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AMBIENTE E DESENVOLVIMENTO

DIVERSITY, DISTRIBUTION AND ECOLOGY OF DRAGONFLIES (ODONATA) FROM THE PAMPA BIOME IN RIO GRANDE DO SUL, BRAZIL

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Lajeado, 2018

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Thesis submitted as part of the requirements for the degree of Doctor on the Environment and Development Postgraduate Program, University of Taquari Valley, Brazil, with the concentration theme Ecology.

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Dedicated to the Odonata conservation.

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Odonata represent one of the most attractive insect groups because their size, color and often conspicuous behavior that make them a popular group for entomologists.

Dragonflies are also positive symbols, as one soldier sent to Angola during the civil war wrote: "A memory that will never fade is watching dragonflies, in their variegated splendour of colour and dazzle, hovering and darting over stagnant pools. They helped me to transport to better things than war. If we found water to fill our canteens and I saw these little creatures, I would always try to get back to the pool later, by myself. And I would find a little piece of heaven."

(Greg Bridges in litt.)

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General Introduction / Contextualization

The Pampa and its landscape

All the biological systems on Earth are, since many years, being impacted by the human population growth. The demands of this fast growing population generates pressure which, in turn, is changing many of the planet's ecosystems, resulting in habitat loss and ecological imbalance. These systems were stable since millions of years. In Brazil this picture is not different and in many aspects it is even worse than the average, given the country's history of occupation/colonization, which yet reflects its actual development levels.

Brazil is gifted with one of the biggest biodiversity of the planet, fact related mostly to its continental dimensions and the biomes existing on it. The Brazilian area is covered by six biomes: Amazon Forest, Atlantic Forest, Cerrado, Caatinga, Pantanal and the Pampa, all remarked by the high species richness, some more fragile than the others (OLIVEIRA et al., 2017).

Amongst the Brazilian biomes is the Pampa, whose name is derived from the indigenous "quéchua", meaning "plain region", being also known as "Southern Fields" (by some authors). In Brazil it represents one of the smallest biomes, covering just 2,07% of the country's territory, and ca. 63% (the southern half) of the area of Rio Grande do Sul state (SANTOS; SILVA, 2011). This biome extends from the 29°S parallel, at its northern limit in the transition from the Atlantic Forest, to the parallel 39°S in its southern limit. It covers the whole Uruguayan territory and good portion of Argentina until it turns again, into to the Patagonian Steppes (OVERBECK et al., 2009).

The Pampa's landscape has ancient origins in transitional ecosystems from the forested to the steppic: actually it is predominantly covered by native grasslands. It is known that the Pampa biome is not a continuum and homogeneous environment, it has several distinctive faces, which are clearly perceptible by the differences in vegetation. ROESCH et al. (2009), in a study based on tree diversity and density, has proposed seven ecoregions for the Pampa:

Savanna, Steppe, Steppic-savanna, Coastal, Transition, Seasonal semi deciduous forest and Seasonal deciduous forest. These different vegetation cover are mostly related to geological processes, which have ruled the evolution of such features.

Its topography is varied from slopes and plains, low mountains and rocky cliffs that favor the occurrence of riparian, gallery and hillside forest formations (MMA, 2016). In general the soils are rocky and sandy, nutrient poor, and very susceptible to erosion. The plain topography favors the occurrence of slow flow rivers and the formation of humid areas, as swamps and bogs in the lower regions (OVERBECK et al., 2009).

If compared to the other Brazilian biomes the Pampa still being one of the less studied and known despite its high levels of biodiversity, fact that makes it more fragile to the anthropogenic impacts (ROESCH et al., 2009). The fauna of the Pampa is still poorly known as the majority of the studies developed in the region are related to its flora: the plant richness is remarkably high, with 2,200 species cataloged, from which 213 are red listed (MMA, 2018). The fauna is diverse, rich in endemic and threatened species, demanding urgent implementation of conservation measures to protect its original areas (OVERBECK et al., 2009).

The human occupation of the Pampa started in the pre-colonial period by indigenous tribes from the "Umbu tradition", which dates back to 10,800 to 10,200 b.C. Later, there was a period of hunting-gathering tribes belonging to the "Tupi-guarani" groups, being those occupations as a continuous migratory flow, until the arrival of the Spanish and Portuguese colonizers (BUENO; DIAS, 2015). The Pampa colonization was greatly marked by territorial conflicts: during this period the actual Brazilian Pampa areas were in transitory hands, between the Portuguese and the Spanish. The Spanish Crown tried a final occupation through the Jesuit fathers, establishing settlements (known as "misiones") and converting the local indigenous people into Christians. It is important to remark that was by this time the first cattle was introduced on the natural grasslands. After some conflicts the Brazilian Pampa was hold as Portuguese land, through the Madrid Treaty stablished in 1750 (BITTENCOURT, 2007).

In the period between 1808 and 1845 the land was finally settled as grazing land. The Portuguese Crown divided the areas into "sesmarias", aiming to populate and occupy the whole territory, by this time the dominant model of rural property was established: extensive soil use for livestock and agriculture (SUERTEGARAY, 1998).

Nowadays, the natural Pampa landscape is highly fragmented mainly due to the removal of the original vegetation for the agricultural processes, livestock and forestry, the last being the most aggressive in terms of environmental impact (PATTA-PILLAR et al., 2009; DE OLIVEIRA et al., 2017). Forestry is growing at alarming rates in the Pampa (SANTOS; SILVA, 2011). According to the Environment Ministry (MMA, 2016), only ca. 36% of the original Pampa vegetation still exists distributed in a very fragmented mosaic. Consequently, introduction of alien species related to the forestry is occurring (*Acacia* sp., *Eucalyptus* sp. e *Pinus* sp.). Also, the introduction of African grasses such as *Eragrostis plana* Nees (Poaceae) is a common practice, aiming to increase the cattle production (MEDEIROS; FOCHT, 2007). The consequences of such practices are negative to the environment and still poorly known.

Another environmental problem which is taking alarming proportions in the Pampa is the appearance of growing sandy patches (desertification processes), which are still without a convincing explanation for their origin. One of the hypotheses for it, is related to the extensive cattle farming, which destroys the thin vegetal layer and exposes the sandy soils of the region. These sandy patches are expanding quickly due to the wind and water action, occupying areas of many hectares. Studies have demonstrated that the original vegetal cover is remarkably difficult to be recovered (OVERBECK et al., 2009; SCOPEL et al., 2013).

Besides the interest on the conservation of the biomes, there is an enormous necessity in the preservation of the aquatic systems within them: the aquatic environments hold and provide breeding sources for most of the biodiversity (ANA, 2016). The levels of diversity on the aquatic systems are also a thermometer of the general situation of a determined region, since it shelters many indicator species and known model taxa for such evaluations (i.e. amphibians, aquatic insects) (ADAMS, 2008; CHOVANEC; RAAB, 1997). In the Pampa, the main threats to the aquatic environments are the removal of riparian zones and contamination by residual forms of pesticides used in the agriculture, impoundments or damming also are changing the water flow and impacting the river basins (ANA, 2016).

In Brazil, most of the preservation and restoring policies are dedicated to forested biomes such as the Amazonian Forest and the Atlantic Forest. Also, government inefficiency and absence, are playing a key problem in the control and restoration of the natural grassland areas (OVERBECK et al., 2013; OVERBECK et al., 2015). Only 0.8% of the total area of the Brazilian Pampa is inserted within protection areas, a fact that makes urgent the demarcation

of additional reserves for the maintenance of such a rich and diverse biome (DOBROVOLSKI et al., 2011; OLIVEIRA et al., 2017).

The steady loss of biodiversity reflects the human interference in the whole region: given the situation, this biome demands urgent conservation measures aiming its maintenance and restoration of degraded areas. It is needed the demarcation of priority areas, sustainable use areas, starting by the water resources from which many of the species depend directly. Thus, it is important to comprehend the impacts of human activities at the landscape level and on the freshwater resources, which are important for both, biodiversity conservation and human welfare.

This poor situation in the Pampa is directly related to the prioritizing of political and economic issues in detriment of environmental values, as can be seen throughout the problems discussed above. The heavy environmental changes taking place in the region are mostly caused by wrong land use and uncontrolled use of natural resources. The actual circumstances requires a clear comprehension of the ecological functions, if the biome is to be subject to efficient conservation measures. Planned actions are the viable way to reverse such situation, but these are still limited due to lack of knowledge and updated information on the ecology and the natural resources of the region (MISSIO et al., 2000).

Landscape ecology and fragmentation

The term landscape was introduced as a geographical concept in the nineteenth century by Alexander von Humbolt, defining the landscape as 'the total character of a part of Earth's surface' (ZONNEVELD, 1989). Comprehending further the landscape structure and its components, Humbolt then considered the physical environment as main factor, instead of the human features (SOARES FILHO, 1998). The concept developed by ZONNEVELD (1979), treats the landscape as "part of the space and terrestrial surface, comprehending a complex of systems featured by the geological activity, water, air, plants and animals, the man and the resulting forms, that could be recognized as entities". From the inclusion of the human perspective in the ecology and in the management of the landscape, the researchers started to add concepts from the social sciences, such as cultural and memorial elements from the human societies (SCHAMA, 1996).

In 1939 the term "landscape ecology" appears in the literature for the first time, resulting from the evolution of the imagery methods, benefited mainly by the aviation, the advance of the mapping techniques and topographic studies (TROLL, 1939). Also by this time were established the basic functions of the landscape: the biological relations of the environment and the man, resulting in a complete system comprehension (METZGER, 2001).

Actually, Metzger (2001) classifies the landscape ecology into two different bases: the geographic, which focuses in the man influence over the landscape, and the ecologic, which emphasizes the spatial ecological relations and its importance for the conservation. The evaluation of the landscape structure has been used as important tool for the studies of temporal variation caused by the human occupation on the land, as it enabled people to evaluate the different ways of soil usage and how land cover creates impact on the landscape (SOARES FILHO, 1998).

The changes on the landscape and ecosystems has been the main negative effect from the human population growth and its technological advances. There are many changes on the natural systems which are only related to human activities. Habitats that in the past covered gigantic extensions, now are modified by agriculture, livestock, cities, roads and many other human structures, resulting in a matrix where the original fragments within, have different shapes and sizes (WIENS, 1989; SAUNDERS et al., 1996; TURNER, 1996; PRIMACK; RODRIGUES, 2001).

The fragmentation is a process where the habitat is partially or totally removed, changing its original configuration. The native vegetation is removed, as the remaining vegetation is turn into fragments scattered in the landscape, inserted in a matrix different from the original. Consequently occurs the reduction of the available total habitat area, resulting in ecological isolation (SAUNDERS et al., 1996; TURNER, 1996; GIMENES; ANJOS, 2003).

Habitat destruction and fragmentation are the biggest threats to biodiversity (MYERS et al., 2000; PIMM; RAVEN, 2000), they reduce the species diversity and its population sizes, affecting the species in different ways. Many studies have shown that species in the upper trophic levels (GOERCK, 1997; HOLT et al. 2013), species specialized in their habitats or food resources (LEGENDRE; LEGENDRE, 1998), species with low dispersion capabilities (STOKS; MCPEEK, 2003), endemic species, and species with fluctuation and low population densities, are the most affected by fragmentation processes (LEGENDRE; LEGENDRE, 1998).

All the environments and ecosystems are influenced by the landscape variables (NAIMAN et al., 1993), the soil usage for agriculture, for example, completely changes the nutrient flow inside such ecosystems. In consequence of these changes, many environments become unsuitable for certain species, especially those that live in more sensitive systems such as aquatic environments.

At ecosystem level, knowledge of the configuration, structure and functioning of the landscape is crucial for the maintenance of its biodiversity (BAKER; CAI, 1992). The probability of a species to occur in certain sites depends greatly on several landscape factors, which act in determined scales. Thus, the definition of a proper scale in such studies is crucial to the knowledge of the influential variables over the communities (SOARES FILHO, 1998).

In this study the landscape was analyzed aiming to know the impacts produced by the human actions on the Odonata, using these model organisms to help in the identification of the factors needed for a diverse community in the Pampa biome.

Conservation

The conservation biology has in its main front of actions, the objective of reduce the impact generated by the human actions and the maintenance of the natural environments in their original shape, consequently resulting in the maintenance of the biodiversity (LAURENCE et al., 2001). The choice of priority areas for conservation is still being based on several criteria such as fragment quality, originality and scenic beauty. It denotes a biased and unspecified method of choice, which is logical of the human species. The conservation units are commonly demarked over remote areas with low economic interest where the exploitation of natural resources is difficult (SCOTT et al., 2001). Thus, more specific criteria to such selection is on urgent demand.

In this context, it is of extreme importance to comprehend how each landscape element influence the species occurrence, the main landscape variables involved and the local issues that lead to species extinction (size and quality of the fragments), the flow capability of ecological corridors (UEZU et al., 2005), the importance of the matrices as secondary habitats, (ANTOGIOVANNI; METZGER, 2005) as well the knowledge of the predator species, parasites and other filters of the biological flow.

It is known that environmental variables (biotic and abiotic) of the landscape influence directly the animal communities, restricting the occurrence of the species, acting selectively on the communities (GALETTI; DIRZO, 2013). The identification of changing patterns at community level along an environmental gradient is a crucial factor for the comprehension and managing of systems under human pressure (GALETTI; DIRZO, 2013). The environmental variables have been extensively used in combination to the species composition to determine the *status* and integrity of natural systems (JUEN et al., 2007; DE MARCO et al., 2014).

In the tropical biomes, the main problem for conservation is the lack of information, which would allow for the establishing of priority areas and practical restoration action. This is mainly due to low availability of faunal inventories, limiting the knowledge on species distribution and abundance. Faunal research is a precious tool for conservation, ecosystem managing and environmental protection (CORBET, 1999; LEWIS, 2006).

Among all the actual environmental problems, the aquatic environments have been those most affected by fragmentation. The management of these habitats and their hydrological basins requires the development of monitoring methods (OERTLI, 2008). Yet, the aquatic environments, both inserted into original remnants or altered ones act as resilience or buffer zones, diminishing the pressure resulting from human development along many years (CORBET, 1999).

Many organisms that live in the riparian zones have biological and ecological features which increase their sensitivity to landscape changes and fragmentation. These features are related to their dispersal capabilities, habitat selection, habitat specificity or the need for bigger areas for their populations to establish (BANKS-LEITE et al., 2012). Not only physical changes on the matrix but small changes in the landscape settings can affect the neighbor populations of species that live on aquatic environments (ESTAVILLO et al., 2013).

Globally, the study of the fragmentation effects over the fauna has been mainly focused on birds and mammals (DE VILLIERS 2009; PIRATELLI et al. 2008), with a comparatively low number of studies dealing with insects (PIMM; RAVEN, 2000; FRANK; MATA, 2004). The insects belonging to the Odonata order can probably act as model organisms showing the effects of the landscape changes given their life cycles, aquatic and terrestrial (CORBET, 1999), their communities are mainly heterogeneous, with species totally different in terms of regulatory capabilities (SIMAIKA; SAMWAYS, 2009; DE MARCO et al., 2015).

The comparison of landscape metrics and environmental variables has been used to analyze the Odonata communities, showing effective results for the comprehension of the integrity of riparian forests over the species compositions (PETERSEN et al., 2004), the effects of vegetation removal and conversion of natural areas into agriculture (VALENTE-NETO et al., 2016). Consequently, the Odonata has been largely used as bio indicators (SIMAIKA; SAMWAYS, 2011; RENNER et al., 2016a).

Comparing environmental variables to insect communities, make it possible to achieve a deeper knowledge of the ecological functioning on the Pampa biome. The present study was developed based on comparisons of the Odonata communities in several types of aquatic environments and its surroundings, from the original and natural ones to the degraded ones. The patterns of composition and distribution were compared to the landscape structures allowing a complete evaluation of these environments. The landscape features that could influence the species were taken into account, as well the type of aquatic environments, as lotic, lentic and temporary. It is possible from this knowledge to suggest possible priority areas for conservation in the Pampa biome.

The Order Odonata (Insecta), ecology and model organisms

Belonging to the Insecta class, the order Odonata is composed by the dragonflies and damselflies. This order is relatively small if compared to orders such as Coleoptera and Diptera, it has only around 7,000 catalogued species. The Odonata is divided into two suborders: Anisoptera (the true dragonflies) and Zygoptera (the damselflies) (KALKMAN et al., 2008). It is a very ancient animal group: the first fossil records of Odonata are dated to the Jurassic and Cretaceous periods, time in which these animals reached gigantic dimensions if compared to the nowadays species. These animals live in a two-phase cycle: aquatic larvae, and terrestrial/aerial adults (CORBET, 1999).

The hyaline wings, inclined thorax, long and thin abdomen, normally longer than the wings, easily recognizes the adults. Active during the daylight these creatures normally display vivid colors, sexual dimorphism and territorial behavior. Usually inhabiting water bodies and their surroundings. These animals are ferocious predators in both life stages, using their very developed sight to detect and ambush prey (CORBET, 1999).

The common name dragonfly is usually referred to the Odonata in general and also to the Anisoptera suborder, while the term damselfly applies only when related to the Zygoptera suborder (GARRISON et al., 2010). In this study I used the distinctive nomenclature for the two suborders: Anisoptera and Zygoptera. The species belonging to the suborder Zygoptera are typically slender, the shape of the fore and hind wings is similar, the flight is slower, as well the wing stroke. The larvae are easily recognized by the long and slender body and by the presence of external gills in the posterior portion of the abdomen. The anisopterans are typically robust, having greater wing load, fore and hind wings in distinct shapes, facilitating the gliding, that allow them to fly longer distances and even migrate (SUHLING et al., 2017). The Anisoptera larvae are also different from Zygoptera, remarkably by their internal abdominal gills (CORBET, 1999).

The Odonata provide several environmental services, from which can be highlighted their function as biological population control over other insect groups such as flies, mosquitos and midges, their main prey. For humans these animals are used as food delicacies, mainly by the eastern people, consumed as appetizers. These animals have also historic aesthetical and cultural values, also mostly related to the eastern culture (CORBET, 1999).

The distribution of the Odonata communities around the globe are remarked by the strict selection of oviposition sites (for the adults), according to the environmental features in a micro geographic scale. The adults are dependent on the features of the water bodies *per se*, as well the features of their surroundings, adjacent vegetation, sunlight conditions, complexity of the local physical structures etc. At the micro habitat scale, for the larvae, there are other influential features, as the availability of oviposition surfaces, quantity and type of aquatic plants, type of bottom (e.g. sand, mud, gravel), as well the presence of fish and other predators (CORBET, 1999; SUHLING et al., 2015). Removal of trees and creation of artificial aquatic environments can promptly change the species spectrum, benefiting the generalist species, which are known as pioneers and colonizers to altered areas (RENNER et al., 2016b). Also, both the kind and distribution of aquatic plants may also affect the numbers and spacing of the larvae which live among them (CORBET, 1999). Therefore, the communities depend upon the overall biological and physical features of the landscape.

Ecologically, the communities organization involves inter and intraspecific relations, as predation, territorial disputes, visual cues and complex pre-copulatory and copulatory behaviors. Remarkably, oviposition behavior is also a decisive factor for habitat selection, as

there are several different mechanisms these animals oviposit, depending on the families/genera they belong to, and in the offer of plants and structures in the habitats (CORBET, 1999). As predators, the Odonata are opportunistic: among its main prey are the wide span of dipterans, among other orders, and inter-specific predation (cannibalism) is common among several species, what makes the order very dependable on the biotic environmental features. In some aquatic systems the Odonata are considered top predators, placed at the top of the food web, fact that makes them very important in terms of ecology (CORBET, 1999; SUHLING et al., 2015).

In the Pampa, as in many other biomes, the Odonata communities have been found to be strictly related to tree cover, vegetation density and type of water body (lotic and lentic). Riparian forests aggregate more species of Zygoptera, which do not depend so directly of sunlight to resume their activities, while the more active Anisoptera are found mostly on less vegetated environments (GARRISON et al., 2010). Intensified land use has resulted in changes in species compositions: specialists tend to be replaced by more widespread generalists following human related changes on the landscape (KOCH et al., 2014). The type or kind of aquatic environments follows the same rule as there are species and families which are specialized in one or another type of environments (e.g. calopterygids and heteragrionids for running waters).

Given their ecology as above, in the conservation biology field the Odonata is well known as a reliable group for environmental quality indication (SAHLÉN; EKESTUBBE, 2001), it has been used in this purpose by many authors (ex.: CARLE, 1979; MOORE, 1984; SCHMIDT, 1985; CASTELLA, 1987; CLARK; SAMWAYS, 1996, RENNER et al., 2016a). Generally these are among the most significant organisms in the aquatic systems, which in turn, are subject to extreme pressure (SAMWAYS, 1999), thus being of great importance for conservation.

