Bioeducation Consortium

Lúrio University, Zambeze University, Manica High-Polietric Institute, Gorongosa

National Park and Lisboa University

Master's Program in Conservation Biology

The ecological niche of the Southern African lungfish *Protopterus annectens*

(Owen, 1839) in Gorongosa National Park, Mozambique

By

Lorena Michel da Encarnação Matos

Dissertation presented to the Master's Program in Conservation Biology as a requirement

to obtain the title of Master in Conservation Biology

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(supervisor)

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Gorongosa National Park, 27 março 2020

The ecologic niche of the Southern African lungfish *Protopterus annectens* (Owen, 1839) in Gorongosa National Park, Mozambique

Declaration

I declare that this thesis, which I hereby submit for the degree 'Master in Conservation Biology' at Bioeducation Consortium: Lúrio University, Zambeze University, Manica High-Polietric Institute, Gorongosa National Park and Lisboa University, is my own work and has not been previously submitted by me for a degree at this or any other tertiary institution.

Signature:

The ecologic niche of the Southern African lungfish *Protopterus annectens* (Owen, 1839) in Gorongosa National Park, Mozambique

Dedication

To my parents Dionisio Matos and Gloria Matos, my fiancé Augusto Bila, my brothers and sisters, Diogo, Natasha, Jenny, Joelle, Denny, and Solange, and my nieces Luna and Allany.

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Acknowledgment

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Abstract

The African lungfish genus *Protoperus* has attracted the attention of researchers for a long time, mostly of those concerned with the evolution from aquatic to terrestrial life, and the survival of dry periods. However, astonishingly little is known about the general ecology of these fish. Lungfish (*Protopterus annectens*) are often permanent residents in poorly oxygenated tropical vleis, pans and swamps. They are obligatory air-breathers, and able to survive extended periods of desiccation. The Gorongosa National Park (GNP) in central Mozambique is an ideal place to study lungfish biology and ecology because of the park's numerous seasonal pans and rivers. The species *Protopterus annectens* is known to occur in the park, but to date there are no comprehensive reports on its biology. This work was undertaken to understand the distribution and habitat selection of *P. annectens* in GNP. Fifty-three pans have been sampled in the wet season from February to April, and the beginning of the dry season from May to June 2019. Two sampling techniques were used, fish funnel traps to assess the presence/absence of *P. annectens*, and the box method to assess associate fauna and flora in those pans. A total of 37 fish were recorded from 21 of the pans. The results show that from the biotic and abiotic variables selected to predicte the occurrence of *P. annectens,* only the pan surface area was predictive. Although not significant, there was a trend that lungfish were more often found in pans with a greater abundance of aquatic vegetation and animals, a slightly acid and neutral pH, low (wet season) and high (dry season) conductivity and large surface area and water depth. The results suggest that *P. annectens* is a very generalized and adaptable species concerning its ecological niche.

Key words: African lungfish, *Protopeterus annectens*, Niche, Habitat selection and Gorongosa pans

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Resumo

O gênero Africano de peixe pulmonado *Protopterus* a sua descoberta atraiu a atenção de pesquisadores, principalmente na área da evolução da vida aquática para a terrestre e a capacidade de sobrevivência a períodos secos. Surpreendentemente, pouco se sabe sobre a ecologia geral dos peixes. O peixe pulmonado (*Protopterus annectens)* são frequentemente residentes permanentes em dambos, lagoas e pântanos tropicais pouco oxigenados, respiram oxigénio atmosférico obrigatoriamente e sobrevivem a longos períodos de dessecação. O Parque Nacional da Gorongosa (PNG), no centro de Moçambique, é o local ideal para estudar a biologia e ecologia do peixe pulmonado, devido às numerosas lagoas e rios sazonais do parque. Sabe-se que o *P. annectens* ocorre no parque, mas até o momento não há relatórios abrangentes sobre sua biologia. Portanto, este trabalho foi realizado para entender a distribuição e seleção de habitats de *P. annectens* no PNG. Foram amostradas cinquenta e três lagoas na estação chuvosa de fevereiro a abril e, no início da estação seca de maio a junho de 2019. Foram utilizadas duas técnicas de amostragem: armadilhas de funil para peixes para avaliar a presença / ausência de *P. annectens* e a caixa metálica para coletar a fauna e flora destas lagoas. Um total de 37 peixes foram registrados em 21 das lagoas. Os resultados mostram que as variáveis bióticas e abióticas selecionadas para predizer a ocorrência de *P. annectens* apenas a área das lagoas foi preditiva. Embora não significantes, os peixes pulmonares foram encontrados com maior frequência em lagoas com maior abundância de vegetação e animais aquáticos, pH levemente ácido e neutro, baixa (estação chuvosa) e alta (estação seca) condutividade e com uma área grande e profundidade da água. Os resultados sugerem que o *P. annectens* quanto a seleção do habitat se mostrou generalistae uama espécie adaptável ao seu nicho ecologico.

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Palavra-chave: Peixe pulmonado africano, *Protopterus annectens,* Nicho, Seleção de habitats e lagoas da Gorongosa

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Chapter 1

General introduction

Lungfish, or Dipnoi have attracted the attention of researchers interested in mechanisms involved in the evolutionary transition from aquatic to terrestrial life (Smith 1931; Delaney et al. 1977; Greenwood 1986; Khidir 2006). Due to those mechanisms that the fish presents, a considerable amount of research has been carried out, dedicated to the anatomy and physiology of these fish, with few studies carried out on the biology of the species. This imbalance is not surprising when considering the generally inhospitable habitats occupied by lungfish, which arouses particular interest in studies on the evolution and phylogeny of vertebrates, and physiologists and biochemists for their ability to breathe oxygen out of the water and aestivate in times of drought (Greenwood 1986). Without studies related to the biology and ecology of lungfish, it is difficult to understand what are the physiological restrictions and needs in terms of resources, according to the microclimate of habitat and how these restrictions determine or affect its distribution.

Understanding species' distribution is a powerful tool to identify critical habitats for the conservation of endangered species, i.e. to propose relevant decision-making strategies (Guisan et al. 2013). Nowadays the effect of climate change and extensive habitat destruction is noticeable, being the most important factors threatening the survival of species. For many species, adapting to new conditions, or move to other areas that offering suitable conditions such as moving to habitat in higher altitudes, is no an option (Hoegh-Guldberg et al. 2008; Chen 2012), and these threats are continually growing and driving the species extinction or force new adaptations.

The suitability of a habitat for a species depends on the habitat's abiotic characteristics and its biological components (i.e. food, competitors, and predators), these

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altogether influencing the fitness of a species, i.e. the number of offspring surviving and reproducing. The habitat suitability will thus be determined by several biotic factors such as food supply and predators (Fretwell 1972). The distribution of fish is often related to other, abiotic factors as well, e.g. habitat quality in form of water chemistry (Joy & Death 2004). Many theories explain how species are distributed across the Earth; among them biogeographic and ecological theories (Eldredge & Cracraft 1982; Acevedo et al. 2016; Crisci 2018).

Biogeography as a science tries to explain the present and past distribution patterns of biological diversity and their underlying environmental and historical causes (Sanmartín 2012). Through the documentation of spatial patterns of biological diversity it aims tounderstand the processes that generate and maintain those patterns (Eldredge & Cracraft 1982). Relevant data for such analyses stem, for instance, from ecology, phylogenetic systematics, and paleontology (Upchurch 1999). The biogeographic research is supported by two different approaches, ecological biogeography (studies the environmental factors that shape the distribution of individual species on spatial scale) and historical biogeography (studies the geographical distribution of organisms in terms of their evolutionary history) (Morrone & Crisci 1995). Alfred Russell Wallace is considered the father of biogeography, having interpreted and documented the distribution of species from an evolutionary perspective (Upchurch 1999).

The evolutionary biogeography (evolucionary perspective) focuses on the idea that the current distribution pattern of a species are the result of a dispersion process from the center of origin of the respective species (Darlington 1957). Hence, the distribution of species on Earth should be in agreement with the response of species to geological, evolutionary and ecological events and mechanisms. Most animals are mobile and thus (to some extent) can choose the habitat in which they live and the environment they

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experience (Levin et al. 2009). According to Rosenzweig (1987) the drivers that promote the behavior during the selection of a habitat also promote or lead to the evolution of characteristics, morphologies and physiologies that will allow the species to colonize a certain habitat.

The use of biogeographic models is important and essential for environmental management and for predicting the impacts of environmental changes, including climate change, on communities and natural ecosystems (Guisan et al. 2006).

The processes that generate and maintain the patterns of biogeographic distribution of a species are related to the ecologic niche of the species (the biotic and abiotic characteristics) because the ecological niche allows the species to occupy particular habitats. Hutchinson (1957) defined the ecological niche as an *n*-dimensional space, which comprises all necessary resources for a species. The axes represent a variety of factors, such as water access, temperature, habitat, food, etc., which are necessary for a species to survive and reproduce.

According to Nichols (2012) citing by Grinnell (1917) defined the niche as the biogeographic distribution of a species based on various abiotic and biotic factors that are ideal for the survival of a particular species. Elton (1927) cited by Nichols (2012) added to niches a functional role, such as a bee's pollination niche, and thus the Eltonian niche is more relate to the position of a species in ecosystems and food chains.

The Grinnellian niche is based on broad-scale variables (climate) that are not affected by species density, while the Eltonian niche relates to fine-scale variables that may be consumed or modified by the species (nutrients) (Hirzel & Lay 2008; Nichols 2012). Hutchinson takes into account the role of other species in niche evolution, in contrast to Grinnell's niche. Essentially, one can think of the Grinnell niche as the fundamental niche in which a species can theoretically be expected to maintain a positive

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population growth rate, disregarding biotic interactions. Hutchinson introduced the realized niche of a species, where a species has positive population growth rates only when biological interactions allow for it, i.e. competitors and predators not driving populations to extinction (Pearman et al. 2007).

The ecological factors of species (resources and conditions) are framed by tolerance limits, where species are eliminated wholly or reduced when (abiotic) conditions and (biotic) resources approach or exceed tolerance limit ideal for species survive. Biotic and abiotic factors are thus very useful to predict species' distributions, because of their synergistic effects on species distribution (Lewis et al. 2017).

The principle of competitive exclusion of Gause in 1954, states that two species cannot occupy the same niche stably, if their niches are overlapping and they are thus competing for the same resources, the stronger species eliminate the other species (Kneitel 2019). The competition for resources may cause species to diverge by natural selection, in how they use their resources, specializing in certain types of resources. The competition is a driving force in the evolution of niche-sharing adaptations, and experimental evidence suggests that the more diverse the community, the stronger the divergence of character traits (Pearson & Dawson 2003).

According to niche widths, species can be divided into two groups, i.e., specialist species, which occupy a narrow niche and generalists, which occupy a broad niche (Brown 1984; Hirzel et al. 2002; Williams et al. 2007; Peers et al. 2012; Ibarra et al. 2014). The specialists might be, for instance specialized on a particular resource (e.g. food type). Under a relatively stable subset of resources, a specialist may achieve a similar or higher level of performance and reach higher density, than a generalist (Devictor et al. 2010; Peers et al. 2012).

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Understanding the adaptability of a species in terms of habitat selection is particularly important when the environment is spatially and temporally variable, as in-stream reaches subject to rapid changes (Capra et al. 2016). A mobile species, as most animals, at least in theory, can decide which habitat it selects according with the resorce that habitats can give. These decisions might vary individually because of size, or type of activity (e.g., feeding, resting or breeding) (Capra et al. 2016). The suitability of a habitat is related to the impact of a habitat for the succeeding of generations of a species, i.e. its effects on fitness. A habitat's suitability will thus be determined by several factors such as food supply and predators (Fretwell 1972).

Habitat suitability and species distribution models

The analysis of the habitat needs of a species is fundamental in the management and conservation of it. One tool for such an analysis is species distributions or ecological niche modelling. These models predict the probability of species occurrence based on environmental variables using the presence / absence data or abundance data (Guisan & Zimmermann 2000; Hirzel & Lay 2008). They use the climate and other variables (e.g. productivity, topography, vegetation cover etc.) of known sites of the species to predict the potential geographic distributions. The predictions may include different levels of habitat suitability (Wiens & Graham 2005). However, rarely ecological and environmental interactions are included in such models (Guisan et al. 2006), where the ecological interations are the relation of the species with other organisms as a parasite, competitor etc., and enviromenal interactions are the relations of the species with the abiotic parameters as water quality, food availability, and others.

The most commonly used tools for habitat suitability models includes important habitat characteristics and habitat relationships of populations occurring at specific sites

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(Mayor et al. 2009). This tool can be used too to evaluate the implementation of alternative actions in terms of predicting changes on species' distributions, or to the quality of habitat where the species occur (Guisan et al. 2006, 2013)

The Habitat suitability models (HSMs) (Hirzel & Lay 2008) and Species distribution models (SDMs) (Guisan et al. 2013) were developed to provide scenarios of future landscapes by projecting changing environmental parameters and are increasingly used to support conservation decision making (Mcshea 2014). The process identifies critical environmental variables for each species or community, and then extrapolates from the known survey locations to the entire target landscape (Mcshea 2014).

The environmental predictors (biotic and abiotic factors) can have a proximal (variables with direct impact on species) or distal (variables with indirect impact species) effect on species distribution (Austin 2002), because the species usually respond to a complex of interdependent factors that consist of many environmental variables (Rydgren et al. 2003). Hence, it is important to select suitable environmental predictors to understand the biology of species well (Hirzel et al. 2002).

The species distribution models are obtained from simple observation data of presence, presence-absence or abundance, random or stratified field sampling or historical collection (Wiens & Graham 2005; Lewis et al. 2017). To run such models, geographic information systems (GIS) are often used to draw environmental data associated with georeferenced sampling sites, using cells with similar environmental characteristics (Kozak & Wiens 2006).

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Lungfish species: Taxonomy and distribution (probably start the lit review with this point)

Studies show that lungfish are the closest living relatives of tetrapods, as evidence by their morphological and physiological characteristics such as air-breathing, lobed fins, and their genetic relatedness (Smith 1931; Greenwood 1986; Otero 2011; Christensen et al. 2015).

Sarcopterygian include three groups of 'fish': the extinct rhipidistians, the coelacanths and the lungfishes or dipnoans (Yokobori et al. 1994). The Dipnoi first appeared in the early Devonian, 400 million years ago, and comprise 50 extinct genera (Morescalchi et al. 2002; Khidir 2006). Today only three genera are known, ***Lepidosiren***, ***Neoceratodus*** and ***Protopterus*** (Morescalchi et al. 2002). The distribution of the three genera of lungfish is a typically Gondwanan distribution, meaning that they occur, apart from Antarctica, on all southern continents (Otero 2011). These genera currently occur in three disjunct regions: Australian with only one species *Neoceratodus forsteri* Krefft, 1870, belonging to the family Ceratodidae; and South American with one species *Lepidosiren paradoxa* Fitzinger, 1836 (Lepidosirenidae). The lungfish from Australia are not obligatory air-breathers, different from lungfish from Africa and South America (Kemp 1987). The genus *Protoperus* is endemic to Africa (Roberts 1975) and its species are obligatory air-breathers, and are able to survive in temporary waters and sometimes for extended periods of desiccation (Greenwood 1986). Africa has four lungfish species: *Protopterus annectens* (Owen, 1839), *P. aethiopicus* Heckel, 1851, *P. dolloi* Boulenger, 1901 and *P. amphibius* Peters, 1844 (Protopteridae) (Smith 1931; Marshall 1986; Goudswaard et al. 2002; Otero 2011). The distribution of the *Protopterus* spp. extends across a large part of Africa, *P. annectens* and *P. dolloi* are essentially West African taxa, and *P. aethiopicus* and *P. amphibius*, are essentially East African, but *P. aethiopicus* also

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occurrs in the Zaire basin, and *P. annectens* extends eastwards into the middle and lower Zambezi systems and the Limpopo system (Greenwood 1986).

In Mozambique lungfish are distributed in the lower Zambezi and the Limpopo systems (Greenwood 1986; Skelton 2001). The genus *Protopterus* is represented in Mozambique by two species *P. annectens* and *P. amphibius* (Greenwood 1986; Skelton 2001). *Protopterus annectens* is distributed in the coastal plain of Mozambique from lower Zambezi to the Incomate, its distribution range extending up into the middle Zambezi valley. *Protopterus amphibius* is distributed in coastal lower Zambezi and East Africa (Skelton 2001).

The lungfish of the Paleozoic were distributed in both marine and freshwater environments, and even predominated in marine environment (Cloutier & Ahlberg 1996), nowadays all species live in freshwater habitats.

The African lungfish inhabit areas that flood in the wet season and dry out in the dry season (Khidir 2006). Their preferred habitats include swampy vegetated areas of lakes and major river systems, which are often prone to drying up during periods of droughts (Greenwood 1986; Mlewa & Green 2004).

Lungfish have a large range of habitats in African savannas, occurring in shallow inshore-water habitats, and occupy both lentic waters (standing) and lotic waters (running), Some populations, of at least one African species, live in permanent waters (e.g. *P. aethiopicus*) and so do not need to estivate, although they apparently retain the ability (Greenwood 1986).

The *P. annectens* tend to be associated with a wide variety of pan, swamp locations and all Rift Valley lakes (Greenwood 1986); frequent habitats are pans, which are at the most 0–20 m deep. This is probably associated with respiratory behavior of lungfish, which requires regular surfacing to breathe (Okafor 2011).

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Biology of lungfish

Breeding

Budgett (1901) and Greenwood (1986) described general aspects of lungfish breeding ecology, including nesting behavior and early development of young larva. In their natural habitat, lungfish are reported to be seasonal breeders. Nests are prepared in shallow vegetated areas of ponds and swamps. During the larval period in the nest, the male *Protopterus* spp. stays with the larvae and guards them (Budgett 1901). The eggs measure 3.5-4.0 mm in diameter. The larvae begin to hatch on the eighth day on average, and by the tenth day the larvae are all attached by their suckers to the side of the nest (Budgett 1901). The nest vary from a simple excavation to a U-shaped tunnel (Greenwood 1986). The architecture of these nests shows marked inter- and intraspecific variability and is likely to be determined by various environmental factors (Greenwood 1986). The lungfish move through dense aquatic vegetation, to burrow, and even to move across barely flooded land.

