infect you with leprosy</i>

3.2.3. Data analysis

To assure that only comments directly linked to the videos were analyzed replies – i.e., comments that respond to other comments – were not included in the analysis. After designating each comment to a corresponding Kellert category, we followed the methodology proposed by Fidino et al. (2018) and fit a Bayesian multinomial model to estimate the most likely opinions held toward armadillos. Our model estimates the probability of each Kellert category would be observed in a comment per video. We assumed an equal prior probability for all Kellert categories in a video by setting all alpha values to 1/8 (0.125) for the eight Kellert categories (see details in Fidino *et al.*, 2018). We used the *besim* R package (Incerti & Jansen, 2019) to run the

posterior distribution which was sampled 80,000 times and then we calculated the corresponding confidence intervals (IC 95%) based on these samples.

To quantify the frequency of the most important word in a comment per Kellert category we first excluded words without meaning itself usually called as stop words (e.g. *the, of, my*) and then conducted the analysis of the *term frequency-inverse document frequency* (TF-IDF) (Salton & Buckley, 1988). The idea of TF-IDF is to find important words for each category by increasing the weight for the most common words within each category (Salton & Buckley, 1988). Given the categories D , a word w , and an individual category $d \in D$, we calculate:

$$w_d = f_{w,d} * \log\left(\frac{|D|}{f_{w,D}}\right)$$

where $f_{w,d}$ equals the number of times w appears in d , $|D|$ represents the categories, and $f_{w,D}$ equals the number of categories in which w appears in D (Salton & Buckley, 1988; Ramos, 2003). This procedure was performed using the *tidytext* package in R program (Silge & Robinson, 2016). To quantify the frequency of the most important words overall we conduct a word cloud analysis (McNaught & Lam, 2010) in the R program (R Core Team, 2018).

3.3. Results

Over 19,264 comments, after removing duplicated comments from the same user, irrelevant comments, and replies, 5,235 (27%) were assignable to a Kellert category. The average number of comments for the videos we assessed was 1,284 (min = 74, max = 4 556). The average number of views was 2.6 million (min = 201,662, max = 7,409,721), likes 17,817 (min = 1,673, max = 84,640), and dislikes 798 (min = 65, max = 3,737) (*Table S1*).

Bayesian multinomial model estimated that humanistic category were the most held opinions toward armadillos (26%, 95% CI = 24–29), followed by scientific (18%, 95% CI = 16–20), negativistic (17%, 95% CI = 16–19) and naturalistic (15%, 95% CI = 13–18) opinions. Humanistic opinions were more likely, respectively, than ecologicistic (3.29 times, 95% CI = 2.98–3.66), moralistic and utilitarian (4.25 times, 95% CI = 3.86–4.68), and dominionistic (12.18 times, 95% CI = 9.71–15.61) opinions, the rarest Kellert categories (*Fig. 1*). The top five most frequently words by each Kellert category are shown in *Fig. 1*. The most frequently used words overall are shown in *Fig. 2*.

3.4. Discussion

Based on comments from YouTube videos (viewed by ~39 million people), we were able to differentiate among the eight types of Kellert categories and thus show that the public online hold diverse attitudes towards armadillos. The humanistic attitude type ranked above all other types, followed by, in descending order, the scientific, negativistic, naturalistic, ecologicistic, moralistic, utilitarian, and dominionistic attitude types.

YouTube videos might have introduced armadillos to a public that would not usually come into contact with them; even so, viewers showed a strong affection for individual armadillos that appeared on videos, demonstrating concern for the well-being of the animals. For example, viewers mentioned an interest in having a pet armadillo (*Fig. 1*). This interest can be interpreted as a positive attitude towards armadillos such as to keep them safe or to provide care to them, but might also represent the influence that video content has on viewers, as some of the videos showed armadillos in captivity or as a pet. Although the word *illegal* was not highlighted as one of the top five words in the moralistic attitude type, a few viewers commented or knew that having a pet armadillo is illegal. To legally adopt an armadillo it is necessary to get appropriate legal permits or be part of a specialized entity dedicated to the care and conservation of animals (e.g. zoos). Many zoos worldwide use armadillos as ambassador species in their educational programs, allowing visitors to observe them while learning about their biology and importance (Meritt, 2006; Clark & Melfi, 2012; Duarte, Trujillo, & Superina, 2016). Still, there are records of the use of armadillos illegally as pets, including the giant armadillo (*Priodontes maximus*), nine-banded armadillo (*Dasybus novemcinctus*), yellow armadillo (*Euphractus sexcinctus*), and three-banded armadillo (*Tolypentes* sp.) (Abba & Superina, 2010; Smith, 2012; Alves *et al.*, 2016; Quiroga *et al.*, 2017; Rodríguez-Durán *et al.*, 2018), some of them threatened of extinction (*P. maximus* and *T. tricinctus*) and/or in declining populations (*P. maximus* and *T. matacus*) (IUCN, 2019). At the same time, viewers demonstrated concern of how armadillos were treated on YouTube videos by highlighting the need of a vet or wildlife professional to better care of armadillos as well as the importance to return them into the wild, as pointed out by the words at the moralistic category (*Fig. 1*).

Despite armadillos' unusual appearance, our results suggest that the species showed on the videos may arouse, at some extent, a positive attractiveness to the public online, as highlighted by the words at the humanistic and naturalistic categories (*Fig. 1*) and by the most frequently mentioned words overall (*Fig. 2*). Perceiving a species as *beautiful* or *ugly* is strongly related to conservation policy-making decisions towards wildlife (Pinho *et al.*, 2014). Maybe armadillos for some are not good looking, but our results indicate they have attributes considered

key-appealing to the public. These include, for example, their relatively large body size, lack of aggressiveness, forward-facing eye and behaviors that are easily anthropomorphized (Batt, 2009; Pinho *et al.*, 2014; Macdonald *et al.*, 2015, 2017), which appear to increase their interest, care, and concern to the public online. In recent years, armadillos have received more attention also by the general public. For instance, there is a growing appealing about using armadillos as flagship species (Melo *et al.*, 2014; Superina, Duarte, & Trujillo, 2019). A high-profile example was the appropriation by the *Fédération Internationale de Football Association* (FIFA) of the Brazilian three-banded armadillo (*Tolypeutes tricinctus*) to serve as the mascot for the 2014 World Cup, although relatively few conservation measures have resulted thus far from this nomination (Bernard & Melo, 2019). Even inconspicuous and poorly known species of armadillos have aroused public interest (Superina *et al.*, 2019). Although only seven species of armadillos were mentioned on YouTube videos, our results suggest that armadillos can attract positive attention from the public online. Thus, further increasing the popularity and visibility of armadillos, especially for poorly known species and/or threatened of extinction, can be an effective strategy for improving conservation practices about this group.

Low negativistic and dominionistic score combined with a high humanistic and naturalistic score also indicates a positive attitude towards armadillos. Although negativistic attitude type ranks at third most likely one, YouTube viewers were not particularly negative; they did show great fear to get diseases, especially leprosy (*Fig. 1* and *Fig. 2*). Some YouTube videos indeed mentioned the possibility of armadillos spread leprosy, but they failed correctly informed that only one species is capable to spread it out. No information about how the disease is disseminated by the armadillo has been mentioned either. As a result, viewers were highly concerned about being infected with leprosy from armadillos in general (*Fig. 1* and *Fig. 2*). Aside from humans, nine-banded armadillo (*D. novemcinctus*) is the only other animal to host the *Mycobacterium leprae*, the causative agent in producing leprosy (Convit & Pinaridi, 1974). The risk of exposure to viable *M. leprae* would likely occur by handling a wild nine-banded armadillo, as the armadillo may cause injuries (Bruce *et al.*, 2000; Deps *et al.*, 2008; Bratschi *et al.*, 2015), or by killing the armadillo and handling the meat for consumption, as blood or other tissue fluids could gain entry through skin cuts (Silva *et al.*, 2018). Armadillos are usually used as food supply as highlighted by the words at the utilitarian category (*Fig. 1*), particularly the nine-banded armadillos (Rodrigues *et al.*, 2019). The consumption of nine-banded armadillo raw meat, especially the liver, would be considered a very high-risk behavior and among the practices most likely leading to successful infection (Silva *et al.*, 2018). We posit, however, that to get leprosy from nine-banded armadillos will depend on particular behaviors above mentioned that can be

easily avoided, apart from several other factors that further hamper its dissemination, including the prevalence of the disease on armadillo population (Loughry *et al.*, 2009) and the low genetic susceptibility of people to be infected by leprosy (Sales *et al.*, 2011; Joyce, 2012). Nevertheless, caution is advised when handling nine-banded armadillos.

Physical attributes and biological functioning of armadillos (scientific attitude type) has aroused great interest in the viewers, but their knowledge was restricted solely to basic physical attributes (*Fig. 1*). As armadillos are the only mammals bearing a carapace that consists of osteoderms covered by epidermal scales (Engelmann, 1985), rather expectedly this physical attribute drew great attention. For instance, viewers over commented about the possibility of armadillos in general curl into a ball. However, only three-banded armadillo *Tolypeutes* encase itself inside its shell as a method of self-defense to ward off predators (Eisenberg & Redford, 1999). Viewers also tried to relate armadillo attributes with other species, especially with the pangolins (Pholidota order), as both have similar morphology and lifestyle (Rose & Gaudin, 2010). Both armadillos and pangolins are typified by adaptations for digging and for feeding on ants and termite, but armadillos also have a varied diet (Redford, 1985), are exclusively terrestrial and can be found in a variety of habitats widely distributed in South and Central America, with one species currently reaching North America (Wetzel, 1985). Pangolins, however, can be arboreal and are confined to the Old World tropics, from sub-Saharan Africa to southeast Asia, mostly inhabiting forested habitats (Rose & Gaudin, 2010). Indeed, no ecological knowledge was highlighted or known by the viewers regarding armadillos, except that they are highly run over in the USA and are rarely found alive, as pointed out by the words in the ecologicistic category (*Fig. 1*). Importantly, armadillos provide essential ecosystem services (natural ecological processes that benefit human society), including regulating, material and non-material contributions (Rodrigues *et al.*, 2019) not mentioned on YouTube videos or comments. As viewers have demonstrated great interesting in armadillos also from scientist perspective, use that interest to increase public support on their research will surely increase our ability to develop sound conservation practices.

3.4.1. Conservation implications

We showed that social media platforms (such as YouTube) can be successfully used to assess public opinions towards armadillos online. Based on the most viewed videos on YouTube about up to seven armadillo species, viewers had a positive attitude regarding armadillos in general. Our findings suggest that social media can be used as a source of data for conservation purposes, and it can be further explored to extend effective conservational practices involving

this group. For instance, in this analysis, we selected the most viewed videos, which likely represent a popular interest in armadillos, and therefore did not choose videos based on their content. Future research could locate videos that cover a multitude of topics (e.g. hunting, education, behavior, entertainment, animation) to determine if comments made apply generally to the species, or are in specific response to the context. Moreover, the present study was focused on only one type of social media (YouTube), thus using data from other social media platforms might increase our knowledge about public perceptions, as their responses may vary in different social media (Stockmann & Luo, 2017). It would also be useful to link quantitative metrics from videos (likes, dislikes, views) to the demographic data of the viewers (e.g. age, gender, country, the highest level of education gained), as it may influence a person's perceptions toward wildlife (Gamborg & Jensen, 2016).

The present study illustrates also the potential of word analysis as a data source for conservation research by highlighting the most relevant topics from the public eye towards armadillos. For instance, we were able to access the most mentioned words overall and at each Kellert category, contributing to identify knowledge gaps and generating conservation insights. Besides, we were able to access that some YouTube videos with informational content did mention erroneous information (e.g. about leprosy) while others did not mention essential information (e.g. ecosystem services provided by armadillos). As approximately 39 million viewers accessed the videos, improving the quality of the contents may increase their understanding and interest as well as their positive attitude towards armadillos online. Importantly, further increasing the production of videos online for armadillos, especially for poorly known species or those threatened of extinction, can be a great strategy to improve armadillo research and conservation. Also, the top 15 YouTube videos were mostly in the English language, whereas most of the armadillo species are found in countries that speak Spanish or Portuguese. So, create subtitles or contents also in Portuguese and Spanish may locally increase armadillo visibility and their importance.

Our study opens a new perspective on using social media platforms and digital applications for assessing opinions online about armadillos towards conservation. Armadillo species have long been neglected by the scientific community and the general public (Superina *et al.*, 2014; Loughry *et al.*, 2015). As a result, according to the IUCN *Red List of Threatened Species*, 10 out of the 20 extant armadillo species have unknown population trends. Further, five species are categorized as *Data Deficient*, five as *Near Threatened* and two as *Vulnerable* (IUCN, 2019). We herein suggested that knowledge of conservation and biological functioning of armadillos should be widespread and emphasized in videos posted on social media. At the same time, an approach

encouraging public participation should be adopted for reducing gaps among scientists, the public and policymakers. The recognition that human values and actions constitute a central element in biodiversity conservation (Bennett *et al.*, 2017) calls for making better use of these newly available types of data in conservation science (Roberge, 2014; Ladle *et al.*, 2016).

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4. SEMI-SUPERVISED IDENTIFICATION OF ARMADILLOS: PRESERVING AN OLD SAMPLING METHOD IN THE TECHNOLOGY ERA

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Abstract

Having accurate information about population parameters of armadillos would improve our ability to conserve and manage them. We investigate the possibility to automatically and accurately identify four armadillo species based on burrow entrance morphometry. We simulate burrow measurements (width, height, and angle) using data found in literature and based on these values we classified unlabelled data through semi-supervised machine learning (SSML), a type of artificial intelligence. We present an R function (*armadilloID*) that automatically identified armadillo species with > 70% accuracy overall. Considering only the data for the known identification, three of four SSML classifiers identified the armadillos with > 80% accuracy. Our results suggest that burrows can be a useful source of information to identify armadillos, allowing ecologists to use a non-invasive low-cost method to study armadillo species.

Keywords: burrow, conservation, machine learning, non-invasive method, ecology, Xenarthra

4.1. Introduction

Estimating population parameters for wildlife is one of the primary interests of scientists and conservationists because of its decisive influence on wildlife management and conservation. However, estimating such parameters is not straightforward, particularly for wide-ranging, low-density, elusive and not well-known species, most of which are threatened (Schipper *et al.*, 2008; Desbiez, Massocato, Kluyber, & Santos, 2018). For example, according to the IUCN *Red List of Threatened Species*, 10 out of the 20 extant armadillo species have unknown population trend information, whilst others six are in decline. Yet, five are categorized as *Data Deficient*, five as *Near*

Threatened, and two as *Vulnerable* (IUCN, 2019). Because it is not practical to employ invasive physical tagging methods to derive armadillo population estimates due to logistical difficulties, high costs and small numbers of captures possible (Loughry & McDonough, 2013; Desbiez *et al.*, 2018), less than 20% of the armadillo studies were based on fieldwork conducted on wild populations (Superina, Pagnutti, & Abba, 2014). Alternatively, a non-invasive method such as camera trapping has been successfully used to assess occupancy for armadillo species (Zimbres *et al.*, 2013; Rodrigues & Chiarello, 2018), however, its disadvantages are the requirement of a large number of cameras (e.g. Rodrigues & Chiarello, 2018), which demands high costs, besides the vulnerability of cameras to animal damage or adverse weather, theft or vandalism and, potentially small number of detections, as some armadillos spend long periods in shelters (Maccarini, Attias, Medri, Marinho-Filho, & Mourão, 2015; Desbiez *et al.*, 2018).

Although armadillos are rarely observed in nature, they dig burrows directly related to the construction of shelter (housing, raising offspring), protection (to hide from predators and to buffer against environmental temperatures), and feed (foraging burrows) (McNab, 1980; Eisenberg & Redford, 1999; Desbiez *et al.*, 2018). Burrows created by armadillos have peculiar shapes and sizes (Carter & Encarnaç o, 1983; Trovati, 2015; Attias, Miranda, Sena, Tomas, & Mourão, 2016; Desbiez *et al.*, 2018), which are influenced by anatomical and morphological differences among the species (e.g. Attias *et al.*, 2016; Desbiez *et al.*, 2018). Several studies have been used armadillo burrows to estimate population parameters including habitat use, density, activity and behaviour (Zimmerman, 1990; McDonough, DeLaney, Blackmore, & Loughry, 2000; Platt, Rainwater, & Brewer, 2004; Arteaga & Venticinque, 2008; Abba, Udrizar-Sauthier, & Vizcaino, 2005; Abba, Zufiaurre, Codesido, & Bilenca, 2015; Sawyer, Brinkman, Walker, Covington, & Stienstraw, 2012; Desbiez *et al.*, 2018). However, correctly identifying armadillos based on their burrows can be challenging (e.g. McDonough *et al.*, 2000; Arteaga & Venticinque, 2010). For instance, to achieve that, Carter and Encarnaç o (1983) fitted four species of armadillos (*Cabassous tatouay*, *Cabassous unicinctus*, *Euphractus sexcinctus*, and *Priodontes maximus*) with radio transmitters and found that the shape of the burrows' entrance differed between the species. By contrast, the fact of solely *Dasybus novemcinctus* be found in the USA has resulted in well-known burrow measurements (Zimmerman, 1990; McDonough *et al.*, 2000; Platt *et al.*, 2004; Sawyer *et al.*, 2012). Other armadillo species were also monitored for describing their burrows measurements (Medri, 2008; Attias *et al.*, 2016; Desbiez *et al.*, 2018). Nevertheless, how to use those reported measurements to correctly identify armadillo species remains poorly explored (e.g. Arteaga & Venticinque, 2010). Few studies reported burrow measurements for different armadillo species, and each reported measure varies among the studies or not always are

associated with their corresponding sampling error estimates (e.g. Carter & Encarnaç o, 1983; Trovati, 2015). Factors such as age, sex, and habitat may increase the correlation among the burrow measurements by different species of armadillos further complicate the identification (Medri, 2008; McDonough *et al.*, 2000; Arteaga & Venticinque, 2010).

Machine learning enables computers to solve tasks analyzing complex patterns without being explicitly programmed to solve them (Sen, 2018). State-of-the-art methods teach machines via supervised learning (i.e., by showing them correct pairs of inputs and outputs from labeled data), unsupervised learning (i.e., finding hidden information or structure from unlabeled data) and semi-supervised learning (i.e., a combination of supervised and unsupervised machine learning technique; Sen, 2018). Its algorithms and models aim to maximize predictability based on data and have demonstrated high accuracy in predicting ecological patterns (Olden, Lawler, & Poff, 2008; Crisci, Ghattas, & Perera, 2012, Thessen, 2016). Machine learning models have been increasingly applied in ecology, including studies of species distribution modelling (e.g. Elith *et al.*, 2006, Phillips, Anderson, & Schapire, 2006), species diversity (e.g., Olden *et al.*, 2008) and distribution (e.g Elith & Leathweck, 2009), and represent great potential for improving species identification methods (e.g. Norouzzadeh *et al.*, 2018).

Species belonging to the genera *Cabassous*, *Dasyplus*, and *Euphractus* are efficient diggers (McDonough *et al.*, 2000; Medri, 2008; Trovati, 2015), have similar body sizes (Eisenberg & Redford, 1999), and can be sympatric (Trovati, 2015; Ferreguetti, Tomas, & Bergallo, 2016). Thus, these genera are ideal to examine for the possibility of correctly identifying them based on their burrows. Considering that the four following armadillo species: *C. tatouay*, *C. unicinctus*, *D. novemcinctus*, and *E. sexcinctus* inhabit a region highly affected by anthropogenic disturbances (Vivo *et al.*, 2011; Egeskog, Freitas, Berndes, Sparovek, & Wirsenius, 2014; Trovati, 2015), improving identification methods might help to ascertain the role of anthropogenic threats for each species of armadillo. Here, we target the following question: is it possible to identify similar body-sized armadillos based on their burrows? Assuming that armadillo burrows have been correctly identified in published studies, we aim to: 1) train data using simulating burrow measurements (width, height, and angle) for the four species of armadillos (*C. tatouay*, *C. unicinctus*, *D. novemcinctus*, and *E. sexcinctus*) based on data found in literature, 2) and then classify unlabelled data using a semi-supervised machine learning. For that purpose, we present an R function that automatically performs those procedures, running several statistical analyses at the same time and displaying output for the identification process.

4.2. Methods

4.2.1. Search strategy and database for simulating data

We searched the *Web of Science* and *Scopus* for articles using all available years and a combination of the following key words: ‘*armadillo**’ OR ‘*dasypus*’ OR ‘*dasyypodi**’ OR ‘*euphract**’ OR ‘*cabassous*’ AND ‘*burrow**’. Searches were conducted in February 2019. We also conducted haphazard searching on *Google Scholar* using some of the key words listed above and by conducting an additional search using the key words in Portuguese and Spanish. In order to be included, the study had to provide directly morphometric measurements (width, height, and angle) for one or more of the following armadillo species: *C. tatouay*, *C. unicinctus*, *D. novemcinctus*, and *E. sexcinctus*. In total, we found 15 studies that directly reported burrow measures for the four species of armadillos (*Table 1*).

Table 1. Species, measurements, and references used to generate the data of burrows. N = number of studies.

Species	N	Measurement	Reference ^a
<i>C. tatouay</i>	2	width, height, angle	Carter & Encarnaç�o (1983), Anacleto (2006) ^a
<i>C. unicinctus</i>	4	width, height, angle	Carter & Encarnaç�o (1983), Anacleto (2006) ^a , Trovati (2009), Desbiez <i>et al.</i> (2018)
<i>D. novemcinctus</i>	5	width, height, angle	Zimmerman (1990), McDonough <i>et al.</i> (2000) ^a – EUA, Platt <i>et al.</i> (2004), Anacleto (2006) ^a , Sawyer <i>et al.</i> (2012)
<i>E. sexcinctus</i>	4	width, height, angle	Carter & Encarnaç�o (1983), Anacleto, (2006) ^a , Medri (2008) ^a , Trovati (2009)

^aangle not reported.

4.2.2. Simulating data

We generate data using the 15 studies that reported morphometric measures of burrows for the four species of armadillos (*Table 1*). We used the mean value \pm standard deviation of width, height, and angle to generate data. By that, we used the *Normal* family of distribution (*rnorm* function), and for those studies that no reported corresponding standard deviation we used the highest value found from other studies for the same species. Particularly, for *C. tatouay* we used the *Poisson* family of distribution (*rpois* function) to generate data for angle as none standard deviation was reported from any found study.

4.2.3. Semi-supervised machine learning

The semi-supervised machine learning was performed using the *selfTraining* function of *ssc* package (Semi-Supervised Classification Methods) (González, Rosado-Falcon, & Rodriguez, 2018) in the R program (R Core Team, 2018). In the self-training method, a predictive model is constructed by using the available labelled instances (i.e. the simulated data in our case). Then it is iteratively retrained with its own most confident predictions over the unlabelled examples. A predictive model has then constructed again and the procedure is repeated until a stopping criterion is satisfied. To establish the possible class of unlabelled instances, the self-training follows a wrapper methodology using a base supervised classifier (González, 2018; González *et al.*, 2018), and by that, we used the four most common ones (Tsai, Hsu, Lin, & Lin, 2009): K-Nearest Neighbors (KNN), Support Vector Machine (SVM), Naïve Bayes Classification (NBC) and C5.0 Decision Tree (C5.0).

4.2.4. Complementary statistical analyses

Differences between groups (*C. tatouay*, *C. unicinctus*, *D. novemcinctus*, and *E. sexcinctus*) for each measurement (width, height, and angle), after the semi-supervised machine learning processes, were tested using analysis of variance (ANOVA) and associated two-by-two Tukey tests, considering an unbalanced sampled size for each species. The ANOVA was performed using *aov* function (Type III) and Tukey test was performed using *TK.test* function of *DTK* package (Lau, 2013) in the R program (R Core Team, 2018).

4.3. The R function

The function *armadilloID* automates burrow identification analysis for the four species of armadillos: *Cabassous tatouay*, *Cabassous unicinctus*, *Dasyurus novemcinctus*, and *Euphractus sexcinctus*. Fully executable R code and detailed manual are provided in Supporting Information.