During the last 30 years this Order has been extensively studied in the Northern hemisphere, although in the Neotropics these investigations are in their first steps. The Neotropics are particularly rich in dragonflies, which are remarkably abundant in the lower regions (GARRISON et al., 2010). In Brazil only around 29% of its area has some kind of study/inventory of the Odonata (DE MARCO; VIANNA, 2005), and in the Rio Grande do Sul state, the studies are mostly related to the Atlantic Forest Biome (KITTEL; ENGELS, 2014; RENNER et al., 2015; RENNER et al., 2016b). For the Pampa specifically, there is one recent

inventory with distribution records, which have demonstrated how diverse the biome is, in terms of Odonata (RENNER et al., 2017, Chapter 3 of this thesis), and for the state there is an updated list which also includes some new records for the Pampa (DALZOCHIO et al., 2018).

Through the knowledge of the Odonata diversity it is possible to develop a perception on the conservation levels around the evaluated regions or sites, as many species of this order have ecological restrictions which are decisive to its occurrence or not. Therefore, these requirements make them reliable as indicators of environmental quality and species richness (SAHLÉN; EKESTUBBE, 2001; RENNER et al., 2016a).

According to Samways and Steytler (1995) and Stewart and Samways (1998), Odonata communities in disturbed environments are characterized by lower species richness, consisting mainly of generalist and common species. Another example of this, from the Neotropics, is the study developed by Machado (2001) in Brazil, where species with wide distribution have shown to be dominant in open fields and disturbed areas while the more specialized species where found only in forested areas. The presence or absence of determined species reflects directly the human activities occurring into or at the surroundings of the aquatic environments (RITH-NARAJAN, 1998; SAHLÉN, 1999) as well the diversity of biotic structures existing in the surveyed environments.

Dunkle (2000), regarded the dragonflies (Anisoptera) and the damselflies (Zygoptera) as the most visible indicators of aquatic environment health and diversity, and confirmed that the monitoring of the species composition can track environmental changes. Due to specific variations, these insects can tolerate certain environmental circumstances being a reliable tool for monitoring the environment condition (BARBOUR et al., 1999).

The selection of indicators from a complete species list seem to be a difficult task given the greatness of taxa occurring in the tropical zones, so the selection of a target taxa is an alternative choice to evaluate the environment condition of a region (PALMER, 1995; RENNER et al., 2016a). The choice of a taxon is mostly based on its responses for environmental changes and the monitoring readiness: it must be cost effective and easy to detect/identify by specialized personnel (KREMEN et al., 1993; SAHLÉN, EKESTUBBE 2001). Species restricted to certain environmental conditions are better indicators than the generalist ones, so the indicators have to be selective for the breeding sites, as well to be

common enough to be easily detected though a brief inventory (SAMWAYS et al., 1996; KALKMAN et al., 2008).

Despite the larval stage be better than the adults in terms of indication, there are still a lack of information on the neotropical larvae (identification keys). Most of the neotropical species can be only identified through the adults instead of the larvae, which are still poorly known, as many of them are not formally described yet (GARRISON et al., 2006; VALENTE-NETO et al., 2016; RENNER et al., 2016a).

Through inventories, it is possible to evaluate statistically the regional species compositions, to acquire a general view on the distribution patterns along the year seasons, and based on this data select potential environmental indicators. Consequently, it is possible to develop further knowledge on the Neotropical Odonata in a biome where it has not been satisfactory studied yet.

In this context, the landscapes studied could be combined with the species occurrences, their distribution on the biome, thus improving information and data needed to the implementation of coherent and efficient conservation measures.

General Objectives

To analyze the Odonata communities structure in the Pampa biome, relating it to the landscape variables, aiming to comprehend the diversity patterns and consequently promote nature conservation.

Specific objectives

- To develop a first Pampa biome species inventory, expanding known distribution records;

- To compare Odonata communities composition and structure among different landscape elements through different scales;

- To compare lotic, lentic and temporary waterbodies in relation to their odonates;

- To determine rare and common species, specialist and generalist species, characteristic for the biome;

- To suggest potential species richness indicators and environmental integrity indicators;

Study area

A total of 131 aquatic environments considered suitable for Odonata as breeding sites were selected. This included lotic, lentic and temporary sites composed of lakes, swamps, streams, river sections, rice fields and erosion sites (temporary waters). The sites were clustered in five main regions: Alegrete / Quaraí / Uruguaiana (N = 26); Manoel Viana / São Francisco de Assis (N = 44); Santana da Boa Vista / Caçapava do Sul (N = 23), Vale do Taquari (N = 23) and Littoral zones (N = 15), ranging from 29°24' to 30°55' S and 53°07' to 56°29' W. As shown in Figure 1.

All the municipalities evaluated in this study are characterized by large areas and have the agriculture as main financial resource. The areas located to the West (Alegrete region) are in the Ibicuí River basin, while the more Southern ones (Caçapava region) are into the Camaquã River basin (IBGE, 2016). The central areas (Vale do Taquari) are in the transition zone from the Atlantic forest to the proper Pampa. The Littoral areas to the East are also classified as Pampa, but are mostly characterized by 'Restinga' vegetation (Figure 2).

The climate in the regions belong to the Cfb type according to the Köppen system: mesothermic humid with mild precipitation equally distributed along the year. The altitudes are

between 50 and 200 meters above the sea level. Rainfall varying from 1,200 to 1,600 millimeters, mean annual temperatures from 13°C to 17.5°C, frost and negative temperatures known to occur between April and November (INPE, 2016).

LEGEND

Atlantic Forest Biome   ✤ Site clusters

Pampa Biome
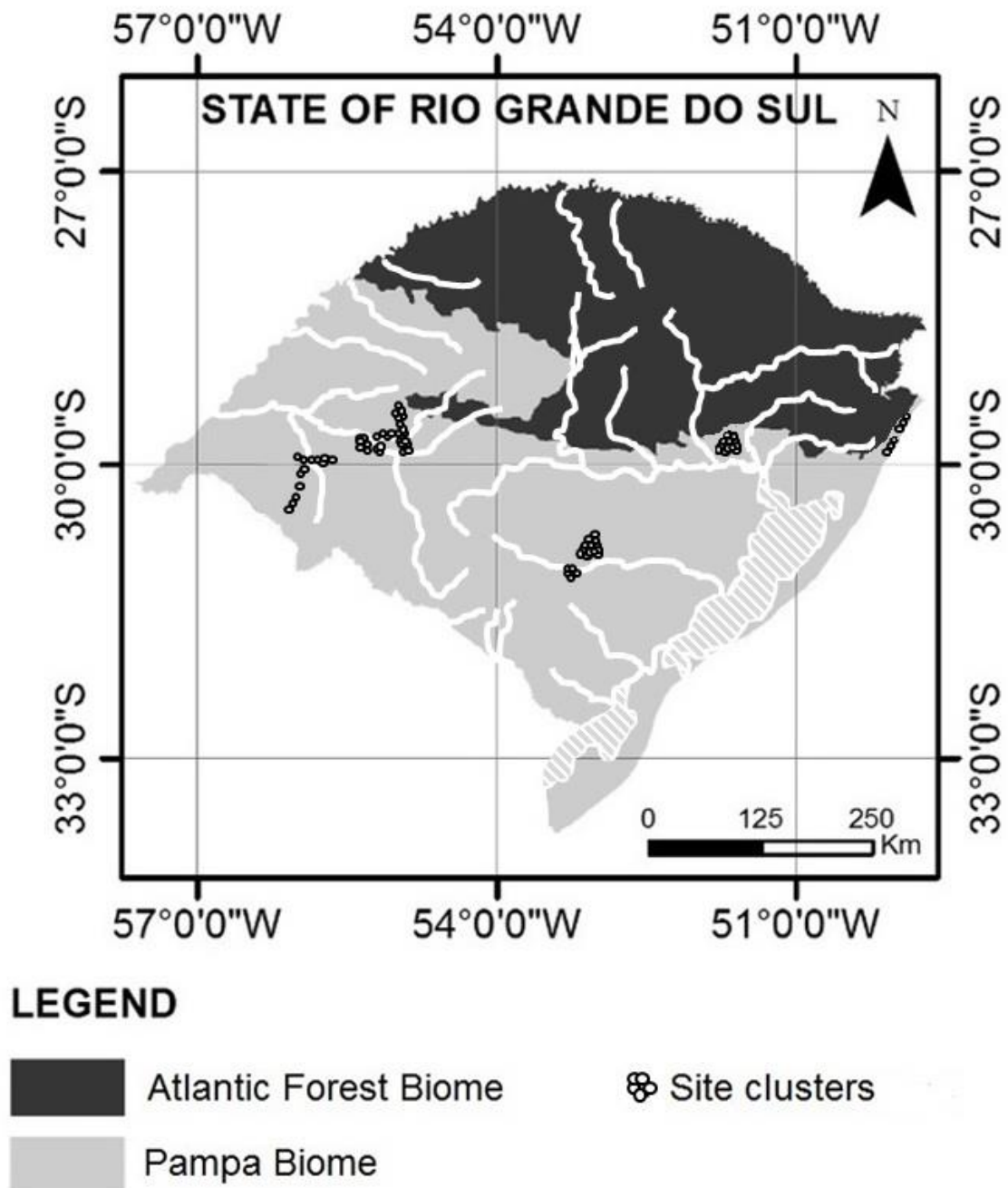
Figure 1 – Clusters of sampling sites along the chosen regions of the Pampa.

Figure 2 – Some examples of the sampling sites: (a) Swampy area, with slowly flowing clear water; (b) Flooding area near to Ibicuí River; (c) Swamp close to a forested edge zone.

Data collection

All localities were visited from one to seven times during the period of development of this study, aiming to a temporal overview. The first visit was dedicated to an environmental assessment of the available natural resources, levels of preservation and GIS data. Field notes were taken on the general condition of the water bodies. Any subsequent visits were made only for sampling purposes. Samplings were performed from 2014 to 2017 with the exception of the Taquari River Valley data, which was acquired during 2012 for the final undergraduate project of the author. The collection permit was issued by the ICMBio under the number Nº 50624-1. The winter season (21st June to 22nd September) was excluded due to the low temperatures and greater reduction on the adult Odonata activity.

The adult sampling method consisted in the use of insect nets by a field team of two persons. It was performed only in sunny days, from 9:00 to 16:00, the peak of odonate activities during the day. The time spent per sampling site had an average time of 45 minutes, it was developed until we found that we have at least one specimen of each species occurring at the site. The specimens were preserved in ethanol 96% for later determination at the Ecology and Evolution Lab (Univates).

The determination was mostly developed using the following literature. In some cases taxonomy experts were contacted.

- Damselfly Genera of the New World: An Illustrated Key to the Zygoptera (GARRISON et a., 2010);
- Dragonfly Genera of the New World: An Illustrated Key to the Anisoptera (GARRISON et al.,, 2006);
- Encyclopedia of South American Aquatic Insects Odonata - Anisoptera: Illustrated Keys to Known Families, Genera and Species in South America (HECKMAN, 2008);
- Encyclopedia of South American Aquatic Insects Odonata - Zygoptera: Illustrated Keys to Known Families, Genera and Species in South America (HECKMAN, 2010);
- The Damselflies of Brazil: An Illustrated Identification Guide 1 - Non-Coenagrionidae families (LENCIONI, 2005).
- The Damselflies of Brazil: An Illustrated Identification Guide 2 - Coenagrionidae (LENCIONI, 2006).

From the species records, the dataset for further analyses was developed. All the statistical analyses developed during this thesis are indicated and justified in the coming chapters.

Thesis structure/organization

This thesis is divided in interrelated but stand-alone chapters. The overlap in the text content between chapters has been kept to a minimum. However, there is some common material presented, particularly at the introductions of the chapters, methods and references. All chapters are published, submitted to scientific journals or manuscripts in development. Although Univates has its own standard format for submission of academic papers, the present thesis, except for chapter one and chapter seven (which obeys the format of Univates), meets the specific standards of each journal. The manuscripts presented in this thesis follow a chronological order, therefore the data (sampling sites) in each subsequent document is increased following the period of development of the studies.

Chapter one presents a general introduction to the main topics studied, a general presentation of the study area and the overall structuring of the thesis. The following chapters,

present each, a manuscript already published, in editorial process or submitted. Chapter two brings the first results from our sampled areas, through a species inventory, showing detailed data on the composition of the odonate communities of the Pampa and several new species records for the state. Chapter three is our first analyses development, using the dataset acquired in the field in comparison to features on the landscape of the Pampa, denoting the variability in the odonate assemblies in relation do the land cover they are within. Chapter four is a specific study, aiming to comprehend how dense are the communities in terms of rare and common species and how the common species, through niche occupation, affect negatively the presence of the rare species. The fifth chapter is based in an ecoregion approach, which has been developed following the tree cover and vegetation density. We explore how the Odonata assemblages differ from ecoregion to ecoregion, demonstrating their specificity to their environments. Chapter six consists in a first attempt to define odonates as bio indicators for the Pampa biome, testing a combination of two popular selection methods. And the last chapter (seven) is dedicated to a general discussion on the main findings of this study and the future works that could be developed. By the end of this document, as an appendix, are presented the prints of publications, submission, and co-authored papers produced during the doctoral period.

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CHAPTER 2

Preliminary dragonfly (Odonata) species list from the Pampa biome in Rio Grande do Sul, Brazil, with ecological notes for 19 new records for the State

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Abstract: An inventory of Odonata was carried out in the southern half of the state of Rio Grande do Sul, Brazil, in the Pampa biome. Originally, this biogeographical region was covered mostly by open fields and grassland, with sections of higher vegetation surrounding water bodies and rocky hills. Today the landscape is fragmented due to agricultural activities, mainly cattle farming, rice crops and forest plantations. Our survey was conducted in three municipalities from this region, between March 2015 and April 2016. Aiming at a general overview of the species composition, our sampling sites were selected on a wide basis, including lakes, bogs, temporary water bodies, small streams and river sections. Eighty two species of Odonata were collected comprising 40 genera and seven families. The dominant families were Libellulidae (56,1%), Coenagrionidae (24,5%) and Aeshnidae (7,3%). We found a diverse odonate assemblage, adding 19 new species records for the state of Rio Grande do Sul.

Key words: Anthropogenic threats, ecology, grassland, Neotropics, southern fields.

Resumo: Um inventário de Odonata foi desenvolvido na metade Sul do estado do Rio Grande do Sul, Brasil, no Bioma Pampa. Originalmente, esta região biogeográfica era coberta principalmente por campos abertos e pastagens, com seções de vegetação mais alta nas imediações de corpos d'água e elevações rochosas. Atualmente a paisagem se encontra fragmentada devido a atividade agrícola, entre as principais, a criação de gado, cultivo de arroz e silvicultura. A pesquisa foi desenvolvida em três municípios da região, entre Março de 2015 e Abril de 2016. Buscando uma visão geral da composição de espécies, os locais de amostragem selecionados incluíram lagos, banhados, corpos d'água temporários e seções de rio. Oitenta e duas espécies foram coletadas compreendendo 40 gêneros e 7 famílias. As famílias dominantes foram Libellulidae (55,1%), Coenagrionidae (24,5%) e Aeshnidae (7,3%). Nós encontramos uma grande diversidade nas comunidades de Odonata, adicionando 19 novos registros de espécies para o estado do Rio Grande do Sul.

Palavras-chave: Ameaças antropogênicas, ecologia, pastagens, região neotropical, campos sulinos.

Introduction

One of the biggest problems towards conservation measures is the lack of knowledge on species distribution, scientifically known as the Wallacean shortfall (Cardoso et al. 2009). Jetz et al. (2012) stated that even when looking at the best known species, knowledge on their occurrence is substantially lower than the amount of available information of other important environmental variables. Insects is the least known group concerning their distribution, mostly due to their high species richness, lack of taxonomic expertise and lack of sampling (Diniz-Filho et al. 2010). In the Neotropical region, and specifically in Brazil, there are still whole biomes which are almost unknown regarding insects (Oliveira et al. 2017). An example is the Pampa biome: extending from the southern half of the state of Rio Grande do Sul (29° S), southwards through the whole Uruguayan territory and within Argentina to the temperate Patagonian steppes, and ending at 39ºS (Roig & Flores 2001). It covers only around 2% of the Brazilian territory but more than 63% of the Rio Grande do Sul State area (IBGE 2016). Although scarce, data from this region has proven high diversity and high levels of endemism, at least regarding the flora (MMA 2002, Behling et al. 2004). The Pampa is under extreme pressure from several human activities such as agriculture, cattle farming, and forestry by the conversion of grasslands into extensive plantations of *Eucalyptus*, *Pinus* and *Acacia* (Bencke 2009, Overbeck et al. 2009, Roesch et al. 2009). Official government data from 2008, shows that only 36% of the original vegetation remains in a fragmented mosaic (MMA 2009). In Brazil, the officially protected areas of the Pampa grasslands cover only about 0.5% of the total biome, thus, more actions are needed to recover and preserve this threatened environment (Overbeck et al. 2009). For conservation purposes, information on species diversity becomes more relevant every day, as well as knowledge on range of distribution (Oliveira et al. 2017). Knowing where species occur and their abundance is fundamental for setting up conservation priorities and red listing. Making information available to scientists and the public is also central to overcome the prevailing lack of distribution knowledge (Jetz et al. 2012). Thus, inventories can provide and improve ongoing and future management efforts (Lewis 2006). Concise information is since long needed for biologists and decision makers to prioritize specific areas for the preservation of biodiversity (Kerr et al. 2000). The Odonata fauna in Brazil is moderately known in terms of species occurrence and distribution: only 29% of the country's territory is adequately surveyed, according to De Marco & Vianna (2005), but this number is probably outdated. For the southeast and central regions several

species lists are available (e.g., Costa et al. 2000, Costa & Oldrini 2005, Anjos-Santos & Costa 2006, Calvão et al. 2014, Bedê et al. 2015), while in the southern part of Brazil these studies are more scarce, the most recently published are Kittel & Engels (2014) and Renner et al. (2015, 2016a, 2016b), which were all conducted in the Atlantic Forest biome. Thus, we were motivated to increase the knowledge of species occurrence to the Pampa biome, the southernmost part of Brazil, where no survey of Odonata has previously been made.