Aestivation

Aestivation is a dormant state occurring during the dry season and, unlike hibernation, reductions of metabolism may occur without any decrease of temperature (Glass 2008). Aestivation is usually accompanied by down-regulation of gas exchange, heart rate (the speed of the heart cycle measured by the number of heart contractions per minute) and cardiac work (the amount of energy that the heart transfers, through the application of a force, to generate displacement of the blood, pumping it through the arteries) (Glass et al. 1997). Aestivation is usually induced by adverse environmental

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conditions such as lack of food or drought (Abe 1995). All four African lungfish species are able to survive prolonged dry periods, when water levels begin to fall in the dry season. *Protopterus aethiopicus*, *P. amphibius,* and *P. annectens* are capable of digging a hole in the mud, in which they lie, using their 'lungs' to breathe air (Greenwood 1986). The metabolic rate slows and the energy necessary for survival comes from the breakdown of the muscle tissue. In this state the *Protopterus* spp. can survive the seasonal periods of drought, which may last 3-9 months (Khidir 2006). The juveniles start to aestivate for the first time before reach 7 - 12 cm length, after three months of growing (Johansen & Svensson 1954). The methods the different species and populations employ for aestivation vary, and include the building of subterranean cocoons, lying-up in water-filled subsurface burrows, or simply burrowing into moist regions of the substrate (Greenwood 1986). To create cocoons, the lungfish secret a mucous from the skin, which hardens to form a waterproof shell that surrounds the body completely, except for a small opening at the mouth. In this subterranean nest, the mouth has a connection to the surface by a narrow breathing channel. During aestivation, the lungfish is obliged to rely entirely on air breathing for its external gas exchange, and is deprived of access to food or water (Delaney et al. 1977). Johnels and Svensson's (1954) cited by Greenwood (1986) give a detailed and well-illustrated description of the cocoon and the so-called sleeping nest of *P. annectens*.

Protopterus annectens is omnivorous, preying on snails, insects and worms, fish and amphibians, and its digestive system is primitive (Adeyemi 2010; Machipane 2010). The prey is sucked into the mouth, repeatedly chewed, and finally sucked into the stomach (Greenwood 1986).

Studies by Mlewa et al. (2005) showed that *P. aethiopicus* daily movements ranged from little or none to 5.2 km. Maximum water depth of its habitats was about 3 m

and fish utilized all depths greater than 1 m. The lungfish are more active during the afternoon and evening when they move around for feeding (Kemp 1987) .

Individual lungfish have overlapping home ranges but individuals restrict their activities to areas smaller than the available lake habitat. Predator avoidance and food availability appear to be the most important factors influencing space use by marbled lungfish (*P. aethiopicus*) in the open waters of Lake Baringo but intraspecific interactions may also be important (Greenwood 1986; Mlewa et al. 2005).

Morphology of Protopterus *spp.*

Lungfish have distinctive elongated tapered bodies and filamentous pectoral and pelvic fins (Skelton 2001). *Protopterus annectens* can reache the total length of 820 cm (Greenwood 1986). According to Tokita et al. (2005) the only effective characters to identify each species of *Protopterus* are the distance from snout to the most anterior point of the dorsal fin (DL); head length (HL); and the distance from snout to most anterior point of anal fin (AL), as well as respective indices as summarized in Table 1. Preserved species can be also identified by the number of their ribs.

Aim of this study

The aim of this study was to understand the distribution and habitat use of a lungfish species, thus potentially contributing to their conservation managementging. The loss of fish diversity in an aquatic system may be a major threat to this ecosystem, given that these species contribute to its dynamics, participates, among others, directly in processes of predation of invertebrates, thus nutrient recycling, being therefore considered one of

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the most factors influencing their respective systems (Melo et al. 2007). The Gorongosa National Park (GNP) in central Mozambique is an ideal place to study lungfish biology and ecology because of the geology and seasonality and the park's numerous seasonal pans and rivers.

This thesis comprises one data chapters, focuses on habitat selection and distribution of lungfish in Gorongosa National Park, where the areas of occupation are, and what the abiotic and biotic characteristics variables influence the lungfish's habitat selection, was studied. The data were collected from 24 pans in GNP, where biotic and abiotic data, and presence and absence of lungfish were collected in two seasons: rainy and dry.

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Chapter 2

Title: Distribution and habitat selection of the Southern lungfish (*Protopterus annectens brieni*) in Gorongosa National Park

Introduction

The way that species are distributed in the world depends on their history and ecology biogeography (Yu et al. 2010; Crisp et al. 2011). This distribution is thus determined by the relative suitability or quality of different habitats (Hirzel & Lay 2008), and the environmental factors that cause natural selection and lead a species to develop particular behavior, through evolutionary processes, to select a particular habitat (Fretwell 1972). The animals select habitats to maximize fitness, and in this processed the natural selection act as a mechanism that tends to produce or alter habitat selection (Brownt & Rosenzweig 1986).

In the natural habitat the species never live in isolation, they coexist with other species.Thus competition, predation, parasitism, or mutualism occur, which may affect species' fitness and behavior (Connel 1961; Pearson & Dawson 2003; Kneitel 2019). These interactions can by direct (interference, such ascompetition and parasitism, and predation) and indirect (when a common resource is depleted or when the species are preyed upon by a common predator) (Hirzel & Lay 2008). The way that species forage can be affected by the variables of habitats (abiotic and biotic interactions - Niche) and the level of resources in a given area (Brownt & Rosenzweig 1986; Pearson & Dawson 2003).

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Many climatic factors during evolution have contributed to African lungfish adapting to their habitat in order to survive in African savannas in dry seasons (Tokita et al. 2005). Today the environmental factors are not the only drivers of habitat selection or distribution of some species as lungfish. Studies conducted by Goudswaard et al. (2002), show that in the African lungfish *Protopterus aethiopios* anthropogenic activitis such as overexploitation through fishing can restrict lungfish to certain refugia.

The African lungfish, *Protopterus* spp*.,* are known to be obligatory air-breathers, able to survive in temporary, poorly oxygenated waters for extended periods of desiccation, when the pans and ponds evaporate. Then lungfish start to aestivate for months (Delaney et al. 1977; Greenwood 1986; Glass 2008) or even years. Many studies on this group have focused on evolution, and few studies addressed the patterns of distribution of lungfish (i.g. Greenwood 1986; Kemp 1987), their ecology, and the way they select their habitat. In order to understand how the species are distributed in a landscape, it is important to understand the biogeography and ecology (Sanmartín 2012).

Recently historical biogeography has begun to use ecological niche modeling to calculate biogeographic reconstructions of the species distribution (Lieberman 2000; Stigall and Lieberman 2005). The natural distribution and assemblage composition of fish within a system can be affected by a number of other factors that could be natural obstacles or man-made and ecological barriers as abiotic conditions of the habitat. But the species physiological and biological tolerances and behaviour patterns finally influence the habitat choosen (Sara et al. 2012).

The ecological niche is defined as a combination of biotic and abiotic environmental conditions necessary for the survival and reproduction of a species in its habitat and is subdivided into a fundamental and realized niche (Hirzel & Lay 2008). The fundamental niche of a species is based on the combination of ideal conditions for a

species to thrive without interference from other species, while the realized niche is the conditions necessary for a species to thrive based on its constraints due to the presence of other species with the species which interact (Nichols 2012). The ecological niche provides a useful framework for understanding how the biotic and abiotic factors affect the range and abundance of species in a habitat (Lewis et al. 2017).

Regarding the occupation of species in a habitat there are two groups of species according to the selection of their habitat specialists who use specific resources and there are generalist species that unlike specialists tend to use a greater variety of resources (Ibarra et al. 2014). Specialized species tend to suffer more from the effects of habitat change than generalist species, as they are common and apparently without conservation concern, exhibiting good adaptability to altered habitats (Segura et al., 2007).

Broad-niche species (generalists) exploit a wide range of diverse habitats, while narrow-niche species (specialists) occupy or exploit habitats where their narrow niche requirements are met (Williams et al. 2006; Ibarra et al. 2014), the specialists species are more vulnerable to changes in their habitat relative to generalist species (Segura et al. 2007). The coexistence between two competing species is favored when one species are specialist (selectively behaving), while the other is generalist (opportunistic behavior) and do not or have little niche overlapping whitin them (Rosenzweig 1987; Segura et al. 2007).

Protopterus annectens are consider omnivore and opportunist foragert. They feed on other fish, insect parts, plant parts, crustaceans, and worms (Adeyemi 2010; Machipane 2010). The opportunist foragers are only semi-opportunists: they exhibit partial preferences by accepting only a fraction of their secondary patches (Brownt & Rosenzweig 1986).

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Niche elasticity theory stipulates that species can either center their choice on resources to exploit them well, or broaden their choice to use resources efficiently (Peers et al. 2012).

The ecological niche use the habitat suitability models to predict the presence and absence or abundance of a species throught use of environmental variables (Hirzel & Lay 2008), as well the Eltonian niche. To know how the species interact with other species and it dispersal capacity in habitat (Soberon & Peterson 2005), i.e the high or low concentration of certain component in fresh water may influence life activities of individual species and can influence their distribution, so the concentration of salts in water can determine the species composition on that habitat (Berezina 2003).

Species behave differently in different habitat types depending on the density of competitors (Rosenzweig 1987). One way to understand how species select their habitat and using models is to explain how these species are distributed in their habitat in the face of biotic and abiotic interactions in their habitat.

Habitat models are used to predict the occurrence of one or more species based on abiotic and biotic habitat variables (Guisan & Zimmermann 2000; Hirzel et al. 2002; Pearman et al. 2007), to quantify habitat species requirements and to help improve understanding of species-habitat relationships (Ahmadi-Nedushan et al. 2006).

The freshwater ecosystems are recognized as the most threatened worldwide, so this ecosystem requires attention for its conservation including the aquatic organisms who live there (López-López & Diaz, 2015). The ways science can assist conservation and management of habitats are the use of species distribution models (SDMs), these models provide future landscape scenarios based on known and projected environmental parameters (Pearman et al. 2007; Guisan et al. 2013; Mcshea 2014).

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The four species of African lungfish are a distributed in savannas, living in shallow inshore waters, including the dense interior swamps, marshes (*P.annectens, P. dolloi and P. amphibias*) and lakes (*P. aethiopicus*) (Greenwood, 1986, Champman et al., 1996). The ability to breathe atmospheric oxygen allows them to occur in areas from which most bony fishes are excluded as permanent residents (Greenwood, 1986), i.e. in poorly oxygenated water of tropical vleis, pans and swamps (Skelton, 2001). *Protopterus annectens* occurs in shallow ponds in west and northeast Africa, and particularly in Mozambique it is distributed in the lower Zambezi, Limpopo (Greenwood, 1986) and Incomate systems (Skelton, 2001).

Gorongosa National Park is known for its diversity of habitats, including rivers, swamps and pans (permanent and temporary), that during the rainy season allow aquatic species to migrate between rivers and permanent or temporary pans. During the wet season waters of Lake Urema flood on the plains, covering about 200 km^2 of land, but during the dry season the waters reduce again to 10 km^2 (Böhme 2005).

Understanding the range of a species is essential for managing the conservation of species (Sinclair & Byrom 2006; Guisan et al. 2013). The lack of knowledge about the ichthyofauna can influence in some way with the lose of the structure of its community (Sara et al. 2012). The loss of fish diversity in an aquatic system may be a major threat to this ecosystem, given that these species contribute to its dynamics, participates, among others, directly in processes of predation of invertebrates, on the nutrient recycling, being therefore considered one of the most factors influencing their respective systems (Melo et al. 2007). Most of the studies on *Protopterus* sp. is devoted to their anatomy and physiology, the particular interest on these animals are in students of evolution and vertebrate phylogeny and the attractions offered to physiologists and biochemists by air-breathing and aestivating fishes. The Knowledge of its biology, however, is still very

incomplete. It is not known how populations of *Protopterus* sp. are changing over time, is important know how *Protopterus annectens* select and disperse in the habitat, and how the biotic and abiotic parameters affect it distribution in the habitat.

Aim:

This study will document the current distribution of lungfish and its habitat characteristics in Gorongosa National Park. I will address three main questions:

(**1.**) Wher does *Protopterus annectens* occur in Gorongosa National park?

(**2.**) What are the abiotic (pond size, water chemistry) and biotic (co-occurring fauna and flora incl. vegetation biomass) parameters of lungfish habitats?

(**3.**) What are the environmental factors that determine the occurrence of the lungfish?

Hypotheses

H1: *Protopterus annectens* occurrences, in particular the selection of specific pans are influenced by the composition of plants and animals in these pans, as well as by the abiotic factor such as pond size and water chemistry.

H2: The abiotic and biotic parameters can be used as predictor variables of presence and absence of *Protopterus annectens.*

Materials and Methods

Species description

Protopterus annectens (Owen 1839)

The lungfish have an eel-like appearance (Goudswaard et al. 2002) (Fig. 1). The body is elongated and tapered to a point at the tail; pectoral and pelvic fins are slender

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and filiform; dorsal and anal fins have soft rays only; the head is robust, snake-like; the nostrils open under the upper lip and are hidden when the mouth is closed. Gill chamber openings are short and restricted to the sides in front of pectoral bases. Small external gills are present above each gill opening in larvae. Anus is positioned behind the pelvic base, offset on one side of body. The coloration is greyish brown with dark brown spots and blotches. Lateral line canals form wavy lines over the head. Scales are soft, cycloid, arranged in 40-50 in lateral series. Adults attains 600 mm total length (Skelton, 2001). The teeth found in this species vary greatly and relatively to its omnivorous food habits.

Study area and study sites (pans)

The study was conducted in the Gorongosa National Park (GNP) (Fig. 2) (from Feberary to July of 2019), which is situated in Sofala Province, in central Mozambique, basically forming the end of the Great Rift Valley system that extends from Ethiopia in East Africa down into Mozambique (PNG, 2016). Gorongosa National Park extends over the districts of Gorongosa, Muanza, Nhamatanda and Cheringoma. It is geographically located between 18 49'49" (latitude) and 34°26'30" (longitude), and has an area of 3719 km^2 plus as buffer zone of 5330 km^2. Together with Mount Gorongosa (367 km^2), the protected area covers 9419 km^2. The climate is predominantly tropical humid, characterized by a change from a dry season (March-November) and rainy season (December to February) (PNG 2016). The mean annual precipitation varies from 354 to 824 mm (Tinley 1977; Massad & Castigo 2016). Rainfall increases as elevation increases to the west and east to ~1200 mm annually (Daskin et al. 2016). In contrast, precipitation on top of Mount Gorongosa reaches 2000 mm per year. Several rivers discharge into Lake Urema, situated in the center of the park, and up to 40% of the surface of Gorongosa floods each year for several months.

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As far as the geology and soils of the study area is concerned the Rift Valley floor is generally characterized by alluvial deposits with colluvial material deposited at the bottom of the Cheringoma plateau. Grey soils (some of which are hydromorphic) occur in the Rift Valley and are derived from detrital fan material and from sands (PNG 2016).

The Hydrology is caracterized by water drainage being mainly from Mount Gorongosa, the Midlands and the Cheringoma Plateau, down into the Rift Valley. Lake Urema is at the epicenter of the drainage with the overflow draining via the Urema River into the Pungue River on its way to the ocean. The eastern boundary of the GNP lies on the watershed on top of the Cheringoma Plateau. Large areas of this part of the Rift Ralley are regularly inundated (Daskin et al. 2016; PNG 2016).

Field methods and data collection

Data were collected at 53 seasonal pans; 24 pans in the wet season and 46 in the dry season (where additional 29 pans were add to the remain pans from the rainy season). Seven pans had dried up at the beginning of the dry season and only 17 pans from wet season persisted and could be resampled in the dry season. In the dry season new 29 pans were added to increase the chances to detect lungfish. Pans were pre-selected randomly along the park's dirt road system in two seasons, the rainy season, herein defined) as February to April, and the beginning of the dry season from medle of May to July 2019 (thereafter only named dry season). Pans were examined for lungfish and other data during 17 days in each season (with one months in between the observations). The data were collected in the field and the fauna and flora collected were identified at the E.O. Wilson biodiversity laboratory. In the field, two sampling techniques were used: fish

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funnel traps (Fig. 3) to assess the presence/absence of *P. annectens*, and the box method (Fig. 4) (Rödel et al. 2009), to record the aquatic fauna and flora.

Assesment o lungfish presence / absence

Four traps were installed randomly in each one of the 53 pans, left for 24h, and checked in the following day. In the pans where the 24h period did not produce lungfish records, the trap were left for another three days (where the initial position of the traps was changed to other places selected randonly of the pan, the ideal was the places with great vegetation cover on the pans and places with few vegetation cover) and checked the following days, to increase the chance to find and to avoid false negative (Mackenzie & Royle 2005; Royle & Ke 2007). If a presence of lungfish was recorded the trap was moved to another pan, and the caught fish measured.

 For morphometric measures, were used a digital caliper and a ruler with an accuracy of $\pm$ 0.5 cm using the identification scheme for freshwater fish provided by Skelton (2001) (Fig. 5).The measures taken were: total length (**TL**), head length **(HL)**, orbital diameter **(OD)** and body depth **(BD)**.

To weigh the fish was used a semi-analytical balance with an accuracy of $\pm$ 0.0001g. In order to weigh the fish, it was put in a zip lock bag, quickly weighed (the Zip-lock bags weight was subtracted from the first measure), and thereafter released into the pan.

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Assessment of aquatic fauna and flora

A metal box (40 x 40 cm, bottom and top open) was used in 14 randomly selected pans for quantitative sampling of the aquatic fauna (Rödel et al. 2009). In each of the pans, four box samples were taken in each cardinal point of the pan (North, South, East and West). After the box had been thrown into the water and it was made sure that the box edges were in the soil, with a plastic dip net (mesh diameter 1 mm) all animals from the box's content were collected. If no more animals were caught with 10 dip net sweeps, sampling was finished. The species collected and identified comprised invertebratess (aquatic insects and their larvae, mollusks, and crabs) and vertebrate (frogs, tadpoles, fish), as well as the plants.

Measurements of abiotic factors in the pan

Five abiotic measures were taken in each pan: water chemistry, pH, electrical conductivity, water depth and altitude, during the wet and dry seasons.

For water chemistry a pH and electrical conductivity (µS/cm) was measured– i.e. the concentration of ions in water. Both measures were taken with a Thermo Scientific Orion Star A329 pH/ISE/Conductivity/RDO/DO meter (accuracy $\pm$ 0.002 pH and $\pm$ 1conductivity). Water depth (in the middle), altitude (measured with a hand hold GPS, Garmin *etrex 10*), and surfcearea of the pan were measured as well (measured with a hand hold GPS, Garmin *etrex 10*). All water parameters and measurements were taken *in situ*. The altitude and the surface of the pan was measured using the function measure area of GPS Garmin. Water depth was taken with a ruler in cm. All these measurements were taken in both seasons, wet and dry, and the pans were the same from both seasons (except for the dried up ones). To estimate the plant cover in a pan a visual estimation was used,

this estimate was taken as a percentage of vegetation cover in the surface of the pan, by only one person.

Laboratory methods

Sample collection and preparation

The invertebrates and vertebrates collected with the box method were kept alive in water-filled buckets and taken to the laboratory, where they were preserved in 70% alcohol and labeled. The identification were made usinga microscope (ZEISS Stemi 305). From each pond the plant samples (emergent and submerse) were washed to remove mud and animals, and then identified and weighed (fresh and dry weight) to calculate biomass. First the fresh plants were weighed, then the plants were dried in an oven at 60 ° C for three days to remove the dry weight. To identify the invertebrates and vertebrates field guides such as were used: "A complete guide to the freshwater fishes of Southern Africa. Africa" by Skelton (2001) and "Freshwater life: A field guide to the plants and animals of Southern Africa" by Griffiths *et al*. (2015). The later guide was also used to identify the plants.