4.3.1. Inputs and parameters

The key parameters of the function are described in *Table 2*. The argument *real_data* refers to the data the user wants to identify. The user must provide a data frame only with three columns, respectively: width (centimeter), height (centimeter) and angle (i.e. slope, in degrees) of the armadillo burrows entrance. The argument *n_sim* refers to the number of burrows the user wants to generate by species. That value must be a single number and multiple of 100. The maximum value the function accepts is 10,000 burrows by species. By default, this argument is

set as 1,000. The argument *n_samp* refers to the proportion of burrows the user wants to randomly select for conducting the analysis. To increase the randomness the user is able to randomly select only part of those generated data by species. That value must be a single number between 0.1 and 1 (10%-100%). By default, this argument is set as 0.7. The argument *id* refers to the base classifier for the semi-supervised machine learning the user wants to use to create final figures and calculating complementary statistical analyses. That value must be a single number between 1 and 4: 1=KNN; 2=SVM; 3=NBC; 4=C5.0. By default, this argument is set as 1.

Table 2. Key parameters of the *armadilloID* function.

Parameters	Description
<i>real_data</i>	Data frame with three columns, respectively: column 1 (width) = values for width in centimeters; column 2 (height) = values for height in centimeters; column 3 (angle) = values for angle in degrees.
<i>n_sim</i>	Numeric vector with a single value and necessarily multiple of 100; $100 \leq n_sim \leq 10,000$. <i>n_sim</i> = 1,000 (default)
<i>n_samp</i>	Numeric vector with a single value and necessarily between $0.1 \leq n_samp \leq 1.0$ (10%-100%). <i>n_samp</i> = 0.7 (default).
<i>id</i>	Numeric vector with a single value and necessarily between $1 \leq id \leq 4$. 1 = K-Nearest Neighbors (KNN); 2 = Support Vector Machine (SVM); 3 = Naive Bayes Classification (NBC); 4 = C5.0 Decision Tree (C5.0). <i>id</i> = 1 (default)

Before running the *armadilloID*, the user must guarantee internet connection because will necessary install the following packages (*ssc*, *DTK*, *car*, *caret*, *e1071*, *C50*) whether the user has not installed them yet. The installation process occurs automatically when the user runs the function.

The semi-supervised machine learning follows the examples provided at the documentation of *ssc* package in the *selfTraining* section (González *et al.*, 2018). Another alternative is the possibility of defining a particular base classifier beyond those used because the function is well-commented and can be easily modified. Thus, with this inputted information, *armadilloID* runs the simulating processes for each species, and the semi-supervised identification by each base classifier is extracted, including the complementary statistical analyses for a chosen base classifier.

4.3.2. Outputs

The function returns a data frame, two R lists, three plots, and prints some complementary statistics. The returned data frame (*final_id*) contains the final semi-supervised identification of armadillos based on their burrows. Regarding this data frame, it is possible to compare those different classifiers helping the user to make a decision towards the identification. That data frame also is exported as *armadillo_ID.csv* into the user working directory. It contains respectively the following columns: *width*, *height*, *angle*, *id_sim*, *id_knn*, *id_svm*, *id_nbc*, and *id_C5.0*. Specifically, the *id_sim* refers to the identification provided during the simulating process, and the corresponding NA values consist of those unlabelled data provided by the user. Others *id_* refers to each base classifier used during the semi-supervised machine learning.

The first R list returned (*result2*) has four levels corresponding to each base classifier (KNN, SVM, NBC, and C5.0 respectively), and contains several important components:

- a) *id*: a factor with the final identification provided after the semi-supervised machine learning;
- b) *confusion matrix*: a table with the confusion matrix between the predicted values from the base classifier and the initial labelled data provided by the simulating process;
- c) *accuracy*: a numeric vector with the proportion of the correct identification based on the values predicted from the base classifier and the initial labelled data provided by the simulating process. The formula over the confusion matrix is: $\text{sum}(\text{diagonal}) / \text{sum}(\text{total})$.

Regarding the second list returned, the plots, and the final complementary statistic, all of them just use one base classifier defined at the *id* argument. They represent a complementary, but not detrimental, statistics, which is created considering the final semi-supervised machine learning identification using the chosen classifier (e.g. KNN, SVM, NBC, or C5.0). Thus, the second R list returned (*result3*) has two levels corresponding to ANOVA and Tukey-Test for the three measurements (width, height, and angle, respectively). Additionally, a plot is created for each measurement and exported into the user working directory. The plotting was divided into two frames: at left, are created four boxplots for each species; and, at right, is created a plot provided from pairwise Tukey-Test comparison. Finally, the function prints the mean \pm standard deviation for each measure (width, height, and angle) for each species. As the objects *final_id*, *result2*, and *result3* are exported to the R global environment the user can use such objects for any posterior analysis.

4.3.3. Identification example

We present a simple example where we applied the function *armadilloID*. This example demonstrates how identification based on different classifiers for the semi-supervised machine learning is able to match with a known identification. Here the known identification is represented from a study assessing burrow characteristics of a single armadillo species, the *D. novemcinctus*. For details on the sampling design, see Zimmerman (1982). We generated 113 burrows (i.e., the number of measured burrows in the study) for width, height, and angle considering the reported mean value \pm standard deviation using the *Normal* family of distribution (*rnorm* function), and store them into *my_data*. This example can be found at the end of the manual in Supporting Material. We expect the identification provided by *armadilloID* for *my_data* being as *D.novemcinctus*. The function was specified as follows: *armadilloID* (*real_data* = *my_data*, *n_sim* = 1000, *n_samp* = 0.7, *id* = 1).

4.4. Results

In the example, the armadillo identification proposed by *armadilloID* varies among the different classifiers and was partly matched with the known identification. Considering all data, the accuracy of identification based on the semi-supervised machine learning was: 0.99 for the KNN; 0.72 for the SVM; 0.70 for the NBC; and, 0.78 for the C5.0. However, considering only the data for the known identification (i.e., 113 last records), the accuracy of identification based on the semi-supervised machine learning was: 0.51 for the KNN; 0.80 for the SVM; 0.87 for the NBC; and, 0.85 for the C5.0.

An example of output plot for one measure (angle) can be seen in *Fig. 1*, and it shows that through basic discriminant analysis (ANOVA and Tukey-test) it is possible significantly discriminate all species based on that measure using the identification provided by the KNN classifier. Additionally, the mean \pm standard deviation using the identification provided by the KNN classifier can be seen in *Table. 3*.

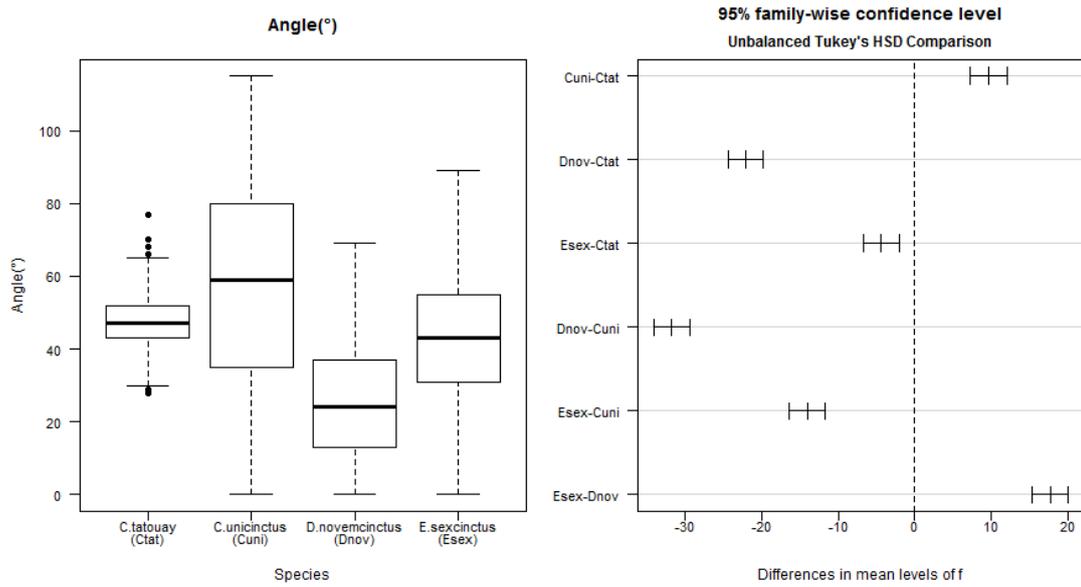


Figure 1. Boxplot illustrating the dispersion of the data between species (left) with two-by-two Tukey tests comparison (right) with significant differences (did not overlap zero) using the identification provided by the KNN classifier as a reference.

Table 3. Mean \pm SD of the three measurements (width, height, and angle) with a significant difference between armadillo species using the identification provided by the KNN as a reference.

Species	Width (cm)	Height (cm)	Angle (°)
<i>C. tatouay</i>	18.93 \pm 1.92	16.61 \pm 2.38 ^a	47.49 \pm 7.23
<i>C. unicinctus</i>	12.71 \pm 2.37	12.56 \pm 2.22	57.13 \pm 26.16
<i>D. novemcinctus</i>	21.09 \pm 5.87	18.48 \pm 4.81	25.45 \pm 15.34
<i>E. sexcinctus</i>	19.96 \pm 2.78	16.97 \pm 3.24 ^a	43.09 \pm 15.71

^ait does not show a significant difference.

4.5. Discussion

Our example demonstrated that it is indeed possible to identify similar body-sized armadillos based on their burrows. The semi-supervised machine learning is an appropriate method able to deal with the complexity of the data by enabling the armadillo identification based on their burrows. Unlike traditional identification methods, it successfully found patterns to classify unlabelled data, and accurately match with the known identification given the example. In such a way, it is a useful tool to conduct scientists to make better decisions towards correct

armadillo identification, and further important by enabling the use of a non-invasive low-cost method to estimate population parameters.

We found that the accuracy of identification provided by the *armadilloID* varies among the classifiers, resulting in between 70% and 99% of accuracy upon all data. Considering only the data from the example the accuracy varies between 51% and 87%. As each classifier has a different algorithm it is expected that they predict a different identification overall. The identification predicted by NBC and C5.0 showed similar and higher accuracy (87% and 85%, respectively) for correctly classifying the unlabelled data, while SVM accuracy was 80%. Nevertheless, the user may prefer to use these multiples classifications to get a *consensus* when defining the species identification instead of comparing them out. Indeed, we posit that identification approach as the most recommendable whether the user has access for complementary factors other than morphometric measurements, such as initial visual classification of the burrow shape (Trovati, 2015), and local features (Sawyer *et al.*, 2012, Desbiez *et al.*, 2018). For instance, according to Carter and Encarnaç o (1983), Redford and Wetzel (1985), and Trovati (2015), *E. sexcinctus* typically constructs burrows with an inverted U-shaped entrance, while the burrows of *C. unicinctus* has an almost perfectly round shape, since individuals rotate their bodies while digging their burrows (Carter & Encarnaç o, 1983; Trovati, 2015) in an almost vertical angle (Trovati, 2015; Desbiez *et al.*, 2018). Moreover, *D. novemcinctus* is the only one that may have as many as five entrances into a single den (Carter & Encarnaç o, 1983), and rotting leaves are often found near the entrances of burrows, especially after rains or floods (Talmage & Buchanan, 1954). Therefore, using qualitative local information together with the morphometric measures the accuracy for correctly identifying armadillos species based on their burrows may be even higher.

On the other hand, the user might decide to choose only one of the classifiers to correctly identify armadillo species. In that case, the potential misidentification is assumed; however, this approach still guarantees great levels of accuracy. Also, when the user chooses only one of the classifiers, complementary statistics analyses are generated helping it to verify it is possible significantly discriminate all species based on the three measurements (width, height, and angle). It represents a traditional statistics commonly used to discriminate between the armadillo species (e.g., Carter & Encarnaç o, 1983; Trovati, 2015; Attias *et al.*, 2016). However, the significant difference will be more frequent as higher the *n_sim* value. Moreover, based on the reported mean \pm standard deviation for the measurements it is possible to compare such values with those reported in the literature. For instance, Trovati (2015) found the mean value of the ratio (width/height) for *C. unicinctus* and *E. sexcinctus* as 1.01 and 1.19, respectively. Using our

reported mean value for width and height for *C. unicinctus* (12.71 and 12.56, respectively) and *E. sexcinctus* (19.96 and 16.97, respectively) it is possible to calculate the ratio as 1.01 and 1.18, corroborating our identification as *C. unicinctus* and *E. sexcinctus*.

As a way to standardization field data, it is common to classify burrows as either active or inactive (Sawyer *et al.*, 2012). An active burrow is the one with compacted forest litter, fresh excavations or tracks at the entrance, being an inactive burrow typically with spider webs and/or debris in the entrance (Sawyer *et al.*, 2012), presenting an eroded shape. Those differences are evident and easily identified in the field, although it does require some degree of experience by the observer. While not tested, considering only measurements from active burrows may also increase the accuracy of armadillo identification. Besides, we highlight that the use of the three measurements (width, height, and angle of the burrows' entrance) when collecting field data is enough for correctly identify armadillo species using the semi-supervised machine learning methods. They are the only measurements consistently present upon the scarce number of studies that reported morphometric measurements for armadillo burrows (see *Table 1*). Regarding the width and height, as pointed out by Carter and Encarnação (1983) they provide more precise information than the diameter. Nevertheless, more data is needed from monitored species of armadillos to improve the accuracy of the *armadilloID*.

The function presented here automates burrow identification analysis for the four species of armadillos: *C. tatouay*, *C. unicinctus*, *D. novemcinctus*, and *E. sexcinctus* allowing ecologists to use a non-invasive low-cost method to study those armadillo species. The function has the potentiality of expanding its options to embrace more armadillo species and more statistical models from other R packages. We encourage R programmers and ecologists to modify the code to satisfy their needs and expand the usage of *armadilloID*.

4.5.1. Conservation implications

Because of the armadillos' lifestyle, i.e. fossorial or semi-fossorial (McBee & Baker, 1982; Redford & Wetzel, 1985; Hayssen, 2014; Desbiez *et al.*, 2018) - their burrows represent the most effective low-cost sampling method for estimating population parameters. Correctly identifying their burrows may increase considerably our knowledge about armadillos, as some of them (e.g. *C. tatouay*, and *C. unicinctus*) spend most of their time underground (Hayssen, 2014; Desbiez *et al.*, 2018). While finding an appropriate method that is functional both for research and for species can be often not an easy task (Arteaga & Venticinque, 2010; Loughry & McDonough, 2013), we found that the use of novel technologies (e.g. machine learning) improving that non-invasive method should be prized, particularly when dealing with low-

density, elusive and not well-known species such as the armadillos (Abba & Superina, 2010; Desbiez *et al.*, 2018). In fact, the deficit of information on armadillo populations in tropical ecosystems is partially due to the lack of reliable cost-effective methodologies allowing managers to obtain data that will eventually lead to the development of appropriate management strategies. The semi-supervised machine learning and the *armadilloID* function considered in this study indicate the potential that both have to identify similar body-sized armadillos based on their burrows.

Additionally, considering that the four following armadillo species: *C. tatouay*, *C. unicinctus*, *D. novemcinctus*, and *E. sexcinctus* inhabit a region highly affected by anthropogenic disturbances (Vivo *et al.*, 2011; Egeskog *et al.*, 2014; Trovati, 2015), it is further important improve identification methods based on their burrows to consider explicitly the role of anthropogenic threats for each species of armadillo. The negative influence of anthropogenic threats can be further higher, as even basic biological information for most armadillo species still is poorly known (Abba & Superina, 2010; Superina *et al.*, 2014). On the other hand, correctly identifying their burrows may increase the knowledge specifically by each species about habitat use, density, activity, behaviour (Zimmerman, 1990; McDonough *et al.*, 2000; Platt *et al.*, 2004; Arteaga & Venticinque, 2008; Abba *et al.*, 2005, Abba *et al.*, 2015; Desbiez *et al.*, 2018), and even ecosystem services such as bioturbation (Sawyer *et al.*, 2012), and ecosystem-engineering (Desbiez & Kluyber, 2013). Therefore, our method provides new insight towards preserving the old sampling methods which is the most cost-effective while using new technologies such as machine learning to enable estimating population parameters of armadillos species. Nevertheless, we posit that using qualitative local information as many as possible together with the semi-supervised machine learning based on the three measurements (width, height, and angle of the burrows' entrance) will surely guarantee a higher accuracy towards the correct armadillo identification.

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5. NATIVE FORESTS WITHIN AND OUTSIDE PROTECTED AREAS ARE KEY FOR NINE-BANDED ARMADILLO (*DASYPUS NOVEMCINCTUS*) OCCUPANCY IN AGRICULTURAL LANDSCAPES

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Abstract

Given the accelerating worldwide expansion of agriculture, biofuel production and managed forest plantations, the future of many tropical mammals depends on understanding why or when some species successfully survive in anthropogenically modified habitats, while others do not. Armadillos are potentially able to adapt to agricultural landscapes and play a key role as ecosystem engineers. However, it is not clear how dependent armadillos are on natural areas in agricultural landscapes and, more specifically, how or if armadillos can use sugar cane or managed forests as alternative habitats. Here, we assessed the relative effects of landscape features, composition and configuration, anthropogenic impacts and degree of protection, as potential predictors of landscape occupancy of the nine-banded armadillo (*Dasypus novemcinctus*). We deployed 203 camera trap stations in three agricultural landscapes of the Brazilian Cerrado, where sugar cane or managed forest cover most (>50%) of the landscape. We found that cover by native forests and proximity to watercourses strongly and positively affect the occupancy of the nine-banded armadillo. In contrast, managed forests mostly composed of *Eucalyptus* spp. had a negative effect on this armadillo's landscape occupancy. We did not detect the effect of sugar cane, although this particular result might be biased due to our sampling design. Overall, our findings indicate that even disturbed native forest strips, particularly those close to watercourses, are important habitats for this armadillo in agricultural matrices, demonstrating the utmost importance of native forests existing both within and outside protected areas. The Brazilian Forest Code protects native vegetation existing in rural private properties in Brazil, but adherence to this law by rural owners is still weak. Therefore, our study supports the strategic role this law plays in conservation in Brazil. Although not endangered by extinction, maintaining the nine-banded armadillo is important for a broader biota because of its putative role as an ecosystem

engineer. The effective implementation of the Forest Code is therefore key not only to maintain this armadillos' populations but also to increase ecosystem services in agricultural landscapes.

Keywords: Agriculture, Brazil, Camera trapping, Cingulata, Cerrado, Cropland

5.1. Introduction

With the increasing demand for agriculture commodities and planted forest products, vast proportions of native forests have been converted into monocultures (Millennium Ecosystem Assessment, 2005). In this scenario of rapid changes in land cover and land use, knowledge on how animal populations cope with those disturbances is essential for improving the management of agricultural areas and developing effective conservation policy for wildlife (Gardner *et al.*, 2009; Melo *et al.*, 2013). Understanding why some species can successfully survive in anthropogenically modified habitats, while others cannot, is a key question in ecology, agriculture and conservation biology (Newbold *et al.*, 2015; Tscharrntke *et al.*, 2005).

In tropical countries such as Brazil, one-third of the land has already been converted, and agricultural frontiers are still expanding (Sparovek *et al.*, 2010). This is especially true for the state of São Paulo, which became dominated, in the last 40 years, by sugar cane monocultures and, to a lesser degree, by managed tree plantations (i.e., *Eucalyptus* spp. and *Pinus* spp.; Egeskog *et al.*, 2014; CONAB, 2014; ABRAF, 2016). Just 17% of its original vegetation remains today (Kronka *et al.*, 2005; Metzger & Rodrigues, 2008). The resulting agricultural landscapes are mostly mosaics formed by a homogeneous matrix of agroecosystem permeated by remnant patches of native vegetation (Metzger & Rodrigues, 2008). Therefore, wildlife conservation in such human-dominated areas requires considering the productive land use, i.e., cropland; (Collins & Fahrig, 2017; Gheler-Costa *et al.*, 2013) from the perspective of the species in focus. Positive and negative effects may both occur; however, ecologically flexible species capable of exploiting these highly modified habitats should be more resilient as human expansion continues (e.g., Rodrigues *et al.*, 2017).

The nine-banded armadillo (*Dasybus novemcinctus*) might have the potential to adapt to agricultural landscapes (Bovo *et al.*, 2018; Dotta & Verdade, 2011; Mcdonough *et al.*, 2000). These are medium-sized mammals (adult body weight: 3-6 kg) with a wide geographic distribution, encompassing most of the Neotropics and the southern tip of the Nearctic (southern United States). The nine-banded armadillo digs burrows for feeding, to raise young, to hide from predators and to buffer against environmental temperatures (McNab, 1980; Eisenberg & Redford, 1999). Given these aspects of their natural history, we can assume that they are directly

dependent on soil surface physical and chemical properties. Therefore, changes in soil quality (e.g., changes in soil morphology and physical-chemical properties due to anthropogenic impacts), together with agrichemical exposure resulting from the widespread use of fertilizers, herbicides, and pesticides typical of modern agriculture, might negatively affect them. Notwithstanding this, it is not clear how or if these armadillos surviving in agricultural landscapes (Dotta & Verdade, 2011) are dependent on native vegetation, such as forest patches. Further, we do not know yet how or if these armadillos use sugar cane or managed forests as alternative habitats. Although the nine-banded armadillo is relatively well studied in the United States (Superina *et al.*, 2014), there is a dearth of ecological information on this species elsewhere (Eisenberg & Redford, 1999; Superina *et al.*, 2014). There is almost no research focusing on habitat preferences or on the extent to which this armadillo can survive in anthropogenic environments. In fact, less than 20% of the armadillo studies were based on fieldwork conducted on wild populations (Loughry *et al.*, 2015; Superina *et al.*, 2014).

This information is relevant, considering the growing scenario of biofuel and managed forest expansion (Egeskog *et al.*, 2014; ABRAF, 2016; Spera *et al.*, 2017). Brazil is one of the world's largest ethanol producers (Monteiro *et al.*, 2012; CONAB, 2014). As a result, sugar cane plantations dominate rural landscapes in some states, particularly São Paulo, where approximately one-third of the Brazilian ethanol production originates from (CONAB, 2014; Egeskog *et al.*, 2014). Brazil also ranks as one of the five largest cellulose producers in the world, with devoted areas to managed forest reaching upwards of 7.7 million hectares, most of which are from exotic species, such as *Eucalyptus* spp. and *Pinus* spp. (ABRAF, 2016). The state of São Paulo has the second largest area of managed forests in the country, with 1.19 million hectares (ABRAF, 2016).

Armadillos, as a whole, have important roles in the Neotropical ecosystems, so understanding how productive lands affect them is also relevant to a larger biota. Specifically, the nine-banded armadillo is a key prey for top and mesocarnivores (Bianchi *et al.*, 2010, 2011; Bueno & Motta-Junior, 2004; Foster *et al.*, 2010). Their burrowing activity alters vegetation, promotes sediment movement and nutrient cycling, and alters soil fertility and mineralization rates which, in turn, affects forest dynamics and regeneration (Sawyer *et al.*, 2012). Their burrows might act as refuges for other vertebrate species and form suitable habitats for vertebrates and invertebrates, similar to what has been found for other armadillos (Desbiez & Kluwyber, 2013; Machicote *et al.*, 2004). Due to these ecological functions, armadillos, as a whole, might be recognized as ecosystem engineers (Desbiez & Kluwyber, 2013; Jones *et al.*, 1994; Machicote *et al.*, 2004).

Here, we evaluate how agricultural and silvicultural landscapes affect nine-banded armadillos with occupancy modeling using camera trap data from three highly modified

landscapes in southeastern Brazil. Specifically, we assessed the relative effects of landscape composition (native forest, sugar cane, and managed forest plantation) and configuration (edge density), as well as anthropogenic impacts (distance from human residences), degree of protection (government-protected areas) and natural features (terrain slope and distance from watercourses) as potential predictors of landscape occupancy. Assuming that nine-banded armadillos are sensitive to anthropogenic disturbance (e.g., Ferregueti *et al.*, 2016), we predict that landscape occupancy is positively affected by areas of remaining natural habitat and negatively affected by distance to water (McDonough *et al.*, 2000) and the amount of anthropogenic land cover types (i.e., sugar cane and forest plantation). Identifying land-use patterns that are positively related to armadillos' occupancy would provide options for maintaining and enhancing armadillos' population and ecosystem services in agricultural regions. These options would be particularly valuable in regions where most of the natural habitats have been lost and in situations where taking cropland out of production for conservation is not feasible.