Material and Methods

Study area

We sampled 63 localities distributed in four municipalities: Alegrete (AL, N = 10), Manoel Viana (MV, N = 9), Santana da Boa Vista (SB, N = 8) and São Francisco de Assis (SF, N = 36); within two different regions (1 and 2) of the Pampa biome (Figure 1). In total, the three municipality areas encompass more than 13,000,000 km² (IBGE 2016). The climate is Temperate (Cfb Köppen), with mean annual temperatures between 13°C and 17°C and altitudes from 50 to 200 m a.s.l. Annual precipitation mean is between 1,200 and 1,600 mm (INPE 2014). Our sites were distributed among several types of standing and running water including all types of habitats that could be considered to be used as reproduction sites for Odonata. We included small temporary pools or flooding areas, perennial waters such as bogs, swamps, ponds, lakes and rivers of various sizes. These sites included Rivers/streams ($N = 27$), Lakes ($N = 18$) and Temporary waters ($N = 18$), see below.
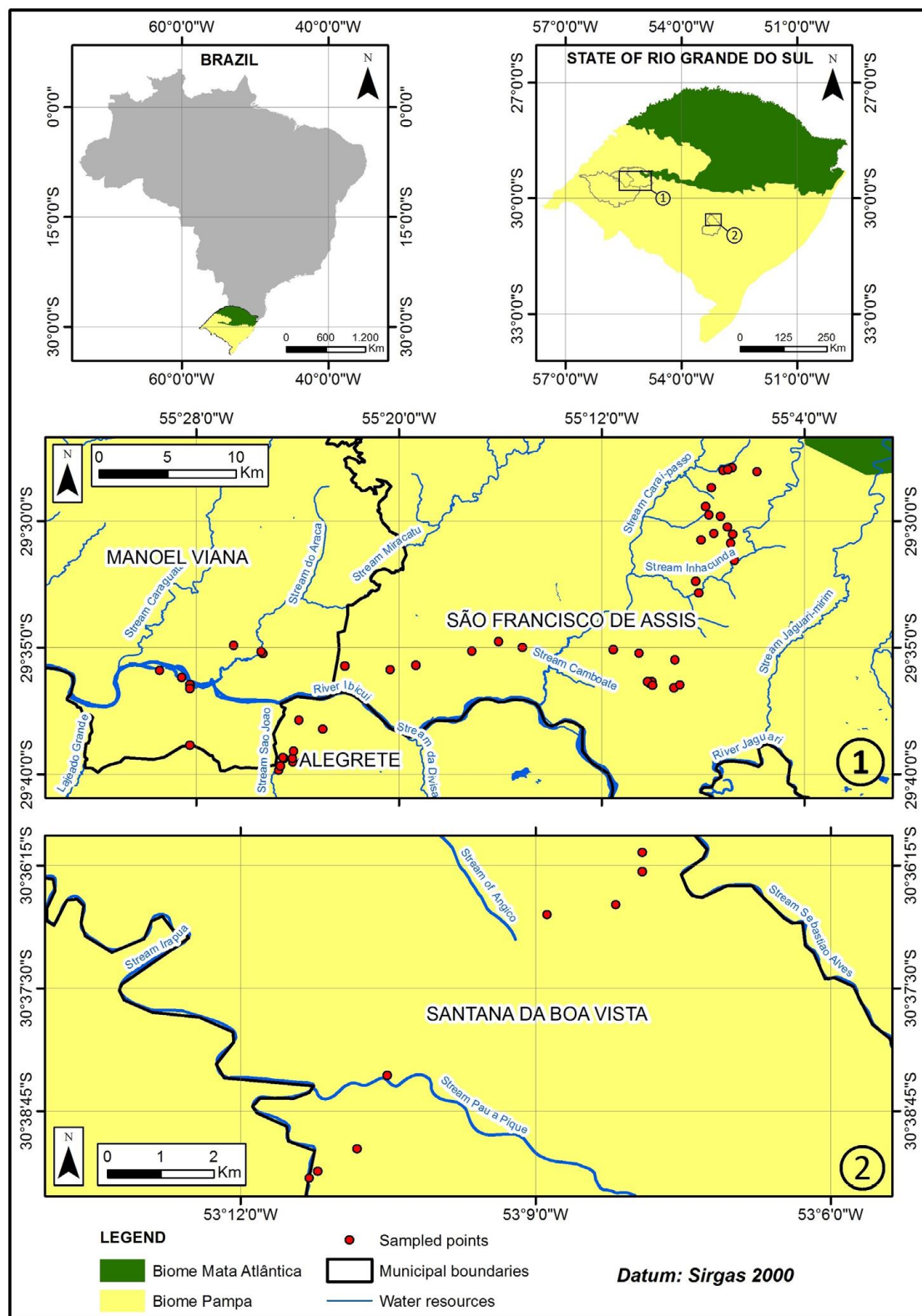
FIGURE 1: Map of Brazil and the Pampa biome domain in Rio Grande do Sul, rectangular insets from the two sampling regions (1 and 2), red dots marking the sampling sites.

Data collection

We sampled adult dragonflies from March 2015 to May 2016, the majority of the sampling sites were visited four times during this period, excluding winter due to the lack of activity of adult Odonata in the low temperatures (below 0° C) during that season. Other sites were visited only once, e.g. temporary water and flooded areas. The sampling method followed Renner et al. (2015): hand-held insect nets by a team of two people, in sunny days, during the peak time of Odonata activity (between 09:00 h to 16:00 h). Each site was sampled during 30 minutes, by walking the edge and marginal zones, the distances walked were dependent on the size and type of waterbodies, varying from ca. 50 to 250 m perimeters. We focused on adults only, since the majority of the larvae are still unknown (e.g., Garrison et al. 2006). Adults are often dispersing long distances (Corbet 1999), and we expect that some of our specimens might therefore derive from other regions. Our aim, however, was not to discern vagrants from reproducing species, but to get an account of species present in the area.

All specimens collected were preserved in 96% ethanol, and later determined to species level according to Garrison et al. (2006, 2010), Heckman (2006, 2010) and Lencioni (2006); species data were compared to the original species descriptions if needed and difficult species were kindly identified with help from Dr. R. W. Garrison, Sacramento, CA, U.S.A. For systematic classification, we followed Dijkstra et al. (2013, 2014). After identification, the specimens were deposited in the Museu de Ciências Naturais da Univates, Lajeado, Rio Grande do Sul, Brazil (MCNU). The collection authorization process was issued by ICMBio, under the number 50624-1. Beyond the municipalities abbreviations (mentioned above), we used the official abbreviations for the Brazilian states, as follows: AM (Amazonas) BA (Bahia), CE (Ceará), ES (Espírito Santo), GO (Goiás), MG (Minas Gerais), MS (Mato Grosso do Sul), MT (Mato Grosso), PA (Pará), PI (Piauí), PR (Paraná), RJ (Rio de Janeiro), RS (Rio Grande do Sul), SC (Santa Catarina), SE (Sergipe), SP (São Paulo) and TO (Tocantins).

To quantify our sampling effort, we choose to present a rarefaction curve (Mao tau) and the Jakkinfe 1 estimator. It is a general statistical technique for reducing the bias of an estimator by removing subsets of the data and recalculating the estimator with the reduced sample. Specifically, Jackknife1 depends only on the uniques (species found in only one sample) because the richness estimated is changed only when a sample that contains one of these species is deleted from a subset of samples (Gotelli & Colwell, 2011). We also quantified our

sampling effort by using a Jackknife estimation of total species richness according to Smith & van Belle (1984).

Results

1. Sampling sites

We sampled many different environments ranging from temporary water bodies (small sites) to big river sections. Some of these places were in good environmental conditions, only marginally affected by human disturbances, and notable by the presence of species considered rare by us. These were small erosion sites with temporary water flow, small streamlets/swamps where cold and clear water was flowing from the underground (Figure 2a), temporary flooding zones at a major river (Figure 2b) and also swampy areas with varied and well vegetated edge zones (Figure 2c). Most of the present threats to such unique environments are related to the expansion of forestry practices, which are growing notably and quickly in the regions where the studies took place.

2. Species List

Eighty-two species belonging to 40 genera and seven families were collected in the three municipalities (Table 1). Seven specimens, newly emerged males and/or females, were impossible to determine to species level; so these were classified as "sp.". Among these we found two specimens of an undescribed species belonging to the family Coenagrionidae. This species is currently under description by Dr. J. Muzón (La Plata, Argentina, personal communication), and no further information is therefore given here. Libellulidae was the dominant family (56,1%, N = 46) followed by Coenagrionidae (24,5%, 20) and, Aeshnidae (7,3%, 6), as shown in Table 2. The richest genus was *Erythrodiplax*, represented by eight species, this genus was also the most abundant in all seasons, occurring in virtually all sampling sites along with *Pantala flavescens* Fabricius, 1798, a known migratory and widely distributed disperser (Troast et al. 2016). Some species occurred only once (uniques) in this study and were considered regionally rare, for example: *Minagrion waltheri* Selys, 1876, *Brechmorhoga nubecula* Rambur, 1842, *Macrothemis lutea* Calvert, 1909 and *Dasythemis venosa* Burmeister, 1839. The rarefaction curve, which was based on the sampling events data, gave us a view of the sampling effectiveness of this study (Figure 3), tending to reach its asympt   ote. According to Smith & van Belle (1984) calculations using Jackknife as

estimator, we expect 101 species to occur in the region, meaning we reached 81% of the total estimated diversity.

3. New records

Excluding the single undescribed species, we found 19 new records for the Rio Grande do Sul State; some of these species we considered rare and some seem to be well distributed in South America. Here we present some habitat preferences and ecological aspects of these species, based on the literature found and on our field observations.

FIGURE 2: Some of the sampling sites which were remarkable by good environmental conditions: (a) Swampy area, with slowly flowing clear water in SF; (b) Flooding area near to Ibicuí River, MV; (c) Swamp close to a forested edge zone in SB.

TABLE 1: Preliminary species list from the Pampa biome in Rio Grande do Sul, Brazil. Municipalities of occurrence and voucher/collection numbers. New records for the state are marked with *.

Suborder	Family	Species	Municipality	Collection ID
Zygoptera	Calopterygidae	*Hetaerina rosea* Selys, 1853	AL, MV, SB, SF	ZAUMCN1119
		Mnesarete lencionii Garrison, 2006	SF	ZAUMCN1120
		Mnesarete pudica (Hagen *in* Selys, 1853)	SF	ZAUMCN1121
	Coenagrionidae	*Acanthagrion cuyabae* Calvert, 1909	AL	ZAUMCN1122
		Acanthagrion gracile Rambur, 1842	AL, MV, SB, SF	ZAUMCN1123
		Acanthagrion lancea Selys 1876	AL, MV, SF	ZAUMCN1124
		Argentagrion ambiguum Ris, 1904	AL, MV, SF	ZAUMCN1125
		Argia albistigma (Hagen *in* Selys, 1865)	MV, SB, SF	ZAUMCN1126
		Argia lilacina Selys, 1865	AL, MV, SF	ZAUMCN1127

		Argia modesta Selys, 1865	SF	ZAUMCN1128
		Argia sp.	SB	ZAUMCN1129
		Homeoura chelifera Selys, 1876	AL, MV, SB, SF	ZAUMCN1130
		Ischnura capreolus Hagen, 1861	AL, MV, SB, SF	ZAUMCN1131
		Ischnura fluviatilis Selys, 1876	AL, MV, SB, SF	ZAUMCN1132
		*Minagrion waltheri Selys, 1876	SF	ZAUMCN1133
		Neoneura leonardoi Machado, 2005	AL	ZAUMCN1134
		Oxyagrion hempeli Calvert, 1909	AL, MV, SB, SF	ZAUMCN1135
		*Oxyagrion rubidum Rambur, 1842	SF	ZAUMCN1136
		Oxyagrion terminale Selys, 1876	AL, MV, SB, SF	ZAUMCN1137
		Telebasis corallina Selys, 1876	SB, SF	ZAUMCN1138
		Telebasis theodori Navás, 1934	MV, SB, SF	ZAUMCN1139
		Telebasis willinki Fraser, 1948	AL, SF	ZAUMCN1140
		*Gen. nov. sp. nov. (under description)	AL	ZAUMCN1141
	Heteragrionidae	*Heteragrion triangulare* (Hagen *in* Selys, 1862)	SF	ZAUMCN1142
	Lestidae	*Lestes bipupillatus* Calvert, 1909	SB, SF	ZAUMCN1143
Anisoptera	Aeshnidae	*Castoraeschna* sp.	SF	ZAUMCN1144
		Limnetron debile Karsch, 1891	SB	ZAUMCN1145
		Remartinia luteipennis Burmeister 1839	SF	ZAUMCN1146
		Rhionaeschna bonariensis Rambur, 1842	SB, SF	ZAUMCN1147
		Rhionaeschna planaltica Calvert, 1952	SF	ZAUMCN1148
		Staurophlebia reticulata Burmeister, 1839	SF	ZAUMCN1149
	Gomphidae	*Aphylla theodorina* Navás, 1933	SB, SF	ZAUMCN1150
		Aphylla molossus Selys, 1869	MV	ZAUMCN1151
		*Archaeogomphus densus Belle, 1982	SB	ZAUMCN1152
		Progomphus basistictus Ris, 1911	MV, SF	ZAUMCN1154
		Progomphus sp.	MV	ZAUMCN1153
	Libellulidae	*Brachymesia furcata* Hagen, 1861	SB, SF	ZAUMCN1155
		*Brechmorhoga nubecula Rambur, 1842	SF	ZAUMCN1200
		*Dasythemis venosa Burmeister, 1839	SF	ZAUMCN1156
		Dasythemis mincki mincki Karsh, 1890	SB, SF	ZAUMCN1157
		Diastatops intensa Montgomery, 1940	MV, SB, SF	ZAUMCN1158

Diastatops obscura Fabricius, 1775	AL	ZAUMCN1159
Dythemis nigra Martin, 1897	SF	ZAUMCN1160
Elasmothemis sp.	SF	ZAUMCN1161
Erythemis peruviana Rambur, 1842	SF	ZAUMCN1162
Erythemis plebeja Burmeister, 1839	SF	ZAUMCN1163
Erythemis vesiculosa Fabricius, 1775	AL, MV	ZAUMCN1164
Erythemis sp.	SF	ZAUMCN1165
Erythrodiplax atroterminata Ris, 1911	AL, MV, SB, SF	ZAUMCN1166
Erythrodiplax hyalina Förster, 1907	AL, MV, SB, SF	ZAUMCN1167
Erythrodiplax lygaea Ris, 1911	SF	ZAUMCN1168
Erythrodiplax media Borror, 1942	AL, MV, SB, SF	ZAUMCN1169
Erythrodiplax melanorubra Borror, 1942	AL, MV, SB, SF	ZAUMCN1170
Erythrodiplax nigricans Rambur, 1842	AL, MV, SB, SF	ZAUMCN1171
Erythrodiplax paraguayensis Förster, 1905	AL, MV, SB, SF	ZAUMCN1172
Erythrodiplax sp.	AL, MV, SB, SF	ZAUMCN1173
Gynothemis venipunctata Calvert, 1909	SF	ZAUMCN1174
Idiataphe longipes Hagen, 1861	SB, SF	ZAUMCN1175
Macrothemis heteronycha Calvert, 1909	MV, SB, SF	ZAUMCN1176
Macrothemis imitans Karsch, 1890	SB, SF	ZAUMCN1177
Macrothemis lutea Calvert, 1909	MV	ZAUMCN1178
Macrothemis marmorata Hagen, 1868	AL, MV, SB, SF	ZAUMCN1179
Miathyria marcella (Selys *in* Sagra, 1857)	AL, MV, SB	ZAUMCN1180
Micrathyria hesperis Ris, 1911	AL, MV, SF	ZAUMCN1181
Micrathyria longifasciata Calvert, 1909	SF	ZAUMCN1182
Micrathyria ocellata Martin, 1897	MV, SB, SF	ZAUMCN1183
Micrathyria spuria Selys, 1900	SB	ZAUMCN1184
Micrathyria tibialis Kirby, 1897	MV, SF	ZAUMCN1185
Micrathyria sp.	SF	ZAUMCN1186
Nephepeltia flavifrons Karsch, 1889	AL, MV, SF	ZAUMCN1187
Orthemis aequilibris Calvert, 1909	AL, MV, SF	ZAUMCN1188
Orthemis ambinigra Calvert, 1909	SF	ZAUMCN1189
Orthemis attenuata Erichson, 1848	AL, MV	ZAUMCN1190

Orthemis discolor Burmeister, 1839	AL, MV, SB, SF	ZAUMCN1191
Pantala flavescens Fabricius, 1798	AL, MV, SB, SF	ZAUMCN1192
Perithemis icteroptera (Selys *in* Sagra, 1857)	AL, MV	ZAUMCN1193
Perithemis mooma Kirby, 1889	AL, MV, SB, SF	ZAUMCN1194
Tauriphila argo Hagen, 1869	MV	ZAUMCN1195
*Tholymis citrina Hagen, 1867	MV	ZAUMCN1196
Tramea abdominalis Rambur, 1842	MV	ZAUMCN1197
Tramea binotata Rambur, 1842	AL, MV, SB, SF	ZAUMCN1198
Tramea cophysa Hagen, 1867	AL, MV, SF	ZAUMCN1199

TABLE 2: Number of Odonata species collected per family in Rio Grande do Sul within the Pampa biome.

FAMILY	No.	%
Zygoptera		
Calopterygidae	3	3,6
Coenagrionidae	20	24,5
Heteragrionidae	1	1,2
Lestidae	1	1,2
Anisoptera		
Aeshnidae	6	7,3
Gomphidae	5	6,1
Libellulidae	46	56,1
TOTAL	82	100%
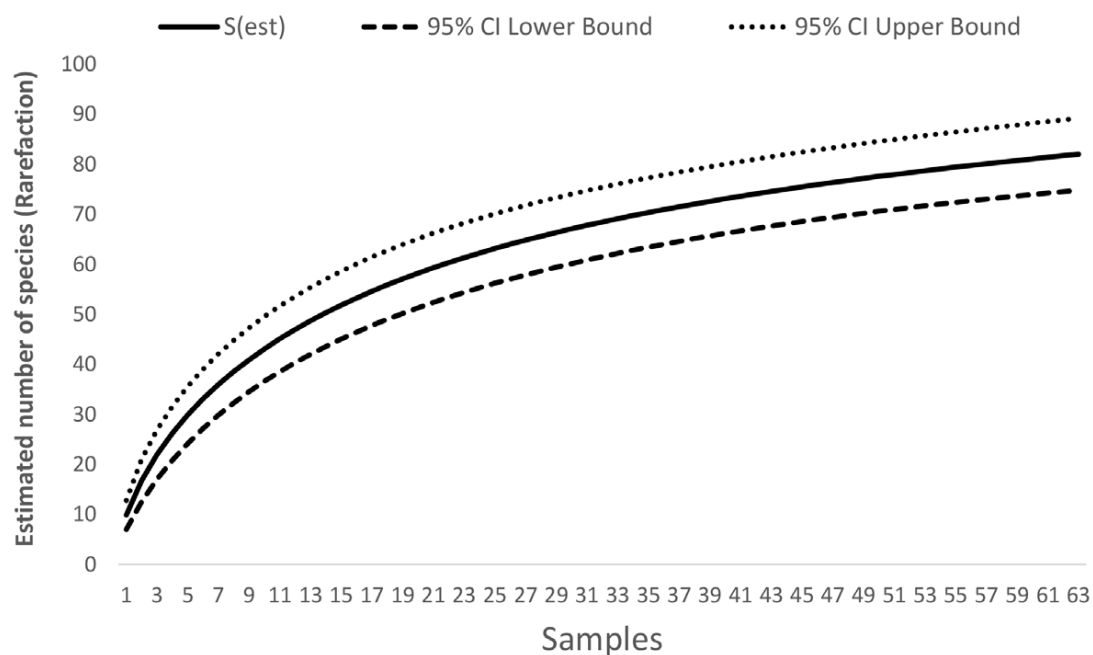
FIGURE 3: Rarefaction curve showing the efficiency of our sampling, stabilization expected to be reached if we continue our efforts. S(est): estimated species number; 95% CI: confidence interval, upper and lower.

3.1 - *Mnesarete lencionii* Garrison, 2006 (Calopterygidae)

Rare, at least for the latitude where our survey took place; this species is thought to be distributed all over Southeastern Brazil (Garrison 2006). The species resembles the congeneric *M. pruinosa* (Hagen *in* Selys, 1853), differing from it by the presence of a dark pseudopterostigma. Only one male was captured, it was found in a small fast flowing rivulet used for drainage of rice fields. At the same place we also found other calopterygids such as *Hetaerina rosea* Selys, 1853, which at the time of sampling, was abundant in the area. This species of *Mnesarete* was recorded from Argentina and Paraguay (Garrison 2006), and from Brazil from MG (Vilela et al. 2016) and SP (Garrison 2006).

3.2 - *Argia lilacina* Selys, 1865 (Coenagrionidae)

An inconspicuous coenagrionid due to its diminutive size (less than 30 mm), whose females shows pale brownish to green coloration and males are a bit more colored, varying from grayish blue to black. This species was quite common and we collected more than 80 specimens. It was mostly found in small streams flowing in open/field areas. According to

Takiya et al. (2016), this species was previously recorded for Bolivia, Paraguay, and Argentina, and in Brazil for CE, TO, MT, GO, MG, MS, ES, SP and RJ.

3.3 - *Minagrion waltheri* Selys, 1876 (Coenagrionidae)

This *Minagrion* species was considered a rare species in our dataset, it occurred in small numbers along the margins of lentic waters, such as swamps and marshes (Garrison et al. 2010). It occurs in areas dominated by cattails (*Typha*), preferring slow moving clear water streams (Santos 1956, 1965). Our specimens occurred at only one sampling site, which had the same environment as that provided by Santos (1956, 1965). The clean water seemed to pertain to an underground flow giving it zero or almost zero turbidity. The previously known records for this species are from MG (Bedê et al. 2015) and SP (Selys 1876; Santos 1965). We thus expand its distribution more than 1,200 km southwards. The species may well occur in between these two regions, but there are no records, probably due to lack of sampling.

3.4 - *Oxyagrion rubidum* (Rambur, 1842) (Coenagrionidae)

This species was locally common, alongside with *O. terminale* Selys, 1876, and difficult to identify in the field due to the resemblance of the two species. The environment where it was found was characterized by dense marginal vegetation on rivers, streams and ponds. This species is known from Uruguay (von Ellenrieder et al. 2009), Paraguay (Heckman 2010), Argentina and Chile (Muzón et al. 2014). From Brazil there is only one record in SP (Costa et al. 2000).