Data analyses

Mapping

To map lungfish occurrences in GNP, each record was marked by its GPS coordinates (pans with presence and absence of *P. annectens*), then the points were uploaded in Quantum GIS 2.18.6 and mapped.

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Prediction model of lungfish occurrence

In order to analyse the occurrences of *P. annectens*, potentially depending on the combination of various abiotic and biotic variables, a logistic regression was performed. This technique is a powerful analytical tool, capable of analyzing the effects of one or several independent variables, discrete or continuous on a (Lee 2007).

To model the probability of occurrence of *P. annectens* to presences/absences, using the logistic regression analysis in the statystucal software *R* (version 3.5.1), a generalized linear models (GLM) for binary data was used. This model were used to analyses the contribution of each abiotic variable (pH, water depth, area, elevation and conductivity) and biotic (plant cover, diversity of fauna, plants species richness and plants biomass) parameters in determination of the occurrence *Protopterus annectens*.

Habitat parameters and water chemistry

The habitat parameters (pan surface area, water depth and altitude) and water chemistry variables (pH and conductivity) were compared between the wet and dry seasons pan surveys, and between pans with (presence) and without (absence) *P. annectens,* by using *Kruskal Wallis test* to perform multiple comparisons, and the *Bonferroni correction* as a post hoc test in case data were significant, using the software R studios *version 3.5.1*. As descriptive statistics were usually provided the mean with standard deviation.

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Faunal diversity in the pans (potential prey)

The diversity of the fauna in pans, were measured using the Shannon and Wienner diversity index, because it is particular sensitive to the rare species in the community (Maguran 1988; Began et al. 2006). To calculated the diversity I used the formula "Shannon_H": H= $-\sum_{i=1}^{S} Pi * \ln Pi$ where **H** is the Shannon diversity index; **Σ** is the sum from species 1 to species S; *Pi* is the fraction of the entire population made up of species I; *S* is the numbers of species encountered, and *ln* is a natural logarithm of the number (Krebs 1989; Jost 2006). The Shannon-Wienner indices H' were calculated using the software Past. Pielou Equitability J or Pielou Index (J) represents the distribution of the number of individuals relative to species. It ranges from 0 to 1, where the value 0 represents the situation in which all species do not have the same abundance and the value 1 represents the situation in which all species have the same abundance, ie the same number of individuals (Magurran 1988); Equitability (E) "Equitability_J": Shannon diversity divided by the logarithm of the number of taxa (Harper, 1999). The Pielou (J) index was determined using the Ecological Past statistical software.

Species Richness of plants

The Species Richness (S) was obteined from the following formula: "Taxa_S": counted as the average number of species per pan (Magurran 1988).

Biomass of pans

The biomass was calculate using the following formula $Biomass = (Wdry/Wwet) * a$, where W_{Dry} is the dry weigh of the plants, W_{Wet} is the wet weigh of plants and the area of the metal box (40x40 cm).

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Similarity of the pans

The similarity between the flora and fauna of pans was calculated with the binary coefficient Jaccard index, which includes only species presence / absence data, regardless of their abundances (Begon et al. 1996). The formula of Jaccard Similarity index is: $SJ = \frac{C}{(A+B+C)}$, where: C is the number of species common to both communities; A is the number of species exclusive to the community A; and B is the number of species unique to community B. The Similarity values thus range from 0 to 1 being that: When all species are shared between "A" and "B", J would be 1. When there are no shared species between "A" and "B", J is 0. This index was calculated to see whether ponds with or without *P. annectens* are equal in faunal and flora composition.

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Results

During the study the wet season was prolonged due to the cyclone Idai that flooded this region in a month of the end of the wet season, and in this period, the first fase of the study (of data collection that should by continuos) was interrupted.

Assesment o lungfish presence / absence

Of the 53 pans investigated for the presence of *Protopterus annectens*, 21 had *P. annectens* (Fig. 6), being Twelve (50%) in the wet season and nine (16.98%) in the dry season. Most of detections in wet season were made during the first (9) and second visit to the pans (3), and the same happened in dry season in the first day (7) and second day (2). In total, were found 37 lungfish, including two juveniles and 35 adults.

Lungfish identification

Thirthy (37) lingfish individuals were captured with the minimum and maximum size (19.2 – 64 cm); and the minimum and maximum weight (19.6 - 1321.08 g) that correspond to the juveniles and adults of lungfish, respectively. In terms of age group, the juveniles were collected in the dry season (June), whereas adults were found in both stations. The morphometric measures collected from the specimens confirm that this sub-species of *Protopterus annectens* in the pans of Gorongosa National Park is *Protopterus annectens brieni*, because most of morphometric measures was the same that Skelton (2001) describe to identify this specie (Tables 2.1) and especially becouse the geographic distribuition.

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Logistic regressions describing presence of P. annectens

Forward and backward selection models describing the presence of lungfish in the wet and dry seasons revealed that the only variable with predictive value was pan size, and this was only significant during the wet season (Tables 2.2 and 2.3). *Protopterus annectens* were more likely to occur in pans with minimum size 1284.3 m^2 and maximum 24700m^2. In the pans without *P. annectens* the minimum size was 451.8 m^2 and maximum size was 54962 m^2. The logistic regression multivariate model to predict the probability of occurrence of *P. annectens*, in both seasons when combining all co-variables (abiotic and biotic) were not significant.

Measurements of abiotic factors in the pan

Abiotic conditions of pans

Comparing the pH means during the wet with the dry season data, as well as pans with and without *P. annectens*, did not detect any statistical differences (after Kruskal Wallis, $X^2 = 28.19$, df = 23, $P = 0.20$). Pans in the wet season all were slightly acidic with (6.71 ±0.3 mean ± SD, N = 12) or without (6.75 ±0.30 mean ± SD, N = 12) *P. annectens*; pH in the dry season was neutral in pans with (7 ± 0.33 (mean ± SD) N = 9) and without (6.8 ± 0.59 mean ± SD, N = 44) *P. annectens* (Fig. 7).

Conductivity did not differ between pans with and without lungfish (after Kruskal Wallis $X^2 = 63.48$, df = 58, $P = 0.29$). Pans in the wet season had low concentration of ions (conductivity) was low with (97.57 µS/cm ± 26.3 mean ± SD, N = 12) or without (90.22 µS/cm ± 16.7 (mean ± SD) N = 12) *P. annectens*. Conductivity in the dry season was two time higher than in the wet season, both in pans with (258.9 µS/cm ± 131 mean ± SD, N= 9) and without (279.5 µS/cm ± 142.03 mean ± SD, N = 44) *P. annectens* (Fig.

8). Comparing the size of pans (area), there was no difference in the mean area in pans with and without *P. annectens* during the wet and dry season (after Kruskal Wallis $X^2 = 61.92$, df = 63, *P* = 0.51). Pan size in the wet season with *P. annectens* seemed to be larger (6037 m^2 ±6998.8 mean ± SD, N = 13) than in pans without *P. annectens* (4397.90 m^2 ± 43868.4 mean ± SD, N = 11). The same I observed as well in the dry season when pans with *P. annectens* were smaller (6442 m^2 ± 7270.24 mean ± SD, N = 9) than with *P. annectens* (6228.5 m^2 ± 15887.15 mean ± SD, N = 44) (Fig. 9).

Comparing water depth there was no significant difference in the mean water depth in pans with and without *P. annectens* during the wet and dry season ($X^2 = 49.27$, df = 39, *P*= 0.13). Water depth in the wet season with *P. annectens* (42.6 cm ± 9.92 mean ± SD, N = 12) seemed, however, to be marginally lower than in pans without *P. annectens* (45.5 cm ± 12.4 mean ± SD, N = 12). The water depth in dry season seemed to be deeper in pans with *P. annectens* (48.6 ± 18.24 mean ± SD, N = 44) compared to the pans without *P. annectens* (34.93 ± 17.3 mean ± SD, N = 9) (Fig. 10).

Assessment of aquatic fauna and flora

Potential prey of the lungfish

Seventy-seven species of aquatic animals belonging to 33 families from 20 orders and seven classes were collected. The most abundant species in the wet season, that were present in more than 50% of the pans, were: *Anisops* sp. (bugs), family Coenagrionidae (damselfly), *Lanistes ovum* (Gastropods), *Amphiops* sp. (beetle), *Appasus* sp. (bugs), *Hyphydrus* sp. (beetles) and *Plea* sp. (bugs). The species that were present in more than 50% of the pans in dry season were: *Anisops* sp. (bugs), family Hydrophilidae sp. 2

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(beetle), *Amphiops* sp. (beetle), *Plea* sp. (bugs), *Appasus* sp. (bugs) and *Hyphydrus* sp. (beetle) (see the Appendix 1 and 2). The most abundant group in the both seasons were insects from the orders Coleoptera and Hemiptera.

Comparing faunal Shannon-Wiener diversity (H') there was no significant difference in the mean Shannon-Wiener diversity (H') in pans with and without *P. annectens* during the wet and dry season (after Kruskal Wallis, $X^2 = 23.51$, df = 23, *P* = 0.43). The Shannon-Wiener diversity in wet season pans with lungfish seemed to be lower (1.65 ± 0.78 mean $\pm$ SD, N = 9) than pans without *P. annectens* (2.3 ± 0.21 mean $\pm$ SD, N=5). The Shannon-Wiener diversity in dry was lower in pans with (1.65 ± 0.95 mean $\pm$ SD, N = 9) or without (1.59 ± 0.99 mean $\pm$ SD, N = 5) *P. annectens* (Fig 11).

In term of abundace of speciments of each species on each pan, the values of Pielou **evenness** (J) in wet and dry season in pans with and without *P. annectens* showed that animal species in most pans were distributed in same abundance during both seasons. The Pielou index (J) values were close to 1, and this values were higher in dry season (Appendix 3).

Faunal similarity

The composition of the fauna (Jaccard similarity index) in the wet season in pans with or without *P. annectens* was lower than 50%, so those pans were not similar. The Jaccard similarity in the dry season showed that pans number 5 (with *P. annectens*) and number 14 (without *P. annectens*) reached 50% similarity, and other were not similar because the Jaccard similarity index was lower than 50% (Appendix 2 and 3).

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Richness of flora and plant biomass

Eleven species from seven plant families were collected in the pans, of which the most abundant in the wet season were *Utricularia gibba*, *Ottelia exserta*, *Pistia stratiotes*, *Azolla filiculoides and Ludwigia adscendens diffusa*. In the dry season the plant species most abundant were *Utricularia gibba*, *Pistia stratiotes Azolla filiculoides*, and *Ottelia exserta* (Appendix 7 and 8).

Comparing the plant richness there was significant difference in the mean of plant richness in pans with and without *P. annectens* during the wet and dry season ($X^2 = 16.56$, df = 24, $P = 0.020$). However, when corrected for multiple testing (Bonferroni correction) the significances disappeared. The plant richness in the wet season was higher in pans with *P. annectens* (4.14 ± 2.09 mean $\pm$ SD, N = 9) than in pans without (3.6 ± 1.76 mean $\pm$ SD, N = 5). The plant richness in dry season was higher in pans with (3.17 ± 1.6 mean $\pm$ SD, N = 9) compared to pans without (1.8 ± 0.4 mean $\pm$ SD, N = 5) *P. annectens* (Fig. 12).

Comparing the plant biomass (floating vegetation and emergent vegetation) there was not significant difference in the mean of plant biomass in pans with and without *P. annectens* during the wet and dry season (Kruskal Wallis, $X^2 = 27$, df $= \pm 25$, $P = 0.35$). The plant biomass mean in wet season had slightly lower biomass pans with *P. annectens* (12.1 g/m^{2}4 ± 5.89 mean $\pm$ SD, N = 12) than those pans without (9.04 g/m$^2 \pm 12.4$ mean $\pm$ SD, N = 12). The plant biomass mean in dry season were lower in pans with *P. annectens* (6.3 g/m$^2 \pm 5.89$ mean $\pm$ SD, N = 44) compared to pans without (9.82 g/m$^2 \pm 5.84$ mean $\pm$ SD, N= 9) (see Fig. 13).

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When comparing the plant cover (floating vegetation) there was no significant difference in the mean of plant cover in pans with and without *P. annectens* during the wet and dry season ($X^2 = 20.30$, df $= 23$, $P = 0.62$). The plant cover in the wet season had low mean plant cover in pans with *P. annectens* (62.15 % $\pm$ 29.4 mean $\pm$ SD, N $= 7$) than in pans without (72.78 % $\pm$ 21.5 mean $\pm$ SD, N $= 7$). The plant cover in dry season were higher in pans with *P. annectens* (70.36 % $\pm$ 31.69 mean $\pm$ SD, N $= 6$) than pans without (34.93 % $\pm$ 17.3 mean $\pm$ SD, N $= 5$) (see Fig. 14).

Flora Similarity

The Jaccard similarity index for flora in wet season between pans with and without lungfish showed that the pans had high similarity in terms of plant composition during the wet season. Most of the pans (from nr. 13 to 14) ranged in their similarity between 50% and 100% (in 4 pans) (see Appendix 9) and those were pans with and without *P. annectens*.

The similarity in terms of plant composition in the dry season was less similar compared to wet season. The highest similarity was observed between pans 5 (with *P. annectens*) and 10 (without *P. annectens*) with 100% similarity in plant composition, most of the pans showed 50% similarity, only one pan showed less than 50% similarity (see Appendix 10). The pans in wet and dry season with and without *P. annectens* showed high similarity in terms of flora composition in between each other.

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Discussion

The subspecies of *Protopterus annectens* identified was *Protopterus annectens brieni*, this subspecies differs to the other subspecies *Protopterus annectens annectens* because of the geographic range, the *Protopterus annectens brieni* occur in Eastern Africa and *Protopterus annectens annectens* occur in Western Africa (Levêque 1990; Khidir 2006). In terms of morphometric characteristics (those two subspecies do not present high morphometrics differences), the *Protopterus annectens annectens* is a bit longer than *Protopterus annectens brieni* (Levêque 1990; Khidir 2006), the *Protopterus annectens annectens* can attain 86cm (Onwude & Fran 2018) and *Protopterus annectens brieni* can attain 60cm (Skelton 2001). In this study the maximum legth was 64cm, suggesting that this subspecies can grow more.

Where does Protopterus annectens *occur in Gorongosa National Park?*

The results showed that *Protopterus annectens* occurs in less than half pans in the southern area of the park (where the study was conducted) with lower altitude and where during the wet season becomes flooded. The detections rates was differet between seasons; in the wet season, the detections were higher (50%) than in the dry season (16.98%). More pans (more than 50%) with lungfish were detected in the landscape Rift valley Alluvial Fan. Machipane (2010) in his studies on Urema ichthyofauna diet, found *P. annectens*, in the landscape Rift valley Lake Urema. These two landscape have the same type of soils, clay and alluvial soil. These two landscapes are in between the Rift valley riverine and floodplain landscapes, with a textured stratified alluvial soil and in this type of soil, *P. annectens* were not detected during data collections. One thing that may influence the lack of detections in dry season was the water level, since when water

starts to dry out, *P. annectens* start preparing their cocoons (Delaney et al. 1977; Greenwood 1986; Icardo et al. 2012).

What are the environmental variables that determine the occurrence of lungfish?

In all models, only surface area was a variable predicting the presence of *P. annectens* in pans, and only in the wet season. Surprisingly, this variable predicted a negative influence of surface area on lungfish. It thus explains why lungfish were not found in large pans. The field observations documented that in very large pans (over 25000 m^2), even those with much vegetation, lungfish were absent, when attempting to catch them through three events. In contrast, they were readily recorded when the pan has shrunk (to less than 3000 m^2). This result can indicate that they indeed avoid largest ponds to avoid predators, such as monitor lizards, birds, and crocodiles.

The island biogeography island principles say that larger areas support more individuals and present more stable populations, but present more and larger predators. Thus the lungfish may need to have ponds of intermediate size: large enough to sustain some lungfish to breed and with enough food, as well as a long enough duration for finishing breeding, but also not too large to avoid lots of fish competitors and very large predators such as crocodiles. The ideal pan then would be of intermediate size. Study by Oertli et al. (2002) in Suisse ponds showed that small ponds had higher species richness compared to large ponds . So the second hypothesis, "The abiotic and biotic parameters can be used as predictor variables of presence and absence of *Protopterus annectens*", was not accepted. Because only one variable (area) was predicted, but in natural all variable interact with each other, so is expected that a group of variables was predictor of the presence of *P. anncetens*.

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The abiotic variable, the area of the pan, can be used to predict the occurence of *P. annectens*. It is important to note, however, that other variables that influence the occurrence of lungfish, and consider lungfish a generalistic species.

In contrast to surface area, the results of all other environmental variables showed that pans with (presence) and without (absence) *P. annectens* did not show any statistical differences, both for abiotic (pH, conductivity, area, water depth and altitude) and biotic (diversity of fauna, diversity of flora, vegetation cover and vegetation biomass) parameters.

Protopterus annectens was more often found in pans which slightly acid pH in the wet season. Similar values were of the pH where reported by Böhme (2005) in Lake Urema and in an *P. aethiopicus* habitat in lake Nawampasa in Uganda (Walakira et al. 2014).

The conductivity was the same fund by Böhme (2005), when the lake had more water the concentration were low but when the water reduce it was high, as the pans but in the pan the conductivity became more high. The pH and conductivity characteristics are highly dependent on the geologic properties of the lakes, ponds or pan (Vidal et al. 2002) these characteristics show been similar to the pans with some geologic properties. *Protopterus annectens* are considerd obligatory freshwater fishes. They are physiologically unable to tolerate salt-water (Roberts 1975). During dry season, when the water-level becomes low and toxic due to the decomposition of the organic materials, the Australian lungfish *Neoceratodus forsteri* exchange branchiae breathing for pulmonar one (Kemp 1987). The ability of *P. annectes* to breathe oxygen of the air make it resist to the toxic water during the dry season. The high temperature in the Carboniferous caused many water bodies to evaporate completely thereby forcing many of the fishes to begin to experiment with life on land (Okafor 2011). The physiology of *P. annectens* evolve in

other to survive during the dry season because in the dry season (Tokita et al. 2005) so they can explore many habitats that many non-air breather cannot survive (Greenwood 1986).

The size of the pan in dry and wet season did no change much (in between 6000-6500m^2, the water depth seemed to be deeper (in between 42- 49cm), the same water depth was see in the habitat of *N. forsteri,* a species that is very selective in the choice of the swamp habitat (Arthington 2009). The diversity of fauna in the wet and dry season was different, in some, it increased (9 pans) and decreased (6 pans), and it could may have influenced the similar between the pans that was not similar. This can be explained because the composition of the pans was more dominated by insects, and that group is the more diverse group in the world, and they have high relation with vegetation (Oertli et al. 2002) so was expected that this pans do not present the same composition of species, and lower values of similarity.