5.2. Methods

5.2.1. Study area

Our study area encompassed an area of approximately 132,000 ha in three agricultural landscapes (*Fig. 1*) within the Cerrado domain (i.e., Brazilian Savannah) of São Paulo State, southeastern Brazil (21°02'–21°43'S and 47°54'–47°16'W). The main municipalities in this area are Luiz Antonio, São Simão, Altinópolis, and Cajuru. The annual temperature varies between 14°C to 28°C, with a mean annual rainfall of 1,470 mm. Rainfall is concentrated in the summer – October to March (CEPAGRI, 2014). Taken together, these three landscapes are characterized by important remnants of natural closed-canopy forest (21%; including a woody savannah – *cerradão*, semi-deciduous, deciduous, and riverine forests), located within and outside of protected areas, and it is surrounded by a heterogeneous matrix made up of *Eucalyptus* spp. (26%), sugar cane plantation (26%), other crops (13%), waterways (1%), and urban areas (3%).

However, the three study landscapes also have important differences. Landscape A is dominated by a large strictly protected area, the Jataí Ecological Station (JES; 9,010 ha), equivalent to a category I protected area from the IUCN (*strict nature reserve*; IUCN, 2018), and by a smaller reserve (Luiz Antônio Experimental Station - LAES; 1,759 ha), equivalent to a category VI protected area from the IUCN (*protected area with sustainable use of natural resources*; IUCN, 2018). Overall, sugar cane is the predominant land cover type (*Table 1*). Landscape B is private property from *International Paper Company* (Cara Preta Farm – CPF; 4,546 ha) and is predominantly covered

with commercial plantations of *Eucalyptus* spp. for paper production. The remaining native forests are protected along rivers and streams (areas of permanent preservation, protected by the Brazilian Forest Code; Brancalion *et al.*, 2016). The third and last landscape (C) is a *mix* between the former two landscapes, with a smaller but still predominant cover by managed forests (*Eucalyptus* spp. and *Pinus* spp.; Table 1). It includes a private farm from *International Paper Company* (Dois Corregos Farm - DCF; 2,017 ha), a protected area with sustainable use of natural resources (Cajuru State Forest - CSF; 1,909 ha) and native forests protected by the Forest Code (Table 1 and Fig. 1).

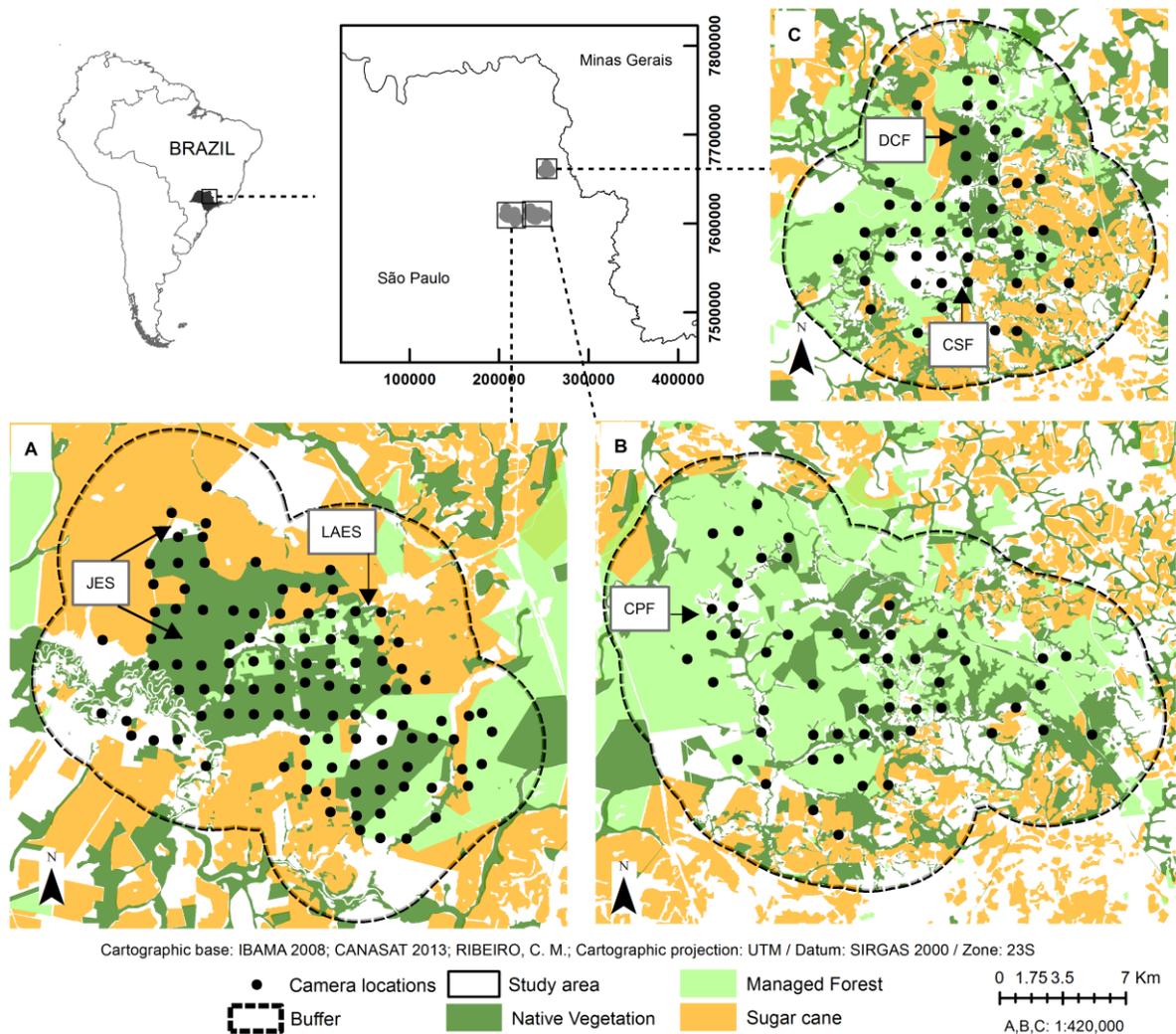


Figure 1. Camera trap points (dots) over 3 study landscapes in the state of São Paulo, southeastern Brazil. Landscape A: Jataí Ecological Station (JES) and Luis Antônio Experimental Station (LAES), B: Cara Preta Farm (CPF), and, C: Dois Córregos Farm (DCF) and Cajuru State Forest (CSF). The most distant points reach up to 2.6 km from the perimeter of each study area. Map adapted from Rodrigues *et al.*, 2017.

Table 1. Mapped area (hectares) of the study landscapes in southeastern Brazil, including corresponding sampling effort with camera traps and main landscape cover amounts in hectares and proportion (parentheses) (see Section 5.2.3 for details).

Study areas	Area*	Camera days	Number of camera sites	Closed-Canopy Forest	Open-Canopy Forest	Sugar cane	Managed forest	Other
Landscape A (JES)	50,206	3,060	102	13,683 (0.27)	241 (0.005)	20,593 (0.41)	6,420 (0.13)	9,269 (0.18)
Landscape B (CPF)	51,860	1,560	52	8,582 (0.17)	3,521 (0.07)	7,278 (0.14)	20,370 (0.39)	12,109 (0.23)
Landscape C (CSF)	30,150	1,470	49	5,887 (0.20)	1,705 (0.06)	7,054 (0.23)	8,236 (0.27)	7,268 (0.24)
Total	132,216	6,090	203	28,152 (0.21)	5,467 (0.04)	34,926 (0.26)	35,026 (0.26)	28,646 (0.22)

*Mapped area includes a 5 km-wide buffer (see Section 2.3).

5.2.2. Armadillo sampling

We obtained data on armadillos (see Section 5.3) from camera trapping and track sampling. The camera trapping was based on a total of 203 sampling sites distributed in a grid of 200-ha cells, with cameras placed at the center of each cell. In some cases, we were unable to access the center of the 200-ha cell to place the camera, so we placed them as close as possible. All cameras were spaced ≈ 1.4 km apart. We systematically placed cameras inside JES-LAES ($n = 52$), CPF ($n = 18$), and CSF-DCF ($n = 19$) and randomly placed a similar number of cameras up to 2.6 km from the perimeter of protected areas and areas of permanent preservation (*Fig. 1*).

We recorded nine-banded armadillo occurrence during the dry season (i.e., from April to September) in 2013 at landscape A and in 2014 at landscapes B and C. Sampling was restricted to only one season in each landscape to satisfy the closure assumption of single-season occupancy models (MacKenzie *et al.*, 2006). A single-camera trap (Reconyx®, digital model HC 500; Reconyx, Holmen, Wisconsin) was fixed on a tree trunk ≈ 50 cm above the ground and was installed in each camera station and programmed to continuously monitor (24 h) over 30 consecutive days. We randomly rotated cameras among sites due to a limited number of cameras. Specifically, we deployed cameras at 18 sites for 30 consecutive days; then, we exchanged batteries and moved the cameras to another 18 random sites. We repeated this process over two years (between April-September) until all 203 sites were sampled. Approximately one-half of the

cameras were deployed on the forest interior and one-half on unpaved roads along forest edges. Further, given logistical and safety constraints, all randomly located points in sugar cane plantations were relocated to the nearest available contact zone between sugar cane and natural closed-canopy forest. In these new locations, cameras were oriented to aim at the originally chosen land cover type (i.e., sugar cane). We sampled armadillo tracks on two occasions during camera set up and during camera removal 30 days later. We did this by actively searching for footprints along approximately 200 m, 100 m on each side of each sampling point. Tracks were identified in situ or photographed for later identification with the help of track guides (Becker & Dalponte, 2013; Borges & Tomas, 2008).

5.2.3. *Landscape covariates*

We mapped the vegetation cover with ArcGIS 10.1 (ESRI, 2011) and Quantum GIS v.2.2 (Quantum GIS Development Team, 2015) at a scale of 1:10,000 using high-resolution orthophotography obtained from the Cartographic and Geographic Institute (São Paulo, Brazil). Our mapping encompassed an area of 132,216 ha (*Table 1*), including a 5-km buffer of our three study landscapes (*Fig. 1*), and it was highly accurate (Cohen's kappa coefficient = 0.897, $P = 0.001$; Cohen, 1960). We extended our mapping to a 5 km-wide buffer to comprise the entire influencing areas of the most distant sampling sites (i.e., those at 2.6 km from the perimeter of protected areas and areas of permanent preservation).

We evaluated the influence of 9 covariates on the occupancy and 12 covariates on the detection of armadillos (*Table 2*). Tested covariates were as follows: *forest* (i.e., proportion of native closed-canopy vegetation represented by *cerradão*, semi-deciduous, deciduous, and riverine forests); *sugarcane* (sugar cane plantation); *managed_forest* (i.e., *Eucalyptus* spp. or *Pinus* spp. plantation); *water* and *residence* (nearest distance between the sampling points and watercourses or residences, including rural installations, respectively); *slope* (i.e., mean slope); and *edge* (i.e., edge density represented by total length of patch edges from closed-canopy forest divided by total area). Furthermore, we classified the sampling points as being located on or off unpaved roads (covariate *road*) and as being located within a protected area (JES, LAES, and CSF; *Fig. 1*) or not (covariate *protected area*). We used a dummy covariate *landscape* to assess the difference between landscape A (considered as our reference category due to the large protected area it contained; JES/LAES) and the other two landscapes (B+C). This grouping is also backed by ongoing analysis from our laboratory (Ph.D. dissertation by Victor Krepschi, in preparation), which indicated that landscapes B and C are more similar to each other than they are to landscape A, regarding the temporal change in the land cover (dynamic of deforestation between 1960-

present). Additionally, we considered the mean temperature (covariate *temperature*) and the total precipitation (covariate *rain*) as potential predictors of detection, both referring to the 30 days of sampling at each sampling point.

Table 2. Covariates and corresponding descriptions hypothesized to affect the detection and occupancy of nine-banded armadillo (*D. novemcinctus*) across agricultural landscapes in São Paulo state, southeastern Brazil.

Covariate name	Covariate notation	Description	Scale	Hypothesized direction of effect	
				ψ	p
Temporal Change Landscape	landscape	Categorical scale: landscape A (0), landscapes B and C (1)	Regional	-	-
Protection Degree	protected_area	Sampling points located within (0) or outside (1) governmental protected areas	Regional	+	-
Road	road	Sampling points located off (0) or on (1) unpaved roads	Local	NA	-
Edge Density	edge	Total length of edges along patches of closed-canopy forest divided by buffer area	798 m radius (200 ha)	-	-
Closed-Canopy Forest Cover	forest	Amount of closed-canopy forest cover in buffer area	179-798 m radius (10, 20, 50, 100 and 200 ha)*	+	+
Sugar cane Cover	sugarcane	Amount of sugar cane cover in buffer area	179-798 m radius (10, 20, 50, 100 and 200 ha)*	-	-
Managed Forest Cover	managed_forest	Amount of managed forest cover in buffer area	179-798 m radius (10, 20, 50, 100 and 200 ha)*	-	-
Mean Slope	slope	Mean slope within buffer area	179-798 m radius (10, 20, 50, 100 and 200 ha)*	+	+
Proximity to Water	water	Nearest distance of camera-trap from water	Local	-	-
Proximity to Building	residence	Nearest distance of camera-trap from buildings	Local	+	+
Temperature	temperature	Average temperature during camera-trapping sampling	Regional	NA	-
Precipitation	rain	Total precipitation during camera-trapping sampling	Regional	NA	-

*scale of effect tested detailed in Section 5.2.4

The covariates *forest*, *sugarcane*, *managed_forest*, *water*, and *residence* were measured using ArcGIS software (ESRI, 2011). We calculated the following: 1) the proportion of land cover

(*forest*, *sugarcane*, and *managed_forest*) using a predefined buffer with different spatial scales (see Section 5.2.4); 2) the nearest distance between the camera position and *water* or *residence* using the *Near* function on ArcGIS software (ESRI, 2011); and 3) the *edge* using the *Edge Density* function upon class-metrics on FRAGSTATS 4.2 (McGarigal *et al.*, 2015), with our forest map as the input layer. We obtained the hydrographic map from the Forest Foundation of São Paulo State (São Paulo, Brazil), and the mean slope at each site from digital elevation models (DEM) available from the Topodata Geomorphic database of Brazil (INPE, 2014). We obtained climate data from the National Institute of Meteorology (INMET, 2013), with some values obtained from the *International Paper Company* (Luiz Antônio, Brazil).

5.2.4. Scales of effect

We tested 5 spatial scales with sampling areas of 10 ha, 20 ha, 50 ha, 100 ha, and 200 ha (i.e., concentric circles with radii of 179-798 m) around each camera trap site. We used this for land cover types and mean slope to determine the best scale at which the association of each predictor with the occurrence of armadillos was strongest, using binomial (logit link) generalized linear models (Martin & Fahrig, 2012; Miguet *et al.*, 2016). The scale with the highest absolute β -coefficient value for the relationship between each variable and the occurrence (incidence records) of armadillos was considered the scale of effect for that predictor (e.g., Koumaris & Fahrig, 2016). We found that the best scales were as follows: *forest* = 10 ha, *sugarcane* = 10 ha, *managed_forest* = 10 ha; and *slope* = 200 ha. We considered the spatial scale of a 200 ha-buffer for *edge*. Furthermore, we used only weakly correlated covariates ($r < 0.50$) in the final model set.

5.2.5. Data analysis

We used the single-season occupancy modeling framework to estimate the occupancy (ψ) of nine-banded armadillos while accounting for heterogeneity in the detection probability (p) (MacKenzie *et al.*, 2002). We used occupancy as a proxy for habitat use, assuming that our sampling equipment, design, and period of study are adequate to satisfy this assumption (MacKenzie *et al.*, 2005; MacKenzie & Bailey, 2004). We built detection histories for nine-banded armadillos for each site over 7 separate occasions (i.e., 6 separate occasions for camera-trap data over 5 days occasion-1 (Mackenzie & Royle, 2005) and 1 separate occasion for footprint data). For each sampling occasion, species detection was recorded as '1', while nondetection was recorded as '0'.

We used a 2-step approach to modeling the occupancy of the nine-banded armadillo (MacKenzie *et al.*, 2006). First, we modeled detection by fixing a general model for ψ (using

uncorrelated covariates, *Table 2*). The covariates used in the general model for ψ were as follows: *landscape*, *protected_area*, *forest*, *sugarcane*, *water*, and *residence*. Then, we tested different covariate combinations for p , either singly or together (up to 2 covariates per parameter), and tested additive effects. In the 2nd step, we fixed the best model for p and tested different covariate combinations for ψ , either singly or together (additive effects, up to 2 covariates per parameter). For the covariates *protected_area* and *landscape*, we also tested interaction effects (up to 2 covariates per parameter).

We generated and analyzed a set of 53 candidate models to assess nine-banded armadillos' occupancy using the Program Mark (White & Burnham, 1999). All tested models represent a biologically plausible hypothesis. We used Akaike's Information Criterion corrected for small samples (AICc) due to the absence of extrabinomial variation of the most parameterized model based on the goodness-of-fit-test (*c-hat* calculated with 10,000 resamples over the most-parametrized model = 1.00; Burnham & Anderson, 2002). For each model, we computed AICc, the difference in AICc from the top-ranked model (ΔAICc), and Akaike weights ($w\text{AICc}$) and used these values to rank models (Burnham & Anderson, 2002). We considered the covariate(s) from the top-ranked model(s) ($\Delta\text{AIC} < 2$) as the best determinant(s) of the species' occupancy. Furthermore, we used the estimated β as an indication of the *significance* of a covariate when its corresponding confidence interval (95%) did not overlap zero, and we estimated ψ using the top-ranked model.

5.3. Results

Over 6,090 camera-trap nights, we detected nine-banded armadillos (*Dasybus novemcinctus*) in 19 of our 203 sampling stations. For occupancy modeling, we added 12 records from *Dasybus* sp. to those 19 detections, which increased the detection to 31 of our 203 sampling stations, resulting in a naïve (uncorrected) occupancy probability of 0.15 (15%). However, although there may be some seven-banded armadillos at sampling stations without proper identification, records from *Dasybus* sp. should likely refer to the most commonly detected species (i.e., *Dasybus novemcinctus*). We only detected the seven-banded armadillo (*Dasybus septemcinctus*) in 1 of our 203 sampling stations, which was discarded from our occupancy modeling. We also detected the yellow-armadillo (*Euphractus sexcinctus*) in 3 of our 203 sampling stations and the southern-naked-tailed armadillo (*Cabassous unicinctus*) in 6 of our 203 sampling stations.

5.3.1. Single-species occupancy models

Two out of 53 total occupancy models tested had $\Delta\text{AICc} \leq 2$ (Table 3). The Akaike weights of these two models represent 59% of relative importance within our model set. The models both include *Distance from water* as a covariate, with a strong negative effect on site occupancy by nine-banded armadillos (Fig. 2B). The top-ranked model also indicates a strong positive effect of *forest* (Fig. 2C), and the second best-ranked model also indicates a strong negative effect of *managed_forest* (Fig. 2D) on site occupancy by nine-banded armadillos in agricultural landscapes. For those covariates, the strong effect can be inferred based on the confidence intervals of the estimated betas, which did not overlap zero. Apart from those three covariates, all other tested covariates had a weak effect on occupancy when individually tested. Considering the heterogeneity on detection probability, we found a corrected occupancy probability of 0.31 ± 0.07 (value \pm SE), which is ≈ 2 times higher than the uncorrected (*naïve*) occupancy probability. The best detection model included *protected_area* and *road* as covariates, but only *road* had a strong, negative effect (Fig. 2A). This indicates that the nine-banded armadillo was less detected on cameras placed on unpaved roads than off-road cameras.

Table 3. Summary of model selection results for the top 10 models (84% relative importance) assessing predictors of nine-banded armadillo (*D. novemcinctus*) occupancy (ψ) within agricultural landscapes in São Paulo state, southeastern Brazil. ΔAICc = 2nd-order AIC, $w\text{AICc}$ = model weight, L = relative model likelihood, K = number of parameters, and Deviance. Equally plausible top models ($\Delta\text{AICc} < 2$) are in bold.

Model	ΔAICc	$w\text{AICc}$	L	K	Deviance
{$p(\text{protected_area}+\text{road})$, $\psi(\text{forest}+\text{water})$}	0.00	0.37	1.00	6	351.69
{$p(\text{protected_area}+\text{road})$, $\psi(\text{managed_forest}+\text{water})$}	0.98	0.22	0.61	6	352.67
{ $p(\text{protected_area}+\text{road})$, $\psi(\text{managed_forest})$ }	4.04	0.05	0.13	5	357.86
{ $p(\text{protected_area}+\text{road})$, $\psi(\text{managed_forest}+\text{ed})$ }	4.39	0.04	0.11	6	356.08
{ $p(\text{protected_area}+\text{road})$, $\psi(\text{global})$ }	4.79	0.03	0.09	10	347.76
{ $p(\text{protected_area}+\text{road})$, $\psi(\text{managed_forest}+\text{slope})$ }	4.89	0.03	0.09	6	356.58
{ $p(\text{protected_area}+\text{road})$, $\psi(\text{managed_forest}+\text{residence})$ }	5.15	0.03	0.08	6	356.84
{ $p(\text{protected_area}+\text{road})$, $\psi(\text{landscape}*\text{managed_forest})$ }	5.18	0.03	0.07	7	354.72
{ $p(\text{protected_area}+\text{road})$, $\psi(\text{landscape}+\text{managed_forest})$ }	5.65	0.02	0.06	6	357.34

The sign (+) indicates additive effects and the sign () indicates interactive effects between 2 covariates.

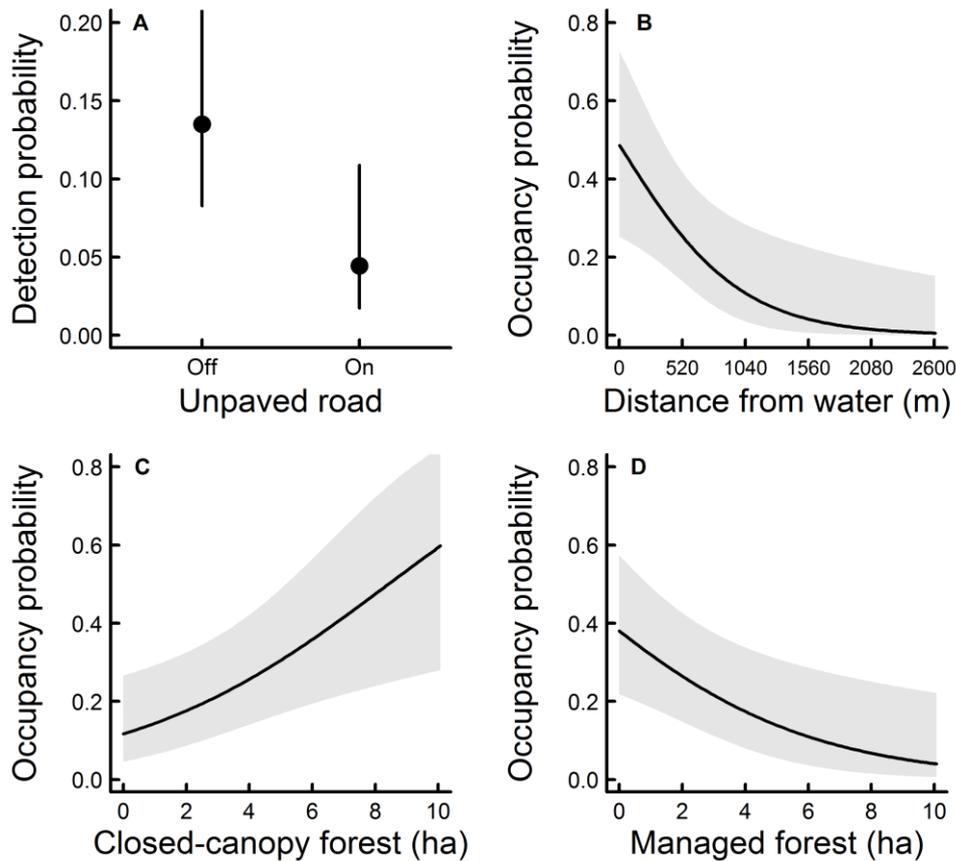


Figure 2. Relationship between covariates from the top models ($\Delta\text{AICc} \leq 2$) of nine-banded armadillo (*Dasypus novemcinctus*) detection and occupancy models, in which the confidence intervals (95%) of the estimated betas (β) did not overlap zero. A: nine-banded armadillo detection probability (\pm 95% CI) as a function of unpaved roads. B, C and D: nine-banded armadillo occupancy probability (\pm 95% CI in gray) as a function of distance from a watercourse (B), closed-canopy forest (C) and the managed forest (D).