3.5 - *Archaeogomphus densus* Belle, 1982 (Gomphidae)

This is a small gomphid, pale colored which makes it inconspicuous in the forest and fields. It is known by its agile and rapid flight that makes it difficult to collect (Belle 1982). This genus is easily identified by its unique characters: two latero-dorsal hooks on the male S10 (Garrison et al. 2006). We consider this species as poorly known since the only records found are the original description from Argentina and MG by Belle (1982). Our unique specimen (male) was caught in a rocky fast flowing stream with sandy margins and covered by low vegetation.

3.6 - *Brechmorhoga nubecula* Rambur, 1842 (Libellulidae)

This species was considered rare to our sampling efforts, since it was found on only one occasion in a fast flowing stream, with a shaded marginal zone. It could be easily confused with some species belonging to the *Macrothemis* genus. According to Kompier (2015) it can be overlooked due to its secretive habitats, which was proven true by our sampling experience. According to Heckman (2006) this species occurs in almost all southern American countries, and in Brazil there are records from CE (Takyia et al. 2016), RJ (Assis et al. 2004, Kompier 2015), MG (Souza et al. 2013, Bedê et al. 2015) and SP (Costa et al. 2000).

3.7 - *Dasythemis venosa* Burmeister, 1839 (Libellulidae)

This forest species was found only in well preserved environments, such as small forest fragments, in shaded areas or natural clearings (at fallen trees), perching on dry twigs above the water. Records of this species are from Argentina and Paraguay (Heckman 2006) and from Brazil there are records from SP (Costa et al. 2000) and MG (Souza et al. 2013).

3.8 - *Diastatops obscura* (Fabricius, 1775) (Libellulidae)

A conspicuous species that has dark colored wings and butterfly-like flying style. Our specimens were found in rich marginal vegetation of streams and lakes. The species can be easily confused with its congener *Diastatops intensa* Montgomery, 1940, which also occurred at the same localities. This species is known from many countries in South America, including Paraguay and Argentina (Heckman 2006); from Brazil there are records from, MG (Bedê et al. 2015, Vilela et al. 2016), MS (Dalzochio et al. 2011), MT (Calvão et al. 2014), RJ (Kompier 2015) and SP (Costa et al. 2000). The species probably occurs in all Brazilian states, but was not previously detected in RS due to lack of sampling.

3.9 - *Dythemis nigra* Martin, 1897 (Libellulidae)

At our sampling sites this species seemed to be rare, found on only one location, a small slow-flowing clear water stream. Our specimen was caught perching on twigs in a shaded marginal zone close to the water. The distribution records for this species, according to Takiya et al. (2016), are from Mexico, Panama, Trinindad and Tobago, Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, Paraguay, Argentina and Brazil: AM, BA, CE, ES, GO, MG, MS, MT, PA, PE, RJ, SC and SP.

3.10 - *Erythemis vesiculosa* Fabricius, 1775 (Libellulidae)

A very conspicuous species, characterized by its flying habits when it is hovering at low height above the water surface. Numerous specimens were observed, mostly at the lakes, and male-to-male territorial disputes and fight behavior was observed on several occasions. This species also has a wide distribution since there are records from many countries in South America. In Brazil the records are from several states: MG (Bedê et al. 2015), MS (Dalzochio et al. 2011), MT (Calvão et al. 2014), RJ (Assis et al. 2004, Kompier 2015) and SP (Costa et al. 2000).

3.11 - *Erythrodiplax lygaea* Ris, 1911 (Libellulidae)

This is a tiny libellulid species whose males have bright yellowish colors that make the identification easy in the field. In our survey it occurred only on two locations, which were slow flowing water areas fed by small streams, corroborating the information provided by Costa et al. (2001) describing the larvae of the species. It is known to occur in Brazil (Pirassununga, SP), Paraguay and Argentina (Jurzitza 1981, Costa et al. 2001, Garrison et al. 2006).

3.12 - *Gynothemis venipunctata* Calvert, 1909 (Libellulidae)

A species which is easily identifiable in the field by the yellowish or amber spots on the male wing bases. Our six specimens were caught flying in a similar motion to that of *Macrothemis*, at about 1.5 m height, above open field areas, corroborating the observations made by Garrison (1983). Also, some were seen at a distance, flying in swarm-like formations consisting of some 5 to 10 specimens close to tree tops of about 10 m height. The species is known from Venezuela (De Marmels 1983) and in Brazil from MS (Costa et al. 1998), RJ (Kompier 2015) and SP (Costa et al. 2000).

3.13 - *Idiataphe longipes* Hagen, 1861 (Libellulidae)

We considered this species as common only in the peak of the summer season (Dec - Feb), since it was found in large numbers, usually perching on dry twigs along the water's edge. It seems to prefer lakes with diverse marginal or aquatic vegetation. There are records from several countries of South America: Colombia, Peru, Venezuela, Paraguay and Guyana. From Brazil the records are from the following states: SP (Costa et al. 2000), RJ (Kompier 2015), ES (Heckman 2006) and MG (Bedê et al. 2015).

3.14 - *Macrothemis heteronycha* Calvert *in* Ris, 1909 (Libellulidae)

Most of our 14 specimens were caught at temporary waters or small creeks with sandy and rocky bottom. Its flight behavior resembles in some ways that of *Gynothemis venipunctata*; a slow and fragile style, very different form the great majority of dragonflies. Also, opposite to most of its congeners, *M. heteronycha* was found mostly in open areas instead of forest with closed canopy. According to the literature, it occurs in Paraguay, Argentina (Ris 1913, Garrison & von Ellenrieder 2006) and Brazil: SP, RJ, MG, MS, ES and SC (Costa et al. 2000, Dalzochio et al. 2011).

3.15 - *Macrothemis lutea* Calvert, 1909 (Libellulidae)

A very interesting and unexpected finding. Our specimens were caught in tandem along a flooding area near to a river sand bank (Figure 2b). At first sight they were thought to be gomphids, due to the long abdomen (big overall size for a *Macrothemis* species) and general appearance. It is a rare species described from Brazil, known to occur in the state of SE which is the species type locality (Calvert 1909) and recently registered in CE (Nobre & Carvalho 2014). Here the distribution of the species is expanded southwards about 4,000 km.

3.16 - *Micrathyria spuria* Selys, 1900 (Libellulidae)

A common species, easily identified by the abdominal markings and the dorsally whitish cerci. We found this species mostly in lakes and swamps with abundant marginal vegetation. It showed the typical *Micrathyria* behavior of perching on tips of emergent vegetation or dry twigs. The females we caught were found away from the water bodies, perching and foraging around trees and bushes. The species is known to occur in Venezuela (De Marmels 1983), Paraguay and Argentina (von Ellenrieder 2009) and Brazil: MG, MS, PR, RJ and SP (Costa et al. 2000, 2002).

3.17 - *Orthemis aequilibris* Calvert, 1909 (Libellulidae)

Most of our specimens were found in the same localities as *M. heteronycha*; temporary waters or small perennial rocky creeks. Some of them were found away from the water. This species has records from Panama, Colombia, Peru, Venezuela, French Guiana, Guyana, Surinam, Bolivia, Paraguay, and from Brazil it has been recorded in BA, ES, MG and RJ (Costa et al. 2000) and AM, CE, MS, PA and PI (Takiya et al. 2016).

3.18 - *Orthemis attenuata* Erichson, 1848 (Libellulidae)

The males resemble a bit the darker species of the genus *Erythemis*, while the females have a typical and unique color scheme: dark brown with yellowish stripes. Most of our specimens were caught in a temporary river flood pool, which was muddy at the time of our sampling efforts, in the spring season. Strong male-to-female harassment was observed, as well as male-to-male territorial disputes. There are records from several countries in South America (von Ellenrieder 2012); in Brazil it is known to occur in PA (Pinto & Carvalho 2009), RJ (Kompier 2015), BA, ES and MT (von Ellenrieder 2012).

3.19 - *Tholymis citrina* Hagen, 1867 (Libellulidae)

This species is known by its crepuscular habits and erratic flight, usually found over marshes hunting mosquitoes (Paulson 2001). Our specimens were caught during the first minutes of our sampling efforts early in the morning (09:00 am), flying at irregular intervals in shaded areas which made them difficult to see and to capture with insect nets. This species was only found in the flooded areas, near to the Ibicuí River. In Brazil the records are known from the following states: MS (Costa et al. 1998), MT (Juen et al. 2014), RJ (Costa et al. 2002) and SP (Costa et al. 2000).

Discussion

Conservation strategies depend basically from information about diversity distribution, biogeography, population and community ecology. Therefore, inventories play a key role for the development of such measures. In this survey, we increased the knowledge on the Odonata fauna of Brazil's Pampa biome. We found 82 species, reflecting the diversity of our sampling sites; including several types of aquatic systems, most of them located in man-influenced areas, mostly by agriculture. Of these species, no less than 19 were new to the state and one new species not described in this paper. Naturally the number of species in the area will increase by including more sample sites and resampling ours, but never-the-less we already can see a highly diverse fauna in the region. We registered a large number (46) of Libellulidae species, which could be the result of many widespread generalists occurring in the mosaic of open fields and agriculture areas with little riparian fragmented forest, a landscape which is known to favor the fast and agile flying dragonflies, supporting the findings of Machado (2001). As suggested by Corbet (1999), there are different responses from Anisoptera and Zygoptera to environmental conditions, since the latter are known as low

range dispersers (Vieira & Cordero-Rivera 2015). In general, there are clear relations between environmental factors (biotic and abiotic) and species composition, these factors acting as determinants of presence and absence of some species due to ecological and physical restrictions (e.g., Paulson 2006, Juen et al. 2007). This is naturally an oversimplified division as Zygoptera is a taxonomical and not an ecological unit and contains both good (Flenner & Sahlén 2008) as well as weak (Lorenzo-Carballa et al. 2015) dispersers, but as an average assumption it is valid also when analysing large scale species patterns (Heiser & Schmitt 2013). We found many rare species in the study (singletons n = 20), all having a restricted occurrence. We consider the following possible explanations: first, we found a high number of species of Coenagrionidae (20), some of which can mirror good ecological conditions even in a highly fragmented region, acting then as bioindicators (Clausnitzer 2003, Suhling et al. 2006, Samways & Sharrat 2010, Renner et al. 2016a). Following this idea, in the open grassland with longer dispersal distances in the open, more exposed surroundings between suitable habitats (Juen et al. 2007), fewer of the smaller bodied species have the possibility to occur. This is due to some genera having ecological restrictions related to aquatic vegetation (i.e. plant diversity) and water quality (e.g., *Argia*, *Homeoura*, *Oxyagrion*) as stated by Garrison et al. (2010). Second, in well preserved areas or large forested areas, higher number of Zygopterans such as Heteragrionidae, Calopterygidae and again coenagrionids are expected to be found, many of which have specific environmental restrictions and ecological needs, mostly regarding to diversity of plants and vegetal structures in the riparian areas (Juen et al. 2014, Carvalho et al. 2013). This fact can explain the occurrence of *Minagrion waltheri* (Coenagrionidae) in only one locality in SA, which is a well-preserved area that keeps its natural features, as well crystal clear water and high diversity of aquatic/riparian vegetation (Figure 2a). These specialized species can function as powerful tools when distinguishing priority areas for preservation, as many of such restricted species have been proposed to be good indicators of environmental quality (Clausnitzer 2003, Sahlén 2006, Koch et al. 2014).

When compared to other studies from the Neotropics (De Marco et al. 2014, Monteiro et al. 2013) our collection efficiency captured only 81% of the expected diversity, tending to reach its asymptote, implying that the actual number of species in the region could be as high as 101 (cf., Figure 3). We have a relatively low number of sampling sites and, hence, cannot see the full picture of the odonate diversity in the Pampa biome, given its dimensions. However, we tried to include every kind of aquatic environment which could shelter any species of

Odonata, from small puddles of temporary water to big rivers, lakes and perennial bogs; more than one of each. To our surprise, we found several interesting habitats in which we recorded most of the species that we considered rare. These habitats could be starting point for future conservation actions to be taken for diversity maintenance in the area. Special focus should therefore be given to the environments whose original features are still preserved, such as small rivulets flowing in ravines, swampy and well vegetated areas supplied by underground waters and forest remnants with waterbodies (Figures 2a, b, c).

Future studies should, if possible, include a bigger selection of environments from more municipalities to obtain a more complete sample of the communities. In addition, more frequent sampling during the seasons might also contribute to the inventory, given that some species are related to specific conditions to be active, e.g. crepuscular flight, which occur among many Aeshnidae that are active only in the twilight. There are also species that are active during rainy conditions (Garrison 1989, Wasscher 1990, Corbet 1999), some of which might occur in the Pampa region.

The knowledge achieved in other biomes of Brazil is much deeper than that from the Pampa. But this biome is considered a highly biodiverse system (Overbeck et al. 2009), and in this context, species surveys can supply valuable initial information for the actions needed to preserve and restore these environments. With this survey we tried to add further information and improve the knowledge of the group Odonata from the Pampa biome of southern Brazil, showing that even under such fragmented and altered conditions diversity is still high; this fact acknowledges that future measurements of conservation and restoration are needed.

Acknowledgements

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CHAPTER 3

Water body type and land cover shape the dragonfly communities

(Odonata) in the Pampa biome, Rio Grande do Sul, Brazil

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Abstract The biogeographical region known as the Pampa Biome in southern Brazil, was originally mainly covered with open fields or grassland, with areas of riparian forest surrounding the water bodies. Today this landscape appears highly fragmented due to agricultural activities such as rice cultivation, extensive cattle farming, and forest plantations. Studies have shown that the Pampa biome has high levels of biodiversity and endemism, but with regard to invertebrates, this biome is still one of the least known in Brazil. We therefore designed a study comparing the dragonfly (Odonata) communities to environmental and landscape features in this area, measuring diversity by species richness, relative abundance and Shannon index. Our results showed that the Pampa is a biome very rich in odonates, and that the species communities are highly dependent on the environmental conditions of the area. Habitats such as rivers/streams, bordered by native grasslands and riparian forests, were shown to harbour communities that were ecologically more complex and sensitive than other habitat types. Man-made lakes and agricultural areas displayed lower levels of biodiversity and odonate communities dominated by generalist species. By combining data on the communities of Odonata and other taxa, our analyses may be instrumental in determining priority areas for future conservation measures within the area.

Introduction

The Brazilian fauna and flora is known to be diverse, although a majority of the studies published so far are related to biomes such as the Atlantic Forest or the Amazonian Forest (Rylands and Brandon, 2005). One of the least known biomes in Brazil is the Pampa Biome, or the Southern Fields. The studies published so far are few and mainly focused on the flora of the area (Roesch et al. 2009), whereas the fauna is quite poorly known (Baldi and Paruelo 2008; Overbeck et al. 2013). Floral studies have shown high levels of diversity and endemism, and some of the species within the area are considered to be endangered (Behling et al. 2004).

The Pampa biome covers only 2% of the Brazilian territory, but more than 63% of the surface of Rio Grande do Sul (IBGE 2016). It changes from small and scattered, partly tree covered patches near the Atlantic Forest into proper grasslands, covering the entire southern half of the state, south of 29° S. Outside Brazil, these grasslands extend south throughout the Uruguay, and in Argentina they extend to the Temperate Patagonian steppes at 39º S (Roig and Flores 2001). During the past 60 years, the pressure from human activities such as agriculture, extensive cattle farming and commercial forestry has grown at an alarming rate (Overbeck et al. 2009; Roesch et al. 2009; Mazia et al. 2010), causing fragmentation and habitat loss. The increasing introduction of non-native species makes matters even worse (Medeiros and Focht 2007). Plantations of exotic species such as *Acacia* sp., *Eucalytpus* sp. and *Pinus* sp. constitute the backbone of commercial forrestry, and African grass species such as *Eragrostis plana* (Poaceae) are being used to improve the grazing for the cattle. The effects of this are assumed to be detrimental to the biome as a whole (Santos and Silva 2007). Another problem is the intriguing desertification process observed locally in several places among the fields

and grasslands. The appearance of sand patches may be a consequence of unsustainable land-use and extensive cattle farming, which expand the existing erosion areas and destroy the fragile remnants of native vegetation (Overbeck et al. 2013).

Data gathered in 2008 demonstrated that only 36% of the original vegetation was still untouched, and that it was configured in a fragmented mosaic (MMA 2009). Also, according to the Ministry of Environment (MMA), only c. 0.5% of the total biome is protected in nature reserves etc.. So far, little has been done in terms of grassland restoration. Studies combining e.g. landscape ecology and conservation biology, which are crucial to successful restoration efforts, are still in their infancy (Bond and Parr 2010).

Landscape changes, especially habitat fragmentation, may affect species composition, since some species need connectivity to maintain stable populations (Bennet et al. 2006). Further, the proportion and amount of certain landscape elements are crucial to the formation and continuity of specific communities (Bond and Parr 2010). In general, the response of species richness to landscape alteration varies depending on the group of species studied; reptiles and amphibians, for example, have shown similar responses (Atauri and de Lucio 2001) while birds, which have higher dispersal capabilities, can adapt to certain landscape changes or migrate (Mörtberg 2001). Beetle communities, on the other hand, have been shown to react negatively to human alterations on the landscape scale (Cajaiba et al. 2017).

In this context, a landscape ecology approach could provide data which improve and enhance measures aiming at restoration, conservation and maintenance of environments affected by human occupancy (cf., Metzger 2001). We know that all elements in the landscape influence its biological communities which, in turn, interact to shape the whole environment (Turner

and Gardner 2001). At ecosystem level, the knowledge of landscape functions has a crucial

impact on the identification of factors needed for long-term maintenance of biodiversity

(Antogiovanni and Metzger 2005). Human disturbance, habitat loss and alteration, change

communities and ecosystem functioning, and areas with high levels of diversity are the most

affected and sensitive (Metzger 2001). By combining landscape information and data on the

distribution/occurrence/abundance of an organism group, it is possible to generate a reliable

method for delineation of areas that can be regarded as particularly species rich, diverse

and/or pristine and well-preserved (Nobrega and De Marco 2011). Such areas could

subsequently have conservation priorities.

To attain data without registering every single organism in an area, the selection of specific

target taxa (Kremen 1994) is a well-known method. Target taxa react on anthropogenic land

alteration. Therefore species distribution and overall diversity of these taxa is proven to be

related to landscape structure or land use variables (Soares Filho 1998). Factors such as

species richness and diversity to measure environmental quality in relation to landscape

metrics may provide clues to understanding ecosystem functions crucial to the maintenance of

a rich community (Samways and Steytler 1995), and to identifcation of variables which shape

these communities (Cunningham et al. 2007). The patterns of species occurrence are related to

the scale of the factors; spanning from a local to a broad (e.g. landscape) context, but the

intensity of all relationships vary depending on the species studied (Cunningham et al. 2007).

To develop this idea in the Pampa biome of southern Brazil, we decided to combine data on

communities and diversity of Odonata (dragonflies and damselflies) with information on the

landscape around and between the aquatic habitats they occupy. Such relationships have

previously been studied by several authors in several other biomes; there are examples from

Amazonia (Monteiro-Junior et al. 2013; Oliveira-Junior et al. 2013), Cerrado (Valente-Neto et

al. 2016) and from other regions of the world, such as Mixed Forests in Central Europe (Stoks and Córdoba-Aguilar 2012) and Afrotropical arid regions from Namibia (Suhling et al. 2006). Odonates are well-known as indicators of good environmental conditions and species diversity, and they are being used in many ecological studies around the world (e.g., Samways and Steytler 1995; Sahlén and Ekestubbe 2001; Koch et al. 2014; Renner et al. 2016a). Another reason to use odonates as model organisms is related to the life stages of the group, as they have aquatic larvae and terrestrial adults, both stages being selective in terms of habitat choice (Suhling et al. 2015).

This study aims at comparing regional dragonfly and damselfly communities among different land cover variables and water body types, studying species composition, species richness and abundance in the Pampa biome. We hypothesise that areas with a more original habitat harbour a higher diversity than areas affected by human activities. We further assume that this original diversity is not measured in species numbers only, but rather in the composition of the entire community, comprehending different ecological groups of species, present or absent. By identifying rich communities and factors determining such species compositions we will take the first steps toward a more thorough understanding of the diversity of water bodies in the Pampa biome and the imminent anthropogenic threats to the area.