The composition of the flora changes according to the seasons, so it was possible to observe that the richness of the vegetation in the wet season is greater than in the dry season. The vegetation cover was high in both seasons, but in the drought becomes higher anthe biomass in the rainy season is higher and decreases in the dry season.

The vegetation in the breeding season is fundamental because the female chose the best nest sites to lay eggs, so the male have to choose a safe habitats at the edge of the pan with high vegetation to build the nests to avoid predator, and to protect the young (Budgett 1901; Greenwood 1986; Mlewa & Green 2004).

The diversity of the pans are influenced by pan variables, vegetation (submerged and floating) cover, connectivity of the pans, quantity of nutrients (Oertli et al. 2002). The *P. aethiopicus* in its habitat during the wet season present aquatic macrophytes (floating and submerged plants) (Walakira et al. 2014) the some as the Australian lungfish

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(Arthington 2014). It could be observed that the sites with higher vegetation cover found more fish (qualitative observations), although the analysis showed that the vegetation does not influence the occurrence of *P. annectens*. The plant richness there had a significant difference, although the post hoc test lost the significance, so the vegegetation cover have an influence on the presence and absence of *Protopterus annectens*. The architecture of these nests is likely determined by various environmental factors, such as the oxygen level, vegetation, and predation (Greenwood, 1986). During the breeding season the male stay more in the edges with dense vegetation and the female stay in the middle of the pan (Greenwood 1986).

It was expected that the pans with *P. annectens* present diferente biotic and abiotic conditios so it was expected that the biotic variables had more influence in the movements and migration of *P. annectens* than the abiotic conditions as happened with *P. aethiopicus* in Lake Baringo, Kenya (Mlewa et al. 2005). The lack of environemnatl differences between the pans with and without *P. annectens*, was possibly related to the type of the landscape that influence them, in particular, the high similarity of plants in the pans and the microclimate of the habitat. The most data were collected in Rift valley Alluvial Fan than others, and results showed that the abiotic and biotic variables was not diferents, and it can be explained because the landscapes had area with specific geomorphology, clime, soil, vegetation pattern and associated fauna, hat gives rise to a predictable and repeatable habitat (Stalmans & Beilfuss 2008).

Protopterus annectens is considered a generalist species because it feeds on various types of food and is not focused on one type of resource and is therefore found in different types of pans (Adeyemi 2010; Machipane 2010). So it was expected that they occur in all pans that have low or high suitability for it occurrence (Perry et al. 2008) as

well as being locally abundant (Williams et al. 2007). The first hypothesis tha "*P. annectens* occurrence, in particular the selection of specific pans, is influenced by the composition of plants and animals in these pans, as well as by the abiotic factor such as pond size, water chemistry", was not confirmed. The species respond to the physiochemical characteristics of the environment, so there is a greater likelihood that species composition will be similar between nearby samples, this is a property of ecological variables (self-correlation) is due to the fact that the samples that are nearby share the same environmental characteristics (Guianuca 2012).

Conclusion

Protopterus annectens occured in southern GNP, in habitats with clay alluvial soil, and it seems that the lungfish are not very selective in terms of habitat characteristics. They occur in pans of intermediate size, likely because of a trade-off between population size of the lungfish, and the occurnces of competitors and predatotors in larger pans and a higher risk of desiccation in smaller ones. Other habitat variables were not significatively different between pans with and without *P. annectens*. However, the lack of clear environmental signals concerning habitat choice of the lungfish might be simply due to the overall high similarity of their abiotic and biotic factors between habitats.

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Chapter 3

General Conclusion

Most of the biotic and abiotic vairiables selected was not predicted variables for determine the presence of *Protopterus annectens* in GNP.The species are found where abiotic conditions are favorable (Acevedo et al. 2016) for their survival and fitness. Most of the samples were collected in pans with same type of the soil so it is important to have the same proportions of the pans in other type of the soils to see the differences of biotic and abiotic variables. The pan surface area was demonstrated to be an important predictor of the lungfish distribution, and it showed that the relationship between the surface area and the lungfish occurrence to be negative.

The logistical regression model predicts that the *P. annectens* occur in pans of intermediate size. The optimal pan size likely fulfills the following criteria: limits the likelihood of large predators; provides enough resources for growth and development; and is persistent enough to allow for complete development but forces aestivation.

The *Protopterus annectens* seems to not care about the habitat however is important to know if it are not selective or if it select the habitat randomly when the GNP are flood. Same pans observed in 2017 with lungfish, in this survey lungfish was not detected in any, in both seasons, and even the habitat did not present the same species composition of 2017. Some of these pans that where detected with lungfish in 2017 (by Lorena Matos) in this survey had present high number of *Claris* sp. so is important know if they compete for the habitat.The study of Machipane (2010) showed that they have 31% of diet overlap. *P. annectens* are known as a territorial species (Greenwood 1986) and they could be competed by habitat, because it seems like a competitive exclusion

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(Kneitel 2019). *Protopterus annectens* are consider a generalist species and its physiology allows it to explore different habitats, but is important now it role in the ecosystem and it relation with other species, so more studies have to be done using genetic or stable isotope analyses to know exactly its diet. Because one thing that can produce changes in the populations, but not are linear is the indirect effect of food web interactions among species (Sinclair & Byrom 2006).

After testing the two hypotheses both showed not to confirm the influence of the abiotic and biotic variables selected in the selection of the habitat by *Protopterus annectens*.

The high or low concentration of certain component in fresh water may influence life activities of individual species and can influence their distribution, so the concentration of salts in water can determine the species composition on that habitat (Berezina 2003).

For the next study is important to investigate the ecological rolr of lungfish in the Gorongosa ecosystem, including its diet (with the use of the stable isotope analysis).

The next study have to consider the use of traps according to the pan size even the metal box to avoid comparing two locations of different sizes using the same number of replicas as recommended by Oertli et al. (2002).

The study of gene flow between populations should be consider to investigate the genetics of the lungfish in Gorongosa to understand the gene in its populations.

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Table 2. Morphological characteristics of *Protopterus* species (copied from Tokita et al., 2005).

Species	Number of ribs	HL/AL (%)	DL/AL (%)	External gills
Protopterus aethiopicus	38–39	24–29.6	62.1–67.1	Absent in adult
Protopterus amphibius	27–30	33.2	45–56	Present in adult
Protopterus annectens	32–37	22.8–28.2	51–57.5	Present in adult
Protopterus dolloi	47–55	16.2–19.6	63.7–66	Absent in adult

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Table 3.1 Morphometric measurments from the specimens collected in the pans, to identify the subspecies of *Protopterus annectens* in Gorongosa National Park

Morphometric measurments	Mean ± SD
Total length (TL)	42.5 ± 9.95
Head length (HL)	5.79 ± 1.67
Orbital diameter (OD)	0.43 ± 0.10
Body depth (BD)	4.99 ± 1.4

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Table 2 1 Logistic regression results describing the presence of lungfish in the wet season. Results are from single variable models; no variables were significant in the multivariate models. For variable definitions see the methods

Variable	**PE**	**AIC**	*P*
pH	0.19	90.1	0.72
Elevation	0.085	36.48	0.39
Conductivity	-0.004	86.66	0.08
Area	-0.0003	85.15	0.04*
Water depth	-0.002	92.07	0.70
Plant cover	-0.02	22.83	0.46
Fauna diversity	-0.11	21.93	0.89
Flora Richness	0.15	23.11	0.59
Plant biomass	9.95	21.93	0.25

*PE = parameter estimate

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Table 2.2. Logistic regression results describing the presence of lungfish in the dry season. Results are from single variable models; no variables were significant in the multivariate models. For variable definitions, see the methods

Variables	PE	AIC	*P*
pH	0.72	90.1	0.31
Elevation	0.08	49.21	0.11
Conductivity	-0.001	49.76	0.70
Area	-0.00007	50.19	0.73
Water depth	0.002	51.08	0.80
Plant cover	0.01	19.81	0.38
Fauna diversity	1.09	18.38	0.41
Flora Richness	0.96	18.47	0.09
Plant biomass	-1.09	19.15	0.91

*PE = parameter estimate

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Figure 1. *Protopterus annectens*.

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Study area
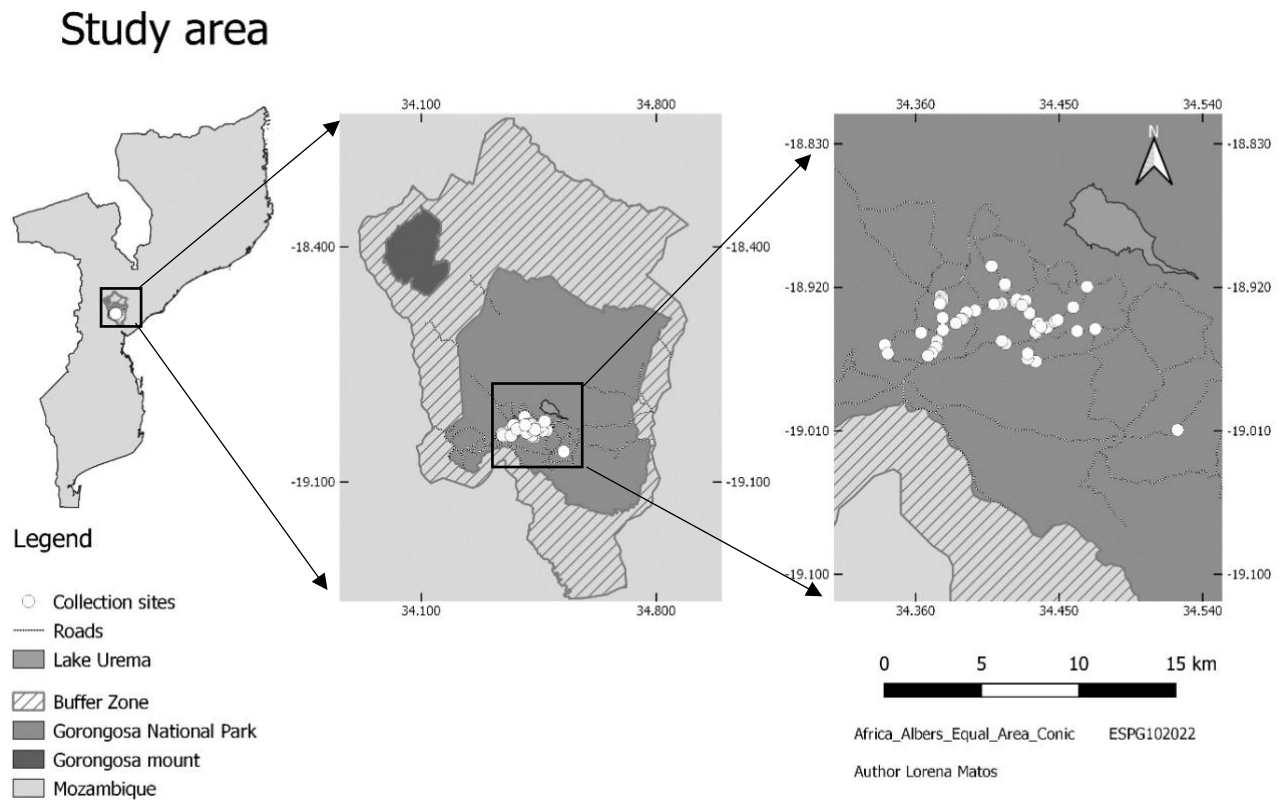
Figure 2. Map showing the location of the Gorongosa National Park in Mozambique (left) and the collections site (right).
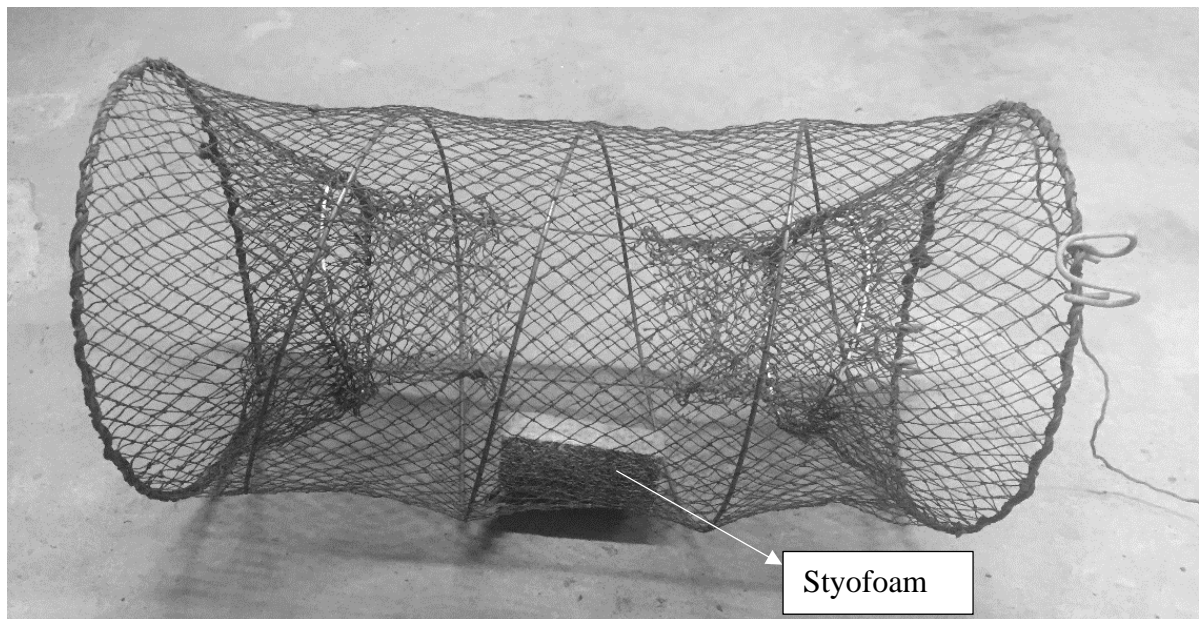
Figure 3.The fish funnel traps to assess the presence/absence of *Protopterus annectens*, with styrofoam inside to prevent fish from drowning.

Figure 4. Realization of the metal box method, during the collections of specimens of fauna and flora in the pans with and without *Protopterus annectes*.
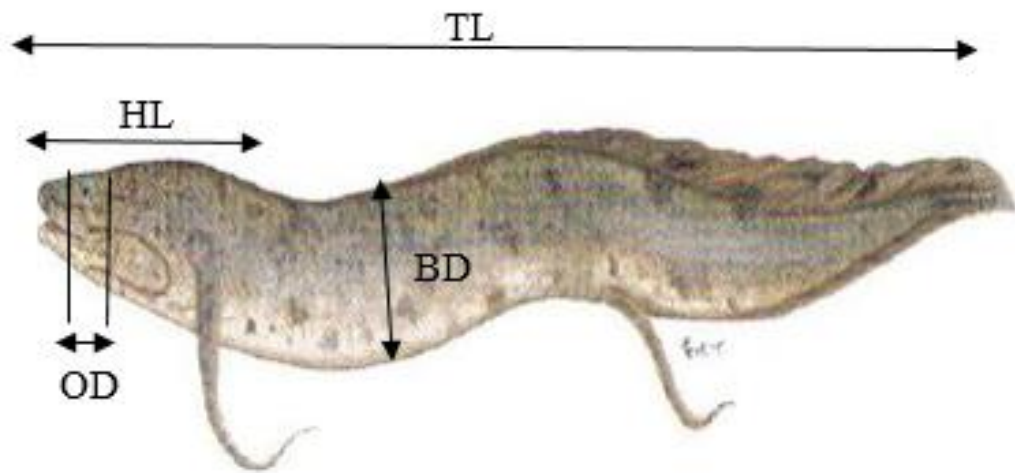
Figure 5. The morphometric measurements that are taken from *Protopterus annectens* to assist in the identification (image copied from Skelton 2001 and measures added by Lorena Matos).

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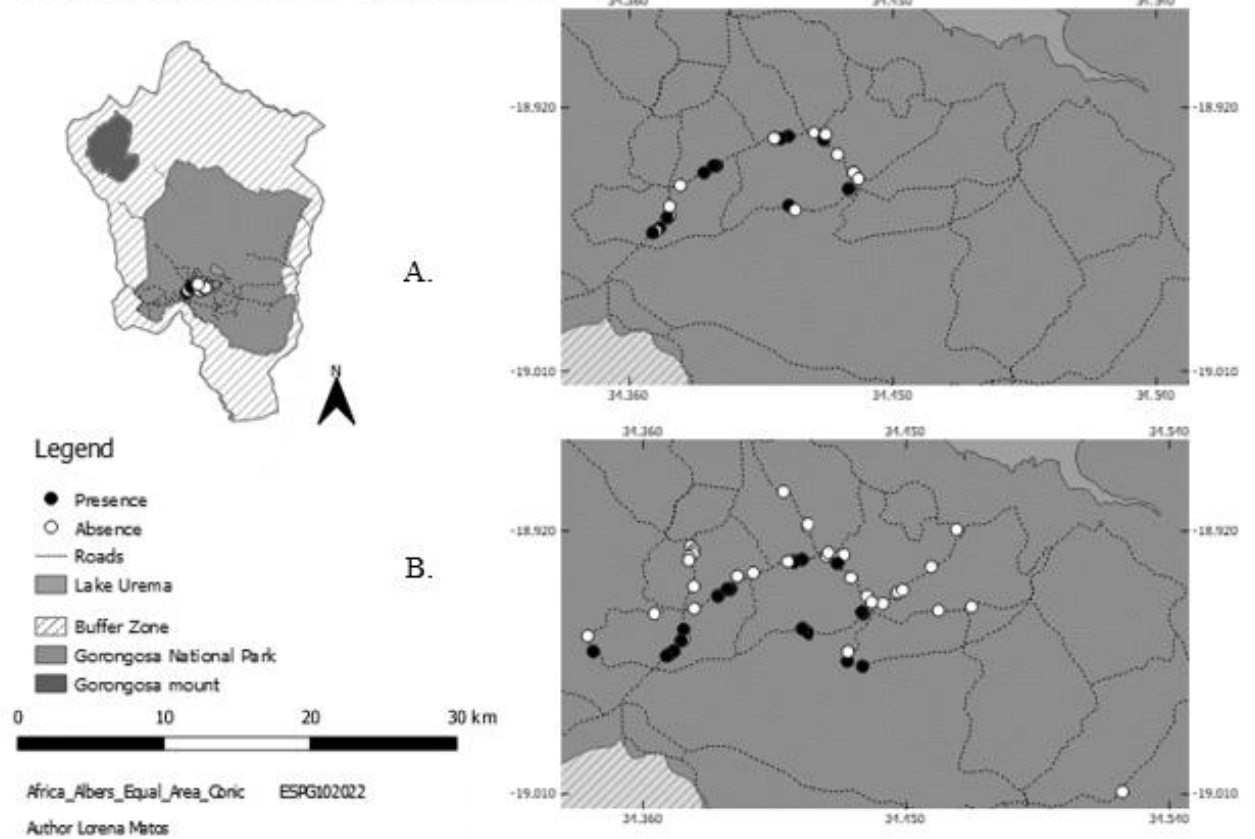
Figure 6. Map of lungfish, *Protopterus annectens*, occurrences in Gorongosa National Park during the wet (A) and dry season (B).