5.4. Discussion

Our results show that *water* and *forest* had strong, positive effects (Fig. 2B-C), and *managed_forest* had a strong, negative effect (Fig. 2D) on landscape occupancy of the nine-banded armadillo, better explaining the variation in this parameter than other land cover types, slope or distance from residences. These findings highlight the importance of closed-canopy forest and watercourses for this species in agricultural landscapes.

The positive effect of closed-canopy forests is consistent with our prediction that the occurrence of the nine-banded armadillo would be positively associated with native forests in different environments (Ferreguetti *et al.*, 2016; Loughry & McDonough, 2013). As armadillos are poor thermal regulators (McNab, 1980), they might prefer sites having more stable temperature

and humidity conditions, such as those found in native forest patches (Laurance *et al.*, 2011), to maintain or optimize their metabolic rates (Attias *et al.*, 2018; Maccarini *et al.*, 2015). Alternatively, this result might also reflect differences in the availability of soil invertebrates, which are the most important food sources for this armadillo (Fitch *et al.*, 1952; McBee & Baker, 1982; Sikes *et al.*, 1990). Although we did not evaluate differences in the insect community within and outside closed-canopy forests, changes in insect community composition and abundance have been recorded in croplands due to their simplified plant community (Franco *et al.*, 2016) and pesticide use (Duelli *et al.*, 1999; Narendra *et al.*, 2011; Vasconcelos, 1999). Consequently, areas with a higher proportion of forests have higher complexity of plant community and are less affected by pesticides, therefore, maintaining a relatively less disturbed and/or more diverse and abundant invertebrate community than croplands.

Given the putative lower quality of cropland as habitats, we expected that our analyses would detect a negative effect of sugar cane on occupancy and/or on detection of the nine-banded armadillo in our study area, something that did not happen. We suspect that the lack of such effect might have resulted from a possible bias in our study design. As we mentioned in the Methods section, to avoid damage or loss of camera traps, we did not install our cameras within sugar cane fields and instead used the nearest available contact zone between sugar cane and native forest (see Section 5.2.2). Therefore, our effect (or, rather, the lack of it) of sugar cane on occupancy should be considered with care, as it might be signaling the effect, not of sugar cane *per se* but the contact zone between sugar cane and native forests.

On the contrary, watercourse use by nine-banded armadillos was consistent with our prediction, since these armadillos appear to need direct access to freshwater to survive (Ferregueti *et al.*, 2016; Loughry & McDonough, 2013) and/or may take advantage of the availability of food resources in areas closest to water (McBee & Baker, 1982). The possible impact on water quality resulting from agriculture activities (runoff water rich in pesticides and chemical fertilizers, among other sources of water pollution; Tanaka *et al.*, 2016; Taniwaki *et al.*, 2017) is not compromising the use of nearby areas by nine-banded armadillos in such agricultural landscapes. The proximity to watercourses becomes even more important when we consider the highly degraded condition of the riparian forests in our system, particularly outside protected areas. Overall, these remaining forest strips are very disturbed, in some places lacking even canopy closure, and exotic grasses are frequent. A study carried out in a large and little disturbed protected area in the Atlantic forest showed that forests close to the reserve's perimeter are avoided by the nine-banded armadillo (Ferregueti *et al.*, 2016). Thus, in landscapes dominated by

agriculture and managed forest, these riparian forests, even those disturbed and probably polluted by runoff water with fertilizers and/or pesticides, are highly prized by this armadillo.

We found a strong negative effect of managed forests on the occupancy of this armadillo, which is consistent with some studies showing a drastic decline of mammal species in Eucalyptus plantations (Barlow *et al.*, 2007; Brockerhoff *et al.*, 2008; Coelho *et al.*, 2014). The impoverished habitat of these managed forests has a reduced taxonomic and functional diversity of the insect community (Fierro *et al.*, 2017; Martello *et al.*, 2018; Suguituru *et al.*, 2011). Furthermore, insects are considered the most important *plague* of Eucalyptus plantations in southeastern Brazil and, consequently, are rigorously controlled by the pulp and paper industry (Ramos *et al.*, 2004). Taken together, these two factors decrease the availability of feeding resources for nine-banded armadillos in these environments. One possible additional factor might result from the high permeability of managed forests to movements of some armadillo predators (e.g., Coelho *et al.*, 2014; Lyra-Jorge *et al.*, 2010). Preliminary analyses indicated that predator species, such as pumas (*Puma concolor*), maned wolf (*Chrysocyon brachyurus*), domestic dogs (*Canis familiaris*), and ocelots (*Leopardus pardalis*), were all recorded in our sampled Eucalyptus plantations.

Our study shows the nine-banded armadillo occupying only a third of our study landscapes. However, occupancy increased to 80% at sites where the forest cover is at a maximum (100% closed-canopy forests within the 10 ha buffers) close to watercourses (< 250 m from the closest watercourse). In contrast, below 20% of closed-canopy forest cover, the occupancy plummets to 5%. This is consistent with the study by Ferreguetti *et al.* (2016), showing that sites located well within the forest reserve (> 750 m from the closest edge) are intensely occupied (80-90%) by this armadillo. Although this dependence on forests indicates that these forest areas are central to the animal, it is likely that it also uses, to a lesser extent, nearby agricultural areas, as suggested by other studies (Gammons *et al.*, 2009; Mcdonough *et al.*, 2000). We conclude that, given the presence of closed-canopy forest patches and watercourses, the occurrence of the nine-banded armadillo is possible in agricultural landscapes.

5.4.1. Conservation implications

We showed that preserving native forests in agricultural landscapes is essential for the nine-banded armadillo, backing what has been found for other species in similar scenarios (Beca *et al.*, 2017; Redford & Fonseca, 1986). Our finding that even degraded forest strips, particularly those close to watercourses, are important habitats for this armadillo, demonstrates the utmost importance of native forests, particularly those existing outside protected areas. Although the

nine-banded armadillo is not under conservation concern, landscapes maintaining it can be helpful to predators and to a host of other smaller vertebrates and invertebrates that benefit from its burrowing activities (Desbiez & Kluyber, 2013; Machicote *et al.*, 2004). In some forest places, nine-banded armadillos dominate the diet of jaguars and pumas (Foster *et al.*, 2010; Novack *et al.*, 2005). For example, a study based on stable isotopes shows that in agricultural landscapes, pumas are frequently consuming nine-banded armadillos (Magioli *et al.*, 2014). Therefore, even though *D.novemcinctus* is a common species, conserving it might contribute to the integrity of food webs in agricultural landscapes.

Our study supports the strategic role (Galetti *et al.*, 2010) played by the *Native Vegetation Protection Law* of Brazil (*Brazilian Forest Code*; Brancalion *et al.*, 2016; Soares-Filho *et al.*, 2014). Among other things, this law mandates that 20% of the area in rural properties be set aside in the form of legal forest reserves (*reservas legais*). Furthermore, an additional amount, varying per property size, location, and other criteria, must be protected as areas of permanent protection (*áreas de proteção permanente*). According to this law, small watercourses (< 10 m wide) must have 30 m wide areas of permanent protection alongside their margins. Correspondingly, considering only the effect of water proximity, our models show that the nine-banded armadillo occupies almost half (45%) the sites located up to 30 m from the closest watercourse, but this decreases to only 7% at sites farther than 250 m from the closest creek or stream.

Empirical data such as these are needed to help increase the implementation of the *Brazilian Forest Code* among rural owners. Unfortunately, most rural property owners do not respect or implement this law yet, resulting in a significant deficit between what the law mandates and what is truly preserved (Soares-Filho *et al.*, 2014; Taniwaki *et al.*, 2018). We acknowledge that preserving and restoring forests may present challenges and entail financial costs to farmers. However, putting together investments for this purpose increases ecosystem services and conservation values, which in turn benefit crop production in several ways (Millennium Ecosystem Assessment, 2005; Tscharntke *et al.*, 2005).

Increasingly, scientific information is demonstrating compatibility, i.e., common ground, between agricultural and conservation interests (Sparovek *et al.*, 2016; Metzger *et al.*, 2017). Producers in general and agricultural markets are progressively complying with nature conservation requirements, while also preparing to meet the increasing demands for agricultural products (Sparovek *et al.*, 2016). Relevant support for civil society activism and surveillance can also increase the likelihood of such compatibility (Sparovek *et al.*, 2015, 2016). Therefore, promoting enforcement frameworks for the *Brazilian Forest Code* is a key strategy to maintain or enhance forest cover in private properties, which, in turn, will surely contribute to sustaining

nine-banded armadillos in agricultural landscapes. Considering that a host of other species, including other armadillos, also benefit from native forest presence or proximity (Attias *et al.*, 2018), such enforcement will doubtlessly ameliorate the capacity of productive rural zones to maintain at least a certain degree of ecosystem services.

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6. FOREST EDGE DENSITY POSITIVELY AFFECTS THE OCCURRENCE OF NAKED-TAILED ARMADILLOS (*CABASSOUS* SP.) IN SUGARCANE DOMINATED LANDSCAPES

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Abstract

Wildlife populations are increasingly confined to human-modified landscapes, in which different spatial variables describing landscape composition and configuration influence species persistence. Therefore, understanding how wildlife responds to such anthropogenic landscapes is essential for improving the management of these areas and developing an effective conservation policy for wildlife. Here, we evaluate how composition and configuration landscape variables affect naked-tailed armadillos (*Cabassous* sp.) occurrence in sugarcane dominated landscapes. We deployed 162 camera-traps in 55 study landscapes in sugarcane dominated region of the Brazilian Cerrado, Brazil. We found that forest edge density strongly and positive affect *Cabassous* sp. occurrence in sugarcane dominated landscapes. Besides indicating that naked-tailed armadillos can occur in such agricultural landscapes, we suggest that forest edge might be an important habitat that makes possible their coexistence with other armadillo species in such landscape context. We highlight that considering the configurational heterogeneity of the landscape is key for the understanding of naked-tailed armadillo (*Cabassous* sp.) occurrence in agricultural landscapes.

Keywords: Agricultural landscapes, camera-trapping, spatial heterogeneity, mammal, Xenarthra.

6.1. Introduction

Agriculture dominates the world's terrestrial area and besides being, by far, the main cause of global change on Earth (Tscharntke *et al.*, 2005; Foley *et al.*, 2005), is still expanding (Ellis, 2013; Riitters *et al.*, 2016). As a result, the amount of natural cover keeps decreasing in many agricultural landscapes and represents a continuing worldwide threat to biodiversity and the ecosystem services they provide (Newbold *et al.*, 2015). Altogether, such emerging landscapes have different spatial structures, ranging widely in their degree of spatial and temporal heterogeneity which can influence both positively and negatively a variety of ecological responses (Tscharntke *et al.*, 2005; Fahrig *et al.*, 2011). By spatial heterogeneity, such landscapes can show different composition (types and proportions of different forms of land covers) and/or different spatial configuration (spatial arrangement of a given land use/land cover) (Fahrig *et al.*, 2011). Each of these landscape variables can not only alter patterns of local diversity (α) but also the structure of remaining assemblages, potentially altering the species turnover (β -diversity) and the whole ecosystem functioning (Carrara *et al.*, 2015; Beca *et al.*, 2017). Ascertaining why some species can successfully survive in anthropogenically modified habitats, while others cannot, remain a key question in ecology, agriculture and conservation biology (Tscharntke *et al.*, 2005; Newbold *et al.*, 2015). Further, understanding how wildlife responds to these human-modified habitats is essential for improving the management of agricultural areas and developing an effective conservation policy for wildlife (Gardner *et al.*, 2009; Melo *et al.*, 2013).

In Brazil, sugarcane (*Saccharum* spp.) is the single plant used for ethanol fuel generation and its production more than doubled over the last decades to meet the growing demand for bioenergy (Bordonal *et al.*, 2018). For instance, to meet only the domestic demand for ethanol in 2021 it has been projected an additional amount of 6.4 Mha of land under sugarcane (Goldemberg *et al.*, 2014), an extent larger than the total area of countries such as Switzerland or Netherlands. Besides, Brazilian sugarcane ethanol has been proposed to be used as an expandable green alternative to crude oil use and for mitigating climate change, which consequently will further promote its expansion (Jaiswal *et al.*, 2017). Facing this scenario of rapid changes in land cover and land use, it is necessary to investigate the adverse effects of this expansion and its direct effects of land-use change on jeopardizing wildlife maintenance, as such impact is poorly known (Verdade *et al.*, 2012). Brazil is the world leader in sugarcane production and about 50% of Brazilian production is from the southeast of the country, where approximately one-third of the Brazilian ethanol production originates (Egeskog *et al.*, 2014). Globally threatened species such as the giant anteater (*Myrmecophaga tridactyla*) as well as regionally threatened species such as the maned wolf (*Chrysocyon brachyurus*), and jaguarundi (*Puma yagouaroundi*) still inhabit this region

immersed in sugarcane dominated landscapes, but few studies have addressed the effect of anthropogenic features on their occurrence (Magioli *et al.*, 2016; Bovo *et al.*, 2018; Bertassoni *et al.*, 2019), or on the occurrence of low-density, elusive and not well-known species, such as the naked-tailed armadillos (*Cabassous* sp.) (Superina, Pagnutti, & Abba, 2014; Loughry *et al.*, 2015).

There are two species of naked-tailed armadillos (genus *Cabassous*) found in Brazil: *Cabassous tatouay* and *Cabassous unicinctus* (Wetzel, 1985; Paglia *et al.*, 2012). Both species seem to feed primarily on terrestrial ants and termites (Redford, 1985), are highly fossorial (Hayssen, 2014; Desbiez *et al.*, 2018), and they dig burrows every day, but do not use the same burrow twice (Carter & Encarnaçao, 1983; Desbiez *et al.*, 2018). Both species are classified by the IUCN *Red List of Threatened Species* as *Least Concern* (IUCN, 2019), although recently *C. tatouay* was considered *Data Deficient* in an evaluation of its extinction risk in Brazil (Anacleto *et al.*, 2015). Both species have been overlooked over the years (Superina *et al.*, 2014; Loughry *et al.*, 2015). Naked-tailed armadillos can be found in open and forested areas, including agricultural landscapes (Abba & Superina, 2010; Hayssen, 2014); however, it is not clear if they can inhabit sugarcane dominated landscapes and how dependent they are on the natural cover or landscape structure. Based on their lifestyle, naked-tailed armadillos would seem likely to experience high exposure to any soil-borne contaminants, either directly from their foraging activities and burrowing, or indirectly via consumption of their soil-dwelling prey, thus decreasing the probability of their occurrence in such landscape. *C. tatouay* seems to be more habitat-sensitive, usually reported as intolerant for areas of intensive agriculture or severely degraded habitats (Aguiar & Fonseca, 2008). Importantly, both species provide key ecosystem services, including ecosystem-engineering, bioturbation, pest control, and seed dispersal (Rodrigues *et al.*, 2019), thus increasing the importance of our understanding of how agricultural lands affect them.

Here, we aim to explore how landscape variables influence the occurrence of *C. tatouay* and *C. unicinctus* in a sugarcane dominated region from the northeastern state of São Paulo, Brazil. We measured two variables of composition (forest cover and anthropogenic cover) and five variables of configuration landscape (forest proximity index, forest shape index, forest edge density, Shannon diversity index, and water density). We hypothesize that variables regarding forest patches (a proxy of habitat amount) – i.e., the main natural cover which still remains immersed in sugarcane dominated landscapes (Metzger & Rodrigues, 2008) – will positively affect the occurrence of naked-tailed armadillos, whereas anthropogenic cover (a proxy of habitat local disturbances), is expected to negatively affect the occurrence of naked-tailed armadillos in sugarcane dominated landscapes. Identifying land-use patterns that are positively related to

armadillos' occurrence would provide options for maintaining and enhancing armadillos' population and ecosystem services in agricultural landscapes.

6.2. Methods

6.2.1. Study area

Our study was conducted in a large fragmented (~34000 km²) region of the Cerrado domain (i.e., Brazilian Savannah) in the state of São Paulo, southeastern Brazil (19°58'– 22°14'S and 49°14'– 47°02'W) (Fig. 1).

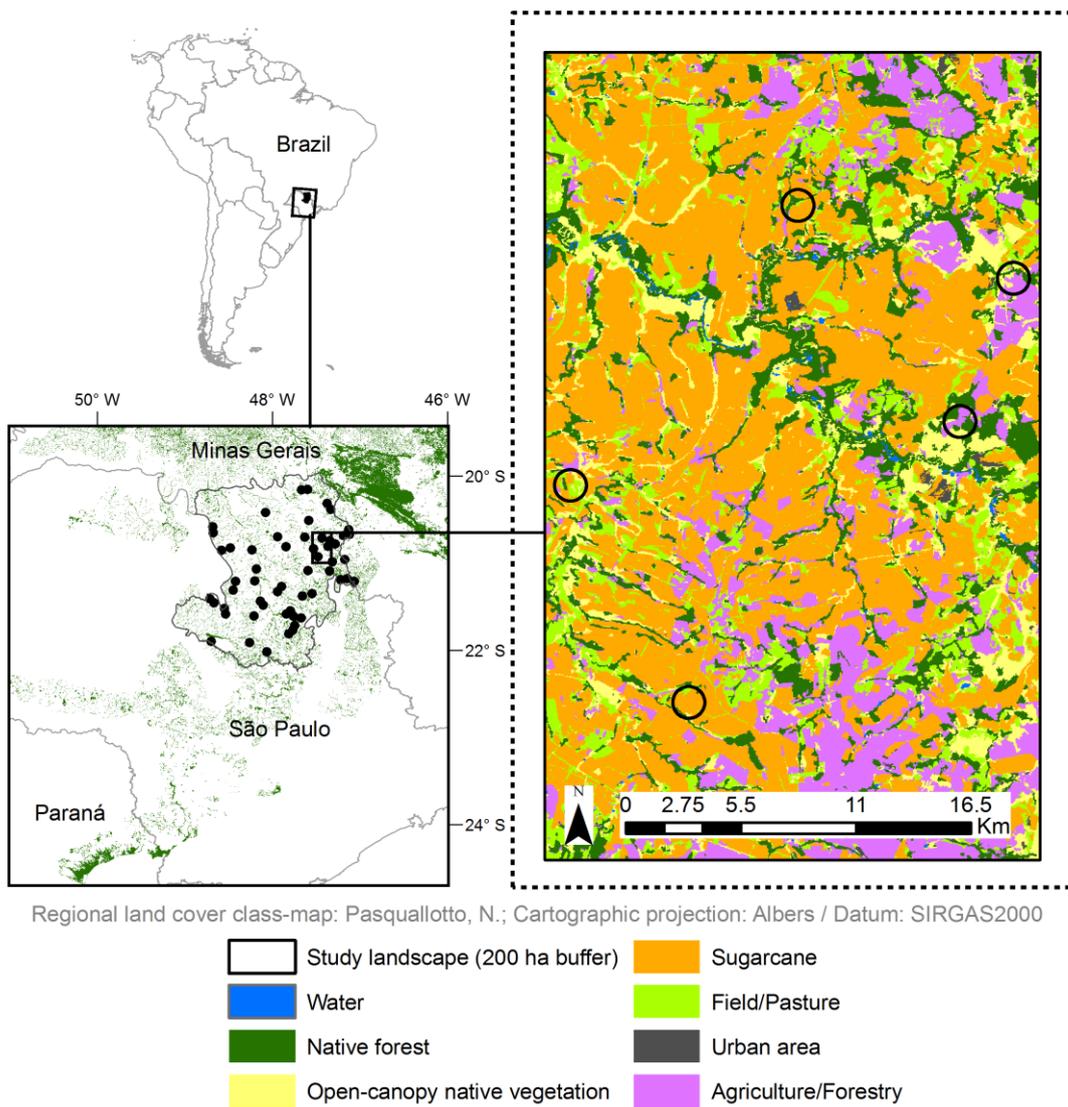


Figure 1. Study landscapes distributed within the Cerrado domain in northeastern of São Paulo State.

The region has an average annual rainfall of 1410 mm and an average annual temperature of 21 °C (<http://climate-data.org>). The best forests in this region started to be cleared in the mid to late 1800's for coffee plantations so that in the 1950's only 20% remained (Victor *et al.*, 2005). From that time on, the wooded and open savannahs started to be cleared so that, over the last 50 years, most of the native type of vegetation had been converted to pastures, managed forests, sugarcane, and other types of crops (Sparovek *et al.*, 2010; Egeskog *et al.*, 2014). Such transformation has left remnants of native vegetation in different conservation levels, immersed in an anthropogenic-dominated matrix (Soares-Filho *et al.*, 2014; Brancalion *et al.*, 2016). Today, sugarcane monocultures comprise the predominant matrix habitat type across the region, which also includes urban settlements and small fractions of pasture lands, eucalyptus monocultures and other cropland such as coffee and citrus (Mapbiomas, 2017). Land tenure is primarily private (different owners) and there are few governmental protected areas (Metzger & Rodrigues, 2008).

6.2.2. Landscape selection

We selected 55 study landscapes (circle of 200 ha each) with their center apart by at least 6.2 km – i.e., to reduce the effect of spatial autocorrelation among these areas (Pasher *et al.*, 2013), and based on three landscape metrics: the Percentage of Landscape (PLAND) and the Largest Patch Index (LPI) for the native forest remnants, and landscape compositional heterogeneity, represented by Shannon Diversity Index (SHDI) (McGarigal *et al.*, 2015). Although the original vegetation of the state of São Paulo is highly heterogeneous (Mapbiomas, 2017), we restricted our landscape selection to forest remnants, not including other native physiognomies (Fig. 1; Mapbiomas, 2017). PLAND and LPI were obtained using a merged map from two recent maps provided by the Brazilian Institute of the Environment and Renewable Natural Resources – IBAMA (IBAMA, 2017), and São Paulo's Rural Environmental Registry – CAR (CAR, 2017). These maps were created based on Landsat images at 1:50,000 scale (30 m spatial resolution; IBAMA) and based on RapidEye images at 1:20,000 scale (10 m resolution; CAR), respectively. The compositional heterogeneity of the landscapes (SHDI) – i.e., number and proportion of different classes of land cover (sugarcane, pasture, forest) – was obtained using a map provided by the project MapBiomas, which was also created based on Landsat images at 1:50,000 scale (30 m spatial resolution; Mapbiomas, 2017).

We first calculated the LPI through a moving window at two different scales, the sampling scale where the species occurrence was collected (i.e., 200 ha; see section 2.3) and the larger possible scale in our research design without overlap between adjacent landscapes (i.e.,

3000 ha). Then, via map algebra, we divided the resulting maps of both scales to find potential landscape centers with the same value of LPI. We did this to ensure that the forest structure of each study landscape would be equal between the two different spatial scales (Pasher *et al.*, 2013). To calculate PLAND and SHDI we used a moving window at the sampling scale. The raster map to calculate SHDI also included the native forest as one of the land covers. Finally, we randomly selected landscapes centers apart by at least 6.2 km from those with the same LPI, ensuring a wide gradient of native forest cover (5–85%) and compositional heterogeneity (0.15–1.6). Albers projection and SIRGAS2000 datum were used as our spatial database reference system. All landscape selection procedures were performed using the software Fragstats (McGarigal *et al.*, 2015) with some procedures on ArcGIS v. 10.1 (ESRI, 2011).