Material and Methods

Study area

We used 60 sampling sites located in four communities situated in two different regions; the Western region: Alegrete (AL; $N = 10$); Manoel Viana (MV; $N = 9$), São Francisco de Assis (SA; $N = 33$); and the South-western region: Santana da Boa Vista (CS; $N = 8$); ranging from 29°24' to 30°39' S and 53°60' to 55°28' W, all within the Pampa biogeographical domain

(Fig. 1). The climate is Temperate (Cfb Köppen) with mean annual temperatures between 13°C and 17°C, altitudes from 50 to 200 m.a.s.l. and mean precipitation between 1,200 to 1,600 mm annually (INPE 2014).
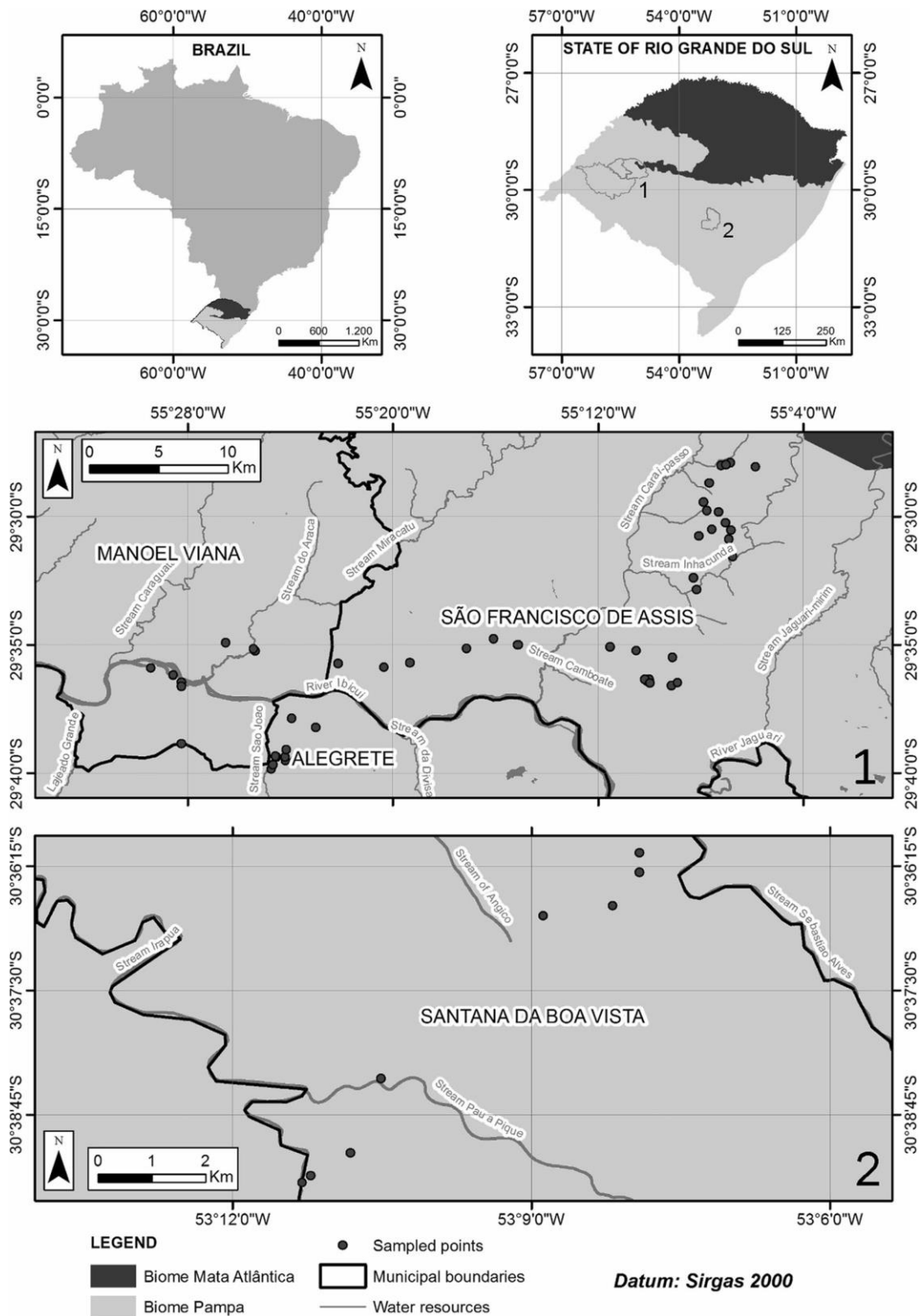
Fig. 1 Map of the survey areas in Rio Grande do Sul, Brazil. Most sampling sites (dark dots) are located in the area of Manoel Viana, Alegrete and São Francisco de Assis (1) with a few in Santana de Boa Vista (2).

Our sites included the whole range of water bodies suitable for Odonata found in the region: river sections, rivulets, streams, lakes, swamps and temporary waters, e.g., small pools and erosion sites (mostly in areas with sand patches, indicating desertification). Most of the sites were relatively small, ranging from 100 m in diameter or length, to some bigger ones (lakes) covering a number of hectares.

Data collection

We sampled adult dragonflies from March 2015 to May 2016: autumn (10 - 29 March); spring (2 - 20 November) and summer (3 - 22 January). Most sampling sites were visited four times during this period, once per season excluding the winter season, as adult Odonata are not active at the prevailing low winter temperatures. Most temporary sites were visited only once. We followed the method described by Renner et al. (2015): hand-held insect nets used by a team of two people in sunny days during the period of peak activity of Odonata (between 09:00 h and 16:00 h). Samples were taken along the edges and marginal zones of the waterbodies; distances varying in length according to the size and shape of the waters. The average time spent per site was 30 minutes, ranging from 15 minutes (species poor sites; often temporary) to 90 minutes (species rich sites or sites with a complex vegetation structure). Using this method, the rarest species at any site is less likely to being detected, but this is a common problem with surveys (Mao and Colwell 2005). We assume the risk of not detecting species to be fairly equal at all sites. Most sites were far apart, with the exception of e.g. impoundments (lake sites) in rivers (running water sites), which were sometimes adjacent to

each other but still treated as separate sites due to the different habitats (cf., Suhling et al., 2006). As we focussed on the adult stage only, we expect that some of our specimens might have dispersed from other regions, but our aim was to evaluate species occurrence records, not reproduction. For each site we noted the species present and the number of each species.

The specimens were preserved in 96% ethanol and identified to species level according to Garrison et al. (2006, 2010) and Lencioni (2006); also consulting the original species descriptions in difficult cases. Several specimens which were problematic to classify, were kindly identified by Dr. R. Garrison (Sacramento, CA). Unidentifiable specimens (young/teneral and some female specimens) were excluded from the analyses. For systematics we followed Dijkstra et al. (2013). After identification, the specimens were deposited at the MCNU (Museu de Ciências Naturais da Univates). The collection authorization process was issued by IBAMA, through the SISBio system under the number 50624-1.

Since statistical approaches to estimate species richness agree that there will always be a fairly big number of undetected, rare species in any area, regardless of sampling effort (e.g., Mao and Colwell 2005), we estimated our sampling effort by using the absolute number of collected specimens for a Mao Tau and Jackknife1 resampling in the Software EstimateS (Colwell 2009), using 1,000 repetitions to build a rarefaction curve, and we also calculated the estimated number of species in the region according to Smith and van Belle (1984).

We tested the spatial independence of the 60 sampling sites related to species composition using a Moran's I Analysis. We used individual species occurrences as variables in a Principal Components Analysis (PCA), where the first axis was used as response variable to the Moran's I with coordinate variables for ten different distance classes. The global Moran's I

analysis did not detect any significant spatial structure of the species composition for any distance classes (minimal distance class average: 0.01 degree; Moran´s I=1.13; p=0.14).

Abundance and rarity

For each site we used occurrence, measured abundance (number of specimens) and relative abundance: 1) single specimens; 2) 'few' (2-5) specimens' or 3) 'many' (>5) specimens. As our aim was to find new species and not to collect all specimens of the abundant species, relative abundance was a better value than absolute abundance. We also used ln (n+1) transformed abundance for the statistical analyses (below) for the same reason. We further calculated the Shannon index, H (Spellerberg and Fedor 2003) based on the occurrence and abundance of all species at each site. These numbers were used to compare the aquatic and terrestrial use groups to each other, as well as the combination of groups (see below). We classified species as 'common' (occurring at 20 or more sites in the dataset), 'rare' (occurring at up to 3 sites) and unique (occurring at only one sampling site) analysing their distribution in relation to the groups (water body type, land cover and combinations of these). Further, the species ß diversity partitioning into species turnover and nestedness proposed by Baselga (2010) was used. For species compositions, three pairwise beta-diversity metrics were calculated: Sørensen dissimilarity index (βsor), which accounts for the total compositional variation between assemblages, including both turnover and nestedness patterns; Simpson dissimilarity index (βsim) which captures only compositional changes due to species turnover; and nestedness-resultant dissimilarity (βsne), calculated as the difference between βsor and βsim. Only species occurrence data were used. Species pairwise β diversity measures were calculated using the betapart package in R (Baselga and Orme 2012; R Core Team 2013).

Local environmental variables

We classified our sites as belonging to one of three water body types:

- Rivers/streams ($N = 27$): lotic waters, including springs and small streams to rivulets, the bigger ones classified into rapid watercourses or river sections;

- Lakes ($N = 15$): lentic waters, mostly comprised by artificial lakes or impoundments, some natural swampy areas with a well vegetated water surface;

- Temporary waters ($N = 18$): mostly related to erosion sites which are fed by rain water, or seasonal springs connected to underground water sources.

Using the most recently (2013-2017) taken satellite images available on the software Google Earth Pro™, we were able to quantify four environmental factors inside a circular area of 1 km² with its centre at the midpoint of the sampling site (water bodies/marginal zones). All areas were clearly visible without clouds, haze or other objects preventing analysis, confirming the landscape features observed during the field work. Through the area measuring tool, we used the percentage of the land surface covered by each environmental factor to divide our set of sampling sites into five groups:

- Grasslands ($N = 23$, cover area $> 50\%$); areas covered by open fields, fields used for cattle grazing, and natural Pampa fields with the typical vegetation of this biome, the latter being characterised by taller vegetation, including bushes and reeds;

- Arable Land ($N = 7$, cover area $> 35\%$); areas with crop plantations, the most common crops in the region being rice, soybeans and corn. These were given second priority over Grasslands and Forests, since these activities also bring great changes to the natural landscape and its ecology, to a varying degree depending on the cultivation method in use (Roesch et al. 2009). As this variable was less common, it was given priority over the natural variables Grasslands and Forests;

- Forested areas ($N = 15$, cover area $> 25\%$); patches of native forest, mainly found in the surroundings of the waterbodies as riparian forest, or in the bordering areas of rock formations scattered in the grasslands. The trees in these patches are similar to those in the semi-deciduous or lowland Atlantic forest;

- Sand patches ($N = 10$, cover area $>5\%$); areas were desertification processes are taking place. Most of these areas are under severe erosion, which leads to loss of vegetation cover. Some of these areas are used by the cattle as trails or resting areas, which may also contribute to the process. These processes have been growing steadily in later years, and are known to be detrimental to the natural landscape of the Pampa (Overbeck et al. 2013). This was also an uncommon variable, and it was given the same priority as Arable Land;

- The remaining sampling sites were grouped as "mixed" areas ($N = 5$), all having lower than the above percentage of all categories.

Comparison and analyses

Our first step was to analyse which combination of landscape variables (i.e. waterbody type and terrestrial habitat) were most important to Odonata species diversity in the Pampa landscape. We used the Odonata richness and abundance, corresponding to the number of taxa and number of individuals found at each site and also the Shannon index. Abundance was ln (n+1) transformed to reduce discrepancies among samples. We removed the "Mixed" variable group as these sites have the characteristics of several land cover variables. We used mixed General Linear Models (GLMM; McCulloch and Neuhaus 2005), treating distance/space as a random factor. Since this factor must be categorical, we transformed the spatial coordinates into four distance classes, based on the location of the sampling site. For richness, we used Poisson distribution, and for abundance and Shannon index we used Gaussian distribution.

The analysis was performed in R with the glmer and glm functions of the statistical package lme4 (Bates et al. 2015). In the next step we used a two-way Permutational Multivariate Analysis of Variance (PERMANOVA) to compare differences in the Odonata species composition between land cover variables and between the different water body types. Here we used $\ln (n+1)$ transformed abundance data for each individual species at all sites. We used pairwise comparisons among and between analysed factors to visualize the main differences in Odonata composition. Although the PERMANOVA here was an unbalanced design, it is considered to be very robust and tolerant (Anderson and Walsh 2013). We are aware that by using unequal group sizes we might get slightly deviating results, but the test was the best choice available for our data. As the last step, we used non-metric multidimensional scaling (NMDS) to test the variation of Odonata composition between land cover variables with water body nested within land cover. The analysis was performed with Bray-Curtis dissimilarity index on two axes. The two last analyses were carried out in PAST 3.14 (Hammer et al. 2001).

Results

We found 82 species in the 60 sites, predominantly belonging to three families: Libellulidae (56%, 46 species), Coenagrionidae (24.5%, 20 species) and Aeshnidae (7.3%, 6 species). The total number of specimens collected was 1,704. Seven specimens could be identified to genus level only and were excluded. A species new to science, which is currently being described by another research group, was also present in our data. The number of species per site varied from 2 to 20, with an average of 10.4 ± 4.42 (SD).

The rarefaction curve was levelling off on, but not reaching its asymptote (Fig. 2). The estimation of total species richness (Smith and van Belle 1984) showed that our sample included >85% of the odonate fauna.
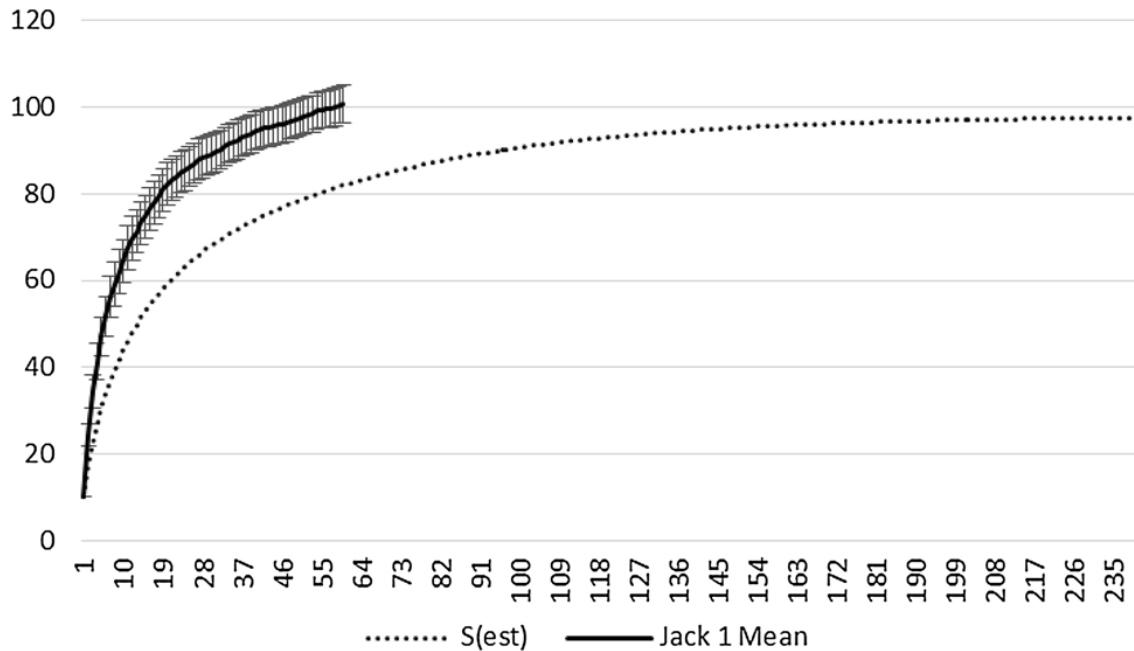
Fig. 2 Rarefaction curve using each sampling event (1 to 4) at each of the 60 sites and 1,000 repetitions. The curve levels but does not reach its asymptote.

Among the land cover variables, the richest group was the Grasslands (60 species). Among water body types, the richest group was Rivers/Streams (61 species). Average richness varied between sites within each land cover variable ($\chi^2 = 24.28$; $p < 0.001$) and between water body types ($\chi^2 = 6.82$; $p < 0.001$). Interaction was not significant ($\chi^2 = 5.46$; $p = 0.486$). Richness in Sand differed from that in Forests and Grasslands, but no significant difference was found when comparing Sand to Arable Land, Forests to Grasslands, Forests to Arable Land and Arable Land to Grasslands (Table 1). Average richness differed between Rivers/streams and Temporary waters, but was similar when comparing Rivers/streams with Lakes and Lakes with Temporary waters (Table 1).

Table 1. Pairwise comparison of land cover groups and water body types from GLMM analysis using richness, abundance and Shannon index data. Bold p values are significant; α<0.05.

Variables/Results	Richness			Abundance (ln+1)			Shannon index		
	Estimate	Std. Error	p	Estimate	Std. Error	p	Estimate	Std. Error	p
Sand x Forests	-0.655	0.178	**0.000**	-0.256	0.160	0.115	0.001	0.301	0.995
Sand x Grasslands	-0.406	0.165	**0.013**	-0.359	0.156	**0.026**	0.06	0.294	0.831
Sand x Arable Land	-0.327	0.243	0.179	-0.286	0.219	0.198	0.168	0.412	0.684
Forests x Grasslands	0.249	0.142	0.080	-0.118	0.159	0.46	0.061	0.202	0.764
Forests x Arable Land	0.329	0.229	0.151	0.422	0.218	0.059	0.167	0.352	0.638
Grasslands x Arable Land	0.079	0.219	0.717	0.541	0.187	**0.005**	0.105	0.347	0.762
Riv/Streams x Lake	0.143	0.263	0.587	-0.185	0.276	0.508	-0.06	0.202	0.734
Riv/Streams x Temporary	-0.368	0.182	**0.043**	0.085	0.169	0.618	0.288	0.294	0.332
Lakes x Temporary	-0.351	0.232	0.130	0.270	0.259	0.303	0.219	0.301	0.470

Among the land cover variables, the group with highest relative abundance was Forests (3.29). Among the water body types, the highest relative abundance was found in Rivers/Streams (1.77). The average relative abundance varied significantly between sites within a given land cover variable ($\chi^2 = 15.63$; $p < 0.001$) but not between water body types ($\chi^2 = 0.0053$; $p = 0.970$). Interaction was not significant ($\chi^2 = 1.90$; $p = 0.952$). The average relative abundance was higher in Grasslands than in Sand, and it was higher in Arable Land than in Forests and Grasslands. The average relative abundance was at a similar level when comparing Sand to Forests, Sand to Arable Land, and Forests and Grasslands (Table 2). The highest Shannon index values were found in Rivers/streams and Lakes (H = 2.01). The average Shannon index value did neither vary between sites within a given land cover type ($\chi^2 = 3.07$; $p = 0.038$), nor between water body types ($\chi^2 = 4.23$; $p = 0.120$). The interaction was not significant ($\chi^2 = 2.022$; $p = 0.918$).