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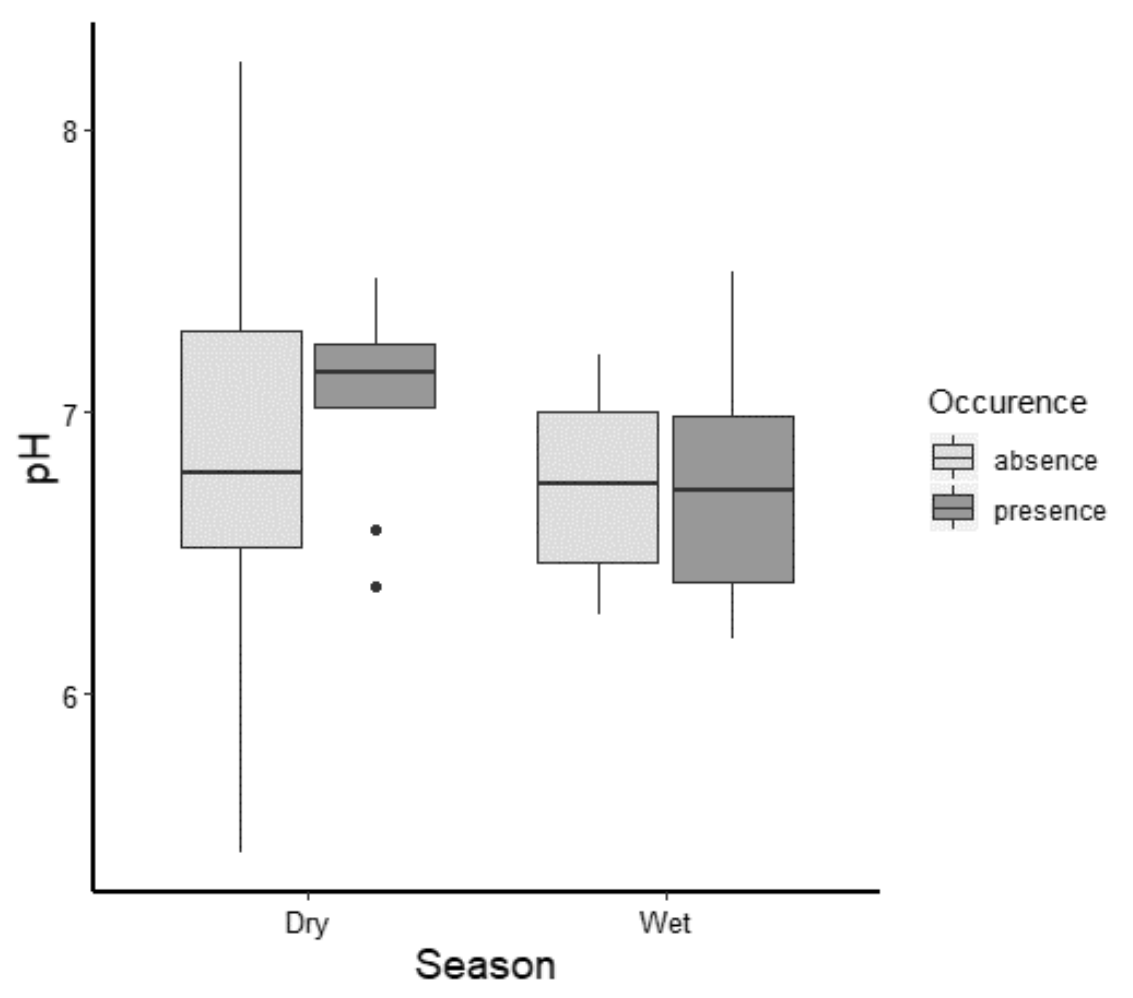
Figure 7. The pH values in the wet and dry seasons, in pans with and without *Protopterus annectens*. The values were not statistically significantly different, neither between seasons, nor between pans with and without lungfish.
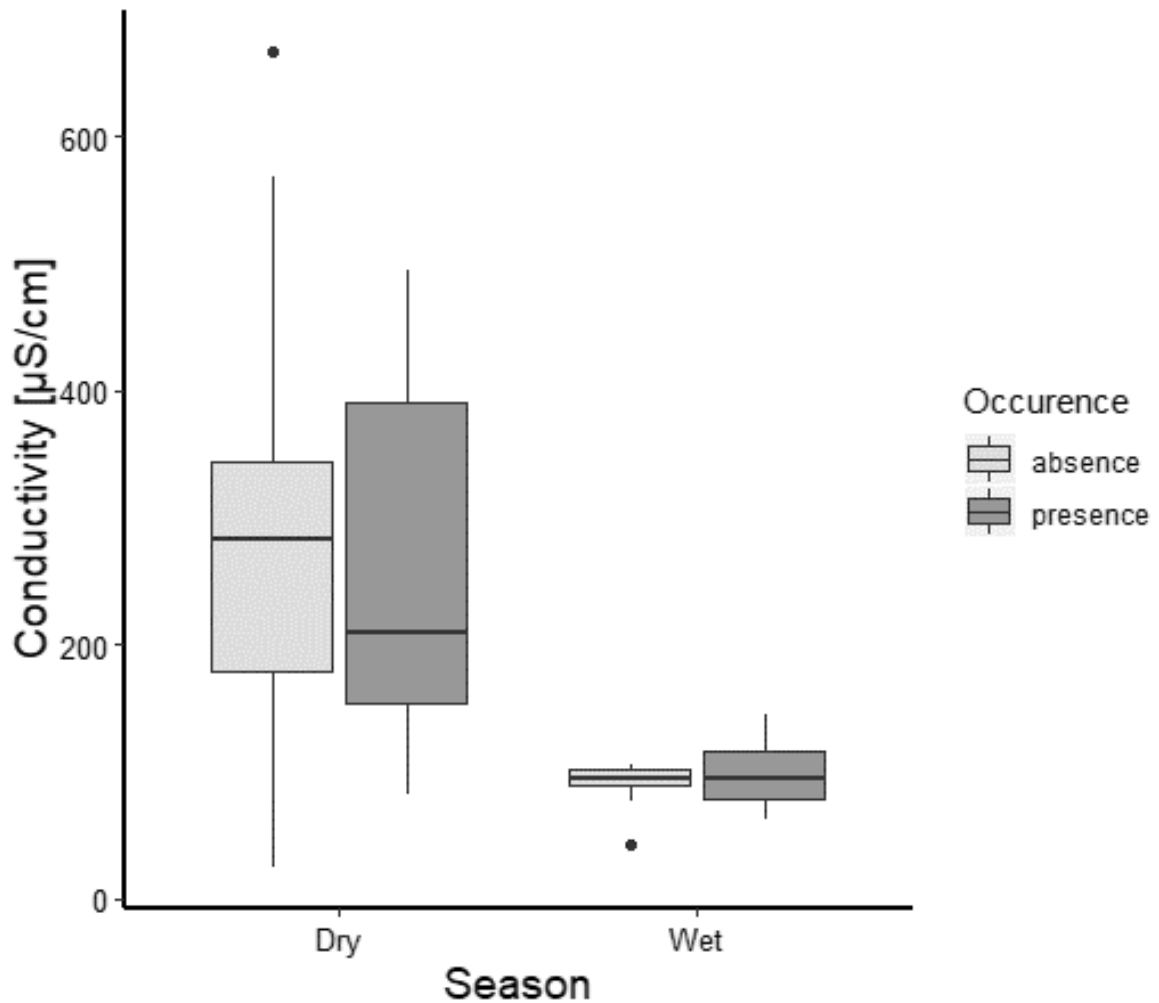
Figure 8. The water conductivity in pans during the wet and dry season with (presence) or without (absence) *Protopterus annectens*. Although the conductivity ranges were much smaller in the wet season, the differences between seasons and between pans with and without lungfish were not statistically different.
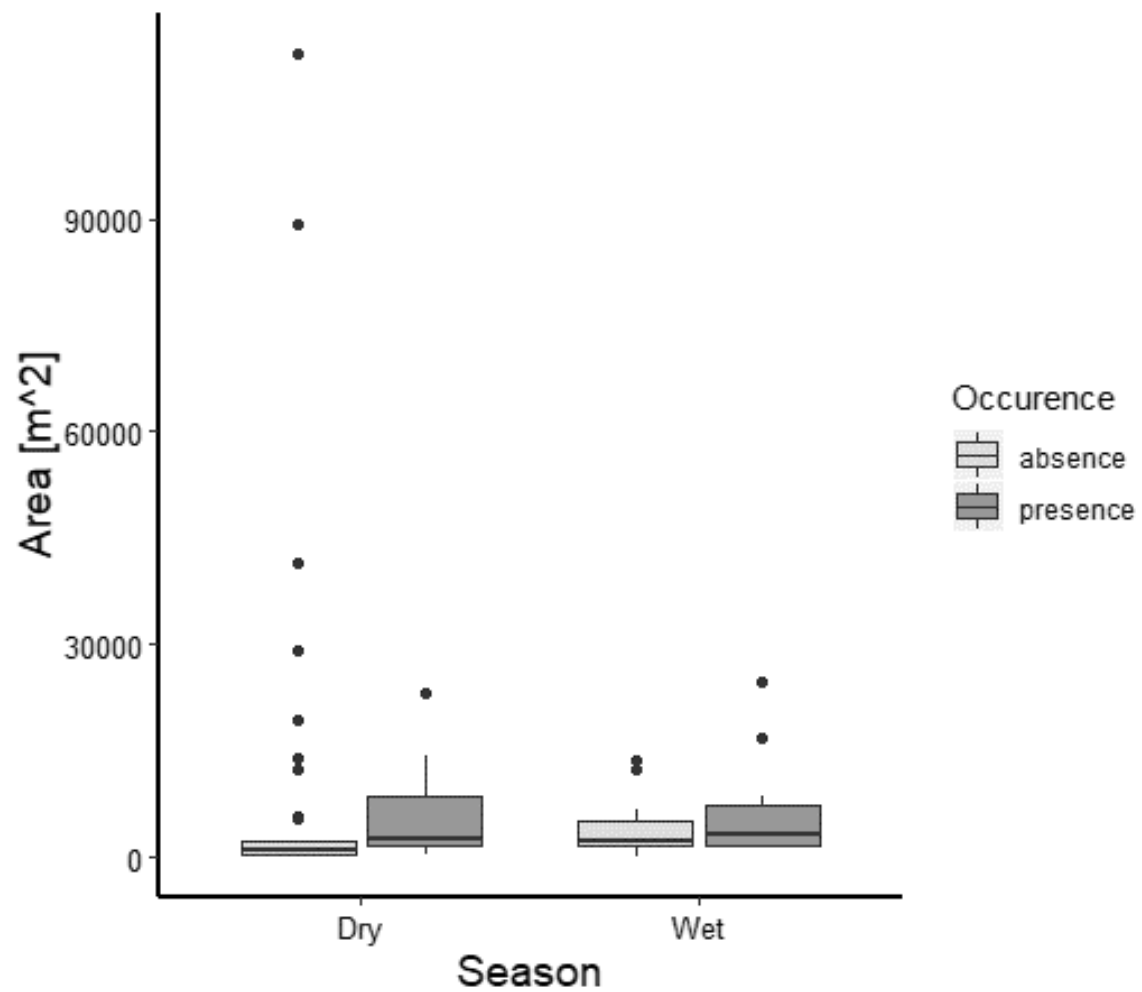
Figure 9. The surface area of the pans during the wet and dry seasons with (presence) and without (absence) *Protopterus annectens*. The differences of pan size were similar between seasons and within seasons.

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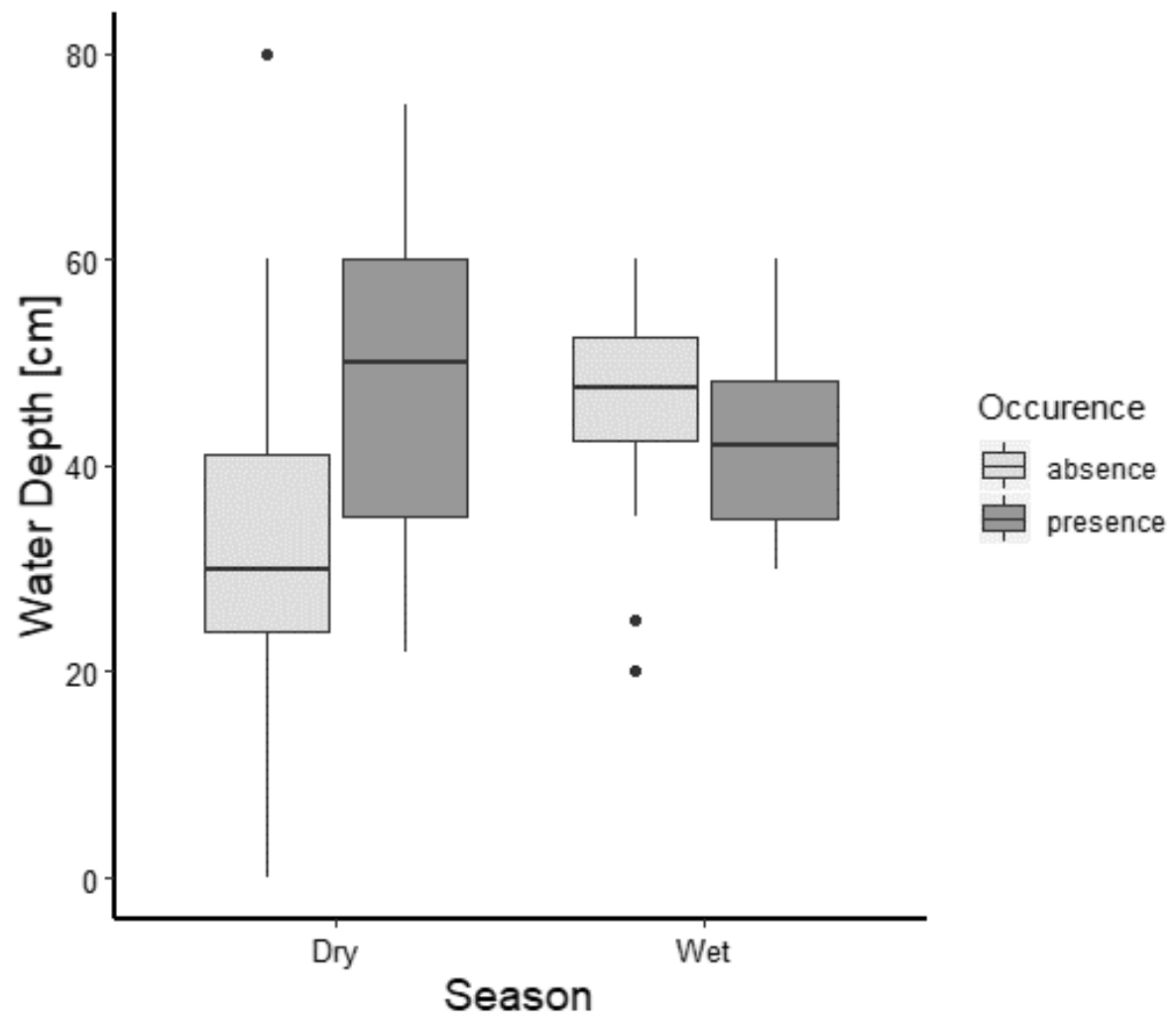
Figure 10. The water depth in pans during the wet and dry seasons with (presence) or without (absence) *Protopterus annectens*. The range of water depth was lower in the wet season. Differences were not statistically significant.

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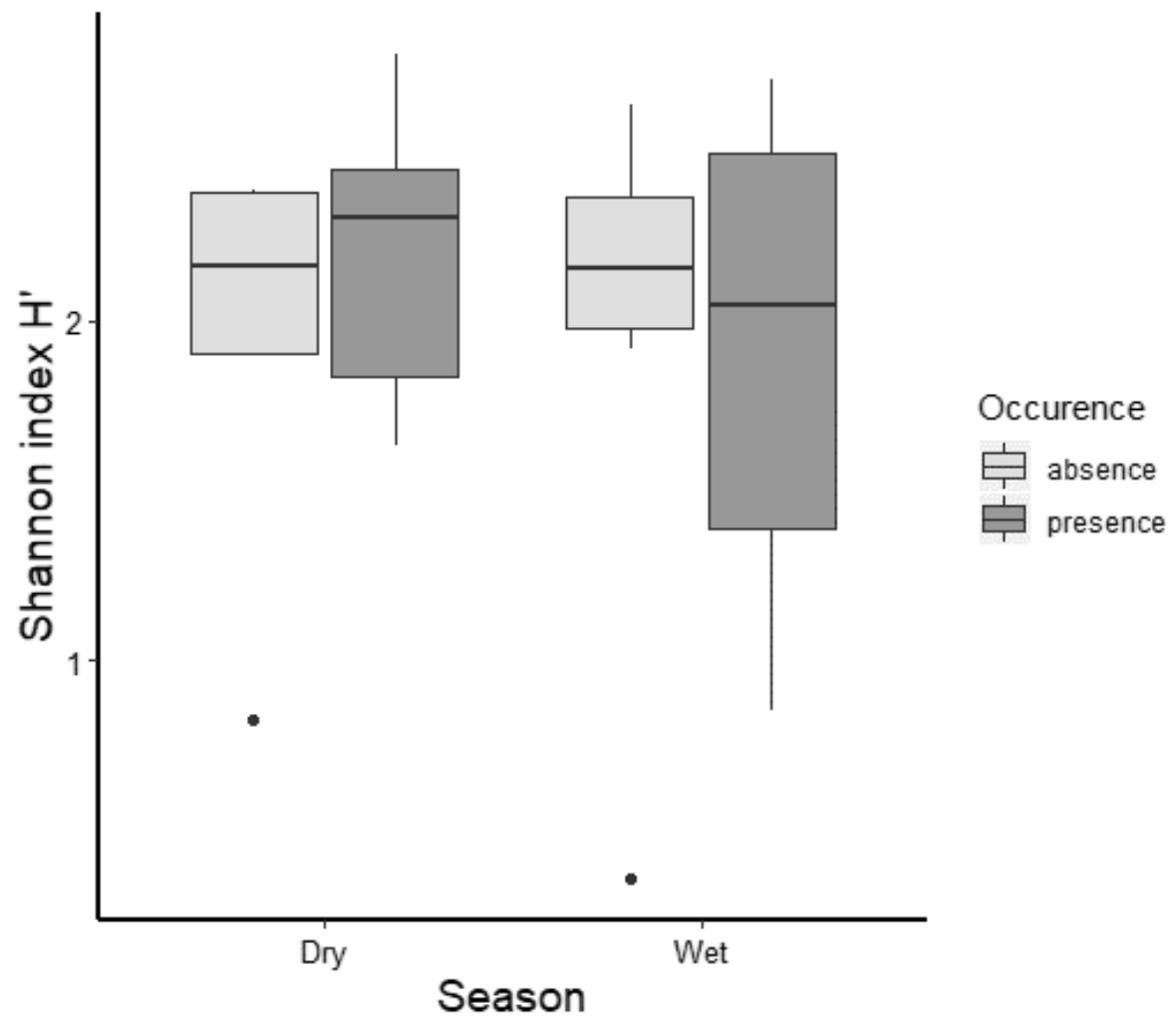
Figure 11. The Shannon diversity for fauna in pans during the wet and dry season, with (presence) or without (absence) *Protopterus annectens*. There were no significant differences in the faunal diversity.