6.2.3. Armadillo sampling

We obtained data on naked-tailed armadillos (see Section 6.3) from camera trapping. At each study landscape, three camera-traps (Reconyx®, digital model HC 500; Reconyx, Holmen, Wisconsin) were fixed on tree trunks ~50 cm above the ground inside remnants of native forest and were programmed to continuously monitor (24 h) over approximately 30 consecutive days. The selected places to install the cameras within landscapes were based on accessibility, but all cameras were spaced at least 50 m apart (480 ± 299 ; mean \pm SD). A total of 162 cameras were used to sample naked-tailed armadillos. We recorded their occurrence during the dry season – i.e., from June to October in 2017 and from April to September in 2018. Specifically, we randomly sampled five study landscapes each month but each landscape was sampled in only one season, either in 2017 or 2018, to adhere to the single-season occupancy protocols (MacKenzie *et al.*, 2018).

6.2.4. Landscape variables

We produced land cover maps of each landscape using high-resolution Google Earth images (1 m spatial resolution). We generated these maps by manual vectorization at 1:10,000 scale (5 m spatial resolution), followed by visual classification with ArcGIS 10.1 (ESRI, 2011). The map was composed of six land cover classes as follows: (a) *water* (i.e. river or lakes); (b) *forest* (i.e., *cerradão*, semideciduous, deciduous, and riverine forests); (c) *open-canopy native vegetation* (i.e., *campo cerrado*, *cerrado sensu stricto*, floodplains and some regenerating areas); (d) *agriculture/forestry* (i.e., mostly citrus, coffee, and eucalyptus); (e) *sugarcane* and (f) *field/pasture* (Fig. 2).

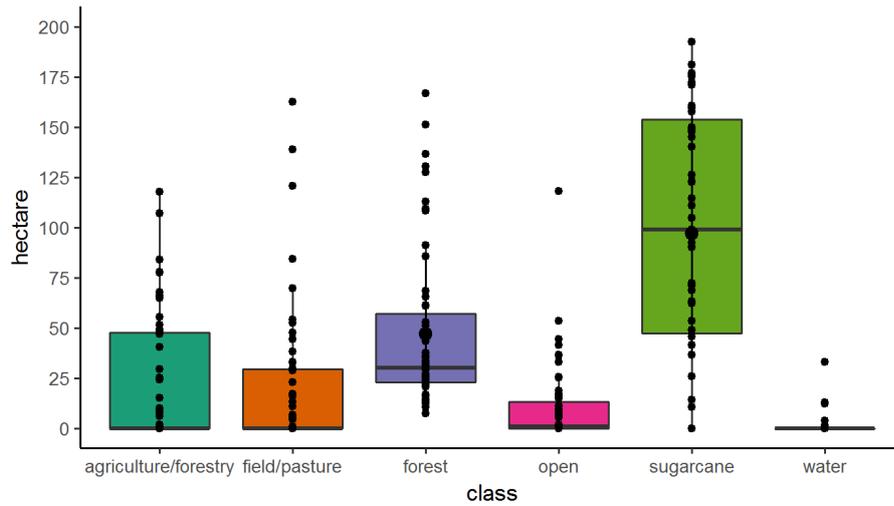


Figure 2. Distribution of the cover classes mapped in the study landscapes.

We calculate seven ecologically informative landscape variables within each study landscape which have been demonstrated to be of high relevance for wildlife in human-modified landscapes (Ewers & Didham, 2006; Fahrig *et al.*, 2011; Fahrig, 2013; Carrara *et al.*, 2015) (*Table 1*), as follows: Area indices: (1) proportion of forest cover (PLAND) and (2) proportion of anthropogenic cover (PLAND), in which forest cover represents the amount of habitat at the landscape scale while anthropogenic cover represents a proxy of proximate human-caused threats regarding agricultural activity. Degree of agglomeration index: (3) forest mean proximity index (PROX_MN), representing the degree of spatial agglomeration or separation of patches in a landscape; used as a surrogate of local habitat connectivity. If a landscape consists of many small patches, the degree of agglomeration is low; when a landscape is composed of a few large patches or if the patches in the same category are adequately connected, the degree of agglomeration is high. Shape index: (4) forest mean shape index (SHAPE_MN). Shape indices are based on the perimeter and area of a patch and represent the complexity of landscape patch shapes. In landscape ecology, shape indices are closely related to edge effects (Li & Wu, 2004). Density indices: (5) forest edge density (ED) and (6) water density (WD). ED represents the amount of edge-affected forests while WD represents the influence of water bodies in the landscape and both also are positively related to the complexity of the landscape. Diversity index: (7) Shannon diversity index (SHDI). It measures the diversity of the landscape. The diversity equals zero when the landscape possesses only one patch type and higher value indicates more diverse landscape

patterns. We calculated all landscape variables in ArcGIS 10.1 (ESRI, 2011) with the V-Late (2013) extension.

Table 1. Landscape variables calculated within each study landscape for using as independent variables on naked-tailed armadillo occurrence in sugarcane dominated landscapes in São Paulo, Brazil.

Variable	Indicators	Meaning
<i>Landscape composition variables</i>		
Forest cover	PLAND ¹	Proportion of landscape area covered by forest
Anthropogenic cover	PLAND ¹	Proportion of landscape area covered by (a) sugarcane (b) field/pasture and (c) agriculture/forestry
<i>Landscape configurational variables</i>		
Forest proximity index	PROX_MN ¹	A proxy of local habitat connectivity, considering the size and proximity of all patches whose edges are within the landscape
Forest edge density	ED ¹	Total perimeter length of all forest patches within the landscape divided by landscape area
Forest shape index	MSI ¹	Patch perimeter divided by the square root of patch area, summarized by the mean for each landscape
Shannon diversity index	SHDI ¹	A proxy of landscape diversity, considering the amount of land cover and the change of their proportions
Water density	WD	Total watercourse length within the landscape divided by landscape area

¹ see details in McGarigal & Marks (1995)

6.2.5. Data analysis

The detection of species is imperfect, and detection probability < 1 can bias the results of standard regression analyses (MacKenzie *et al.*, 2006). Approaches have been developed to take this into account in regression models (MacKenzie *et al.*, 2006), but they generally require a certain number of observations or recaptures over time, making the application of these methods difficult for rare species (Banks-leite *et al.*, 2014). The definition of rarity often varies with study system and taxa (Rabinowitz, 1981; Yu & Dobson, 2000), and while it is undeniable that species that were only captured once or twice in such a large sample effort are rare, few would consider a species to be rare if it failed to occur in at least eight out of 11 sites (Ferraz *et al.*, 2007; Banks-leite *et al.*, 2014). When a species or individual is poorly detected, detectability models may not

converge to a solution even for a species occurring across 50% of the sites (Welsh, Lindenmayer, & Donnelly, 2013). Given the scarcity of naked-tailed armadillos records (see Section 6.3), we, therefore, used Generalized Linear Models (GLMs).

Before the analysis, we standardized $(X - \mu/\sigma)$ independent variables to compare effect sizes, used Pearson correlation coefficient (r) matrices and variance inflation factor (VIF) estimation to identify and assess the extent of collinearity (Zuur, Hilbe, & Ieno, 2013). We retained variables with $VIF < 3$ and Pearson's $r < 0.6$ for the full global model. We used Generalized Linear Models (GLMs) with a binomial distribution to test the influence of landscape variables (independent variables; *Table 1*) on the occurrence of naked-tailed armadillos (*Cabassous* sp.) based on their presence-absence in each landscape (dependent variable). Model fit was conducted through a stepwise procedure, using backward elimination. All independent effects were included, and the effect that contributed the least to the model was removed at each step. We also included models with a single predictor at the time, and a null model against a null, intercept only model, representing the absence of effect of any predictor. Akaike's Information Criterion (AIC) was used to rank models based on $\Delta AIC < 2$ (Burnham & Anderson, 2002). Model assumptions were verified by plotting residuals versus fitted values (Zuur & Ieno, 2016). All statistical analyses were conducted in the R software (R Core Team, 2018). Code is available as supplementary material.

6.3. Results

Over a total survey of 4,822 camera-trap nights (an average of 87.67 trap nights at each landscape), we detected naked-tailed armadillos (*Cabassous* sp.) in 12 landscapes ($12/55 = 22\%$). We were not able to discriminate between the species (*C. tatouay* and *C. unicinctus*) based on the photographs, except in three landscapes in which we were able to correctly identify the species as *C. tatouay*. The top-ranked model included only a significant and positive effect of the predictor forest edge density (ED) on the naked-tailed armadillo occurrence in sugarcane dominated landscapes (*Fig. 3*). Although four out of 17 models tested had $\Delta AIC < 2$, they had predictors with no significant influence (95% confidence intervals of the corresponding betas overlapping zero) on the occurrence of naked-tailed armadillos, except the ED for the second and third models (*Table 2*). Model validation indicated no problems (see supplementary material).

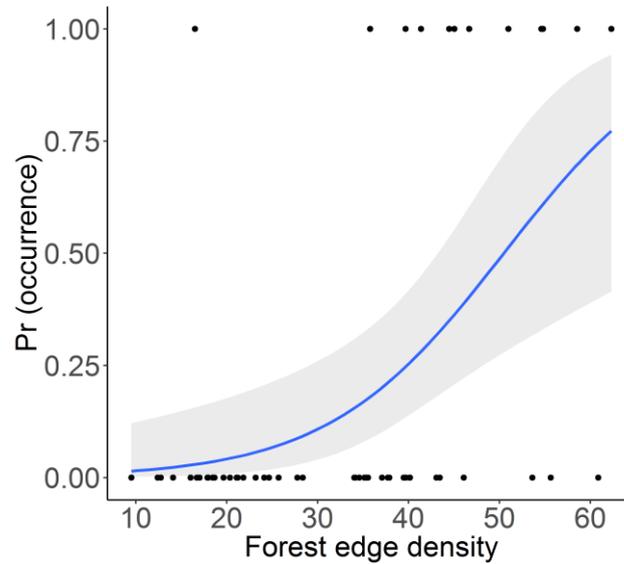


Figure 3. Relationship between the variable forest edge density from the top model ($\Delta\text{AIC} = 0.00$) on the naked-tailed occurrence (*Cabassous* sp.), in which the confidence intervals (95% CI in gray) of the estimated beta (β) did not overlap zero.

Table 2. Variables used and results of the binomial Generalized Linear Models (GLMs) on the occurrence of naked-tailed armadillos in sugarcane dominated landscapes, Brazil. Values in bold indicate a significant effect of the predictor (β), considering a significance at $P < 0.05$.

	Intercept	ED	Field	Forest	Forestry	MPI	MSI	SHDI	WD	Sugar cane	DF	Log Lik	AIC	ΔAIC	Weight
m8	-1.76	1.44									2	-22.04	48.31	0.00	0.26
m5	-2.14	1.89		-0.87	-0.73			0.83			5	-18.70	48.61	0.31	0.22
m7	-1.85	1.26						0.59			3	-21.17	48.80	0.49	0.20
m6	-1.98	1.36			-0.69			0.97			4	-20.00	48.80	0.49	0.20
m4	-2.19	1.83		-0.85	-0.76		0.27	0.78			6	-18.45	50.66	2.35	0.08
m3	-2.17	1.75		-0.89	-0.69	0.18	0.32	0.70			7	-18.36	53.11	4.80	0.02
m16	-1.51							0.94			2	-25.54	55.32	7.01	0.01
m2	-2.16	1.78	-0.16	-0.92	-0.66	0.19	0.30	0.70			8	-18.31	55.74	7.44	0.01
m14	-1.29					0.78					2	-26.97	58.17	9.87	0.00
m15	-1.36						0.60				2	-27.05	58.33	10.02	0.00
m1	-2.27	1.78	-0.18	-0.90	-0.67	0.19	0.27	0.72	0.01		9	-18.30	58.59	10.28	0.00
m9	-1.28										1	-28.85	59.78	11.47	0.00
m17	-1.75								0.06		2	-28.31	60.85	12.54	0.00
m12	-1.28		0.14								2	-28.75	61.72	13.41	0.00
m11	-1.28									-0.15	2	-28.75	61.73	13.42	0.00
m10	-1.28			0.07							2	-28.83	61.89	13.58	0.00
m13	-1.28				0.06						2	-28.84	61.91	13.60	0.00

6.4. Discussion

Rather surprisingly, the effect of forest edge density (i.e., landscape structure) had the strongest positive effect on the occurrence of naked-tailed armadillos (*Cabassous* sp.) in sugarcane dominated landscapes. Forest edge density was the only predictor that also showed a significant effect in equally plausible models (Table 2). Our results indicate that naked-tailed armadillos might occur in landscapes with monocultures of sugarcane as long as these areas have immersed native forest patches in a more complex spatial arrangement, with higher forest edge densities. Thus, considering the configurational heterogeneity of the landscape is key for the understanding of naked-tailed armadillo (*Cabassous* sp.) occurrence in agricultural landscapes.

Contrary to the currently known that *C. tatouay* is normally absent in areas of intensive agriculture or severely degraded habitats (Redford & Eisenberg, 1992; Fonseca & Aguiar, 2004), our findings confirm its occurrence in sugarcane dominated landscapes. However, both species (*Cabassous* sp.) overall depend on native forest patches, which are immersed in human-modified landscapes, potentially because of the habitat structure and prey communities. As armadillos, in general, are poor thermal regulators (McNab, 1980), they might prefer sites having more stable temperature and humidity conditions, such as those found in native forest patches (Laurance *et al.*, 2011) to maintain or optimize their metabolic rates (Maccarini *et al.*, 2015; Attias *et al.*, 2018). The availability of resource might also be influencing their occurrence in such forest patches as changes in insect community composition and abundance have been recorded in croplands due to their simplified plant community (Franco *et al.*, 2016) and pesticide use (Duelli, Obrist, & Schmatz, 1999; Vasconcelos, 1999; Narendra, Gibb, & Ali, 2011).

Forest edge density is also related to patch shape complexity (Ewers & Didham, 2006). Landscapes with greater edge density can be of lower quality because, among other threats, animals may be more exposed to unfavorable habitat in the edge and matrix (Laurance *et al.*, 2011; Thornton, Branch, & Sunquist, 2011). However, as naked-tailed armadillos are highly fossorial (Hayssen, 2014; Desbiez *et al.*, 2018), they might be more effective in tolerating forest edge-effects, which result from a variety of causes (Laurance *et al.*, 2011). Further, both habitat heterogeneity and the primary productivity associated with secondary forests near forest edges can be higher in more complex patches, increasing resource availability for many species, including armadillos (Dalponte & Tavares-Filho, 2004; Meyer, Leal, & Wirth, 2009; González-Zamora *et al.*, 2012; Garmendia *et al.*, 2013; Rodrigues & Chiarello, 2018). For example, leaf-cutting ants profoundly benefit from edge creation in Neotropical forests (Meyer *et al.*, 2009), indeed increasing resource availability for *Cabassous* sp. The likelihood that species will enter the matrix and use complementary or supplementary resources from it also may be higher in more

complex-shaped patches (Dunning, Danielson, & Pulliam, 1992), and armadillos may take advantage of that. For instance, the yellow armadillo (*Euphractus sexcinctus*), which share the same landscape with *Cabassous* sp. (Vivo *et al.*, 2011; Trovati, 2015), has feeding tendencies in marginal road habitats, taking advantage also from the available resources on the matrix (Dalponte & Tavares-Filho, 2004). The northern naked-tailed armadillo (*Cabassous centralis*) seems to show the same pattern to use habitat edges for feeding or traveling (González-Zamora *et al.*, 2012; Garmendia *et al.*, 2013). Additionally, patches with more irregular shapes have a higher probability of being randomly occupied by a given individual, increasing the colonization rates within these patches (Ewers & Didham, 2006). As naked-tailed armadillos never use the same burrow twice (Carter & Encarnaçao, 1983; Desbiez *et al.*, 2018), this feature might favor the maintenance of naked-tailed armadillos in such landscapes.

Our results also indicate that *Cabassous* sp. has a habitat requirement different from *Dasyopus novemcinctus* and *Euphractus sexcinctus*, which also occur in sugarcane dominated landscapes at our study region (Vivo *et al.*, 2011; Trovati, 2015; Rodrigues & Chiarello, 2018), a result that might suggest niche partitioning among them. Although forest patches immersed in agricultural landscapes are also important for *D. novemcinctus*, they are strongly attracted to, and perhaps even are dependent upon, forest areas close to watercourses (Ferregueti, Tomas, & Bergallo, 2016; Rodrigues & Chiarello, 2018). In fact, Ferregueti *et al.* (2016) highlighted that *D. novemcinctus* strongly avoided forest edges, occupying more intensively the interior of the forest. On the other hand, *E. sexcinctus* appears to be more common in open areas with scattered trees and bushes, including in agricultural matrix (Redford & Wetzel, 1985; Dalponte & Tavares-Filho, 2004), and no individuals have been recorded in gallery forests (Carter & Encarnaçao, 1983). Therefore, our findings highlight the importance of forest edge density for *Cabassous* sp., which represents a different habitat requirement comparing with other armadillos found in the same landscape context.

Our study highlights the importance of considering native forest patches immersed in agricultural landscapes for the understanding of naked-tailed armadillo (*Cabassous* sp.) occurrence in sugarcane dominated landscapes. Most importantly, we showed that considered the landscape structure and the complexity of forest patches in such landscape context are key to broaden our understanding of the habitat requirement for *Cabassous* sp. Our study supports the strategic role (Galetti *et al.*, 2010) played by the *Native Vegetation Protection Law* of Brazil (*Brazilian Forest Code*; Soares-Filho *et al.*, 2014; Brancalion *et al.*, 2016) in protecting native forests within private properties, since native forest patches in such landscape context are essential also to guarantee the conservation of armadillos as well as the provision of their ecosystem services (Rodrigues *et*

al., 2019). As part of the Brazilian agribusiness sector does not agree or implement this law (Soares-Filho *et al.*, 2014), empirical data such as these are also essential to help increase the importance of the *Brazilian Forest Code* among rural owners (e.g. Metzger *et al.*, 2019).

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7. CONCLUDING REMARKS

Throughout the five chapters of this thesis, I studied how and why armadillos represent an important group of mammals; at the same time, I offered novel perspectives that favor research, management, and conservation practices for these amazing species. More than documenting new examples of research on armadillo ecology, which by the way represents a key front line for the understanding of this group, we went a step further, elucidating ecosystem services, public perceptions and consequences of human-modified landscapes in a context of high anthropogenic disturbance, combining modern and classic approaches.

In *Chapter 1* (Rodrigues *et al.*, 2019), we identify the ecosystem services provided by armadillos. Besides identifying each ecosystem service provided by armadillos and the corresponding key knowledge gaps, we connect their ecological functions with research fields considering social, economic, cultural, environmental, and biological aspects, something never tried before. Surprisingly, we found that armadillos supply important regulating (e.g. bioturbation, ecosystem engineering, seed dispersal, pest control), material (e.g. meat, medicine), and non-material (e.g. learning, inspiration) contributions all over the Americas for centuries. Our review also interprets and presents scientific data on armadillos in an interdisciplinary fashion that makes them appealing to other scientists who are not working with armadillos, thus broadening avenues towards armadillo research, management, and conservation.

In *Chapter 2*, we investigate the public attitudes towards armadillos based on YouTube videos' comments, a popular social media website, to gain conservation insights. Our results suggest that the public online has a positive attitude towards individual armadillos that appeared on videos, demonstrating strong affection for the animals. As public interest largely drives public policy, we can use that interest to increase research on armadillos and so our ability to develop sound conservation practices, including online. We were also able to access the most relevant topics under the perspective of the public, contributing to identify knowledge gaps and clarifying them. Our findings suggest that social media can be used as a source of data for conservation purposes, and it can be further explored to extend effective conservational practices involving armadillos.

In *Chapter 3*, we investigate the possibility to automatically and accurately identify four armadillo species (*C. tatouay*, *C. unicinctus*, *D. novemcinctus*, and *E. sexcinctus*), that inhabit a region highly affected by anthropogenic disturbances, based on burrow entrance morphometry. Our results suggest that burrows can be a useful source of information to identify armadillos, allowing ecologists to use a non-invasive low-cost method to study armadillo species. We also make

available an R function (*armadilloID*) that automatically identify these species of armadillos with > 70% accuracy overall. Our findings advance on the use of novel technologies (e.g. machine learning) enabling the use of a non-invasive method for dealing with low-density, elusive and not well-known species such as the armadillos.

In *Chapter 4* (Rodrigues & Chiarello, 2018), we assess the relative effects of landscape variables, including anthropogenic impacts and degree of protection, as potential predictors of landscape occupancy of the nine-banded armadillo (*Dasybus novemcinctus*) in agricultural landscapes. Our results indicate that forest cover and proximity to watercourses strongly and positively affect the occupancy of the nine-banded armadillo, whereas managed forests negative affect them. Even disturbed native forest strips, particularly those close to watercourses, are important habitats for this armadillo in agricultural matrices, demonstrating the utmost importance of native forests existing both within and outside protected areas. Our findings also support the strategic role played by the *Brazilian Forest Code*, which is key not only to maintain or enhance forest cover in private properties but also to sustaining nine-banded armadillos that provide key ecosystem services also in agricultural landscapes (Rodrigues *et al.*, 2019).

Lastly, in *Chapter 5*, we investigate how variables of composition and configuration landscape influence the occurrence of naked-tailed armadillos (*Cabassous unicinctus* and *Cabassous tatouay*) in a sugarcane dominated region. Our results indicate that forest edge density strongly and positive affect *Cabassous* sp. occurrence in landscapes where intensive monocultures of sugarcane cover, on average, >40% of the land surface. Besides indicating that naked-tailed armadillos can occur in such agricultural landscapes, we suggest that forest edge might be an important habitat that makes possible their coexistence with other armadillo species in such landscape context. We highlight that considering the configurational heterogeneity of the landscape is key for the understanding of naked-tailed armadillo (*Cabassous* sp.) occurrence in agricultural landscapes.

I believe this thesis contributes to the understanding (i) of the ecological processes provided by armadillos that benefit human well-being and (ii) how they are perceived by the public, as well as (iii) the landscape variables that influence the occurrence between different armadillo species in highly altered human-modified landscapes. Furthermore, we propose some new methodological approaches that may be useful in later studies of ecology, human dimensions, and conservation of armadillos *per se*. Future studies on armadillos could be even more integrative, finding the potential effects, whether positive or negative, of armadillos on ecosystem services based on modern technologies, including digital media and machine learning approaches. At the same time, it would be promising an approach encouraging public

participation in armadillo studies for reducing gaps among scientists, the public and policymakers. As a last remark, I hope the results of this thesis encourage researchers and readers to seek to understand more about the amazing armadillos.

“Somewhere, something incredible is waiting to be known”

– Carl Sagan.

End.

Chapter 1. Rodrigues, T. F., Mantellatto, A. M., Superina, M. and Chiarello, A. G. (2019), Ecosystem services provided by armadillos. *Biological Reviews*. doi:10.1111/brv.12551.

Chapter 4. Rodrigues, T.F., Chiarello, A.G. (2018) Native forests within and outside protected areas are key for nine-banded armadillo (*Dasybus novemcinctus*) occupancy in agricultural landscapes. *Agric. Ecosyst. Environ.* **266**, 133–141.