The highest dissimilarity value (βsor) was found when comparing Sand and Forests (βsor = 0.45), followed by Sand and Arable Land (βsor = 0.40) and Forests and Grasslands (βsor=0.39). The lowest βsor was found comparing Sand and Grasslands (βsor = 0.32). Pairwise comparison of ß diversity partitioning into species turnover (βsim) and nestedness (βsne) showed the highest component of βsne in Grasslands vs. Arable Land, where more than 50% was due to nestedness. The level was lower in the other comparisons with Sand vs. Arable Land as well as Forests vs. Grasslands, having almost no βsne component at all (Fig. 3a). Pairwise comparison of water body types revealed that Lakes vs. Rivers/streams had the highest βsim and Rivers/streams vs. Temporary waters the lowest (Fig. 3b).
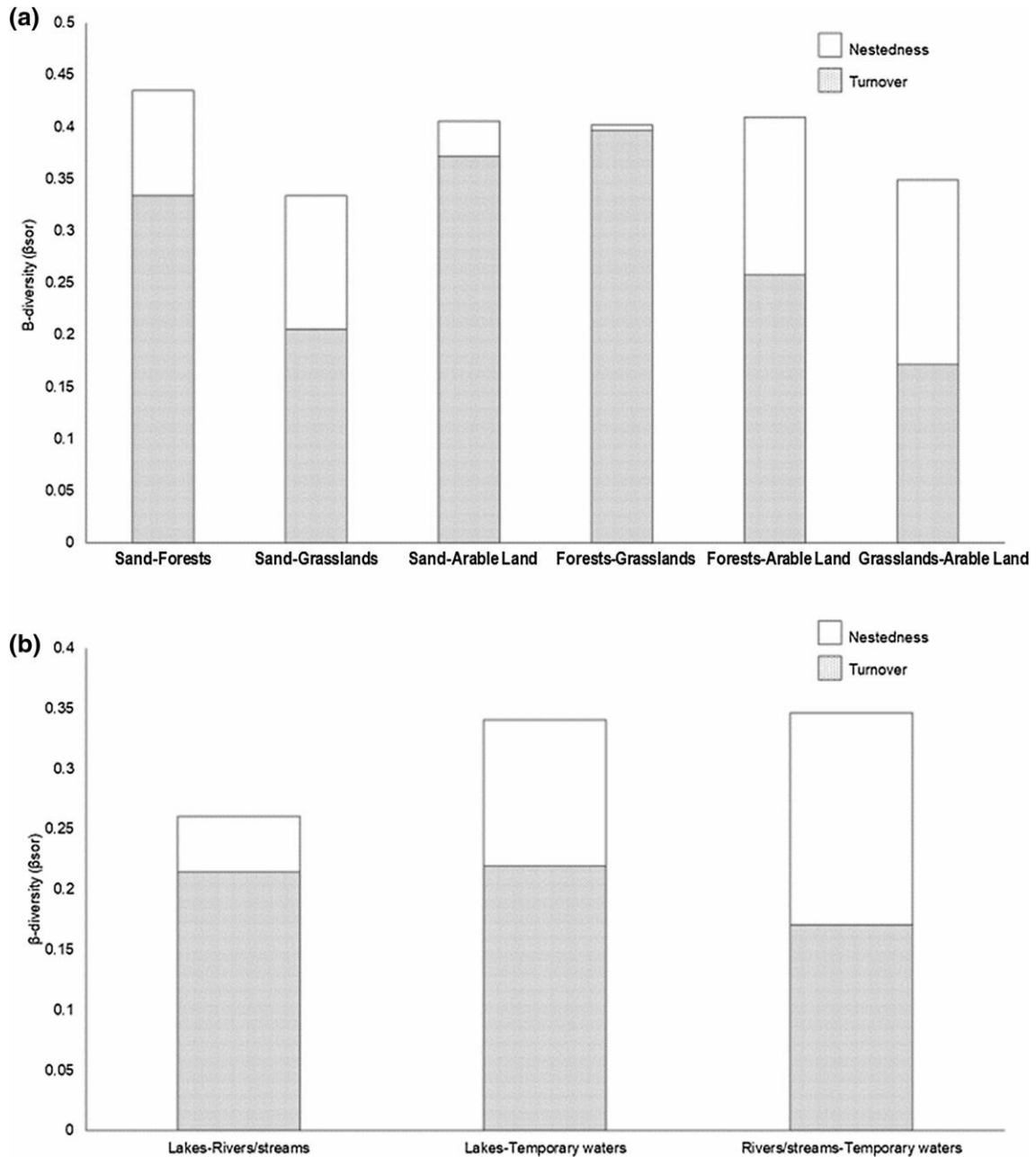
Fig. 3 Pairwise comparison of ß diversity (measured as Sørensen dissimilarity index, βsor) partitioned into species turnover (Simpson dissimilarity index, βsim) and nestedness-resultant dissimilarity (βsne). a) A big component of of βsim is seen when comparing Sand and Arable Land as well as Forests and Grasslands. For the rest of the comparisons, βsne constituted a bigger part of the diversity. b) The βsim component vary in the pairwise comparisons from the lowest part in Rivers/streams vs. Temporary waters to the highest in Lakes vs. Rivers/streams.

We classified 9 species as common (occurring at more than 30% of the sampling sites) and 39 species as rare (registered at three sampling sites or less; Supplementary material). The water body type that hosted the highest number of unique species was Rivers/Streams (9), while the land cover variable for this was Forests (17). The nine common species were found in every group, except in the Sand areas, whereas the distribution of the rare species was more heterogenic, most of them occurring in only one type of water body or land use group (Table 2). Some examples of rare species in the region are: *Mnesarete lencionii*, *Brechmorhoga nubecula* and *Macrothemis lutea*. The eight most common species were: *Acanthagrion gracile*, *Ischnura fluviatilis*, *Erythrodiplax atroterminata*, *Erythrodiplax paraguayensis*, *Erythrodiplax media*, *Orthemis discolor*, *Pantala flavescens*, and *Perithemis mooma*.

Table 2. Water body types and land cover groups with values for average species richness per site (α) ± standard deviation, total richness for all sites included (γ), mean relative abundance and Shannon index (± sd), common, rare and unique species. Number of sites per type/group given as N.

Variable/Result	Avg richness (α)	γ	Rel abundance	Shannon index	Common	Rare	Uniques
Riv/Streams (N=27)	10,03 ±5,04	63	1,77	2,01 (1,19 - 2,69)	9 (11%)	22 (26,8%)	9 (11%)
Lakes (N=15)	10,47 ±5,73	56	1,57	2,01 (0,86 - 2,25)	9 (11%)	19 (23,2%)	4 (4,9%)
Temporary (N=18)	9,16 ±3,66	45	1,67	1,88 (0,63 - 2,48)	9 (11%)	9 (11%)	4 (4,9%)
Sand (N=10)	8,6 ±4,14	39	1,64	1,60 (0,86 - 2,32)	6 (7,3%)	8 (9,7%)	8 (9,7%)
Arable Land (N=7)	13,42 ±4,15	39	1,77	2,08 (1,67 - 2,49)	9 (11%)	9 (11%)	8 (9,7%)
Grasslands (N=23)	10,34 ±3,95	54	2,02	1,91 (1,63- 2,49)	9 (11%)	16 (19,5%)	10 (12,2%)
Forests (N=15)	8,77 ±6,06	54	3,29	2,08 (0,63 - 2,48)	9 (11%)	19 (23,2%)	17 (20,7%)
Mixed (N=5)	11 ±4,89	55	1,14	1,28 (1,86 - 2,69)	9 (11%)	5 (6,1%)	4 (4,9%)
TOTAL (N=60)	10,36 ±4,84	82	2,17	1,95 (0,63 - 2,69)	9 (11%)	39 (47,6%)	19 (23,2%)

The species composition varied significantly between sites within a given land cover type (pseudo-$F_{3,54}$ = 1.26; p = 0.0001) and between water body types (pseudo-$F_{2,54}$ = 1.50; p = 0.0001) with no significant interaction (pseudo-$F_{6,54}$ = -2.76; p = 0.44). The Odonata composition differed between Sand and Grasslands (t = 1.72; p = 0.04), Sand and Arable Land (t = 3.617; p = 0.0005), Forests and Grasslands (t = 2.229; p = 0.004), Forests and Arable Land (t = 2.369; p = 0.008) and between Grasslands and Arable Land (t = 2.303; p=0.005). Sand and Forests were only marginally different (t = 1.613; p = 0.060). With regard to the water body types, the Odonata composition differed significantly between Rivers/Streams and Lakes (t = 2.651; p = 0.002), Rivers/Streams and Temporary water (t = 2.423; p = 0.003) and between Lakes and Temporary water (t = 2.684; p = 0.001). The

similarity in Odonata community composition was represented by two axes in the ordination analysis, where the first explained 71% of the variance (NMDS, stress=0.04), shown in Fig. 4. The two original land cover types (Grasslands and Forests) were found near the center of the plot, but were separated along axis 2. The two most altered habitats are found far from the center with Sand to the negative and Arable Land to the positive end of axis 1, indicating clearly different species compositions. The water body types were ordered in the same direction along axis 1 within all land cover groups, with Rivers/Streams having the lowest values, followed by Lakes and Temporary waters (Fig. 4).
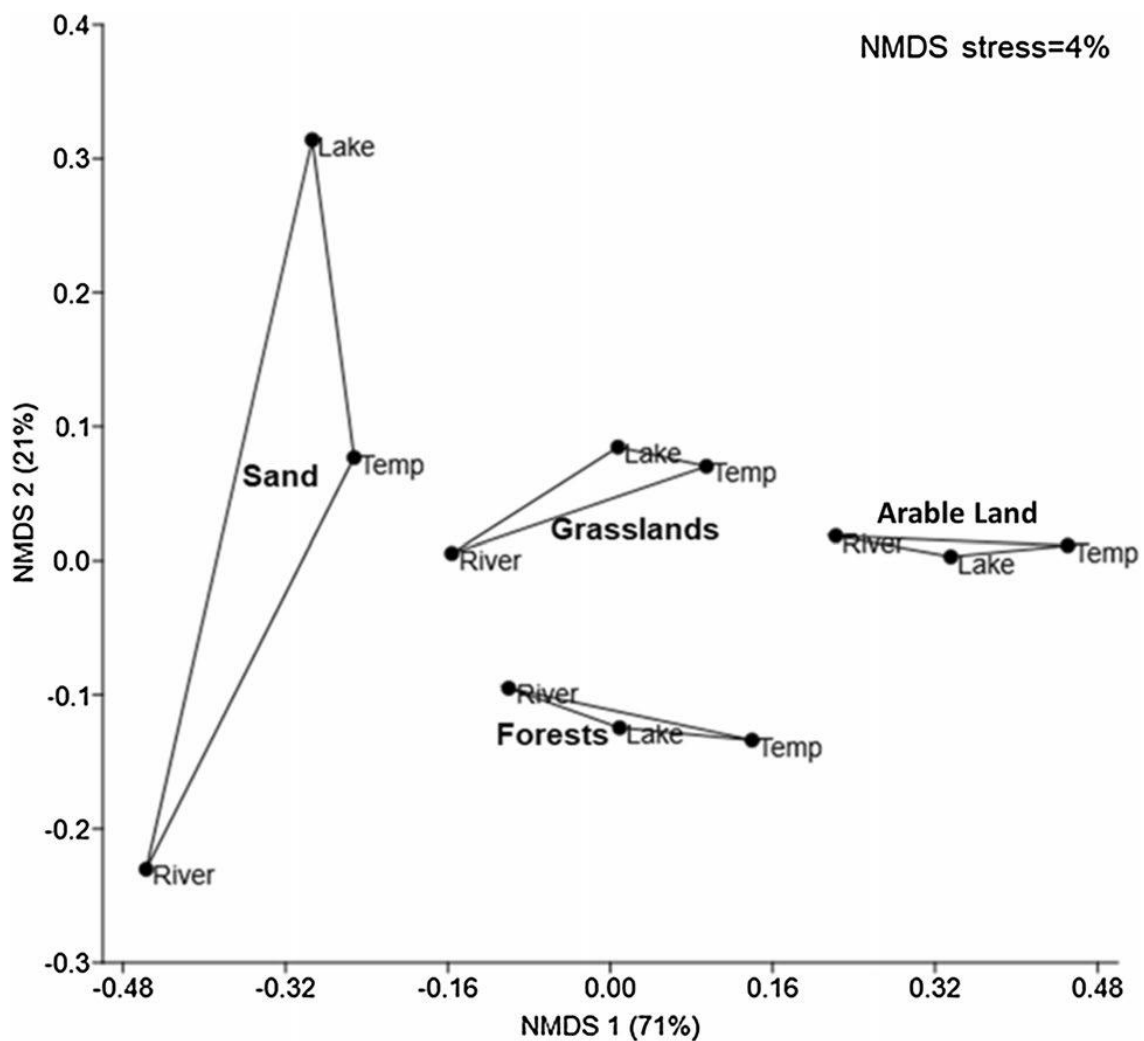
Fig. 4 NMDS plot showing the similarity of the Odonata communities for each of the land cover and water type groups. The original land cover types are found near the centre of the plot with the altered habitats on the negative (Sand) and the positive (Arable Land) side. The

water body types are ordered in the same way along axis 1 in all four land cover groups possibly indicating a general similarity in composition.

Discussion

Our analysis revealed information on how dragonfly community assemblages in the Brazilian Pampa are dependent on both water body type and land cover. Firstly, measuring diversity can be done in many different ways, and looking at mean species richness, mean abundance and the Shannon index each variable resulted in different outcomes. While the Shannon index differed marginally between water body types and land cover groups, species richness and species composition varied between land cover groups and between the aquatic habitat types. Abundance, however, varied only between land cover groups and not between the aquatic habitat types. This kind of variation is to be expected, as Lammert and Allan (1999) noted that effects of local land use were more important than those of regional land use on the macroinvertebrate community in rivers, but local habitat conditions had the highest influence. We found large differences between sites (from only two up to 20 species of Odonata coexisting), and we predict that the heterogeneity of the habitats within the region might be one of the obstacles to overcome in future conservation discussions for the Pampa. For forests, preserving landscape heterogeneity has been proposed as one of the guiding principles (Lindenmayer et al. 2006), while Hendrickx et al. (2007) showed that increased habitat diversity appeared to be only of secondary importance to species richness in agricultural areas. We found that a pattern of species assemblages related to environmental variables does exist, at least for the odonate communities. This pattern has also been found in similar biomes such as the Cerrado, both for odonates (Ferreira-Peruquetti and Fonseca-Gessner, 2003) and Ephemeroptera (Shimano et al. 2010). For the Pampa, we suggest that studies like ours should

be expanded to other organism groups in order to determine a more general pattern of biodiversity occupancy for the biome as a whole.

We noted that the more original land cover types (Grasslands and Forests) had a much higher species richness (γ-diversity; Table 1) than the altered environments (Arable Land and Sand). Ward (1998) showed that natural environmental gradients and disturbances lead to high levels of aquatic biodiversity. On the other hand, anthropogenic impact typically reduces biodiversity. The patterns we observed fit this general theory, if we assume that the differences in diversity are not only caused by differences in sample site numbers. Our results further suggest a strong dominance of species turnover in Forests compared to other land use variables and Rivers/Streams vs. Lakes. It reflects the effect of environmental sorting on species which enhance community replacement towards generalist species (Baselga 2010). If we infer that most of the original land cover of the Pampa was similar to the Grasslands we see today (albeit changed due to anthropogenic activities; cf., Santos and Silva 2007) we may hypothesize that the habitats within this land cover type would be most suitable for the original species composition in the biome. This has been shown in other studies comparing dragonfly communities in original patches of the environment to those of altered habitats (Juen et al. 2014; Renner et al. 2016b), and also in other taxonomic groups such as soil microbes (Lupatini et al. 2013), birds (Mörtberg 2001) and in studies comparing organism groups occurring together, e.g. birds, amphibians, reptiles and lepidopterans (Atauri and de Lucio 2001). Rivers in the area meander, changing their courses during heavy rains (cf., Latrubesse et al. 2005), and lake communities are constantly renewed as Lakes are man-made (below). Temporary water is, by definition, ephemeral. These factors combined would ensure new successions of species communities, thus favouring mobile species and pioneers. Renner et al. (2016c) noted that man-made lakes in forested environments mainly attracted vagrant

and generalist species from surrounding areas, a well-known pattern in dragonflies (cf., Juen et al 2014). In our case we see another pattern: the constantly changing landscape of the Grasslands will favour dispersal and colonization and, hence, we suspect that part of the original species community in this biome consisted of good colonizers.

High species richness, variation and dispersal would create possibilities for formation of unique communities, and in our area we noted that small streamlets/swamps where clear and cold water surfaces from underground sources hosted some of the most unique species assemblages (Renner et al. *in press*). Looking at the occurrence of common, rare and unique species in our water body types we see that the commonly occurring species appear in equal numbers in all three habitat types. According to the Jackknife1 calculation and the species accumulation curve, we expect that we have missed a number of species occurring in the area, but as sampling was made in a similar way but at random daytime (10:00 - 16:00) at all localities we expect a similar amount of 'noice' at all localities and in all our groups. Our findings are easily explained by the fact that many of the common odonate species are indeed good dispersers and usually have a generalist distribution pattern (Nobrega and De Marco 2011; Renner et al. 2016b). The rare species show a different pattern as the Temporary water sites host less than half the number of such species compared to the two permanent habitat types. It is a common pattern that Temporary water bodies, in comparison with other aquatic habitat types, host few rare and many generalist species (Collinson et al. 1995). Temporary water bodies are ephemeral, and the fact that species with long life cycles cannot reproduce in this habitat is the basic reason behind the low numbers. But looking at the unique species, only four of them were found in Temporary water; the same number as in our Lakes. Here we suspect that as lakes are to a large part man-made in the Pampa, fewer unique species have had time to establish there compared to Rivers/streams, which constitute the original aquatic

environment and attracted nine unique species in our study. (Table 1). Therefore, both

Rivers/streams and Lakes have a diverse fauna, but the fauna in Lakes has formed recently

and is largely dependent on human activities. This pattern was shown in Atlantic Forest by

Renner et al. (2016c), where communities in man-made lakes and natural aquatic systems

were compared. The same pattern was seen in Namibia where lakes in an arid area had a

distinct species composition, predominantly comprising generalist species with good dispersal

abilities (Suhling et al. 2006). Thus, Lake communities consisted of widespread, and in many

case generalist species, which we assume might be a universal pattern for dragonflies.

We also see this pattern when considering the land cover variables. It is well known that

terrestrial factors are very important to adult odonates, while the aquatic factors are more

crucial to larvae (Suhling et al. 2015). Terrestrial factors may limit the dispersal of certain

species and prevent their egg laying, while at the same time favouring other species (e.g.,

Stoks and Cordoba-Aguilar 2012). It has also been shown that different species inhabiting

different environments disperse differently, for instance, McPeek (1989) showed that

damselfly species breeding in fishless environments dispersed more than species breeding in

environments with fish. In our area all land cover types except Sand had the same number of

generalist species (9; Table 1) and, as mentioned above, differences increased for the rare and

unique species. The land cover types which were originally occurring in the Pampa,

Grasslands and Forests, have double the amount of rare species compared to the more recent

types Arable Land and Sand. The number of unique species was highest in Forests (17), but in

Grasslands only 10 such species were encountered - a number comparable to that found in the

other land cover types. The unique species found at any forested sampling site are often small

zygopterans, which are assumed to be weak dispersers (Paulson 2006; Juen et al. 2007). This

is naturally an oversimplified division, as Zygoptera is a taxonomical and not an ecological

unit which contains both good (Flenner and Sahlén 2008) and weak (Lorenzo-Carballa et al. 2015) dispersers, but as a generalized assumption it is valid also when analysing large scale species patterns (Heiser and Schmitt 2013). Following this idea; in the open grassland, where distances between suitable habitats are longer and the surroundings more exposed (cf., Corbet 1999), fewer of the smaller bodied species are able to occur. Our study thus revealed that Rivers/streams in the two more original land cover types Grasslands and Forests house the distinctly most complex and species rich communities in the Pampa, the variation of species being highest in the riparian forests.

Bunn and Arthington (2002) showed how precipitation regimes may affect aquatic organisms, but they stated that it is difficult to separate changes deriving from land use to those caused by the flow change. In our study, we can now make a preliminary evaluation of the community patterns we see in our respective land use groups. In the NMDS (Fig. 4) the three water body types are oriented in the same way in all four land cover groups. Wellborn et al. (1996) showed that the community structure across the gradient of temporary to permanent water is determined by physical as well as biotic effects, the latter driven by ecological interactions. In our case we have the two permanent water types (Rivers/Streams and Lakes) at one end and the temporary habitats at the other end; surrounded by our four different types of land cover. The presence of a general pattern in the community structure is clear. Heino (2010), reviewing cross-taxon congruence in indicator species, stated that there was no evidence that many species occurring in a single group can predict the amount of species in another. Instead, we have seen a pattern where different ecological – functional groups of Odonata are always present in the environment, regardless of land cover and type of water body. The species differ between sites, but their function/position in the food web might be the same. Some examples are the 6 species in the family Aeshnidae (Supplementary material) which all

occur in Rivers, 4 of them also in some Temporary water and 3 of these in some Lakes as well. Thus, the presence of Aeshnidae species, mainly in Rivers, and in all land cover types, might constitute one determinant for the species community. Three other examples are the damselflies *Neoneura leonardoi*, *Oxyagrion hempeli* and *Oxyagrion rubidum,* which are also selective and were found only in Rivers in Forests and Grasslands. An opposite example is the genus *Erythrodiplax*. We found 8 species in our study, all but 1 occurring in all water types and all land cover types. This genus has a generalist habitat selection (Valente-Neto et al. 2016) and will not be a determinant of the community structure. The number of specimens and the number of sites is still too low to make a complete analysis, and hence, with our limited data, we cannot determine a standardised community structure for our aquatic and land cover groups. As our sampling effort and timing during the day and over the seasons will also affect our analyses, we recommend more dense and even more standardised sampling for further studies. Our examples of species and communities might serve as preliminary candidates, but further work is needed. We predict that a focus on the primary Pampa habitat Rivers/Streams with riparian forest in Grassland, would be rewarding.

We also have the sandy areas to consider, and from a colonisation perspective these are probably the newest addition to the biome (Overbeck et al. 2013). A clear difference compared to the other land cover areas was that not all common species were present at the sandy sampling sites. We assume this indicates that not all generalists can cope with the conditions prevailing there. This type of environment harbours a peculiar set of species, possibly adapted to dry/hot conditions. Three interesting examples from our dataset are *Aphylla molossus*, *Orthemis aequilibris* and *Tholymis citrina* (Supplementary material), all being rare and found in temporary water only.