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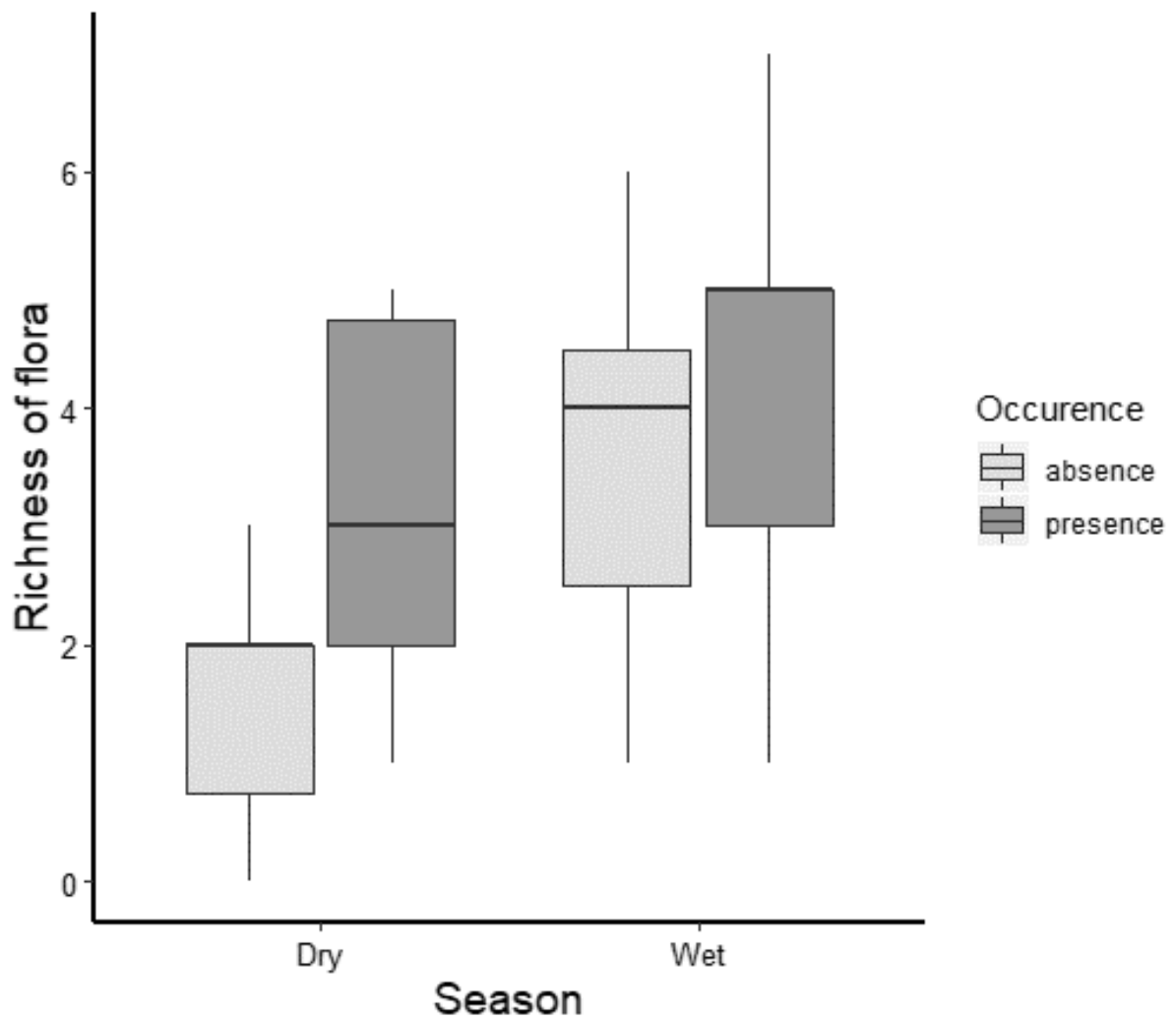
Figure 12. Floral species richness in pans during the wet and dry season, with (presence) or without (absence) *Protopterus annectens*. There were no significant differences in the in flora species richness.
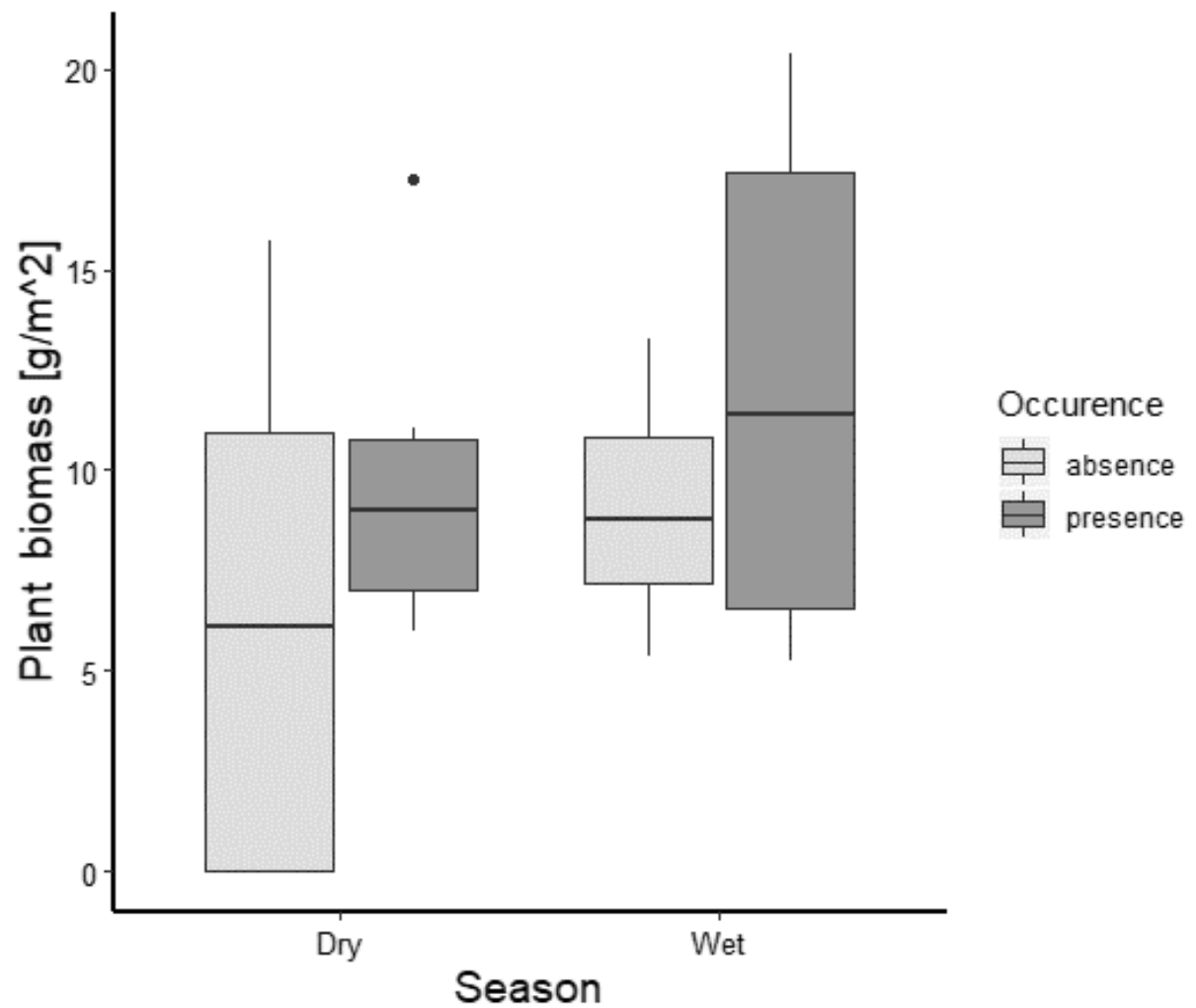
Figure 13. Plant average biomass variation in pans during the wet and dry season, with (presence) or without (absence) *Protopterus annectens*. There were no significant differences in the plant biomass.
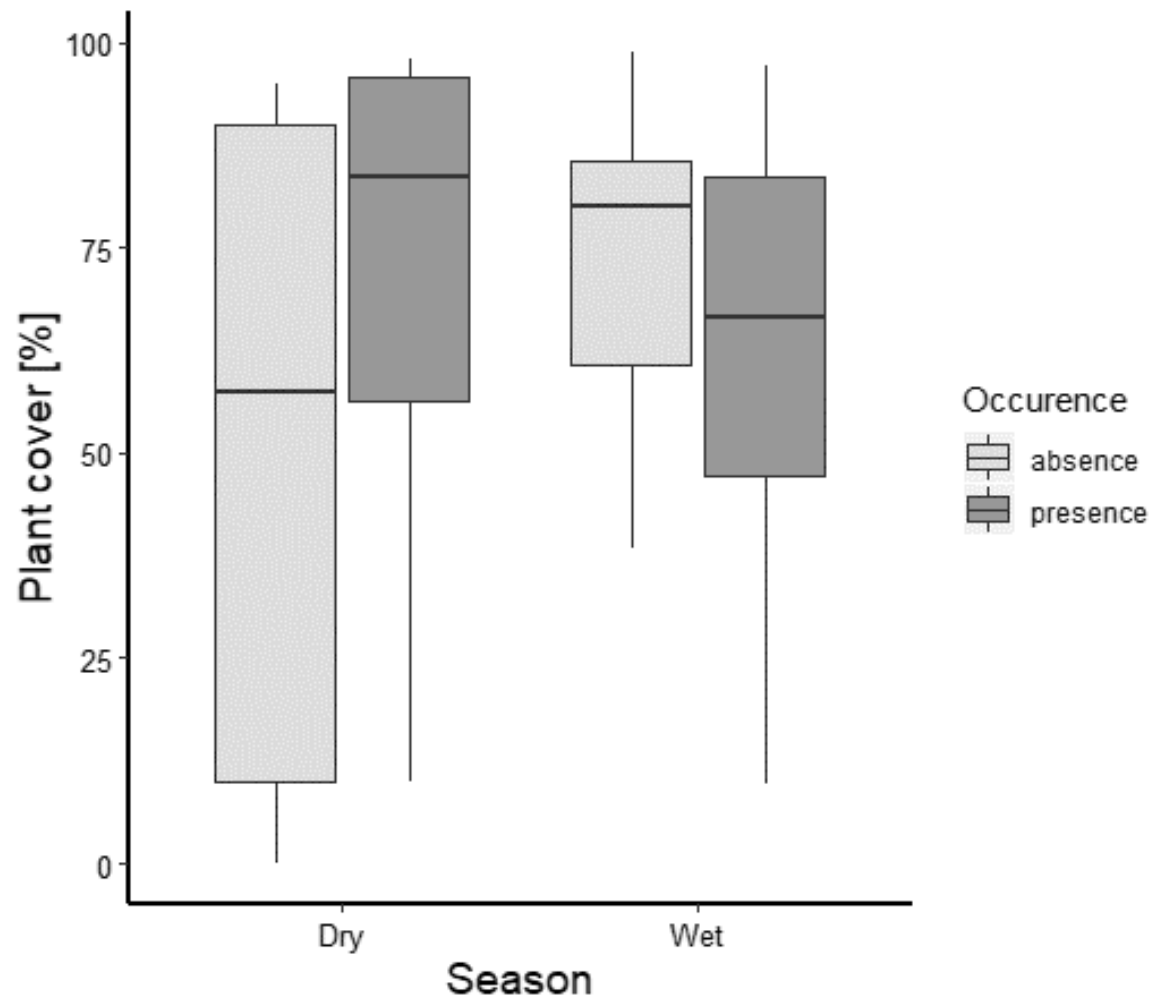
Figure 14. Plant cover in percentage in the wet and dry seasons in pans with and without

Protopterus annectens. The median within season and between occurrences of

Protopterus annectens different, however the differences were not significantly.

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References

1. Abe AS. 1995. Estivation in south american amphibians and reptiles. Brazilian Journal of Medical and Biological Research **28**:1241–1247.

2. Acevedo P, Jiménez-valverde A, Aragón P, Niamir A. 2016. New developments in the study of species distribution. Current Trends in Wildlife Research **1**:151–175.

3. Adeyemi SO. 2010. Food and feeding habits of *Protopterus annectens* (Owen) (lungfish) at Idah area of River Niger, Nigeria. African Journal Online **6**:69–74.

4. Ahmadi-Nedushan B, St-Hilaire A, Bérubé M, Robichaud É, Thiémonge N, Bobée B. 2006. A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. River Research and Applications **22**:503–523.

5. Arthington AH. 2009. Australian lungfish , *Neoceratodus forsteri* , threatened by a new dam. Environmental Biology of Fishes. **84:** 211–221.

6. Austin MP. 2002. Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. Ecological Modelling **157**:101–118.

7. Begon M, Harper JL, Townsend CR. 1996. Ecology, individuals, populations and communities, 3rd editio. Blackwell Science, London.

8. Berezina NA. 2003. Tolerance of freshwater invertebrates to changes in water salinity. Russian Journal of Ecology **34**:261–266.

9. Böhme B. 2005. Geo-ecology of the Lake Urema, central Mozambique. Freiberg Online Geology **14**:112. Available from http://www.geo.tu-freiberg.de/fog/FOG_Vol_28.pdf.

10. Brown JH. 1984. On the relationship between abundance and distribution of

species. American Naturalist **124**: 255–279.

11. Brownt JS, Rosenzweig ML. 1986. Habitat selection in slowly regenerating environments isoleg analysis. Jornal of Theoric Biology **123**:151–171.

12. Budgett JS. 1901. On the breeding-habits of some West-African fishes, with an account of the external features in development of *Protopterus annectens*, and a description of the larva of *Polypterus lapradei*. Transactions of the Zoological Society of London. **16**:115–136.

13. Capra H, Plichard L, Bergé J, Pella H, Ovidio M, Mcneil E, Lamouroux N. 2016. Science of the total environment fish habitat selection in a large hydropeaking river : Strong individual and temporal variations revealed by telemetry. Science of the Total Environment. Elsevier B.V. Available from http://dx.doi.org/10.1016/j.scitotenv.2016.10.155.

14. Chen I. 2012. Rapid range shifts of species. Science **1024**:17–20.

15. Christensen CB, Christensen-dalsgaard J, Madsen PT. 2015. Hearing of the African lungfish (*Protopterus annectens*) suggests underwater pressure detection and rudimentary aerial hearing in early tetrapods. Experimental Biology **218**:381–387.

16. Connel JH. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle. Ecological Society of Ecology **42**:710–723.

17. Crisci J V. 2018. The voice of historical biogeography the voice of historical biogeography. Journal of Biogeography **28**:157–168.

18. Crisp MD, Trewick SA, Cook LG. 2011. Hypothesis testing in biogeography. Treds in Ecology and Evolution **26**:66–72.

19. Darlington PJJ. 1957. Zoogeography: The geographical distribution of animals. Robert E. Krieger Publshing Company, Florida.

20. Daskin JH, Stalmans M, Pringle RM. 2016. Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. Journal of Ecology **104**:79–89.

21. Delaney RG, Lahiri S, Hamilton R, Fishman AP. 1977. Acid-base balance and plasma composition in the aestivating lungfish (*Protopterus*). American Journal Physiology **232**:10–17.

22. Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, Venail P, Villéger S, Mouquet N. 2010. Defining and measuring ecological specialization. Journal of Applied Ecology **47**:15–25.

23. Eldredge N, Cracraft J. 1982. Phylogenetic patterns and the evolutionary process. Method and Theory in Comparative Biology. Geological Magazine, Reviews 103–104.

24. Fretwell SD. 1972. Theory of habitat selection in populations in a seasonal environment. Princeton University Press. Princeton, NJ.

25. Glass ML. 2008. The enigma of aestivation in the African lungfish *Protopterus dolloi* – Commentary on the paper by Perry et al . Science Direct **160**:18–20.

26. Glass ML, Fernandes MS, Soncini R, Glass H, Wasser J. 1997. Effects of dry season dormancy on oxygen uptake, heart rate, and blood pressures in the toad Bufo paracnemis. Experimental Zoology **279**:330–336.

27. Goudswaard KPC, Witte F, Chapman LJ. 2002. Decline of the African lungfish (*Protopterus aethiopicus*) in Lake Victoria (East Africa). African Journal of Ecology **40**:42–52.

28. Greenwood PH. 1986. The natural history of African ungfishes. Morphology Supplement **1**:163–179.

29. Guianuca AT. 2012. Análise de gradientes ecológicos: distribuição espacial e

regras de montagem das comunidades de aves no litoral sul do Brasil. Postgraduate dissertation.Universidade Federal de Santa Catarina, Florianópolis.

30. Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**:147–186.

31. Guisan A, Lehmann A, Ferrier S, Austin M, Overton JMCC, Aspinall R, Hastie T. 2006. Making better biogeographical predictions of species ' distributions. Journal of Applied Ecology **43**:386–392.

32. Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM. 2013. Predicting species distributions for conservation decisions. Ecology Letters **16**:1424–1435.

33. Hirzel AH, Ausser JH, Hessel DC. 2002. Ecological-Niche factor analysis : How to compute habitat-suitability maps without absence data? **83**:2027–2036.

34. Hirzel AH, Lay GL. 2008. Habitat suitability modelling and niche theory. Applied Ecology **45**:1372–1381.

35. Hoegh-Guldberg O, Hughes L, Mcintyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD. 2008. Assisted Colonization and Rapid. Science **321**:345–347.

36. Hutchinson GE. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology. The founding paper of the population persistence niche concept. **2**:415427.

37. Ibarra JT, Martin K, Drever MC, Vergara G. 2014. Occurrence patterns and niche relationships of sympatric owls in South American temperate forests: A multi-

scale approach. Forest Ecology and Management **331**:281–291.

38. Icardo M, Loong AIM, Colvee E, Wong WAIP. 2012. The alimentary canal of the African lungfish *Protopterus annectens* during aestivation and after arousal. The Anatomical Record **295**:60–72.

39. Johnels AG, Svensson GSO. 1954. On the biology of *Protopterus annectens* (Owen). Arkiv Zoologi **7:** 131–164.

40. Jost L. 2006. Entropy and diversity. Opinion **2**:363–375.

41. Joy MK, Death RG. 2004. Application of the index of biotic integrity methodology to new zealand freshwater fish communities. Environmental Management **34**:415–428.

42. Kemp A. 1987. The biology of the Australian lungfish, *Neoceratodus forsteri*. Journal Of Morphology Supplement **1**:181–198.

43. Khidir ASO. 2006. Morphometric traits, karyotypic features and protein polymorphism of the African lungfish (Um Koro). Master dissertation. University of Khartoum.