8. APPENDICES

Appendix A – Chapter 1, DATA COLLECTION PROCEDURES

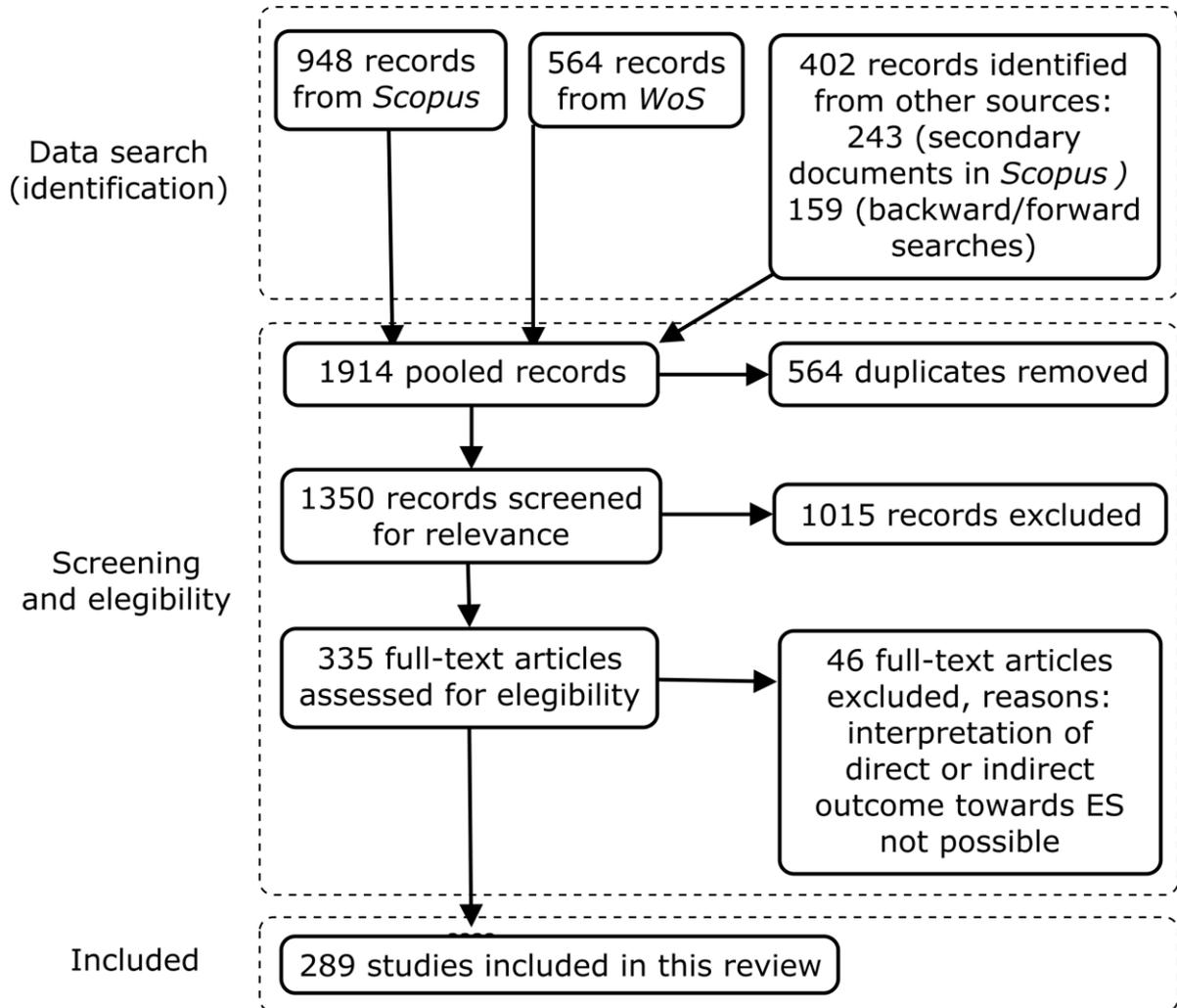


Figure S1. PRISMA flow diagram (Moher *et al.*, 2009) of our literature search and data collection.

Appendix B – Chapter 2, THE ONLINE PUBLIC VISIBILITY

Table S1. Summary of online public interactions over the 15 selected YouTube videos.

YouTube ID	Code	Category	View count	Likes	Dislikes	Comments	Published at
110iUX1Ursk	v01	Information	7,409,721	84,640	1,425	3,844	12/31/2013
SkXDQxgs_Pw	v02	Behaviour	7,187,115	9,262	3,737	332	05/23/2014
LGrNXUXn6Js	v03	Information	6,511,822	8,132	1,427	359	05/22/2014
HhNGdnuFQYM	v04	Behaviour	3,948,795	21,356	346	1,041	05/03/2014
3fs8tqTxEcM	v05	Behaviour	2,700,108	19,309	998	2,151	05/19/2015
LFxRkS7V0sE	v06	Information	2,308,515	41,139	722	4,556	11/10/2017
zrbFeZOSKf8	v07	Behaviour	2,273,461	3,177	661	597	05/02/2013
oteYDnHGhGE	v08	Behaviour	1,698,276	4,072	598	231	12/11/2017
wNQg1AS_94U	v09	Behaviour	1,328,561	36,769	509	2,434	09/27/2018
dIUC5eGMSFY	v10	Behaviour	1,156,487	1,987	256	356	02/07/2006
FQH2rISdaWw	v11	Information	856,269	2,932	311	261	11/19/2014
UBVxJLABNuk	v12	Behaviour	807,678	1,673	343	74	11/01/2008
GO7GisWODDg	v13	Information	625,568	16,828	318	1,650	09/10/2017
ib4bWAQIYns	v14	Information	285,825	9,175	249	925	01/23/2019
xl4bN6QQlrc	v15	Information	201,662	6,804	65	453	10/11/2017
Total			39,299,863	267,255	11,965	19,264	

armadilloID: an R function

Semi-supervised analysis to identify four species of armadillos

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October 2019

Description

Function *armadilloID* attempts to automate semi-supervised machine learning analysis to identify four species of armadillos (*Cabassous tatouay*, *Cabassous unicinctus*, *Dasypus novemcinctus*, and *Euphractus sexcinctus*) based on three burrow entrance measurements – width, height, and angle. The user provides a data.frame containing three columns, respectively: width (centimeter), height (centimeter) and angle (i.e. slope, in degrees) of the armadillo burrow entrance. Also, the user must provide the number of burrows to generate by species, the proportion of burrows to randomly select for conducting the analysis, and the base classifier (i.e. machine learning algorithm) for the semi-supervised machine learning. The function's output includes the following elements: a final data.frame containing the semi-supervised identification of armadillos, two R lists with relevant information, three plots, and prints some complementary statistics.

Dependencies

The function requires the correspondent packages: *ssc* (González *et al.*, 2018), *DTK* (Lau, 2013) *car* (Fox & Weisberg, 2011), *caret* (Kuhn, 2008), *e1071* (Meyer *et al.*, 2018), and *C50* (Kuhn & Quinlan, 2018).

Usage

```
armadilloID <- function(real_data, n_sim = 1000, n_samp = 0.7, id = 1)
```

Arguments

<code>real_data</code>	Data.frame with three columns, respectively: column 1 (width) = values for width in centimetres; column 2 (height) = values for height in centimetres; column 3 (angle) = values for angle in degrees
<code>n_sim</code>	Numeric vector with a single value and necessarily multiple of 100; $100 \leq n_sim \leq 10,000$. <code>n_sim = 1,000</code> (default)
<code>n_samp</code>	Numeric vector with a single value and necessarily between $0.1 \leq n_samp \leq 1.0$ (10%-100%). <code>n_samp = 0.7</code> (default)
<code>id</code>	Numeric vector with a single value and necessarily between $1 \leq id \leq 4$. 1 = K-Nearest Neighbors (KNN); 2 = Support Vector Machine (SVM); 3 = Naive Bayes Classification (NBC); 4 = C5.0 Decision Tree (C5.0). <code>id = 1</code> (default)

Details

First of all, the user must possess a data.frame with solely three columns as specified above. This data.frame must be specified in the argument `real_data` of the function.

The user must provide the number of burrows to generate by species in the argument `n_sim` of the function. This argument simulates burrow measurements for each armadillo species based on data found in the literature (mean and standard deviation reported by different studies) and it is used as a labeled data (or reference) in the semi-supervised machine learning identification.

The argument `n_samp` must be fulfilled with the proportion of burrows the user wants to randomly select for conducting the analysis. The user is able to randomly select only part of those generated data by species. This argument is used to increase the accuracy of the generated labeled data.

The argument `id` refers to the base classifier for the semi-supervised machine learning that the user wants to use to create final figures and calculating complementary statistical analyses. As the user may choose to identify armadillo species based on only one base classifier, this argument provides a complementary analysis using the final identification provided by the selected base classifier.

Value

armadilloID returns the following components:

<code>final_id</code>	Data.frame containing the final semi-supervised identification of armadillos based on their burrows. This data.frame also is exported as <i>armadillo_ID.csv</i> into the user working directory. It contains respectively the following columns: <i>width</i> , <i>height</i> , <i>angle</i> , <i>id_sim</i> , <i>id_knn</i> , <i>id_svm</i> , <i>id_nbc</i> , and <i>id_C5.0</i>
<code>result2</code>	R list with four levels corresponding to each base classifier (KNN, SVM, NBC, and C5.0 respectively): <ul style="list-style-type: none"> a) <i>id</i>: a factor with the final identification provided after the semi-supervised machine learning b) <i>confusion matrix</i>: a table with the confusion matrix between the predicted values from the base classifier and the initial labelled data provided by the simulating process c) <i>accuracy</i>: a numeric vector with the proportion of the correct identification based on the values predicted from the base classifier and the initial labelled data provided by the simulating process. The formula over the confusion matrix is: $sum(diagonal) / sum(total)$
<code>result3</code>	R list with two levels corresponding to ANOVA and Tukey-Test for the three measurements (width, height, and angle, respectively)
<code>plot</code>	Three plots created for each measurement and exported into the user working directory
<code>print</code>	Print of mean \pm standard deviation for each measure (width, height, and angle) for each species based on one base classifier

The objects *final_id*, *result2*, and *result3* are exported to the R global environment.

Warning

Before running the *armadilloID*, the user must guarantee internet connection because will necessary install packages whether the user has not installed them yet. The installation process occurs automatically when the user runs the function.

If the arguments are entered incorrectly, the function is not executed.

When executing the function, it is expected to take a while as the procedure of generating burrow measurements demands a great processing of the computer memory.

Note

So far, *armadilloID* can only be applied for the four armadillo species: *Cabassous tatouay*, *Cabassous unicinctus*, *Dasypus novemcinctus*, and *Euphractus sexcinctus*. So, we recommended its use only if the user suspects that the burrow measurements may represent one of this species in particular.

The semi-supervised machine learning follows the examples provided at the documentation of *ssv* package in the *selfTraining* section (González *et al.*, 2018). Another alternative is the possibility of defining a particular base classifier beyond those used because the function is well-commented and can be easily modified.

Example

```
## Generating data based on Zimmerman (1982)##
# N(reported) = 113; Species = Dasypus novemcinctus

set.seed(33)
w <- round(rnorm(n = 113, mean = 21.9, sd = 3.64), 1) #width
h <- round(rnorm(n = 113, mean = 19.8, sd = 4.24), 1) #height
a <- abs(round(rnorm(n = 113, mean = 16.2, sd = 16.1), 0)) #angle

my_data <- data.frame(width = w, height = h, angle = a)

#Simulating 1000 burrows by species and randomly selecting only 70% of them
for conduct the analysis. Also, plot figures and calculate analyses for the
first machine learning classifier (knn) - (Default)

armadilloID(real_data = my_data)

#Verifying accuracy using the example data
final_id[2801:2913,4] #unlabelled data provided by the example
final_id[2801:2913,4] <- rep("D.novemcinctus", each=113) #changing them to
D.novemcinctus

for (k in 5:8) {
  a <- table(final_id[,4], final_id[,k])
  print(a)
  b <- round(sum(diag(a))/sum(a), 2)
  print(b)
}

#Verifying the accuracy only for the unlabeled example data
for (k in 5:8) {
  a <- table(final_id[2801:2913,4], final_id[2801:2913,k])
  print(a)
  b <- round(1-sum(a[1],a[2],a[4])/a[3], 2)
  print(b)
}
```

Author of the R function:

Thiago Ferreira Rodrigues – thiagorodriguess@gmail.com

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Appendix D – Chapter 3, FULLY EXECUTABLE R CODE (*armadilloID*)

```

## ArmadilloID
## Author: Thiago Ferreira Rodrigues
## thiagorodriguess@gmail.com

## START OF THE FUNCTION

armadilloID <- function(real_data, n_sim = 1000, n_samp = 0.7, id = 1){

  ## MESSAGES OF WARNINGS

  if(class(n_sim)!="numeric" | class(n_samp)!="numeric")
  {
    stop("\n\n WARNING: 'n_sim' and 'n_samp' must be a numeric vector \n\n")
  }

  if(length(n_sim)!= 1 | length(n_samp)!= 1)
  {
    stop("\n\n WARNING: 'n_sim' and 'n_samp' must be a numeric vector with a s
ingle value \n\n")
  }

  if(n_sim < 100 | n_sim > 10000)
  {
    stop("\n\n WARNING: the value must be 100 <= n_sim <= 10000 \n\n")
  }

  if(n_sim %% 100 != 0)
  {
    stop("\n\n WARNING: the value must be multiple of 100 \n\n")
  }

  if(n_sim!=round(n_sim, 0))
  {
    stop("\n\n WARNING: 'n_sim' must be an integer number \n\n")
  }

  if(n_samp < 0.1 | n_samp > 1)
  {
    stop("\n\n WARNING: the value must be 0.1 <= n_samp <= 1 \n\n")
  }

  if(missing(real_data)==TRUE)
  {
    stop("\n\n WARNING: the real data is needed to correctly run the function
\n\n")
  }

  if(class(real_data)!="data.frame")
  {
    stop("\n\n WARNING: the real data must be within a data.frame \n\n")
  }

  if(length(real_data)!=3)
  {
    stop("\n\n WARNING: the data.frame must have 3 columns:
column 1 (width)= values for width in centimeters

```

```

        columna 2 (height)= values for height in centimeters
        columna 3 (angle)= values for angle in centimeters \n\n")
    }

    if(class(real_data[,1])!="numeric")
    {
        stop("\n\n WARNING: the column 1 must corresponding to WIDTH and necessarily
ly be a 'numeric' class \n\n")
    }

    if(class(real_data[,2])!="numeric")
    {
        stop("\n\n the column 2 must corresponding to HEIGHT and necessarily be a
'numeric' class \n\n")
    }

    if(class(real_data[,3])!="numeric")
    {
        stop("\n\n the column 3 must corresponding to ANGLE and necessarily be a '
numeric' class \n\n")
    }

    if(any(is.na(real_data[,c(1:3)])))
    {
        real_data <- (na.omit(real_data))
        message("\n\n NAs values were removed from data.frame \n\n")
    }

    if(class(id)!="numeric")
    {
        stop("\n\n WARNING: 'id' must be a numeric vector \n\n")
    }

    if(id < 1 | id > 4)
    {
        stop("\n\n WARNING: the value must be 1 <= n_samp <= 4 \n\n")
    }

    if(id!=round(id, 0))
    {
        stop("\n\n WARNING: 'id' must be an integer number \n\n")
    }

    ## PACKAGES NEEDED

    for (l in c("ssc", "DTK", "car", "caret", "e1071", "C50")) {
        if (!require(l, character.only=TRUE)) install.packages(l, repos="http://cran.us.r-project.org")
    }

    if(n_sim >= 100)
    {
        message("\n CHILL OUT: IT'S FINE SO FAR, MAY TAKE SOME TIME THOUGH \n")
    }

    ## START: SIMULATING DATA

    #Loop to automatically simulate burrows measurements (width, height and angle)
from all available studies

```

```

for(i in n_sim){
  n1 <- i #Number of burrows by species

  ## Euphractus sexcinctus

  # Carter and Encarnação (1983)
  # Only mean was reported
  # SD based on highest value from other studies

  # width
  cart_lar_sp1 <- round(rnorm(n = n1/4, mean = 22.2, sd = 2.115),1)
  # height
  cart_alt_sp1 <- round(rnorm(n = n1/4, mean = 20, sd = 2.329),1)
  # angle
  cart_dec_sp1 <- abs(round(rnorm(n = n1/4, mean = 32.4, sd = (0.65*sqrt(n1/
4))), 0))

  # Trovati (2009)
  # Mean and SD reported

  # width
  trov_lar_sp1 <- round(rnorm(n = n1/4, mean = 19.9, sd = (0.16*sqrt(n1/4)))
, 1)
  # height
  trov_alt_sp1 <- round(rnorm(n = n1/4, mean = 14.5, sd = (0.14*sqrt(n1/4)))
, 1)
  # angle
  trov_dec_sp1 <- abs(round(rnorm(n = n1/4, mean = 55.6, sd = (0.65*sqrt(n1/
4))), 0))

  # Medri (2008)
  # Mean and SD reported

  # width
  medr_lar <- round(rnorm(n = n1/4, mean = 19.456, sd = 2.115),1)
  # height
  medr_alt <- round(rnorm(n = n1/4, mean = 15.47, sd = 2.329),1)

  # Anacleto (2006)
  # Mean and SD reported

  # width
  anac_lar_sp2 <- round(rnorm(n = n1/4, mean = 17.6, sd = 2), 1)
  # height
  anac_alt_sp2 <- round(rnorm(n = n1/4, mean = 17.2, sd = 2.2), 1)

  # Angle: simulating data for Medri and Anacleto:
  # 50% based on Carter and 50% based on Trovati
  # Unique available information
  cart_dec1 <- abs(round(rnorm(n = n1/4, mean = 32.4, sd = (0.65*sqrt(n1/4))
), 0))
  trov_dec1 <- abs(round(rnorm(n = n1/4, mean = 55.6, sd = (0.65*sqrt(n1/4))
), 0))
  cart_trov_dec <- sample(round(c(cart_dec1,trov_dec1), 0))

  # data.frame with all generated data
  esex <- data.frame(
    width = c(cart_lar_sp1, trov_lar_sp1, medr_lar, anac_lar_sp2),
    height = c(cart_alt_sp1, trov_alt_sp1, medr_alt, anac_alt_sp2),

```

```

    angle = c(cart_dec_sp1, trov_dec_sp1, cart_trov_dec),
    sp = rep("E.sexcinctus", n1))

## Dasyopus novemcinctus

# Sawyer et al. (2012)
# Mean and SD reported

# width
sawy_lar <- round(rnorm(n = n1/5, mean = 25.7, sd = 8), 1)
# height
sawy_alt <- round(rnorm(n = n1/5, mean = 20.4, sd = 4.7), 1)
# angle
sawy_dec <- abs(round(rnorm(n = n1/5, mean = 33.5, sd = 13.8), 0))

# Zimmerman (1990)
# Mean and SD reported

# width
zimm_lar <- round(rnorm(n = n1/5, mean = 21.9, sd = 3.64), 1)
# height
zimm_alt <- round(rnorm(n = n1/5, mean = 19.8, sd = 4.24), 1)
# angle - Zimmerman (1982)
zimm_dec <- abs(round(rnorm(n = n1/5, mean = 16.2, sd = 16.1), 0))

# Anacleto (2006)
# Mean and SD reported

# width
anac_lar_sp4 <- round(rnorm(n = n1/5, mean = 18.0, sd = 2.4), 1)
# height
anac_alt_sp4 <- round(rnorm(n = n1/5, mean = 20.3, sd = 3), 1)

# Platt et al. (2004)
# Mean and SD reported

# width
plat_lar <- round(rnorm(n1/5, mean = 18.6, sd = 3), 1)
# height
plat_alt <- round(rnorm(n1/5, mean = 13.7, sd = 2.5), 1)

# McDonough et al. (2000) - (EUA)
# Mean and SD reported

# width; it was used the highest sd reported
mcdol_lar <- round(rnorm(n1/5, mean = (20.5+19.38+21.03+19)/4, sd = 5.96),
1)
# height; it was used the highest sd reported
mcdol_alt <- round(rnorm(n1/5, mean = (15.33+15.02+15.79+15.38)/4, sd = 5.6
9), 1)

# Angle: simulating data for Anacleto, Platt and McDonough.
# 50% based on Zimmerman and 50% based on Sawyer
# Unique available information
zimm_dec1 <- abs(round(rnorm(n = n1/5, mean = 16, sd = 16.1), 0))
sawy_dec1 <- abs(round(rnorm(n = (n1/5)*2, mean = 33.5, sd = 13.8), 0))
zimm_sawy_dec1 <- sample(round(c(zimm_dec1,sawy_dec1),0))

# data.frame with all generated data

```

```

dnov <- data.frame(
  width = c(sawy_lar, zimm_lar, anac_lar_sp4, plat_lar, mcdo_lar),
  height = c(sawy_alt, zimm_alt, anac_alt_sp4, plat_alt, mcdo_alt),
  angle = c(sawy_dec, zimm_dec, zimm_sawy_dec1),
  sp = rep("D.novemcinctus", n1))

## Cabassous tatouay

# Carter and Encarnação (1983)
# Only mean was reported
# SD based on highest value from other studies

# width
cart_lar_sp3 <- round(rnorm(n = n1/2, mean = 20.1, sd = 1.4), 1)
# height
cart_alt_sp3 <- round(rnorm(n = n1/2, mean = 15.1, sd = 1.9), 1)
# angle
# mean is the unique information available; we used poisson family
cart_dec_sp3 <- abs(rpois(n = n1, lambda = 47.7))

# Anacleto (2006)
# Mean and SD reported

# width
anac_lar_sp5 <- round(rnorm(n = n1/2, mean = 17.7, sd = 1.4), 1)
# height
anac_alt_sp5 <- round(rnorm(n = n1/2, mean = 18.1, sd = 1.9), 1)

# Angle: simulating data for Anacleto; 100% based on Carter
# Unique available information).

# data.frame with all generated data
ctat <- data.frame(width = c(cart_lar_sp3, anac_lar_sp5),
  height = c(cart_alt_sp3, anac_alt_sp5),
  angle = cart_dec_sp3,
  sp = rep("C.tatouay", n1))

## Cabassous uncinctus

# Carter and Encarnação (1983)
# Only mean was reported
# SD based on highest value from other studies

# width
cart_lar_sp2 <- round(rnorm(n = n1/4, mean = 15.4, sd = 1.3), 1)
# height
cart_alt_sp2 <- round(rnorm(n = n1/4, mean = 15.1, sd = 1.2), 1)
# angle
cart_dec_sp2 <- abs(round(rnorm(n = n1/4, mean = 35.3, sd = (0.86*sqrt(n1/
4))), 0))

# Trovati (2009)
# Mean and SD reported

# width
trov_lar_sp2 <- round(rnorm(n = n1/4, mean = 13.0, sd = (0.10*sqrt(n1/4)))
, 1)
# height
trov_alt_sp2 <- round(rnorm(n = n1/4, mean = 13.0, sd = (0.10*sqrt(n1/4)))

```

```

, 1)
  # angle
  trov_dec_sp2 <- abs(round(rnorm(n = n1/4, mean = 77.1, sd = (0.86*sqrt(n1/
4))), 0))

  # Desbiez et al. (2018)
  # Mean and SD reported

  # width
  desb_lar <- round(rnorm(n = n1/4, mean = 10, sd = 1.32), 1)
  # height
  desb_alt <- round(rnorm(n = n1/4, mean = 10, sd = 1.44), 1)

  # Anacleto (2006)
  # Mean and SD reported

  # width
  anac_lar_sp6 <- round(rnorm(n = n1/4, mean = 12.1, sd = 1.3), 1)
  # height
  anac_alt_sp6 <- round(rnorm(n = n1/4, mean = 12.4, sd = 1.2), 1)

  # Angle: simulating data for Desbiez and Anacleto.
  # 50% based on Carter and 50% based on Trovati
  # Unique available information
  cart_dec1_sp2 <- abs(round(rnorm(n = n1/4, mean = 35.3, sd = (0.86*sqrt(n1
/4))), 0))
  trov_dec2_sp2 <- abs(round(rnorm(n = n1/4, mean = 77.1, sd = (0.86*sqrt(n1
/4))), 0))
  cart_trov_dec2 <- sample(round(c(cart_dec1_sp2, trov_dec2_sp2), 0))

  # data.frame with all generated data
  cuni <- data.frame(
    width = c(cart_lar_sp2, trov_lar_sp2, desb_lar, anac_lar_sp6),
    height = c(cart_alt_sp2, trov_alt_sp2, desb_alt, anac_alt_sp6),
    angle = c(cart_dec_sp2, trov_dec_sp2, cart_trov_dec2),
    sp = rep("C.unicinctus", n1))

  # Selecting "n_samp" randomly burrows
  esex_f <- esex[sample(x = 1:nrow(esex), nrow(esex) * n_samp, replace = FAL
SE),] #E.sexinctus
  dnov_f <- dnov[sample(x = 1:nrow(dnov), nrow(dnov) * n_samp, replace = FAL
SE),] #D.novemcinctus
  ctat_f <- ctat[sample(x = 1:nrow(ctat), nrow(ctat) * n_samp, replace = FAL
SE),] #C.tatouay
  cuni_f <- cuni[sample(x = 1:nrow(cuni), nrow(cuni) * n_samp, replace = FAL
SE),] #C.unicinctus

  # Final dataset with generated data
  result1 <- rbind(esex_f, dnov_f, ctat_f, cuni_f)
  #write.csv(result1, file = paste0("sim_", i*n_samp, "_burrows", ".csv"), r
ow.names=FALSE) #export as "file".csv
}

## END:SIMULATING DATA
##
## START:MACHINE LEARNING

#Data preparation
data_df <- data.frame(width = c(result1[,1], real_data[,1]),