Conclusion

Here we present the first evidence of community patterns where certain constellations of Odonata species, probably occupying different ecological niches, form species communities in the Pampa of southern Brazil. We believe that the same components can be found in the communities of Lakes, Streams/Rivers and Temporary water regardless of the type of land cover surrounding the sites. The highest diversity was found in Rivers/Streams and in Forests and Grasslands. These habitat types are probably the most ancient and established ones in the biome, possibly still harbouring the most original species pool within this area. The original patches of Pampa in the region are known for their high levels of endemism within other organism groups, and we see a constantly growing problem of increasing human impact. The great variation between our sites in the original habitat types also makes these localities highly sensitive to disturbance. While the species most original or characteristic of the Pampa biome are found around rivers and streams with native riparian forest in grassland areas, the numbers of altered or degraded habitats increase rapidly (e.g. man-made lakes and agricultural areas). Such environments may develop species rich communities consisting of a high proportion of generalist species, quickly shifting the whole species pool towards a less complex and much less unique species community. We therefore suggest that conservation efforts should focus on the original habitat types, but we would also like to stress that there are still many questions regarding what factors are essential to the occurrence of the original species. Hence, further research, accumulating data on a range of target taxa, is necessary. In doing so, we should be able to determine priority areas for conservation of the biome as a whole.

Conflict of interest: The authors declare that they have no conflict of interest.

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CHAPTER 4

The balance of common vs. rare: a study of dragonfly (Odonata) assemblages in the Brazilian Pampa biome

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Running title: **Common vs. rare in Odonata assemblages**

Abstract: We surveyed dragonflies (Odonata) at 87 sites in the anthropologically changed Pampa biome of southern Brazil to evaluate how regionally rare and common species form species assemblages in different types of water and the relationship between assemblages, habitat structures and environmental factors in the area. We classified 9 out of the 90 species encountered as regionally common and 59 as regionally rare. A discriminant analysis confirmed that localities with only a few common species were characteristic in the set of rare species present, while localities housing more common showed no clear pattern. A PCA revealed that a subset of the common species were strongly positively associated to water temperature, quality and pH, but negatively associated to desertification. In contrast, rare species were positively associated to grassland habitat but negatively to agriculture, salinity and conductivity. In general the associations of the rare species were weaker. Finally, a correlation confirmed that sites with six or more common species present had a reduced number of rare species compared to sites with fewer common species. It is possible that the common species reduce the available niche space for weaker competitors among the rare species. We conclude that the original species assemblages in the biome may have been species poor with few regionally common species. Current anthropogenic change has increased the number of common species which in turn have had negative effects on the survival possibilities for rare species.

Key words: anthropogenic change, commonness, competition, niche space, rarity, Neotropics

Introduction

In general, animal communities and their distributions are shaped by environmental factors and biotic interactions (Leibold *et al* 2004, Brasil *et al* 2017). The complexity of assemblage structure and distribution is the result of an interplay of patch dynamics, neutral effects, species sorting and dispersal capabilities (Soberón 2007). In natural systems, the geographic separation between communities or metacommunities acts as a major factor: communities inhabiting patchy environments are shaped by the interaction between these 'islands', and these interactions mostly occur by the means of emigration and immigration at local and regional scales (Hanski 1982, Šizling *et al* 2009).

Although not always determinant for range size at regional or even global scale (Lester *et al* 2007), dispersal capability is a key component, which also directly influences the local community (Taylor 1990). The influx of immigrant species or specimens is important, but in turn dependent on how long the range of dispersal for a given species is. Long range dispersal is a well-studied (Rosindell & Cornell 2009) and common phenomenon in birds (Milot *et al* 2008) and mammals (Sutherland *et al* 2000) but more rarely studied in arthropods (but cf. Green & Figuerola 2005, Viana *et al* 2013, for long range dispersal via water birds). The most striking examples of long range dispersal in insects are probably those of *Pantala flavescens* Fabricius 1798 (Odonata: Libellulidae), which were shown to migrate at global scales (Troast *et al* 2016) and the Monarch butterfly (Urquhart & Urquhart 1978), but most arthropods move shorter distances. Also at local scale, biotic interactions, such as interspecific competition, has proven to be of great importance in community structuring dynamics (Hanski 1982, Gutiérrez *et al* 2014). Another example is the spatial competition hypothesis addressed by Rosindell & Cornell (2009). We therefore know that common species influence the presence of rare species, as proven e.g., by studies on several animal groups such as butterflies (Thomas &

Mallorie 1985), ants (Kunin & Gaston 1993), and also among vertebrates (Berg & Tjernberg 1996, Maguran & Henderson 2003).

Regarding aquatic systems, at small spatial scales the environmental conditions are among the most important factors determining community structure (Novelo-Gutiérrez & Gómez-Anaya 2009, Monteiro-Júnior *et al* 2014, Oliveira-Junior *et al* 2015), since the presence or absence of species will depend on the prevailing conditions, e.g. species sorting (van der Gucht *et al* 2007). This pattern was shown for North African damselflies, where prevailing environmental conditions were determinant for the presence of certain species (Ferreira *et al* 2015). On niche scale, habitat heterogeneity and the amount of structural elements are determinant to composition and dynamics of animal populations (Hutchinson 1957). Moreover, on this scale, physical parameters, such as water conditions (temperature, pH, oxygen, etc.) are crucial components acting as 'selection variables' for species niche occupancy (Leibold 1995, Otto *et al* 2014). Further, the intensification of human disturbances is one of the main triggers of assemblage changes over time (Wagner *et al* 2000), resulting in species declines, loss and changes in species composition (Benton *et al* 2003; Hendrickx *et al* 2007), affecting specialist (more sensitive) and generalist (highly adaptive) species alike (Renner *et al* 2016a).

All communities are composed of a small number of common species and a larger set of rare ones (Bulmer 1974). The term rare does not automatically imply that a species is threatened in any way as there are many different reasons for a species to appear less commonly in an area. According to general theory this pattern is universal, but in many cases there are even more rare species than expected (Magurran & Henderson 2003). Surveying common species is easy, as they should be present in a large percentage of the samples, but it is always difficult to survey for rare species, as has been discussed when selecting indicator species (Sahlén &

Ekestubbe 2001 and references therein). Further, most of the known species tend to be rare and have small ranges (Pimm *et al* 2014). The turnover rates for rare species are higher, they disappear more often from sites, and if they are locally extinct they require longer time to re-immigrate than do common species (Volkov *et al* 2003). However, the rare species are often more interesting from a conservation point of view and many decision makers rely on information about rare species alone (Gärdenfors 2001, Gauthier *et al* 2010). We hence found it challenging to investigate how common species regulate the occurrence of rare species in a set of aquatic species assemblies in a not so well surveyed area of Pampa, southern grassland, in southern Brazil.

We used dragonflies (Odonata) as model organisms; this group has been frequently used in ecological studies and is known to react to landscape change (Juen *et al* 2007, Brasil *et al* 2017), climate change (De Block *et al* 2013) and water chemistry (Al Jahaweri & Sahlén 2016). It has been suggested as a useful bioindicator group (Corbet 1999, Sahlén & Ekestubbe 2001, Renner *et al* 2015). As the group is semiaquatic with aquatic larva and a terrestrial adult, both stages are selective in terms of habitat choice (cf., Corbet 1999).

We asked the following questions: 1) How will regionally common species interact with or affect rare ones, and the overall species assemblages in different types of water in the area? 2) What are the relationships between these assemblages and the habitat structures and environmental factors present in and around these water bodies. We hope that the knowledge gained here may shed more light onto the complex interaction of species, in our case aquatic insects, in an assemblage or in a community in general.

Materials and Methods

Study area

The study was performed in the Pampa biome in southern Brazil. This biome is one of the least known in the Neotropics (Overbeck *et al* 2013). Several studies performed in this area have shown that certain organism groups have high diversity and high levels of endemism, at least regarding the flora (MMA 2009, Behling *et al* 2004). These grasslands are under high pressure from cattle farming, agriculture and forestry; especially the latter has resulted in the conversion of vast areas into exotic tree plantations of *Eucalyptus, Pinus* and *Acacia* (Bencke 2009, Overbeck *et al* 2013, Roesch *et al* 2009). Already ten years ago government data showed that only 36% of the original vegetation remains in a highly fragmented mosaic (MMA 2009), this should be put in relation to the fact that only 0.5% of the biome is officially protected (Overbeck *et al* 2013).

We sampled adult odonates in 87 sites within the Pampa biogeographical domain. The sites were clustered in seven regions: Alegrete (N = 14); Quaraí (N = 5); Uruguaiana (N = 7); Manoel Viana (N = 13), São Francisco de Assis (N = 32); Santana da Boa Vista (N = 11); Caçapava do Sul (N = 5), ranging from 29°24' to 30°55' S and 53°07' to 56°29' W (Fig. 1). The areas have mean annual temperatures between 13°C and 17°C, altitudes from 50 to 200 m.a.s.l. and mean precipitation between 1,200 to 1,600 mm annually (INPE 2014) corresponding to temperate climate (Cfb Köppen).
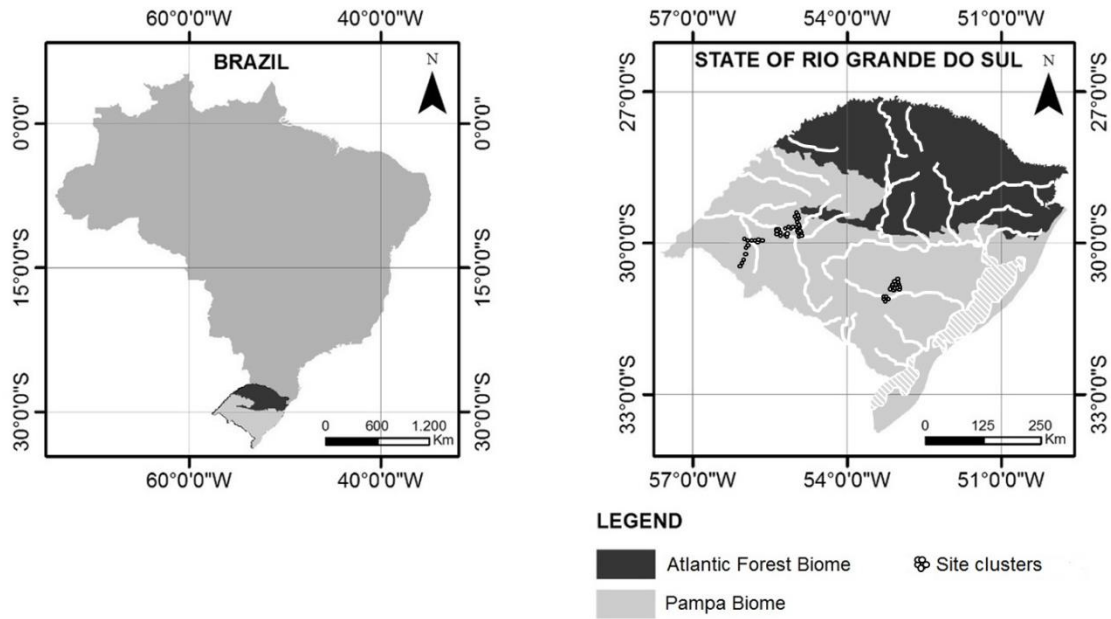
Fig 1 Map of Brazil, Rio Grande do Sul state in the south highlighted, with Atlantic forest biome in black and Pampa biome in light grey. Sampling sites clustered in seven regions, shown as open dots. Some sites overlap at this scale. Large rivers in white with lagoons shaded.

Species sampling

Our species appear as clusters at a range of sites in a varying landscape, i.e. we have not a homogeneous landscape, and consequently more of pattern diversity (cf., Scheiner 1992). As pattern based diversity is fairly insensitive to the intensity of sampling (of rare species) we strived for an average sampling effort per site and not to find all possible species in the habitat. We sampled adult dragonflies from March 2015 to January 2017, visiting sampling sites 1-5 times during this period, often once per season excluding winter months (May-August). Temporary sites were, with some exceptions, visited only once. We used the method described by Renner *et al* (2015): hand-held insect nets by a team of two people in sunny days during the peak activity of Odonata (09:00 h to 16:00 h). We collected along the edges and marginal zones of waterbodies; distances varying in length according to the size and shape of

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the water; the average time spent per site was 30 minutes. For each site we noted the species present and the number collected. The sampling sites included the whole range of different waterbodies in the region, suitable for Odonata: from large river sections, to man-made lakes and temporary water. Our sites were mostly small in size, often around 100 m in length (for lotic environments) or diameter (for lentic water bodies) up to bigger lakes with a surface area of many hectares. Part of this dataset has been used to evaluate effects on land use on species composition in the area (Renner *et al* 2018).

The specimens were determined to species level according to Garrison *et al* (2006, 2010), Heckman (2006, 2010) and Lencioni (2006, 2017); consulting original species descriptions and external experts when needed. The specimens were deposited in the MCNU (Museu de Ciências Naturais da Univates). The collection authorization process was issued by ICMBio, through the SISBio system under the number 50624-1.

Environmental variables

Using recent (2013-2016) satellite images available via Google Earth Pro™, we quantified seven land use variables inside a circular perimeter of 1 km² with its center at the midpoint of the sampling site. Using the program's area measuring tool, we quantified the cover percentage of each variable inside the perimeter. All areas were visible in the map program without any presence of clouds or haze. The land use variables were chosen as follows:
- forest: mostly riparian forests which are the commonest formations in the area, also isolated gallery forest patches scattered in the landscape as 'islands';
- forestry: often plantations of exotic trees with commercial purposes, in the Pampa the most common species used are *Eucalyptus* sp., *Pinus* sp. and *Acacia* sp.;

- grassland: areas used for cattle grazing, considered both native and also areas with exotic grass species, e.g. *Eragrostis plana* (Poaceae), an African grass species;

- agriculture: planted areas for crop production, the most common crops grown in the region are rice, soybeans and corn;

- water surface: areas covered by the water bodies within the perimeter; some water bodies, e.g., large rivers, continued outside the circle);

- human built structures: roads, buildings and urbanized areas;

- sand: erosion sites caused by the loss of vegetal layer and on-going desertification processes which are taking place in several localities of the Pampa.

At each site we also measured temperature, pH, conductivity, turbidity, dissolved O_2, total dissolved solids and salinity using a Horiba multi-parameter water quality meter (Horiba Co., Japan). At some temporary locations (20) these measurements had to be excluded due to low water levels.

Species numbers and classification

In total, the dataset contained 90 species. We classified them into regionally common (occurring at ≥30 localities in the dataset; 9 species in total) and regionally rare (occurring at ≤ 10; 59). There is no consensus of what constitutes a rare vs. a widespread (common) species and, as pointed out by Hartley & Kunin (2003), rarity should if possible be explained by different factors. This is, however, often not possible when dealing with species where ecological information is scarce (Fattorini 2013) such as the Pampa of southern Brazil. We therefore use a simple classification of common vs. rare, similar to that used for dragonflies in two other studies. Sahlén & Ekestubbe (2001) and Suhling *et al* (2006) used percentages to

classify species as 'moderately common', we adapted this method based on our dataset,

allowing for lower and higher percentages respectively.

We further classified the localities into three categories based on the number of common

species encountered: 1) 0 - 2 species present; 2) 3 - 5 species present; and 3) 6 - 8 species

present; no locality had all 9 common species present. Based on this we classified the rare

species according to their occurrence at localities with different numbers of common species:

a) species present only at localities with up to 2 common species; b) present at localities with

up to 5 common species, and c) present at localities with up to 8 common species.

Data analyses

We tested the spatial independence of the 87 sampling sites related to species composition

using a Moran's I analysis. We used individual species occurrence as variables in a Principal

Components Analysis (PCA) where the first axis was used as response variable to the

Moran's I with coordinate variables for ten different distance classes. The global Moran's I

analysis did not detect any significant spatial structure of the species composition for any

distance classes (minimal distance class average: 0.01 degree; Moran´s I=2.29; p=0.61), and,

hence, spatial structure was not included in further statistical analysis.

We performed a discriminant analysis to investigate whether the distribution of the rare

species at sites with different numbers of common species present were random or not. As the

collecting method tend to favor rare species over common ones as all specimens of common

species are not collected, we used the relative abundance of the species at all sites as

independent variables, using ln(n+1) transformation to level out high differences in numbers

of collected specimens. We used the three categories of common species (above) as grouping

variable. This procedure results in two discriminant functions, each with an Eigenvalue informing of the efficiency of the function and a Wilks' lambda value measuring how well the function separate cases into groups. The latter value corresponds to the proportion of the total variance not explained by differences among the groups, meaning that a smaller value mirror a higher discriminant ability of the function. The classification results presents how well the three groups formed by the presence of a number of common species can be predicted by the species assemblage of rare species. The analysis was carried out in SPSS v20.

In a second analysis we wanted to verify which of the environmental variables had the highest impact over the Odonata assemblies to investigate whether common and rare species reacted differently. To do this, all environmental variables were entered in a PCA using the varimax method, first to investigate any interrelationships between them and also to reduce the number of variables for the CCA analyses (below). We used the scree method to determine the number of factors retained. We used ln (n+1) transformed data to normalize variation within and between variables. Associations with eigenvectors higher than 0.65 (positive or negative) were considered relevant in the evaluation. The analysis was carried out in SPSS v20.

We used the principal components derived from the environmental variables for two CCA analyses: In the first we used the ln(n+1) transformed relative abundance values for the rare species to identify species or species groups which are strongly impacted on by the PCs. The second analysis used the same type of dataset but for the common species. The CCA model used forward selection with 999 permutations. As the relationships between species and environmental variables are assumed to be unimodal in a CCA, rare species suffer by not occurring in a high enough number of sites. For the evaluation of the rare species we therefore

focused on species found in at least three sites in the dataset, removing the others from the analysis. The analyses were carried out in PAST v3.14 (Hammer 2015).

Finally we made partial Spearman correlations between the number of common and rare species present at the sites, separated according to the span of occurrence of the rare species; groups as above. The data were controlled for the total number of species observed at the site. The objective here was to see whether the number of common species at a locality was correlated to the number of co-occurring rare species.

Results

Our results indicated that the number of rare as well as common species at each site was low. We noted that sites with few common species had a characteristic composition of rare species while sites with more common species were dissimilar in rare species composition. Further, our CCAs showed that all common species but one were affected by environmental variables (as per PCs), while most of the rare species were not. Correlations showed that fewer rare species were noted at sites with a high number of common species present. Below we present the results in more detail.

We found at least one common and one rare species at 86% of the sites (N = 75). We found no common species at 3 of the sites (3.4%) and no rare species at 9 sites (10.3%). The average number of common species at all sites was 3.90 ± 2.01 SD while the average number of rare species was 2.43 ± 1.74. The most species poor site with both species categories present had 2 (1 rare and 1 common) species. The most species rich site had 13 (7, 6).

The discriminant analysis used two discriminant functions of which the first was significant (Eigenvalue = 5.134, Wilks' lambda = 0.085, χ^2 = 139.1, df = 112, p = 0.042) and explained 84.9% of the variance. In total, 89.7% of all habitats could be classified according to the number of common species present based on their rare species assemblage structures. Our classification separated all sites with 0-2 common species present (group 1) from the rest, while groups 2 and 3 were slightly mixed (with 9 of the localities wrongly classified; Fig. 2). Sites with only a few common species could thereby be identified based on the rare species occurring while this pattern becomes unclear for sites with a higher number of common species.
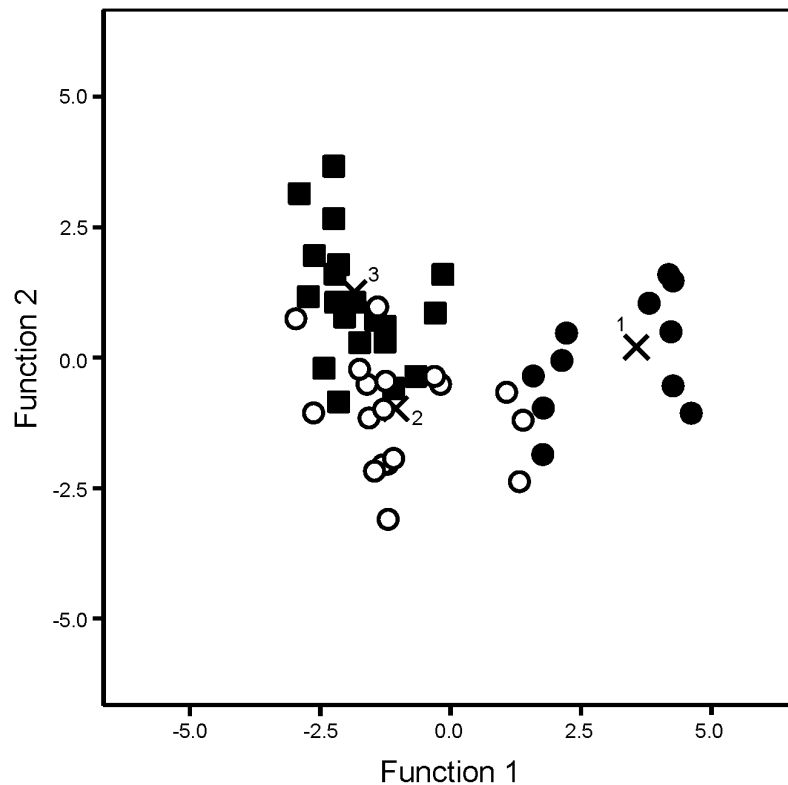
Fig 2 Discriminant analysis for three groups of common species using the relative abundance, (ln (n+1) transformed) of the rare species as independent variables. 1 (black circles) = 0-2

common species, 2 (open circles) = 3-5 common species and 3 (black squares) = 6-8 common

species at the locality. Group centroids marked as 'x'. Several localities appear on top of each

other and are not visible in the figure. Localities with only a few common species have a more

distinct composition of rare species than localities with a higher number of common species.