44. Kneitel JM. 2019. Gause′s competitive exclusion principle. Page Encyclopedia of Ecology, 2nd edition. Elsevier Inc. Available from http://dx.doi.org/10.1016/B978-0-12-409548-9.00816-2.

45. Kozak KH, Wiens JJ. 2006. Does niche conservatism promote speciation ? a case study in north american salamanders. Evolution **60**:2604–2621.

46. Krebs CJ. 1989. Ecological methodoloy. Harper Collins Publishers, USA.Chichester.

47. Laland KN, Odling-Smee FJ, Feldman MW. 1996. The evolutionary consequences of niche construction: A theoretical investigation using two-locus theory. Journal of Evolutionary Biology **9**:293–316.

48. Lee S. 2007. Application of logistic regression model and its validation for landslide susceptibility mapping using GIS and remote sensing data**.** International Journal of Remote Sensing, **26:**1477-1491.

49. Lévêque C. 1991. Protopteridae. Page 76-78 in C. Lévêque D. Paugy and G.G Teugels, editors. The fresh and brackish water fishes of West Africa. Volume 1. Coll. faune tropicale 28. Institut francais de recherche scientifique pour le développement en coopération, Paris, France, Musée Royal de I'Afrique Centrale, Tervuren, Belgium, 386pp.

50. Levin PS, Fogarty MJ, Murawski SA, Fluharty D. 2009. Integrated ecosystem assessments: Developing the scientific basis for ecosystem-based management of the ocean. PLoS Biology **7:**23-28.

51. Lewis JS, Farnsworth ML, Burdett CL, Theobald DM, Gray M, Miller RS. 2017. Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. Scientific Reports **7**:1–12.

52. Machipane ME. 2010. A Comunidade Ictiológica do Lago Urema, sua Diversidade e Interações Tróficas. Graduate thesis. Universidade Eduardo Mondlane.

53. Mackenzie DI, Royle JA. 2005. Designing occupancy studies : general advice and allocating survey effort. Journal of Applied Ecology **42**:1105–1114.

54. Magurran AE. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton.

55. Marshall CR. 1986. Lungfish: Phylogeny and parsimony. Journal of Morphology **190**:151–162.

56. Massad TJ, Castigo T. 2016. Investigation possible effects of climate change on tree recruitment: responses of abundant species to water stress in Gorongosa

national park. South African Journal of Botany **106**:96–100.

57. Mayor SJ, Schneider DC, Schaefer JA, Mahoney SP. 2009. Habitat selection at multiple scales. Écoscience **16**:238–247.

58. Mcshea WJ. 2014. What are the roles of species distribution models in conservation planning? Environmental Conservation **41**:93–96.

59. Melo TL de, Tejerina-GarroL. F, Melo CE de. 2007. Diversidade biológica da comunidade de peixes no baixo rio das Mortes, Mato Grosso, Brasil. Revista Brasileira de Zoologia **24**:657–665.

60. Mlewa CM, Green JM. 2004. Biology of the marbled lungfish , *Protopterus aethiopicus* Heckel, in Lake Baringo, Kenya. African Journal of Ecology **42**:338–345.

61. Mlewa CM, Green JM, Simms A. 2005. Movement and habitat use by the marbled lungfish *Protopterus aethiopicus* Heckel 1851 in Lake Baringo, Kenya. Hydrobiologia **537**:229–238.

62. Morescalchi MA, Rocco L, Stingo V. 2002. Cytogenetic and molecular studies in a lungfish , Protopterus annectens **295**:279–287.

63. Morrone JJ, Crisci JV. 1995. Historical biogeography: Introduction to methods. Annual Review of Ecology and Systematics **26**:373–401.

64. Nichols R. 2012. Coexistence in ungulate communities: niches, resource partitioning, competition & facilitation. Page Introductory Research Essay 7.

65. Oertli B, Joye DA, Castella E, Cambin D, Lachavanne J. 2002. Does size matter ? The relationship between pond area and biodiversity. Biological Conservation **104**:59–70.

66. Okafor AI. 2011. The habits of the African lungfish , *Protopterus annectens* in laboratory aquaria. Research in Environment and Life Sciences **4**:137–140.

67. Onwude AM, Fran AE. 2018. The morphometric and meristic characteristics of *Protopterus annectens* (Owen, 1839) in river Niger at Agenebode, Edo state, Nigeria. Journal of Fisheries and Aquatic Science **13**: 76-81.

68. Otero O. 2011. Current knowledge and new assumptions on the evolutionary history of the African lungfish , *Protopterus*, based on a review of its fossil record. Fish And Fisheries **12**:235–255

69. Pearman PB, Guisan A, Broennimann O, Randin CF. 2007. Niche dynamics in space and time. Trends in Ecology and Evolution **23:**149-151.

70. Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology & Biogeography **12**:361–371.

71. Peers MJL, Thornton DH, Murray DL. 2012. Reconsidering the specialist-generalist paradigm in niche breadth dynamics : resource gradient selection by canada lynx and bobcat. PLoS ONE **7:**1–10.

72. Perry SF, Euverman R, Wang T, Loong AM, Chew SF, Ip YK, Gilmour KM. 2008. Control of breathing in African lungfish (*Protopterus dolloi*): A comparison of aquatic and cocooned (terrestrialized) animals. Respiratory Physiology & Neurobiology **160**:8–17.

73. PNG. 2016. Plano de Maneio Parque do Nacional da Gorongosa.

74. Roberts TR. 1975. Geographical distribution of African freshwater fishes. Zoological Journal of the Linnean Society **57**:249–319.

75. Rödel M-O, Grözinger F, Pfahler A, Thein J, Glos J. 2009. A simple quantitative method to assess larval amphibians and other aquatic organisms. Zeitschrift für Feldherpetologie **15**: 243–256.

76. Rosenzweig ML. 1987. Habitat selection as a source of biological diversity.

Evolutionary Ecology **1**:315–330.

77. Royle JA, Ke M. 2007. A bayesian state-space formulation of dynamic occupancy models. Ecological Modelling **88**:1813–1823.

78. Sanmartín I. 2012. Historical biogeography : Evolution in time and space. Geographyand Evolution **5**:555–568.

79. Sara JR, Moyo N a G, Smit WJ, Geldenhuys G, Theron J. 2012. An ichthyological and bio-monitoring survey of fish assemblages in the vunduzi river from it source on gorongosa mountain to its lower reaches in the gorongosa national park, moçambique. Aquaculture Research. pp71.

80. Segura C, Feriche M, Pleguezuelos JM, Santos X. 2007. Specialist and generalist species in habitat use: Implications for conservation assessment in snakes. Journal of Natural History **41**:2765–2774.

81. Sinclair ARE, Byrom AE. 2006. Understanding ecosystem dynamics for conservation of biota. Journal of Animal Ecology **75**:64–79.

82. Skelton P. 2001. A complete guide to the freshwater fishes of Southern Africa. New editio. Struik Nature, Cape Town, South Africa.

83. Smith HW. 1931. African lungfish biology. Ecology **12**:164–181.

84. Soberon J, Peterson AT. 2005. Soberon, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics **2**:1–10.

85. Stalmans M, Beilfuss R. 2008. Landscapes of Gorongosa National Park.

86. Tinley KL. 1977. Framework of the Gorongosa ecosystem. Doctoral dissertation. University of Pretoria, S. Africa.

87. Tokita M, Okamoto T, Hikida T. 2005. Evolutionary history of African lungfish: a hypothesis from molecular phylogeny. Molecular Phylogenetic and Evolution

35:281–286.

88. Upchurch P. 1999. Brown JH, Lomolino MV. 1998. Biogeography.Sunderland (Massachusetts): Sinauer Associate; distributed in the UK by Macmillan. Price & pound 35–95 (hard covers). ISBN 0 87893 073 6. Geological Magazine, Book Review **136**:475–478.

89. Vidal ML, Bassères A, Narbonne JF. 2002. Influence of temperature, pH, oxygenation, water-type and substrate on biomarker responses in the freshwater clam *Corbicula fluminea* (Müller). Comparative Biochemistry and Physiology. Toxicology and Pharmacology **132**:93–104.

90. Walakira JK, Molnar JJ, Phelps R, Terhune J. 2014. Culturing the African lungfish in Uganda : Effects of exogenous fish feed on growth performance in tanks Uganda. Journal of Agricultural Sciences **15**:137–155.

91. Wiens JJ, Graham CH. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics **36**:519–539.

92. Williams YM, Williams SE, Alford RA, Waycott M, Johnson CN. 2006. Niche breadth and geographical range: ecological compensation for geographical rarity in rainforest frogs. Biology Letters **2**:532–535.

93. Yokobori S, Hasegawa M, Ueda T, Okada N, Nishikawa K, Watanabe K. 1994. Relationship among coelacanths, lungfishes and tetrapods: a phylogenetic analysis based on mitochondrial cytochrome oxidase I gene sequences. Molecular Evolution **38**:602–609.

94. Yu Y, Harris AJ, He X. 2010. S-DIVA (Statistical Dispersal-Vicariance Analysis): A tool for inferring biogeographic histories. Molecular Phylogenetics and Evolution **56**:848–850. Elsevier Inc. Available from

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Appendix

Appendix 1. Table of species of potential prey found in pans with (presence- **p**) and without (absence- **a**) *Protopterus annectens* during the wet season. Species that occur in most pans are bolded.

Classe	Ordem	Familia	Genera	Species	Life	Pans															Nr. of pan occurred
						1a	3p	4a	5p	7p	9a	10a	11a	12p	13p	14p	15p	16p	17p	
Insecta	**Hemiptera**	**Notonectidae**	**Anisops**	**sp.**	**adult**	24	0	456	2	20	2	1	5	10	2	10	7	21	17	12
	Coleoptera	Hydrophilidae		sp. 1	larvae	3	0	2	0	0	1	0	0	0	0	0	0	2	1	5
	Odonata (Zygoptera)	**Coenagrionidae**		**sp.**	**nymphs**	5	0	0	3	0	1	16	2	31	4	7	4	2	4	11
	Odonata (Anisoptera)	Libelullidae		sp. 1	nymphs	6	0	0	0	0	5	1	0	0	0	0	4	1	0	5
	Coleoptera	**Noteridae**		**sp. 2**	**larvae**	26	0	4	0	1	0	5	9	0	3	3	9	0	3	9
	Coleoptera	Hydrophilidae	Allocotocerus	sp.	adult	1	0	0	0	0	0	0	2	23	1	0	1	1	0	6
	Coleoptera	**Hydrophilidae**	**Amphiops**	**sp.**	**adult**	1	0	0	1	0	2	0	20	31	4	3	16	7	20	10
	Coleoptera	**Noteridae**		**sp. 3**	**nymphs**	1	0	0	0	0	0	1	0	3	3	0	10	1	3	7
	Coleoptera	Elmidae	Elpidelmis	sp.	adult	3	0	0	0	0	0	0	0	0	0	0	1	1	4	4
	Coleoptera	Hydrophilidae		sp. 1	larvae	1	0	0	1	0	0	0	0	0	0	0	0	0	0	2
	Coleoptera	**Dytiscidae**	**Hyphydrus**	**sp.**	**adult**	1	0	0	1	0	1	0	0	0	1	0	4	2	2	7
	Coleoptera	Haliplidae	Haliplus	sp.	adult	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	Diptera	Chironomidae		sp.	larvae	2	2	0	0	0	0	0	0	0	0	0	0	1	407	4
	Ephemeroptera	Baetidae	Cheleocloeon	sp.	nymphs	1	0	0	0	0	0	0	0	0	0	0	9	0	0	2

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Diptera	Chironomidae		sp. 1	larvae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Diptera	Culicidae		sp.	larvae	0	1	0	0	1	0	0	0	0	0	0	1	0	0	3
Cyprinodontiformes	Nothobranchiidae	Nothobranchius	sp.	adult	0	0	1	0	0	0	1	0	0	0	0	0	0	0	2
Coleoptera	Dytiscidae		sp. 1	larvae	0	0	1	0	1	0	0	0	10	2	0	5	0	0	5
Hemiptera	Mesoveliidae	Mesovelia	sp.	adult	0	0	3	0	0	1	0	1	0	0	1	0	0	0	4
Hemiptera	Micronectidae	Micronecta	sp.	adult	0	0	2	0	0	0	0	0	0	0	0	0	0	1	2
Coleoptera	Elmidae	Elpidelmis	sp. 2	adult	0	0	2	0	0	2	0	0	0	0	0	0	0	1	3
Anisoptera	Libellulidae		sp. 3	larvae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Anisoptera	Libellulidae		sp. 2	larvae	0	0	0	0	2	0	1	0	20	0	1	0	0	0	3
Coleoptera	Noteridae		sp. 3	larvae	0	0	0	3	1	0	0	0	0	0	0	0	0	0	2
Coleoptera	Dytiscidae		sp.	larvae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Coleoptera	Histeroidea		sp.	larvae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Coleoptera	Dytiscidae	Cybister	Sp	adult	0	0	0	1	0	3	0	0	4	0	0	0	0	0	3
Hemiptera	**Pleidae**	**Plea**	**sp.**	**adult**	**0**	**0**	**0**	**2**	**0**	**10**	**4**	**0**	**0**	**4**	**4**	**0**	**1**	**5**	**7**
Coleoptera	Curculionidae	Cyrtobagous	sp.	adult	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Hemiptera	Naucoridae	Naucoris	sp.	adult	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1
Odonata (Zygoptera)	cf. Synlestidae		sp.	nymphs	0	0	0	0	0	2	0	0	0	0	0	0	2	0	2
Hemiptera	**Belostomatidae**	**Appasus**	**sp.**	**adult**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**2**	**15**	**1**	**0**	**1**	**6**	**1**	**7**
Hemiptera	Nepidae	Ranatra	sp.	adult	0	0	0	0	0	1	0	0	0	0	1	0	0	1	3
Anisoptera	Libellulidae	Orthetrum	sp.	adult	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2
Coleoptera	Dytiscidae	Rhantus	sp.	adult	0	0	0	0	0	0	4	0	4	0	0	3	1	3	5
Ephemeroptera	Baetidae	Cheleocloeon	sp.	adult	0	0	0	0	0	0	0	4	0	0	0	0	0	0	1
Coleoptera	Elmidae		sp.	larvae	0	0	0	0	0	0	0	1	0	5	0	1	1	1	5
Coleoptera	Hydrophilidae	Regimbartia	sp.	adult	0	0	0	0	0	0	0	0	14	0	0	30	0	6	3
Hemiptera	Belostomatidae	Lethocerus	sp.	adult	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Diptera	Ceratopogonidae	Palpomyia	sp.	adult	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Coleoptera	Curculionidae		sp.	larvae	0	0	0	0	0	0	0	0	0	1	0	0	0	1	2

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Group	Order	Family	Genus	Species	Stage															
	Ephemeroptera	Baetidae	Afroptilum	sp.	nymphs	0	0	0	0	0	0	0	0	0	1	0	0	6	2	3
	Coleoptera	Dytiscidae		sp. 5	larvae	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
	Coleoptera	Dytiscidae		sp. 1	larvae	0	0	0	0	0	0	0	0	0	0	2	0	1	0	2
	Coleoptera	Dytiscidae		sp. 6	larvae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
	Diptera	Culicidae	Culex	sp.	larvae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
	Coleoptera	Chrysomelidae		sp. 2	larvae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
	Zygoptera	Lestidae		sp.	larvae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
	Coleoptera	Elmidae		sp.2	larvae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
	Diptera	Tipulidae		sp.	larvae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	Hemiptera	Belostomatidae		sp.	larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1
	Coleoptera	Hydrophilidae		sp. 2	larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	Coleoptera	Hydrophiloidea		sp. 1	larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	Diptera	Tipulidae		sp.	larvae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Gastropoda	Basommatophora	Planorbidae	Bulinus	cf. forskalii	adult	1	0	0	0	2	0	33	0	0	0	0	0	0	1	4
	Basommatophora	Planorbidae	Bulinus	sp.	adult	0	0	0	0	0	0	1	0	3	0	0	3	0	5	3
	Architaenioglossa	**Ampullariidae**	**Lanistes**	**ovum**	**adult**	**1**	**1**	**3**	**3**	**2**	**1**	**2**	**2**	**5**	**1**	**0**	**0**	**0**	**0**	**9**
Crustaceans	Decapoda	Potamonautidae	Potamonautes	sp.	adult	0	0	1	1	0	0	0	0	0	0	0	3	0	0	2
Branchiopoda	Cladocera	Daphnidae	Daphnia	sp.	adult	0	0	0	0	1	0	0	0	0	0	1	3	0	0	3
Ostracoda	Podocopida	Cyprididae	Megalocypris	sp.	adult	0	0	0	0	1	3	5	0	0	0	0	1	0	0	4
	Anura	Phrynobatrachidae	Phrynobatrachus	sp.	larvae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	Anura	Hyperoliidae	Hyperolius	marmoratus	larvae	0	0	0	0	0	17	0	0	0	0	0	29	2	0	3
	Anura	Hyperoliidae	Hyperolius	sp.	larvae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Amphibia	Anura	Hyperoliidae	Semnodactylus	sp.	larvae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	Anura	Hyperoliidae	Afrixalus	sp.	larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	Anura	Hyperoliidae	Hyperolius	sp. 1	larvae	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1
	Anura	Hyperoliidae	Hyperolius	sp. 2	larvae	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1
Osteichthyes	Cichliformes	Cichlidae	Tilapia	sp.	jovenile	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1

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	Cyprinodontiformes	Nothobranchiidae	Nothobranchius	kuhntae	adult	0	0	0	0	2	0	0	0	4	0	0	0	0	0	2
	Cyprinodontiformes	Nothobranchiidae	Nothobranchius	orthonotus	adult	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1
	Silurifor	Clariidae	Clarias	sp.	jovenile	9	23	8	2	0	0	0	0	0	0	0	0	0	0	4
Branchiopoda	Conchostraca	Leptestheriidae	Leptestheria	sp.	adult	0	0	0	0	0	1	4	0	0	0	0	4	11	2	5
Arachnida	Acarina (Hydracarina)			sp.	adult	0	0	0	0	0	3	0	0	0	0	0	0		0	1
Nematoda	Gordioidea	Chordodidae	Paragordius	sp.	adult	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Oligochaeta	Oligochaeta	Naididae	Tubifex	sp.	adult	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Reptilia	Testudines	Pelomedusidae	Pelusios	sp.	jovenile	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2

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Appendix 2. Table of species of potential prey found in pans with (presence- **p**) and without (absence- **a**) *Protopterus annectens* during the dry season. Species are listed in descending order, with the most abundant first.