```

```

        height = c(result1[,2], real_data[,2]),
        angle = c(result1[,3], real_data[,3]))

result1$sp <- as.character(result1$sp)
sp_df <- c(result1$sp, rep(NA, nrow(real_data)))
sp_df <- as.factor(sp_df)

#Data preparation for input over ssc package
x <- as.matrix(data_df)
x <- scale(x, center = TRUE, scale = TRUE)
y <- sp_df

## Semi-Supervised Machine Learning

# Machine Learning from a set of instances with 1-NN
# k-nearest neighbors as the base classifier
id1 <- selfTraining(x = x, #matrix with labeled and unlabeled data
                   y = y, #factor with the name of the species; unlabeled dat
a must be reported as NA
                   x.inst = TRUE, #indicate that x is a matrix
                   learner = caret::knn3, #type of algorithm used
                   learner.pars = list(k = 1), #k=1 means to classify with ju
st one class
                   pred = "predict") #predicted values

# Machine Learning from a set of instances with SVM
# Support Vector Machine as the base classifier
learner <- e1071::svm #type of algorithm used
learner.pars <- list(type = "C-classification", #categorical data
                    kernel="radial", #type of algorithm processing
                    probability = TRUE,
                    scale = TRUE)

pred <- function(m, x){
  r <- predict(m, x, probability = TRUE)
  prob <- attr(r, "probabilities")
  prob
}

id2 <- selfTraining(x = x, #matrix with labeled and unlabeled data
                   y = y, #factor with the name of the species; unlabeled dat
a must be reported as NA
                   learner = learner, # type of algorithm used
                   learner.pars = learner.pars, #parameters of svm
                   pred = pred) #predicted values

# Machine Learning from a set of instances with Naive-Bayes
# as the base classifier
id3 <- selfTraining(x = x, #matrix with labeled and unlabeled data
                   y = y, #factor with the name of the species; unlabeled dat
a must be reported as NA
                   learner = function(x, y) e1071::naiveBayes(x, y), # type o
f algorithm used
                   pred = "predict", #predicted values
                   pred.pars = list(type = "raw")) #parameters of nbc

# Machine Learning from a set of instances with C5.0
# as the base classifier.
id4 <- selfTraining(x = x, #matrix with labeled and unlabeled data

```

```

        y = y, #factor with the name of the species; unlabeled data
a must be reported as NA
        learner = C50::C5.0, #type of algorithm used
        pred = "predict", #predicted values
        pred.pars = list(type = "prob")) #parameters of C50

# List containing all machine learning results
id_tot <- list(id1,id2,id3,id4)

# Creating an empty Lists
pred <- list()
tab <- list()
accuracy <- list()
result2 <<- list()

# Final List with the predicted values, confusion matrix,
# and identification accuracy from all Learning processes
for (n in 1:4) {
  pred[[n]] <- predict(id_tot[[n]], x) #classification based on semi-supervised
machine learning
  tab[[n]] <- table(pred[[n]], y) #confusion matrix
  accuracy[[n]] <- sum(diag(tab[[n]]))/sum(tab[[n]]) #accuracy

  # ALL results together
  result2[[n]] <<- list(id=pred[[n]],confusion_matrix=tab[[n]],accuracy=accuracy[[n]])
}

#Final data.frame
sp_sim <- c(result1$sp, rep(NA, nrow(real_data)))
id_ml <- list()

for (a in 1:4) {
  id_ml[[a]] <- as.character(result2[[a]][[1]])
}

data_df[, c("sp_sim", "id_knn", "id_svm", "id_nbc", "id_C5.0")] <- c(sp_sim, id_ml[[1]],id_ml[[2]],id_ml[[3]],id_ml[[4]])

# Final dataframe exported to R global environment
final_id <<- data_df

# Final dataframe exported to the user working directory
write.table(data_df, "armadillo_ID.csv", sep="," , row.names = FALSE)

## END:MACHINE LEARNING
##
## START:ANOVA, TUKEY-TEST AND FIGURES

if(id == 1){
  mach_learn <- as.factor(data_df$id_knn)
  nam <- names(data_df[5])
  message("\n\t ANOVA and Post-hoc TuKEY test (result3), mean \u00b1 SD (printed) and exported figures
calculating using K-Nearest Neighbors (knn) classification \n")
}

if(id == 2){
  mach_learn <- as.factor(data_df$id_svm)

```

```

    nam <- names(data_df[6])
    message("\n\t ANOVA and Post-hoc TuKEY test (result3), mean \u00b1 SD (printed) and exported figures
           calculating using Support Vector Machine (svm) classification \n")
  }

  if(id == 3){
    mach_learn <- as.factor(data_df$id_nbc)
    nam <- names(data_df[7])
    message("\n\t ANOVA and Post-hoc TuKEY test (result3), mean \u00b1 SD (printed) and exported figures
           calculating using Naive Bayes Classification (naiveBayes) classification \n")
  }

  if(id == 4){
    mach_learn <- as.factor(data_df$id_C5.0)
    nam <- names(data_df[8])
    message("\n\t ANOVA and Post-hoc TuKEY test (result3), mean \u00b1 SD (printed) and exported figures
           calculating using C5.0 Decision tree classification \n")
  }

  # Calculating ANOVA and Post-hoc TUKEY test for the chosen
  # machine Learning classifier

  # Creating an empty List
  my_aov <- list()
  tt <- list()
  result3 <- list()

  for (j in 1:3) {
    # ANOVA (considering unbalanced samples by species)
    my_aov[[j]] <- Anova(aov(data_df[,j]~mach_learn), type = "III")
    # Post-hoc Tukey test (considering unbalanced samples by species)
    tt[[j]] <- TK.test(x = data_df[,j], f = mach_learn, a = 0.05)
  }

  # List with ANOVA and TT for all measurement following each machine
  # Learning identification
  result3 <- list(anova = my_aov, tukey_test = tt)

  # Calculating the mean and sd for the chosen base classifier
  mn_sd <- list()
  for (k in 1:3) {
    mn_sd[[k]] <- aggregate(x = data_df[,k], by=list(mach_learn), FUN = function(x) c(mn = round(mean(x),2),sd = round(sd(x),2)))
  }

  # Text with mean and sd
  tx_w <- rep(NA, 4)
  tx_h <- rep(NA, 4)
  tx_a <- rep(NA, 4)

  for (i in 1:4) {
    tx_w[i] <- paste(mn_sd[[1]]$x[i,1], sep=" \u00b1 ", collapse = "\t", mn_sd[[1]]$x[i,2])
    tx_h[i] <- paste(mn_sd[[2]]$x[i,1], sep=" \u00b1 ", collapse = "\t", mn_sd[[2]]$x[i,2])
  }

```

```

    tx_a[i] <- paste(mn_sd[[3]]$x[i,1], sep=" \u00b1 ", collapse = "\t", mn_sd
[[3]]$x[i,2])
  }

  # Generating figures
  lab0 <- c("width", "height", "angle")
  lab <- c("Width(cm)", "Height(cm)", "Angle(°)")

  for (f in 1:3) {
    png(filename = paste0(nam, "_", lab0[f], "_", n_sim*n_samp, ".png"), width
= 900, height = 500)
    par(mfrow=c(1,2))

    #FigLeft
    plot(data_df[,f]~mach_learn, pch=19, las=1, cex.axis=0.9, xaxt="n",
        ylab= lab[f], xlab="Species", main = lab[f])
    axis(side = 1, at=1:4, cex.axis=0.9, las=1, mgp=c(3,0.3,0),
        labels = c("C.tatouay", "C.unicinctus", "D.novemcinctus", "E.sexcinctus"
))
    mtext(side = 1, at= 1:4, cex = 0.9, line=1,
        text = c("(Ctat)", "(Cuni)", "(Dnov)", "(Esex)"))

    # FigRight
    plot(result3$tukey_test[[f]], mgp=c(3,0.3,0), cex.axis = 0.9, las=1, yaxt=
"n")
    axis(side = 2, at = 1:6, cex.axis=0.9, las=1,
        labels = c("Esex-Dnov", "Esex-Cuni", "Dnov-Cuni", "Esex-Ctat",
            "Dnov-Ctat", "Cuni-Ctat"))
    mtext(side = 3, text = "Unbalanced Tukey's HSD Comparison", line = 0.5, fo
nt=2)
    dev.off()
  }

  mn_sd_df <- data.frame(Species = mn_sd[[1]]$Group.1, Width = tx_w, Height = tx
_h, Angle = tx_a)
  return(mn_sd_df)
}

##END OF FUNCTION##

```

Appendix E – Chapter 5, R CODE AND OTHER RELEVANT INFORMATION

The following pages contain all the R code to run the analyses and plot the figures of the chapter 5. In this document, the R code is highlighted, immediately followed by the output signaled by #. See an example:

```
x <- 2 + 2
y <- 20
print(x/y)

## [1] 0.2
```

1. LOAD R PACKAGES AND CUSTOM FUNCTIONS

```
if(!require(dplyr)){install.packages('dplyr'); library(dplyr)}
if(!require(MuMIn)){install.packages('MuMIn'); library(MuMIn)}
if(!require(statmod)){install.packages('statmod'); library(statmod)}
if(!require(pander)){install.packages('pander'); library(pander)}
if(!require(hnp)){install.packages('hnp'); library(hnp)}
if(!require(ellipse)){install.packages('ellipse'); library(ellipse)}
if(!require(corrplot)){install.packages('corrplot'); library(corrplot)}
if(!require(car)){install.packages('car'); library(car)}
if(!require(ggplot2)){install.packages('ggplot2'); library(ggplot2)}
```

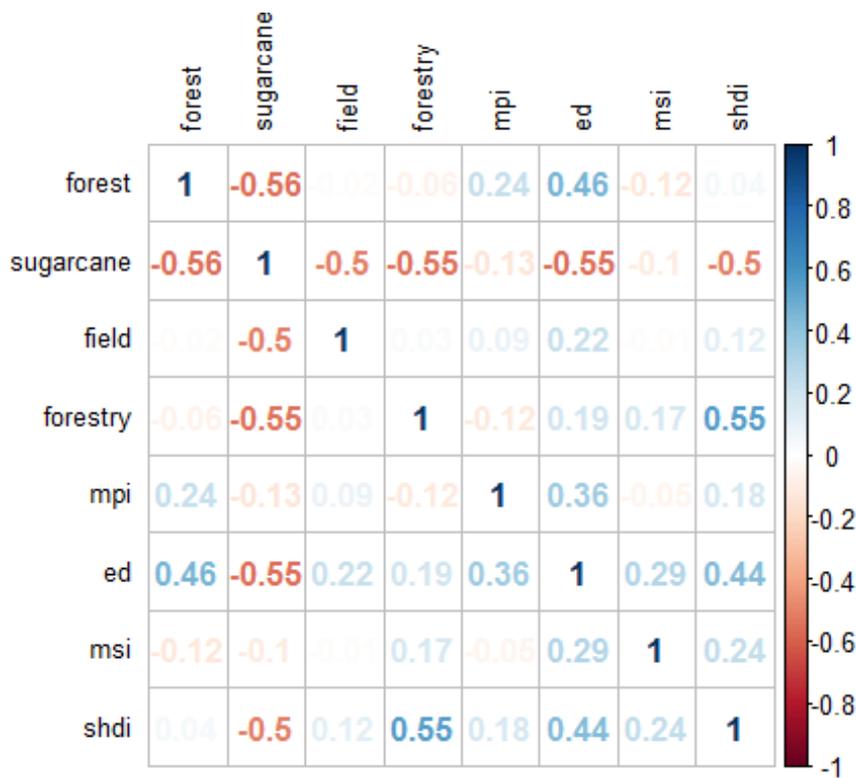
2. CHECK THE STRUCTURE OF THE DATA

```
df_cabassous <- read.csv2(file = "./data_cabassous.csv")
str(df_cabassous)

## 'data.frame': 55 obs. of 11 variables:
## $ sites : Factor w/ 55 levels "P003","P006",...: 1 2 3 4 5 6 7 8 9 1
## 0 ...
## $ p1 : int 0 0 0 0 1 0 0 0 0 0 ...
## $ forest : num 27.1 12.4 14.1 20.8 30.9 ...
## $ sugarcane: num 68.9 149.6 181.2 171.5 122.5 ...
## $ field : num 0 38.1 0 0 28.9 ...
## $ forestry : num 67.82 0 0 7.76 9.49 ...
## $ mpi : num 21.4 0.21 60.53 18.7 2.25 ...
## $ ed : num 27.8 12.7 19.6 35.5 39.7 ...
## $ msi : num 2.12 1.52 2.05 1.52 2.66 ...
## $ shdi : num 1.314 0.705 0.366 0.493 1.143 ...
## $ wd : num 10.45 0 7 9.89 13.89 ...
```

3. PEARSON'S CORRELATION ANALYSIS

```
corr_data <- subset(df_cabassous, select=c(3:10))
corr <- cor(corr_data, method = 'pearson')
corrplot(corr, method = "number", tl.cex=0.8, tl.col=1)
```



4. SCALING THE INDEPENDENT VARIABLES

The motivation of this type of scaling, named standardization, is to make the feature coefficient scales comparable with each other and to facilitate the convergence of the regression algorithm.

```
df_cabassous2 <- df_cabassous %>%
  mutate_at(c(3:11), funs(c(scale(.))))
str(df_cabassous2)

## 'data.frame':   55 obs. of  11 variables:
## $ sites      : Factor w/ 55 levels "P003","P006",...: 1 2 3 4 5 6 7 8 9 1
## $ p1         : int  0 0 0 0 1 0 0 0 0 0 ...
## $ forest     : num  -0.506 -0.879 -0.836 -0.667 -0.409 ...
## $ sugarcane  : num  -0.449 0.837 1.341 1.187 0.406 ...
## $ field      : num  -0.567 0.496 -0.567 -0.567 0.241 ...
## $ forestry   : num  1.441 -0.689 -0.689 -0.446 -0.391 ...
## $ mpi        : num  0.0215 -0.36 0.726 -0.0271 -0.3233 ...
## $ ed         : num  -0.402 -1.479 -0.984 0.153 0.448 ...
## $ msi        : num  0.359 -0.826 0.216 -0.82 1.419 ...
## $ shdi       : num  1.297 -0.521 -1.533 -1.154 0.787 ...
## $ wd         : num  0.5793 -1.327 -0.0502 0.4767 1.208 ...
```

4. GENERALIZED LINEAR MODELS (GLMS)

We used Generalized Linear Models (GLMs) with a binomial distribution to test the influence of composition and configuration landscape variables on the occurrence of naked-tailed armadillos (*Cabassous* sp.) The response variable was the presence-absence of the *Cabassous* sp. over 55 study landscapes.

Defining the global model

```
mglobal <- glm(p1~forest+field+sugarcane+forestry+mpi+ed+msi+shdi+wd,
              family = "binomial", data = df_cabassous2)
summary(mglobal)

##
## Call:
## glm(formula = p1 ~ forest + field + sugarcane + forestry + mpi +
##      ed + msi + shdi + wd, family = "binomial", data = df_cabassous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.29624  -0.42151  -0.22103  -0.08925   2.93465
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -2.2944     0.6886  -3.332 0.000863 ***
## forest         1.0801     1.6318   0.662 0.508036
## field         1.1649     1.1495   1.013 0.310871
## sugarcane     3.2108     2.4759   1.297 0.194685
## forestry      0.7065     1.1599   0.609 0.542435
## mpi           0.1425     0.5114   0.279 0.780582
## ed            1.7363     0.7620   2.279 0.022690 *
## msi           0.4358     0.5197   0.839 0.401692
## shdi          1.3704     0.8649   1.584 0.113087
## wd           -0.1598     0.5778  -0.277 0.782052
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 57.706  on 54  degrees of freedom
## Residual deviance: 34.215  on 45  degrees of freedom
## AIC: 54.215
##
## Number of Fisher Scoring iterations: 6
```

Checking for multicollinearity (VIF)

```
vif(mglobal)

##      forest      field sugarcane forestry      mpi      ed      msi
## 10.972432  3.765457 24.539359  6.439271  1.317192  1.915635  1.642313
##      shdi      wd
##  3.071335  1.565470
```

Removing the variable sugarcane which represents the highest value of VIF

```
mglobal2 <- glm(p1~forest+field+forestry+mpi+ed+msi+shdi+wd,
               family = "binomial", data = df_cabassous2)
summary(mglobal2)

##
## Call:
## glm(formula = p1 ~ forest + field + forestry + mpi + ed + msi +
##      shdi + wd, family = "binomial", data = df_cabassous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.35852  -0.49787  -0.23249  -0.09463   2.98473
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept) -2.17126    0.62686  -3.464 0.000533 ***
## forest      -0.90351    0.63939  -1.413 0.157632
## field       -0.17632    0.50199  -0.351 0.725401
## forestry    -0.66731    0.54301  -1.229 0.219110
## mpi         0.18623    0.44911   0.415 0.678387
## ed          1.78018    0.73434   2.424 0.015343 *
## msi         0.26541    0.46922   0.566 0.571643
## shdi        0.71866    0.61758   1.164 0.244561
## wd          0.07419    0.48674   0.152 0.878854
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 57.706  on 54  degrees of freedom
## Residual deviance: 36.590  on 46  degrees of freedom
## AIC: 54.59
##
## Number of Fisher Scoring iterations: 6
```

Checking for multicollinearity (VIF)

```
vif(mglobal2)

## forest field forestry mpi ed msi shdi wd
## 1.645728 1.179612 1.592686 1.332218 1.766164 1.361879 1.614300 1.291566
```

Stepwise, with backward elimination, using the mglobal2 (renamed as m1)

```
m1 <- glm(p1~forest+field+forestry+mpi+ed+msi+shdi+wd,
          family = "binomial", data = df_cabassous2)
summary(m1)

##
## Call:
## glm(formula = p1 ~ forest + field + forestry + mpi + ed + msi +
```

```

##      shdi + wd, family = "binomial", data = df_cabassous2)
##
## Deviance Residuals:
##      Min        1Q      Median        3Q        Max
## -1.35852  -0.49787  -0.23249  -0.09463   2.98473
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept) -2.17126    0.62686  -3.464 0.000533 ***
## forest      -0.90351    0.63939  -1.413 0.157632
## field       -0.17632    0.50199  -0.351 0.725401
## forestry    -0.66731    0.54301  -1.229 0.219110
## mpi         0.18623    0.44911   0.415 0.678387
## ed          1.78018    0.73434   2.424 0.015343 *
## msi         0.26541    0.46922   0.566 0.571643
## shdi        0.71866    0.61758   1.164 0.244561
## wd          0.07419    0.48674   0.152 0.878854
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 57.706  on 54  degrees of freedom
## Residual deviance: 36.590  on 46  degrees of freedom
## AIC: 54.59
##
## Number of Fisher Scoring iterations: 6

m2 <- glm(p1~forest+field+forestry+mpi+ed+msi+shdi,
          family = "binomial", data = df_cabassous2)
summary(m2)

##
## Call:
## glm(formula = p1 ~ forest + field + forestry + mpi + ed + msi +
##      shdi, family = "binomial", data = df_cabassous2)
##
## Deviance Residuals:
##      Min        1Q      Median        3Q        Max
## -1.3763  -0.5029  -0.2349  -0.0986   2.9563
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept) -2.1637    0.6229  -3.474 0.000513 ***
## forest      -0.9152    0.6369  -1.437 0.150742
## field       -0.1580    0.4916  -0.321 0.747928
## forestry    -0.6576    0.5367  -1.225 0.220407
## mpi         0.1873    0.4483   0.418 0.676160
## ed          1.7813    0.7319   2.434 0.014932 *
## msi         0.2946    0.4266   0.691 0.489827
## shdi        0.7027    0.6095   1.153 0.248917
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##

```

```

## (Dispersion parameter for binomial family taken to be 1)
##
## Null deviance: 57.706 on 54 degrees of freedom
## Residual deviance: 36.613 on 47 degrees of freedom
## AIC: 52.613
##
## Number of Fisher Scoring iterations: 6

m3 <- glm(p1~forest+forestry+mpi+ed+msi+shdi,
          family = "binomial", data = df_cabassous2)
summary(m3)

##
## Call:
## glm(formula = p1 ~ forest + forestry + mpi + ed + msi + shdi,
##      family = "binomial", data = df_cabassous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.3431  -0.4906  -0.2273  -0.1008   2.9844
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -2.1708     0.6240  -3.479 0.000503 ***
## forest        -0.8869     0.6336  -1.400 0.161540
## forestry      -0.6846     0.5451  -1.256 0.209136
## mpi           0.1798     0.4530   0.397 0.691477
## ed            1.7536     0.7307   2.400 0.016399 *
## msi           0.3212     0.4192   0.766 0.443655
## shdi          0.7011     0.6127   1.144 0.252471
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

## (Dispersion parameter for binomial family taken to be 1)
##
## Null deviance: 57.706 on 54 degrees of freedom
## Residual deviance: 36.725 on 48 degrees of freedom
## AIC: 50.725
##
## Number of Fisher Scoring iterations: 6

m4 <- glm(p1~forest+forestry+ed+msi+shdi,
          family = "binomial", data = df_cabassous2)
summary(m4)

##
## Call:
## glm(formula = p1 ~ forest + forestry + ed + msi + shdi, family = "binomial",
##      data = df_cabassous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.3373  -0.4841  -0.2067  -0.1006   3.0122
##

```

```

## Coefficients:
##           Estimate Std. Error z value Pr(>|z|)
## (Intercept) -2.1935     0.6256  -3.507 0.000454 ***
## forest      -0.8473     0.6132  -1.382 0.167071
## forestry    -0.7599     0.5239  -1.450 0.146971
## ed           1.8259     0.7176   2.545 0.010942 *
## msi          0.2745     0.4029   0.681 0.495713
## shdi         0.7844     0.5862   1.338 0.180882
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
## Null deviance: 57.706 on 54 degrees of freedom
## Residual deviance: 36.909 on 49 degrees of freedom
## AIC: 48.909
##
## Number of Fisher Scoring iterations: 6

m5 <- glm(p1~forest+forestry+ed+shdi,
          family = "binomial", data = df_cabassous2)
summary(m5)

##
## Call:
## glm(formula = p1 ~ forest + forestry + ed + shdi, family = "binomial",
## data = df_cabassous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.3422  -0.5348  -0.2220  -0.1105   2.9500
##
## Coefficients:
##           Estimate Std. Error z value Pr(>|z|)
## (Intercept) -2.1401     0.6034  -3.547 0.00039 ***
## forest      -0.8718     0.6051  -1.441 0.14969
## forestry    -0.7334     0.4988  -1.470 0.14149
## ed           1.8894     0.7038   2.685 0.00726 **
## shdi         0.8288     0.5746   1.442 0.14920
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
## Null deviance: 57.706 on 54 degrees of freedom
## Residual deviance: 37.390 on 50 degrees of freedom
## AIC: 47.39
##
## Number of Fisher Scoring iterations: 6

m6 <- glm(p1~forestry+ed+shdi,
          family = "binomial", data = df_cabassous2)
summary(m6)