Classe	Ordem	Family	Genus	Specie	Specie	1a	4a	5p	7p	10a	11a	12p	14p	15p	16p	17p	Nr. of pan occurred
	Anura	Hyperoliidae	Hyperolius	marmoratus	larvae	0	3	0	0	0	0	0	0	3	0	0	2
	Anura	Hyperoliidae	Hyperolius	sp.	larvae	0	1	0	0	0	0	1	0	0	0	0	2
	Anura	Hyperoliidae	Hyperolius	sp. 2	larvae	0	1	0	0	0	0	0	0	0	0	1	2
	Anura	Hyperoliidae	Hyperolius	sp. 1	larvae	0	1	0	0	0	0	0	0	0	0	1	2
Classe	Anura	Hyperoliidae	Semnodactylus	sp.	larvae	2	1	0	0	0	0	0	0	0	0	0	2
Arachnida	Acarina (Hydracarina)			sp.	adult	0	1	0	0	2	0	0	0	0	0	0	2
	Acarina (Hydracarina)	Sperchonidae	cf. Sperchon	sp.	adult	0	2	0	0	0	0	1	1	0	0	0	3
Branchiopoda	Conchostraca	Leptestheriidae	Leptestheria	sp.	adult	11	3	0	0	0	0	0	0	0	0	1	3
Hirudinea	Rhynchobdellida	Glossiphoniidae	Marsupiobdella	sp.	adult	0	1	0	0	0	0	0	1	0	0	0	2
	Rhynchobdellida	Glossiphoniidae	Marsupiobdella	africana	adult	0	1	0	0	0	1	0	0	0	0	0	2
Gastropods	Basommatophora	Planorbidae	Bulinus	cf. forskalii	adult	18	2	0	0	0	0	0	2	0	0	0	3
	Architaenioglossa	Ampullariidae	Lanistes	ovum	adult	2	2	0	0	0	0	0	0	1	0	0	3
	Basommatophora	Planorbidae	Bulinus	sp.	adult	4	3	1	0	0	0	1	0	0	0	0	4
	Basommatophora	Planorbidae	Gyraulus	sp.	adult	1	3	0	0	0	0	0	1	0	0	0	3
	Basommatophora	Planorbidae	Ceratophallus	sp.	adult	0	1	0	0	0	2	0	0	0	0	0	2
	Basommatophora	Planorbidae		sp.	adult	0	1	0	0	0	0	1	0	0	0	0	2
	Littorinimorpha	Pomatiopsidae		sp.	adult	0	1	0	0	0	0	1	0	0	0	0	2
Insecta	Hemiptera	Notonectidae		sp. 1	nymph	0	2	0	0	5	0	0	0	0	0	3	1
	Hemiptera	**Notonectidae**	**Anisops**	**sp.**	**adult**	**42**	**9**	**6**	**1**	**37**	**2**	**11**	**43**	**0**	**6**	**0**	**9**
	Hemiptera	Naucoridae	Laccocoris	sp.	adult	0	3	0	3	0	0	19	0	0	0	1	4
	Hemiptera	Naucoridae	Neomacrocoris	sp.	adult	0	2	0	1	5	0	0	0	0	0	0	3

Coleoptera	**Hydrophilidae**		**sp. 2**	**larvae**	0	6	5	0	7	0	2	9	0	2	3	**7**
Odonata (Zygoptera)	Coenagrionidae		sp. 1	larvae	0	5	1	21	0	8	16	0	0	0	1	**6**
Odonata (Zygoptera)	Coenagrionidae		sp.	larvae	28	3	0	0	0	0	35	0	0	11	0	4
Odonata (Anisoptera)	Libellulidae	Orthetrum	chrysostigma	larvae	0	1	0	0	0	0	0	0	0	0	0	1
Odonata (Anisoptera)	Libellulidae		sp. 3	larvae	4	1	0	0	0	0	0	0	0	0	0	5
Odonata (Anisoptera)	Libelullidae		sp. 1	larvae	3	3	0	0	21	0	0	0	0	14	0	4
Coleoptera	Noteridae		sp. 2	larvae	32	4	0	0	0	4	46	0	0	0	0	4
Coleoptera	Hydrophilidae	Allocotocerus	sp.	adult	0	1	0	0	0	34	0	0	0	0	0	2
Coleoptera	**Hydrophilidae**	**Amphiops**	**sp.**	**adult**	19	7	1	0	0	4	11	2	0	3	2	**8**
Coleoptera	Noteridae		sp. 1	adult	0	1	0	0	0	1	0	0	0	0	0	2
Coleoptera	Elminae	Elpidelmis	sp.	adult	0	1	0	0	0	0	0	0	0	0	0	1
Coleoptera	Hydrophilidae		sp. 1	larvae	6	5	1	0	0	0	0	4	0	1	1	6
Coleoptera	Dytiscidae	Hyphydrus	sp. 3	adult	0	1	0	1	0	0	0	0	0	0	0	2
Coleoptera	**Dytiscidae**	**Hyphydrus**	**sp.**	**adult**	0	7	10	0	4	2	4	13	4	6	0	**8**
Diptera	Chironomidae		sp.	larvae	0	5	0	5	14	0	0	0	0	3	1	5
Ephemeroptera	Baetidae	Cheleocloeon	sp.	nymph	0	3	0	5	22	0	2	0	0	0	0	4
Ephemeroptera	Leptophlebiidae	Adenophlebiodes	sp	nymph	0	1	0	1	0	0	0	0	0	0	0	2
Coleoptera	Dytiscidae		sp. 1	larvae	0	3	0	0	12	1	0	0	0	0	3	4
Hemiptera	Mesoveliidae	Mesovelia	sp.	adult	7	1	0	0	0	0	0	0	0	0	0	2
Hemiptera	Micronectidae	Micronecta	sp.	adult	0	3	0	2	0	0	1	8	0	0	0	4
Coleoptera	Noteridae		sp. 3	adult	0	3	0	0	0	1	1	0	0	2	0	4
Cladocera	Daphnidae	Daphnia	sp.	adult	0	1	2	0	0	0	0	0	0	0	0	2
Coleoptera	Dytiscidae	Cybister	sp.	adult	0	2	0	2	0	0	0	0	1	0	0	3
Hemiptera	**Pleidae**	**Plea**	**sp.**	**adult**	82	8	0	6	6	2	13	0	0	3	1	**8**

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					48	6	0	1	4	0	7	0	0	1	1	7
Hemiptera	**Belostomatidae**	**Appasus**	**sp.**	**adult**												
Anisoptera	Libellulidae	Orthetrum	sp.	adult	3	2	0	0	0	0	0	0	0	1	0	6
Coleoptera	Dytiscidae	Rhantus	sp.	adult	1	4	0	0	0	0	1	0	0	6	0	4
Coleoptera	Elmidae		sp.	larvae	2	2	0	0	0	1	0	0	0	0	0	3
Coleoptera	Hydrophiloidea	Regimbartia	sp.	adult	2	4	0	0	0	19	0	0	0	3	2	5
Diptera	Ceratopogonidae	Palpomyia	sp.	adult	0	1	0	0	0	0	0	0	2	0	0	2
Coleoptera	Curculionidae		sp.	larvae	0	1	0	0	1	0	0	0	0	0	0	2
Ephemeroptera	Baetidae	Afroptilum	sp.	nymph	0	3	0	1	7	1	0	0	0	0	0	4
Coleoptera	Dytiscidae		sp. 4	larvae	0	1	0	0	0	0	0	0	0	0	0	1
Coleoptera	Dytiscidae		sp. 2	larvae	2	3	0	0	0	0	0	0	0	0	1	3
Coleoptera	Dytiscidae		sp. 3	larvae	0	2	0	0	0	0	4	0	0	0	0	2
Diptera	Culicidae	Culex	sp.	larvae	0	3	0	0	0	3	6	0	0	7	0	4
Coleoptera	Hydrophiloidea		sp. 1	larvae	0	2	0	0	0	1	17	0	0	0	0	3
Diptera	Tabanidae		sp.	larvae	1	1	0	0	0	0	0	0	0	0	0	2
Coleoptera	Hydrophilidae		sp. 7	larvae	1	1	0	0	0	0	0	0	0	0	0	2
Coleoptera	Hydrophiloidea	Hydrophilus	sp.	adult	0	2	0	0	0	1	0	0	0	0	0	2
Diptera	Ceratopogonidae	Palpomyia	sp.	adult	0	2	0	3	0	0	0	0	0	6	0	3
Coleoptera	Scarabaeidae	Rhyssemus	sp.	adult	0	1	0	0	0	0	0	0	0	0	0	1
Hemiptera	Gerridae	Neogerris	sp.	adult	0	1	0	0	0	0	0	0	0	0	0	1
Coleoptera	Heteroceridae		sp. 1	larvae	0	1	0	0	1	0	0	0	0	0	0	2
Coleoptera	Lampyridae		sp. 1	larvae	0	1	0	0	1	0	0	0	0	0	0	2
Coleoptera			sp. 2	larvae	0	1	0	0	1	0	0	0	0	0	0	2
Hemiptera	Naucoridae	Macrocoris	sp.	adult	0	1	0	0	0	2	0	0	0	0	0	2
Hemiptera	Notonectidae	Enithares	sp.	adult	0	1	0	0	0	1	0	0	0	0	0	2
Anisoptera	Libellulidae		sp. 2	nymph	0	2	0	0	0	6	0	1	0	7	0	4
Coleoptera	Dryopidae		sp. 1	larvae	0	1	0	0	0	0	1	0	0	0	0	2
Hemiptera	Belostomatidae		sp.	nymph	0	1	0	0	0	0	0	1	0	0	0	2
Coleoptera	Hydrophilidae		sp.	larvae	0	2	0	0	0	0	0	1	0	3	0	3

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	Order	Family	Genus	Species	Stage												Total
	Diptera	Muscidae		sp.	larvae	0	1	0	0	0	0	0	1	0	0	0	2
	Coleoptera	Ptilodactylidae		sp.		0	1	0	0	0	0	0	1	0	0	0	2
	Diptera	Tabanidae	cf. Tabanus	sp.	larvae	0	1	0	0	0	0	0	1	0	0	0	2
	Hemiptera	Nepidae	Borborophilus	sp.	adult	0	3	0	0	0	0	0	0	1	1	1	4
	Hemiptera			sp.	nymph	0	1	0	0	0	0	0	0	0	1	0	2
	Coleoptera	Hydrophiloidea	Hydrophilus	cf. senegalensis	larvae	0	1	0	0	0	0	0	0	0	2	0	2
	Coleoptera	Hydrophilidae		sp. 3	larvae	0	1	0	0	0	0	0	0	0	0	12	2
	Zygoptera			sp. 1	nymph	0	1	0	0	0	0	0	0	0	0	20	2
	Diptera	Syrphidae		sp.	larvae	0	1	0	0	0	0	0	0	0	0	1	2
Osteichthyes	Silurifor	Clariidae	Clarias	sp.	adult	1	4	0	2	1	2	0	0	0	0	0	5
	Cichliformes	Cichlidae	Tilapia	sp.	adult	0	2	0	0	0	2	0	2	0	0	0	3
Ostrocoda	Podocopida	Cyprididae	Megalocypris	sp.	adult	0	1	0	0	0	0	0	0	0	0	0	1

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Appendix 3. Diversity of fauna in pans with and without *Protopterus annectens* during the wet and dry season

Pan	1a	3p	4a	5p	7p	9a	10a	11a	12p	13p	14p	15p	16p	17p
H' wet season	2,15	2,55	2,04	1,28	1,81	2,44	2,64	2,28	2,71	2,44	0,96	0,85	0,36	1,92
H' dry season	2,38	0	0,82	1,7	2,16	0	2,38	2,36	2,47	0	1,9	1,63	2,79	2,25
Evenness wet season	0,48	0,39	0,11	0,9	0,45	0,61	0,45	0,61	0,67	0,82	0,7	0,56	0,55	0,1
Evenness dry season	0,75	0	0,3	0,82	0,8	0	0,82	0,75	0,79	0	0,67	0,91	0,9	0,76

*(a) absence of Protopterus annectens and (p) presence of Protopterus annectens

Appendix 4. Jaccard similarity index values of potential prey species in pans with and without lungfish in the wet season

Pans	1ª	3p	4a	5p	7p	9a	10a	11a	12p	13p	14p	15p	16p	17p
1a	1	0,2	0,24	0,32	0,14	0,22	0,25	0,27	0,21	0,30	0,14	0,29	0,34	0,29
3p		1	0,19	0,13	0,11	0,04	0,05	0,07	0,05	0,05	0	0,03	0,04	0,03
4a			1	0,2	0,17	0,17	0,15	0,22	0,11	0,15	0,13	0,11	0,06	0,15
5p				1	0,13	0,28	0,17	0,24	0,22	0,27	0,19	0,12	0,19	0,16
7p					1	0,09	0,23	0,14	0,19	0,14	0,16	0,17	0,03	0,08
9a						1	0,22	0,24	0,19	0,27	0,21	0,23	0,37	0,27
10a							1	0,17	0,26	0,21	0,19	0,26	0,23	0,26
11a								1	0,29	0,42	0,26	0,23	0,24	0,2
12p									1	0,31	0,15	0,29	0,23	0,23
13p										1	0,19	0,33	0,36	0,34
14p											1	0,14	0,17	0,18
15p												1	0,37	0,33
16p													1	0,42
17p														1

*(a) absence of Protopterus annectens and (p) presence of Protopterus annectens

The ecologic niche of the Southern African lungfish *Protopterus annectens* (Owen, 1839) in Gorongosa National Park, Mozambique

Appendix 5. Table of Jaccard similarity index in the dry season with presence and absence of *Protopterus annectens*, of the composition of fauna.

Pans	1a	4a	5p	7p	10a	11a	12p	14p	15p	16p	17p
1a	1	0.13	0.2	0.1	0.17	0.24	0.22	0.29	0.08	0.31	0.12
4a		1	0.08	0.13	0.14	0.14	0.13	0.08	0	0.14	0.08
5p			1	0.13	0.21	0.31	0.38	0.56	0.11	0.42	0.36
7p				1	0.31	0.17	0.29	0.13	0.08	0.11	0.19
10a					1	0.25	0.24	0.21	0.08	0.33	0.29
11a						1	0.4	0.21	0.08	0.25	0.2
12p							1	0.38	0.08	0.4	0.27
14p								1	0.11	0.42	0.25
15p									1	0.08	0
16p										1	0.29
17p											1

*(a) absence of Protopterus annectens and (p) presence of Protopterus annectens

The ecologic niche of the Southern African lungfish *Protopterus annectens* (Owen, 1839) in Gorongosa National Park, Mozambique

Appendix 6. Table of Richness of flora in the wet season with presence and absence of *Protopterus annectens*

Species	Pans														Nr. of pan occurred
	1a	3p	4a	5p	7p	9a	10a	11a	12p	13p	14p	15p	16p	17p	
Cyperus sp. 1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	3
Cyperus sp. 2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2
Grass	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ludwigia adscendens diffusa	1	0	0	1	0	0	0	0	1	1	0	1	1	0	6
Ottelia exserta	1	0	0	1	1	0	1	0	1	1	1	1	0	1	9
Pistia stratiotes	1	0	0	0	0	0	0	0	1	1	1	0	1	1	6
Spirodela polyrrhiza	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Utricularia gibba	1	1	1	1	0	1	1	1	0	1	0	1	1	0	10
Azolla filiculoides	0	0	0	1	1	0	1	0	1	1	1	1	0	0	7
Nymphaea sp.	0	0	0	0	1	0	1	0	0	0	1	0	0	0	3
Marsilea macrocarpa	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2

*(a) absence of Protopterus annectens and (p) presence of Protopterus annectens

The ecologic niche of the Southern African lungfish *Protopterus annectens* (Owen, 1839) in Gorongosa National Park, Mozambique

Appendix 7. Table of Richness of flora in the dry season with presence and absence of *Protopterus annectens*

Species	1a	4p	5p	7p	10a	11p	12p	13p	14p	15p	16p	17p	Nr. of pan occurred
Cyperus **sp. 1**	1	0	0	0	0	0	0	0	0	1	1	1	**4**
Cyperus **sp. 2**	0	0	0	0	0	0	1	1	0	0	0	0	2
Grass	0	0	0	0	0	0	0	0	0	0	0	0	0
Ludwigia adscendens diffusa	0	0	0	0	0	1	1	0	0	0	0	0	2
Ottelia exserta	0	0	1	0	1	1	1	0	0	0	0	0	**4**
Pistia stratiotes	0	0	0	0	0	0	1	1	1	0	1	1	**5**
Spirodela polyrrhiza	1	0	0	0	0	0	0	0	0	0	0	0	1
Utricularia gibba	0	1	1	1	1	1	0	0	0	0	0	0	**5**
Azolla filiculoides	0	0	0	1	0	0	1	1	1	0	0	1	**5**
Nymphaea sp.	0	0	0	0	0	1	0	0	0	0	0	0	1
Marsilea macrocarpa	0	0	0	0	0	1	0	0	0	0	0	1	2

*(a) absence of Protopterus annectens and (p) presence of Protopterus annectens

Appendix 8. Table of Jaccard similarity index in the wet season with presence and absence of *Protopterus annectens*, the composition of flora

Pans	1a	3p	4a	5p	7p	9a	10a	11a	12p	13p	14p	15p	16p	17p
1a	1	0,2	0,2	0,5	0,13	0,2	0,29	0,2	0,43	0,57	0,43	0,67	0,5	0,33
3p		1	1	0,25	0	1	0,25	1	0	0,17	0	0,2	0,25	0
4p			1	0,25	0	1	0,25	1	0	0,17	0	0,2	0,25	0
5p				1	0,33	0,25	0,6	0,25	0,5	0,67	0,29	0,8	0,33	0,17
7p					1	0	0,6	0	0,29	0,25	0,5	0,29	0	0,17
9a						1	0,25	1	0	0,17	0	0,2	0,25	0
10a							1	0,25	0,29	0,43	0,5	0,5	0,14	0,17
11p								1	0	0,17	0	0,2	0,25	0
12p									1	0,83	0,43	0,43	0,29	0,33
13p										1	0,375	0,57	0,43	0,29
14p											1	0,43	0,13	0,33
15p												1	0,29	0,14
16p													1	0,4
17p														1

*(a) absence of Protopterus annectens and (p) presence of Protopterus annectens

The ecologic niche of the Southern African lungfish *Protopterus annectens* (Owen, 1839) in Gorongosa National Park, Mozambique

Appendix 9. Table of Jaccard similarity index in the dry season with presence and absence of *Protopterus annectens*, the composition of flora

Pans	1a	4a	5p	7p	10a	11a	12p	13p	14p	15p	16p	17p
1a	1	0	0	0	0	0	0	0	0	0,5	0,33	0,2
4p		1	0,5	0,5	0,5	0,2	0	0	0	0	0	0
5p				0,33	1	0,4	0,17	0	0	0	0	0
7p				1	0,33	0,17	0,17	0,25	0,33	0	0	0,2
10a					1	0,4	0,17	0	0	0	0	0
11p						1	0,25	0	0	0	0	0,13
12p							1	0,6	0,4	0	0,17	0,29
13p								1	0,67	0	0,25	0,4
14p									1	0	0,33	0,5
15p										1	0,5	0,25
16p											1	0,5
17p												1

*(a) absence of Protopterus annectens and (p) presence of Protopterus annectens

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