```

```

##
## Call:
## glm(formula = p1 ~ forestry + ed + shdi, family = "binomial",
##      data = df_cabassous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.7241  -0.5628  -0.2720  -0.1341   2.9393
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -1.9793     0.5321  -3.720   0.0002 ***
## forestry      -0.6924     0.4989  -1.388   0.1652
## ed            1.3580     0.5273   2.575   0.0100 *
## shdi          0.9740     0.5565   1.750   0.0801 .
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 57.706  on 54  degrees of freedom
## Residual deviance: 40.000  on 51  degrees of freedom
## AIC: 48
##
## Number of Fisher Scoring iterations: 6
m7 <- glm(p1~ed+shdi,
          family = binomial(link='logit'), data = df_cabassous2)
summary(m7)
##
## Call:
## glm(formula = p1 ~ ed + shdi, family = binomial(link = "logit"),
##      data = df_cabassous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.3676  -0.6235  -0.3107  -0.1679   2.8642
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -1.8545     0.4932  -3.760   0.00017 ***
## ed            1.2620     0.4843   2.606   0.00916 **
## shdi          0.5904     0.4556   1.296   0.19504
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 57.706  on 54  degrees of freedom
## Residual deviance: 42.329  on 52  degrees of freedom
## AIC: 48.329
##
## Number of Fisher Scoring iterations: 5

```

```

m8 <- glm(p1~ed,
          family = binomial(link='logit'), data = df_cabassous2)
summary(m8)

##
## Call:
## glm(formula = p1 ~ ed, family = binomial(link = "logit"), data = df_cab
## assous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.6532  -0.6453  -0.3181  -0.1987   2.6604
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -1.7644     0.4677  -3.772 0.000162 ***
## ed            1.4426     0.4735   3.046 0.002317 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 57.706  on 54  degrees of freedom
## Residual deviance: 44.077  on 53  degrees of freedom
## AIC: 48.077
##
## Number of Fisher Scoring iterations: 5

```

NULL Model

```

m9 <- glm(p1~1, family = binomial(link='logit'), data = df_cabassous2)
summary(m9)

##
## Call:
## glm(formula = p1 ~ 1, family = binomial(link = "logit"), data = df_caba
## ssous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -0.7016  -0.7016  -0.7016  -0.7016   1.7450
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -1.2763     0.3265  -3.909 9.26e-05 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 57.706  on 54  degrees of freedom
## Residual deviance: 57.706  on 54  degrees of freedom
## AIC: 59.706
##
## Number of Fisher Scoring iterations: 4

```

Each predictor at the time

```
m10 <- glm(p1~forest, family = binomial(link='logit'), data = df_cabassous2)
summary(m10)

##
## Call:
## glm(formula = p1 ~ forest, family = binomial(link = "logit"),
##      data = df_cabassous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -0.7693  -0.6954  -0.6882  -0.6818   1.7660
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept) -1.27764    0.32685  -3.909 9.27e-05 ***
## forest       0.06975    0.32056   0.218  0.828
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 57.706  on 54  degrees of freedom
## Residual deviance: 57.659  on 53  degrees of freedom
## AIC: 61.659
##
## Number of Fisher Scoring iterations: 4

m11 <- glm(p1~sugarcane, family = binomial(link='logit'), data = df_cabassous2)
summary(m11)

##
## Call:
## glm(formula = p1 ~ sugarcane, family = binomial(link = "logit"),
##      data = df_cabassous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -0.7745  -0.7229  -0.6630  -0.6409   1.8278
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept) -1.2825    0.3282  -3.907 9.33e-05 ***
## sugarcane   -0.1499    0.3282  -0.457  0.648
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 57.706  on 54  degrees of freedom
```

```

## Residual deviance: 57.497 on 53 degrees of freedom
## AIC: 61.497
##
## Number of Fisher Scoring iterations: 4

m12 <- glm(p1~field, family = binomial(link='logit'), data = df_cabassous2
)
summary(m12)

##
## Call:
## glm(formula = p1 ~ field, family = binomial(link = "logit"),
## data = df_cabassous2)
##
## Deviance Residuals:
## Min 1Q Median 3Q Max
## -0.8945 -0.6897 -0.6748 -0.6748 1.7840
##
## Coefficients:
## Estimate Std. Error z value Pr(>|z|)
## (Intercept) -1.2819 0.3280 -3.908 9.29e-05 ***
## field 0.1441 0.3046 0.473 0.636
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
## Null deviance: 57.706 on 54 degrees of freedom
## Residual deviance: 57.492 on 53 degrees of freedom
## AIC: 61.492
##
## Number of Fisher Scoring iterations: 4

m13 <- glm(p1~forestry, family = binomial(link='logit'), data = df_cabassous2)
summary(m13)

##
## Call:
## glm(formula = p1 ~ forestry, family = binomial(link = "logit"),
## data = df_cabassous2)
##
## Deviance Residuals:
## Min 1Q Median 3Q Max
## -0.7549 -0.7002 -0.6895 -0.6895 1.7625
##
## Coefficients:
## Estimate Std. Error z value Pr(>|z|)
## (Intercept) -1.27715 0.32672 -3.909 9.27e-05 ***
## forestry 0.05572 0.32331 0.172 0.863
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)

```

```

##
## Null deviance: 57.706 on 54 degrees of freedom
## Residual deviance: 57.676 on 53 degrees of freedom
## AIC: 61.676
##
## Number of Fisher Scoring iterations: 4

m14 <- glm(p1~mpi, family = binomial(link='logit'), data = df_cabassous2)
summary(m14)

##
## Call:
## glm(formula = p1 ~ mpi, family = binomial(link = "logit"), data = df_cabassous2)
##
## Deviance Residuals:
## Min 1Q Median 3Q Max
## -1.1048 -0.6567 -0.6153 -0.6144 1.8763
##
## Coefficients:
## Estimate Std. Error z value Pr(>|z|)
## (Intercept) -1.2870 0.3422 -3.761 0.00017 ***
## mpi 0.7821 0.6546 1.195 0.23214
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
## Null deviance: 57.706 on 54 degrees of freedom
## Residual deviance: 53.943 on 53 degrees of freedom
## AIC: 57.943
##
## Number of Fisher Scoring iterations: 5

m15 <- glm(p1~msi, family = binomial(link='logit'), data = df_cabassous2)
summary(m15)

##
## Call:
## glm(formula = p1 ~ msi, family = binomial(link = "logit"), data = df_cabassous2)
##
## Deviance Residuals:
## Min 1Q Median 3Q Max
## -1.0941 -0.7376 -0.5810 -0.4760 2.0366
##
## Coefficients:
## Estimate Std. Error z value Pr(>|z|)
## (Intercept) -1.3596 0.3480 -3.907 9.36e-05 ***
## msi 0.5983 0.3279 1.825 0.068 .
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##

```

```

##      Null deviance: 57.706  on 54  degrees of freedom
## Residual deviance: 54.097  on 53  degrees of freedom
## AIC: 58.097
##
## Number of Fisher Scoring iterations: 4

m16 <- glm(p1~shdi, family = binomial(link='logit'), data = df_cabassous2)
summary(m16)

##
## Call:
## glm(formula = p1 ~ shdi, family = binomial(link = "logit"), data = df_c
abassous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.1747  -0.7444  -0.4805  -0.3192   2.3197
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -1.5046     0.3938  -3.820 0.000133 ***
## shdi          0.9354     0.3993   2.342 0.019163 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 57.706  on 54  degrees of freedom
## Residual deviance: 51.087  on 53  degrees of freedom
## AIC: 55.087
##
## Number of Fisher Scoring iterations: 5

m17 <- glm(p1~wd, family = binomial(link='logit'), data = df_cabassous2)
summary(m17)

##
## Call:
## glm(formula = p1 ~ wd, family = binomial(link = "logit"), data = df_cab
assous2)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.1062  -0.7359  -0.6442  -0.5660   1.9548
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -1.3062     0.3346  -3.904 9.45e-05 ***
## wd           0.3347     0.3213   1.042  0.298
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##

```

```
## Null deviance: 57.706 on 54 degrees of freedom
## Residual deviance: 56.620 on 53 degrees of freedom
## AIC: 60.62
##
## Number of Fisher Scoring iterations: 4
```

5. MODEL SELECTION: R code below will generate the Table 2 and Figure 3 in Chapter 5

```
df.model <- as.data.frame(model.sel(m1,m2,m3,m4,m5,m6,m7,m8,m9,m10,m11,m12,
,m13,m14,m15,m16,m17))
round(df.model,2)
```

Figure 3:

```
ggplot(df_cabassous, aes(x = ed, y = p1)) +
  geom_point() +
  stat_smooth(method = "glm", method.args = list(family = "binomial"), f
ormula = y~x, alpha = 0.2, size = 1) +
  scale_y_continuous(breaks = c(.00, .25, .50, .75, 1)) +
  scale_x_continuous(breaks = c(seq(0,80, 10))) +
  xlab("Forest edge density") + ylab("Pr (occurrence)") +
  geom_point() + theme_bw() +
  theme(panel.border = element_blank(), panel.grid.major = element_blank
(), panel.grid.minor = element_blank(), axis.line = element_line(colour =
"black"), legend.position = "none")
```

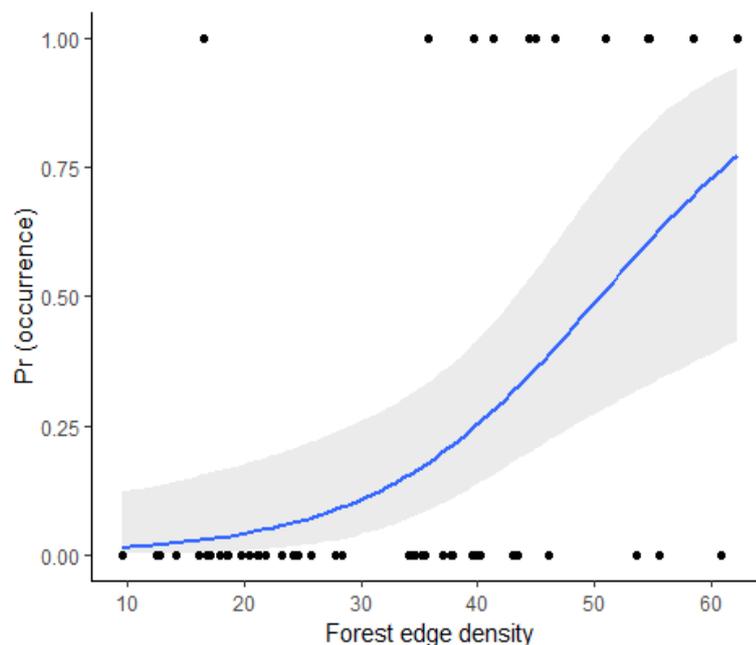


Figure 3. Relationship between the variable forest edge density from the top model ($\Delta AICc < 2$) on the naked-tailed occurrence (*Cabassous* sp.), in which the confidence intervals (95% CI in gray) of the estimated values did not overlap zero.

Comparing the full model with the top-ranked model

```
anova(m8, m1, test = 'Chisq')
```

```
## Analysis of Deviance Table
```

```
##
```

```
## Model 1: p1 ~ ed
```

```
## Model 2: p1 ~ forest + field + forestry + mpi + ed + msi + shdi + wd
```

```
## Resid. Df Resid. Dev Df Deviance Pr(>Chi)
```

```
## 1      53      44.077
```

```
## 2      46      36.590  7   7.4877  0.3799
```

The result suggesting that the top-ranked model with one predictor fits as well as the full model. Then, by the principle of parsimony, we favor the simpler model. Therefore, we identified the model **m8** as the most parsimonious of these models. That is, only forest edge density (ED) influences on the occurrence of naked-tailed armadillos in sugarcane dominated landscapes.

```
pander(as.data.frame(broom::tidy(m8)), split.tables = Inf)
```

term	estimate	std.error	statistic	p.value
(Intercept)	-1.764	0.4677	-3.772	0.0001617
Ed	1.443	0.4735	3.046	0.002317

6. CHECKING MODEL ASSUMPTIONS

We plot the residuals and recommended half-normal plot with simulation envelopes to check for model assumptions. Both model validations indicated no problems.

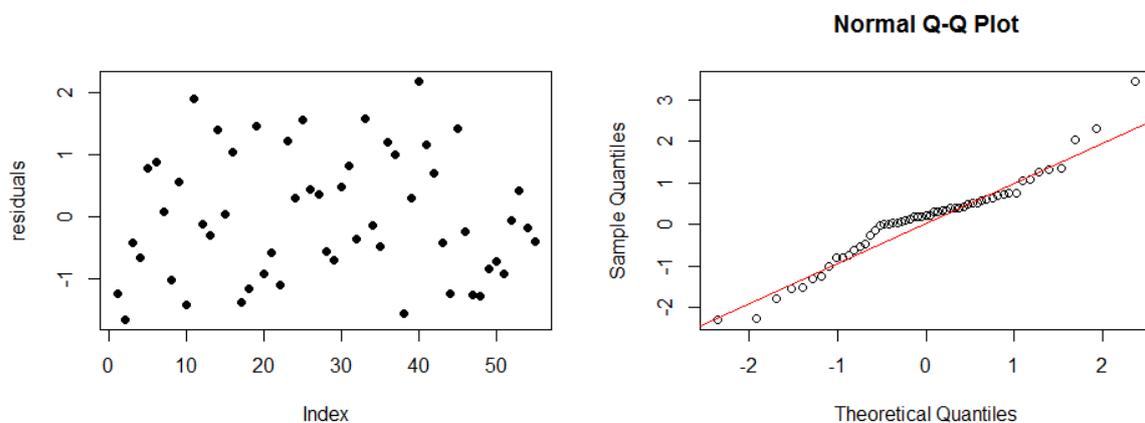
```
# Plotting Randomized Quantile Residuals
```

```
plot(qresiduals(m8), pch = 19, ylab = 'residuals')
```

```
# Plotting Normal Q-Q Plot
```

```
qqnorm(qresiduals(m8))
```

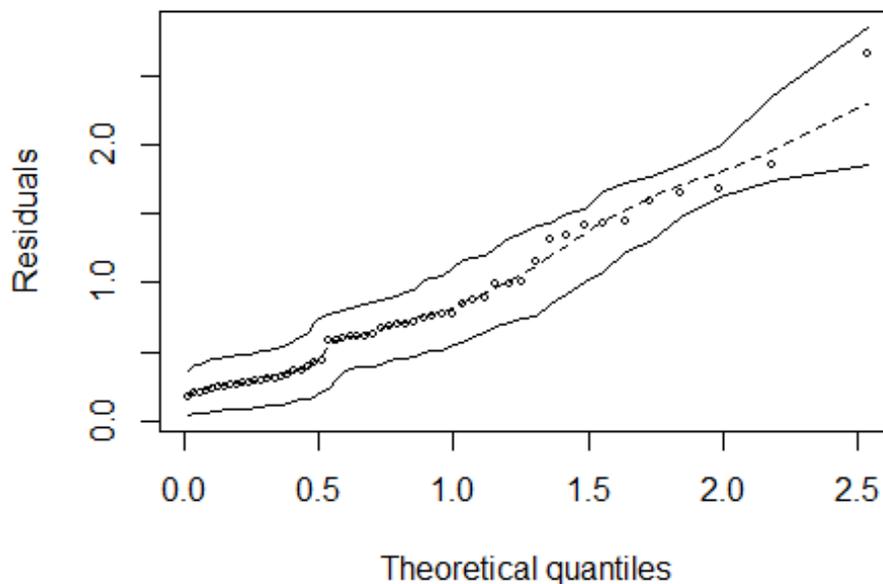
```
qqline(qresiduals(m8), col = 2)
```



```
#Plotting a half-normal plot with simulation envelopes
```

```
hnp(m8)
```

```
## Binomial model
```



Dispersion of the full model

```
summary(m1)$deviance/summary(m1)$df.residual
```

```
## [1] 0.7954272
```

8. SESSION INFO

Information about the R session and packages used to run the analyses and generate this document.

```
sessionInfo()
```

```
## R version 3.5.1 (2018-07-02)
## Platform: x86_64-w64-mingw32/x64 (64-bit)
## Running under: Windows 8.1 x64 (build 9600)
##
## Matrix products: default
##
## locale:
## [1] LC_COLLATE=Portuguese_Brazil.1252 LC_CTYPE=Portuguese_Brazil.1252
## [3] LC_MONETARY=Portuguese_Brazil.1252 LC_NUMERIC=C
## [5] LC_TIME=Portuguese_Brazil.1252
##
## attached base packages:
## [1] stats graphics grDevices utils datasets methods base
##
## other attached packages:
## [1] ggplot2_3.1.0 car_3.0-2 carData_3.0-2 corrplot_0.84
```

```
## [5] ellipse_0.4.1 hnp_1.2-6 MASS_7.3-50 pander_0.6.3
## [9] statmod_1.4.32 MuMIn_1.42.1 dplyr_0.8.3
##
## loaded via a namespace (and not attached):
## [1] tidyselect_0.2.5 purrr_0.3.0 haven_2.0.0
## [4] lattice_0.20-35 generics_0.0.2 colorspace_1.4-0
## [7] htmltools_0.3.6 stats4_3.5.1 yaml_2.2.0
## [10] rlang_0.4.0 pillar_1.3.1 foreign_0.8-70
## [13] glue_1.3.0 withr_2.1.2 readxl_1.1.0
## [16] plyr_1.8.4 stringr_1.4.0 munsell_0.5.0
## [19] gtable_0.2.0 cellranger_1.1.0 zip_1.0.0
## [22] evaluate_0.12 knitr_1.20 rio_0.5.10
## [25] forcats_0.3.0 curl_3.2 broom_0.5.2
## [28] Rcpp_1.0.1 backports_1.1.5 scales_1.0.0
## [31] abind_1.4-5 hms_0.4.2 digest_0.6.18
## [34] stringi_1.2.4 openxlsx_4.1.0 grid_3.5.1
## [37] rprojroot_1.3-2 tools_3.5.1 magrittr_1.5
## [40] lazyeval_0.2.1 tibble_2.0.1 tidyr_0.8.2
## [43] crayon_1.3.4 pkgconfig_2.0.2 Matrix_1.2-14
## [46] data.table_1.11.8 assertthat_0.2.1 rmarkdown_1.10
## [49] R6_2.3.0 nlme_3.1-137 compiler_3.5.1
```




Quem somos?
Nós somos uma equipe de professores e alunos da Universidade de São Paulo, em Ribeirão Preto.



CONTATO
Professor Responsável:
Adriano G. Chiarello

Alunos pós-graduandos:
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Marcella Pônzio
Nielson Pasqualotto
Paulo Bobrowiec
Thiago Rodrigues
Victor Krepschi

Projeto de Pesquisa FAPESP: Ocorrência de Mamíferos e Invasão Biológica em Remanescentes de Cerrado de Paisagens Agrícolas

Instituição Sede: Departamento de Biologia da Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Universidade de São Paulo

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QUAL BICHO MORA AQUI?



Nós estudamos os animais da nossa região e gostaríamos de saber onde eles vivem:

Será que o tatu mora na plantação de cana?

Será que a onça vive nas plantações de eucalipto?

E o tamanduá, onde ele mora?

As Reservas Legais e Áreas de Proteção Permanente são importantes para os animais?

Vamos conhecer mais os animais que vivem na nossa região!

Você é muito importante para o nosso estudo! Nos ajude a cuidar das câmeras que vamos colocar nas árvores!

Para tentar saber mais sobre esses e outros bichos nós estamos usando uma máquina fotográfica que fica presa nas árvores.





Ela tira foto dos animais que passam por aqui e depois nós conseguimos saber onde eles estão morando.




Figure S2. Folder used to ask for rural owners and employees permission to use their properties as study landscapes. Text (*Portuguese*) and Desing: Marcella do Carmo Pônzio.

Com a sua colaboração, nós conseguimos fotografar vários bichos que moram na nossa região e na sua fazenda!



SEMPRE QUE PRECISAR, ENTRE EM CONTATO COM A GENTE

Professor Responsável:
Adriano G. Chiarello

Alunos pós-graduandos:
Marcella Ponzio
Nielson Pasqualotto
Thiago Rodrigues

Projeto de Pesquisa FAPESP: Ocorrência de Mamíferos e Invasão Biológica em Remanescentes de Cerrado de Paisagens Agrícolas

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O PROJETO
'QUAL BICHO MORA AQUI?'
AGRADECE A SUA AJUDA




USP LAEC FAPESP

Durante dois anos, nós visitamos várias propriedades rurais na região de Ribeirão Preto e Araraquara, pedindo autorização para instalarmos câmeras fotográficas dentro das fazendas.

Você foi nosso parceiro!



Tamanduá-bandeira



Veado catigueiro

Obrigado!



Macaco-prego



Irara




Figure S3. Folder used to thank rural owners and employees for the permission gave to us, delivered it at the end of the field campaigns. Text (*Portuguese*) and Desing: Marcella do Carmo Ponzio.

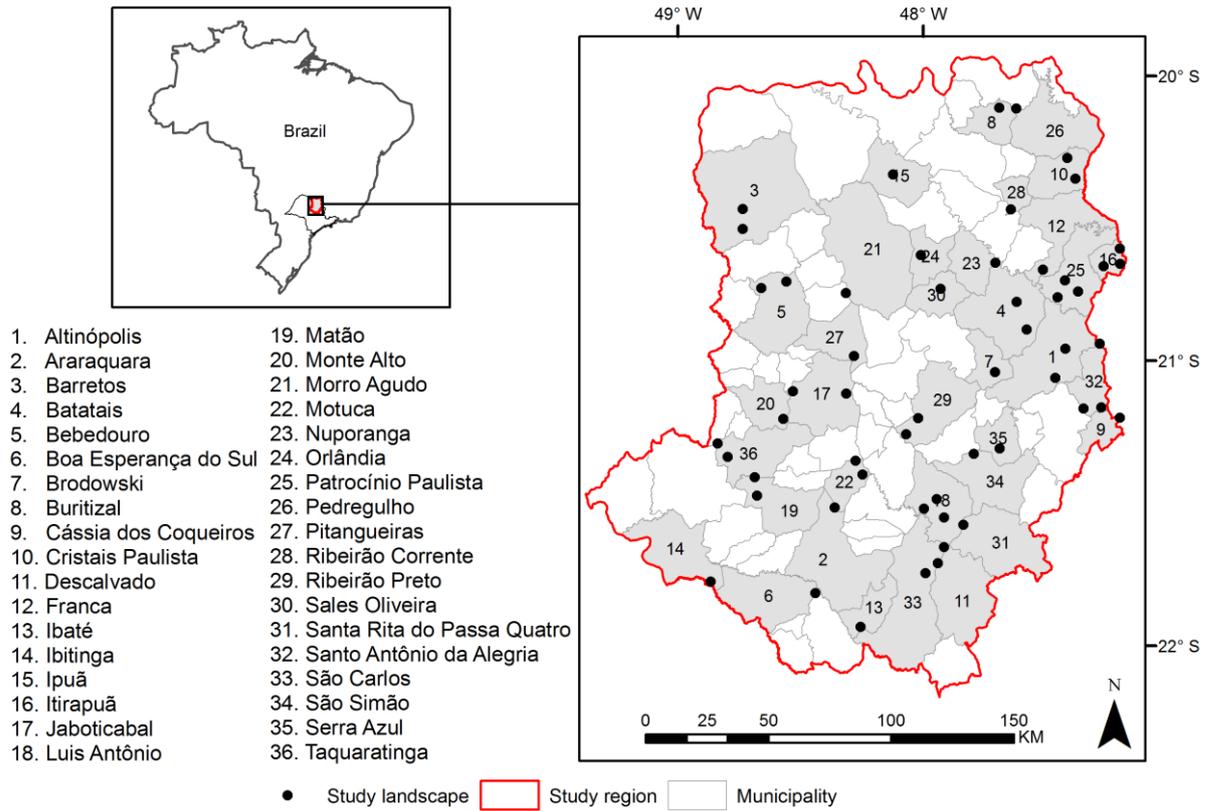


Figure S4. Municipality' names (1–36) containing the study landscapes for sampling armadillos in northeastern of state of São Paulo, Brazil.