The scree method extracted four factors from the PCA explaining 68% of the total variance.

Principle component 1 (PC1) explained 31.4% of the variance and was strongly associated to

temperature and pH, but also to turbidity, and dissolved O_2. Further, it was negatively

associated to sand (Table 1). PC2 explained 15.6% of the variance and was negatively

associated to conductivity and salinity. PC3 explained 12.7% of the variance and was strongly

associated to grassland and negatively associated to agriculture. The last factor, PC4,

explained 8.4% of the variance and was associated to forestry (Table 1). There were no

associations to the four original variables forest, water surface, human structures and total

dissolved solids.

Table 1 Results of principal component analysis on environmental variables measured at the collecting sites. Bold digits indicate high eigenvector values.

Original variable	Principal Component			
	1	**2**	**3**	**4**
Temperature	**0,913**	0,295	0,137	0,031
pH	**0,928**	0,202	0,114	0,074
Conductivity	**0,614**	**-0,650**	0,156	0,031
Turbidity	**0,695**	0,391	-0,004	-0,181
Diss. O_2	**0,742**	0,450	0,039	0,057
Total diss. solids	0,389	-0,538	0,284	-0,206
Salinity	0,308	**-0,773**	0,203	0,033
Forest	-0,099	0,487	0,299	-0,500
Forestry	-0,242	0,169	0,034	**0,751**
Grassland	-0,232	-0,080	**0,850**	0,078
Agriculture	0,355	-0,146	**-0,739**	0,055
Water	0,481	-0,135	-0,247	0,251
Man-made struct.	0,121	0,264	0,424	0,454
Sand	**-0,738**	0,082	-0,053	0,010

Only the second axis in our CCA for the rare species was significant. It explained 30.25% (Eigenvalue 0.3512, P = 0.042) of the cumulative variance (Fig. 3). Along axis 2, PC2 and 3 (positive to grassland, negative to agriculture, salinity and conductivity) had the biggest effect on the occurrence of the rare species. The species *Neoneura leonardoi* Machado, 2005, *Coryphaeashna perrensi* McLachlan, 1887, *Cyanallagma bonariense* Ris, 1913, *Oxyagrion hempeli* Calvert, 1909, *Macrothemis imitans* Karsch, 1890*, Miathyria marcella* Selys *in* Sagra 1857 were positively correlated to these components while *Negriagrion* sp., *Micrathyria*

longifasciata Carlvert, 1909, *Orthemis atenuata* Erichson, 1848, *Macrothemis lutea* Calvert, 1909, *Telebasis theodori* Navás, 1934, *Tholymis citrina* Hagen, 1867, *Erythemis vesiculosa* Fabricius, 1775 and *Rhionaeschna planaltica* Calvert, 1952 are negatively correlated.
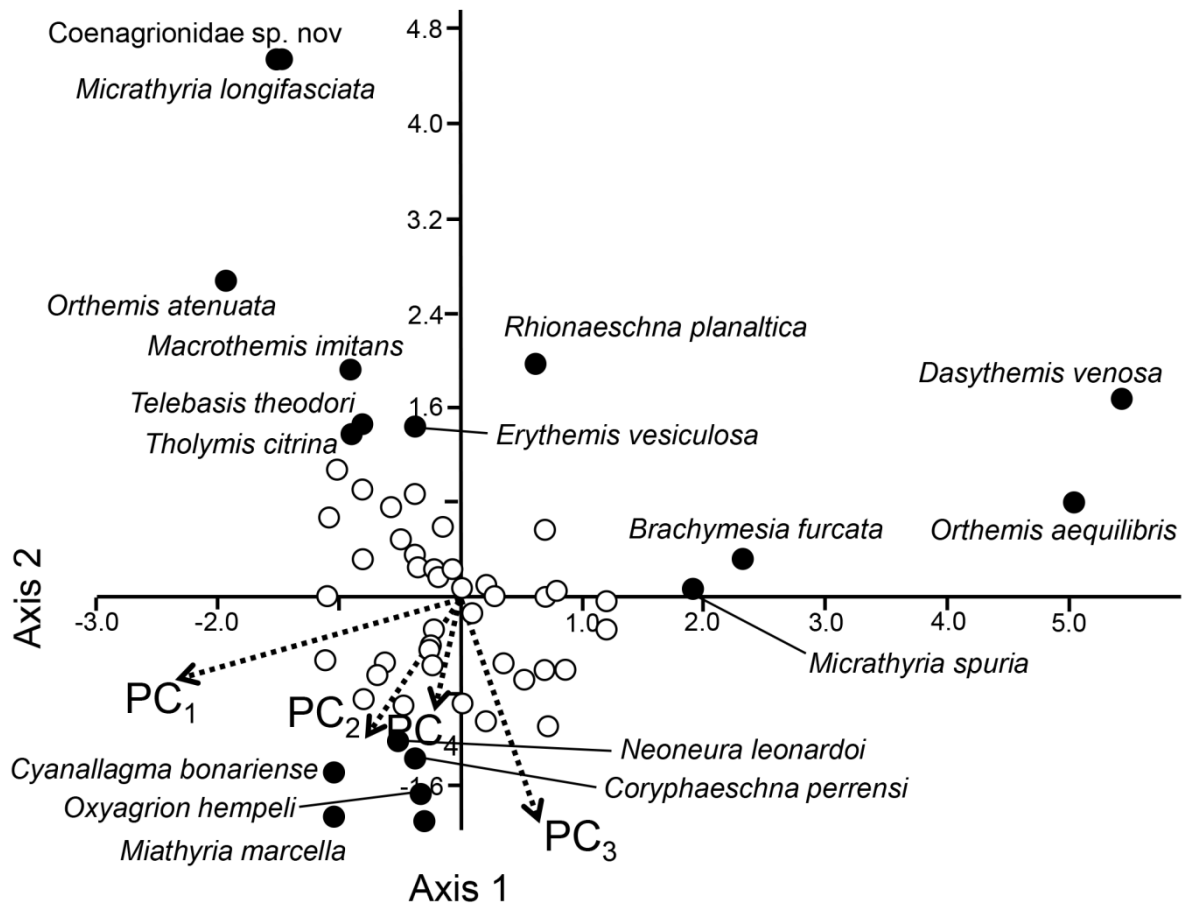
Fig 3 CCA plot based on the relative abundance of rare species and the four principal components. Most common species (empty circles) appear near the centre of the ordination and are only moderately affected by the PCs. A small set of species, e.g., *Micrathyria longifasciata*, *Orthemis aequilibris* and *Dasythemis venosa* are strongly (negatively) affected by PC1 and PC3 while the rest of the rare species (filled circles) are moderately affected.

In the CCA for the common species the first two axes were significant (Axis 1 explaining 62.32 % of the cumulative variance, Eigenvalue 0.050, P = 0.001; axis 2 explaining 21.71 %,

Eigenvalue 0.017, P = 0.043; Fig. 4). PC1 had the most pronounced effect on the occurrence of species, with higher values corresponding to high relative abundance of *Ischnura fluviatilis* Selys, 1876*, Acanthagrion gracile* Rambur, 1842 and *Perithemis mooma* Kirby, 1889. Further, *Pantala flavescens* was negatively affected by PC1. PC1 correspond to high temperature, pH, turbidity and dissolved O_2 and also to low amounts of sand. PC2 had the same direction as PC1 but the effects were much weaker. PC3 and 4 correlates positively to *Erythrodiplax atroterminata* Ris, 1911 and *Erythrodiplax* sp. (1), and negatively to *Perithemis mooma*. These components correspond to a high amount of forestry and grassland and a low amount of agriculture.
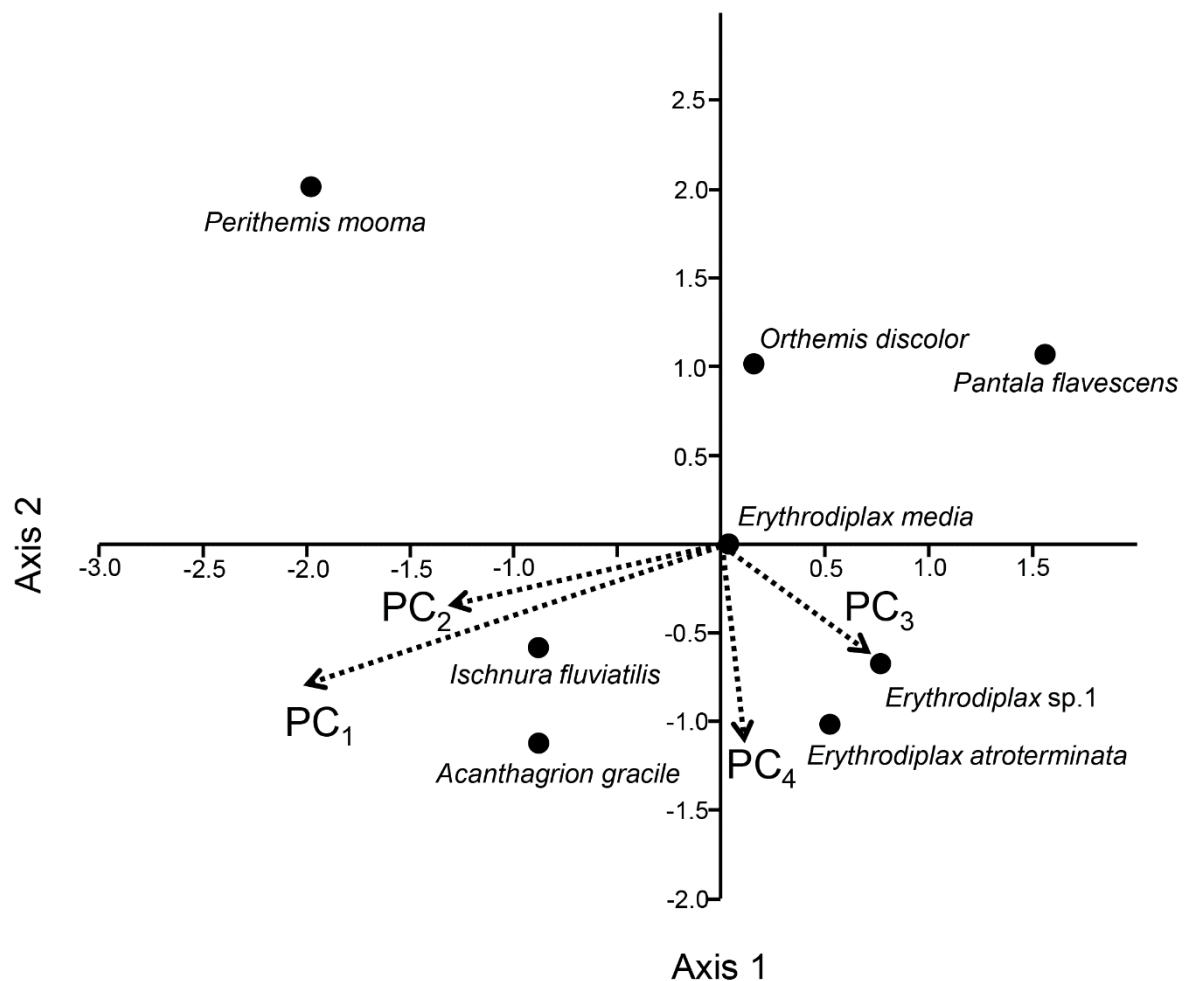
Fig 4 CCA plot based on the relative abundance of the common species and the four principal components. The small damselflies *I. fluviatilis* and *A. gracile* are positively associated to PC1 and 2 while the *P. flavescens* is negatively associated. Further, two *Erythrodiplax* species are positively associated to PC3 and 4, with *P. mooma* negatively associated. *Erythrodiplax media* is not affected by any of the variables corresponding to the PCs.

The number of rare species per site was not correlated with the number of common species (Spearman correlation; $p = 0.115$) when controlling for total species number. Looking at the abundance groups of common vs. rare species we noted that when the number of common species per site was high (6-8 species; group 3) there was a negative correlation with the number of rare species at the sites (group c; Spearman correlation, $p = 0.014$, $r = -0.49$) when controlling for total species number. There was no correlation between the groups of few common/few rare species (1 vs. a; $p = 0.57$) or between groups 2 and b ($p = 0.86$). There were fewer rare species present when there was a higher number of common species present.

Discussion

In this study we showed two main things: First, when only few common species occur at a site, the rare species composition differed from that at locations with a higher number of common species present. Second, localities with more than five common species harbored fewer rare species than localities with a low number of common species. Hence, the Odonata communities in the Pampa biome are to a big extent shaped according to the presence or absence of a small set of regionally common species.

In an earlier paper we showed how landscape variables and habitat types affect species diversity of Odonata in the Pampa (Renner *et al* 2018). Here we studied the effect of the

species themselves in shaping and affecting the species assemblages apart from the landscape environmental variables. The fact that the density or amount of common species is regulating the occurrence of the rare species in the ecosystem has been shown by e.g., Kunin & Gaston (1993) and Siqueira *et al* (2012). There are several aspects that differentiate common from rare species; dispersal capabilities are generally higher in common species (Suhling & Suhling 2013, Borthagaray *et al* 2014), their life-history strategies involve more competition and are accelerated (Nylin & Gotthard 1998, Johansson & Rowe 1999, Therry *et al* 2014), and they in general have a wider environmental preference (Cornwell & Ackerly 2010). From this we can achieve a deeper comprehension of the patterns of dragonfly niche occupancy in the Pampa biome. Patch occupancy has also been considered one of the major factors regulating the proportion of rare vs. common species, since specialized species are known to require a set of specific ecological features to inhabit a location (Kassen 2002, Paulson 2006) and with the global homogenization of habitats specialized species are declining (Clavel *et al* 2011). If niche overlap between common and rare species is high at a location, the competition for resources affects foremost the rare species negatively, as these are inferior competitors and more sensitive to both intra- and interspecific competition (Yenni *et al* 2017), as well as to changes in the environment (Renner *et al* 2016c).

In an assemblage with a high number of common species most niches will be occupied, making it difficult for populations of rare species to establish or persist; this was shown by us in the lower number of rare species at locations with six or more common species. Further, many common and generalist species grow more rapidly and have shorter life cycles than specialized species and are able to have several generations each year. One such example was shown in arid regions in southern Africa by Suhling *et al* (2003), who noted that big, highly mobile and multivoltine species (e.g. *Pantala*, *Sympetrum* and *Crocothemis*) impaired the occurrence of rare and specialized species and prevailed over many slow-growing and rare

species. Similar patterns were observed in other studies comparing rare to common species (e.g., Southwood 1996, Magurran & Henderson 2003). These authors suggested that the balance of common vs. rare insect species might to a great extent be affected by the inflow of migrants, this may also be the case in our study area as many of our common species are known to be good dispersers (i.e., genera such as *Pantala*, *Orthemis* and *Tramea*).

Besides the rare/common relation in the communities, we also for the first time in this biome observed the major effects of land use and environmental variables on the whole Odonata assemblies. Here we show that common species are, to a higher degree than rare species, affected by environmental variables. The CCA values (Figs. 3 and 4) indicate that rare species are affected by grassland (positive) and agriculture, salinity and conductivity (negatively). Common species, on the other hand, are strongly affected by high temperature, pH, turbidity and dissolved O_2 and also by low amounts of sand. We deduct that the factors influencing the common species would all be apparent in open, windy areas where species would need to tolerate a high mineral content, and open lake areas (a man-made habitat in the area) with high nutrient concentration. These type of habitats are less common in areas with desertification. If we infer that most of the ancient/original land cover of the Pampa was similar to the remaining grasslands we see today (albeit changed due to many anthropogenic activities; cf., Santos & Silva 2007), we may hypothesize that these habitats would be the most suitable for the original species composition in the biome. This has been shown in other studies comparing dragonfly communities from original patches of the environment to altered ones (Juen 2015, Renner *et al* 2016b), and also in other taxonomic groups such as soil microbes (Lupatini *et al* 2013), birds (Mörtberg 2001) and among groups occurring together: birds, amphibians, reptiles and lepidopterans (Atauri & de Lucio 2001). The basic pattern we revealed here is that most of the assemblages seems to be composed of just a small selection of species and could even be considered species poor (2-13 species per locality in the area).

This number may e.g., be compared to northern European environments (Sahlén & Ekestubbe 2001, Koch *et al* 2014), where the regional species pool is as low as 30-40 species compared to the 90 registered for the Pampa region in this study. It is therefore likely that a 'normal' species assembly in this biome is one of very few species. As the original dominating type of environment here is the natural grasslands, we can imply that the openness of these is more favorable to species with high dispersal capabilities (cf., Corbet 1999); several of these were also common in our study.

Previous studies on dragonfly species composition to test the effects of environmental changes caused by man (Raebel *et al* 2012) and on dragonflies with different life-histories affected differently by environmental changes (Kadoya *et al* 2008) corroborate our results, leading us to some speculation about species-specific ecological needs. Many rare species have been shown to be negatively affected by local scale changes (Raebel *et al* 2012, Renner *et al* 2016c), as well as by large scale human modifications of the environment. Also, the migratory or long-range dispersers depend on the quality of the features in the terrestrial landscape (Raebel *et al* 2012), not only for migration purposes, but also for feeding and roosting (Samways & Steytler 1996, Corbet 1999). There is still a severe shortage of ecological knowledge on most Neotropical dragonflies (Garrison *et al* 2010), and, hence, we need to discuss environmental factors instead of specific requirements. Further, there is a similar lack of information whether the rare species also are threatened, since there are big gaps in species assessments compared to other regions (Clausnitzer *et al* 2009). IUCN red list assessments have recently started for the Neotropic odonates (Muzón *et al* 2017), but most of the species are regarded as "Data deficient" (Muzón & Lozano 2016).

Assessing the status of rare species is difficult also from another point: a rare species is disproportionately vulnerable to extinction in the short term (Gaston 2008), due to human

interference, habitat loss, degradation or other factors. Nevertheless, rare species may also be affected by factors which are more difficult to quantify, mainly biotic ones; an example is our main result, which shows that the abundance of common species directly affects the density of the rare ones. Common species on the other hand respond to more conspicuous environment variables as shown by Lennon *et al* (2004) using birds, Sheldon (1988) using fishes and Arita *et al* (1990) using forest mammals. The sensibility of rare species and their higher risk of extinction stimulate the choice of selecting them as references for conservation purposes, as shown in many publications (e.g. Caughley & Gunn 1995, Gaston & Blackburn 2000, Baillie *et al* 2004). In this context, comparative studies of the interaction between rare and common species are important and could help in acquiring the knowledge needed regarding rare species survival. Given the vast number of rare species and how little is known about them (Kuning & Gaston 1993) vs. the generally small number of common ones, this is a promising field for further studies.

As Hodgson (1993) showed, the number of attributes determining species abundance is high and ecological factors therefore often complex. For Amazonian trees, environmental and spatial variables could explain a set of attributes of common species but not for rare ones (Bispo *et al* 2017). But certain sets of common and rare species have been shown to react to similar environmental gradients (Siqueira *et al* 2011), suggesting that species sorting is the dominant process structuring communities. We showed that the number of common species seems to influence the rare species presence or absence in the assemblage, thus adding more support to the findings of Siqueira *et al* (2011). As rare species are more prone to go locally extinct and take longer time to re-establish (Volkov *et al* 2003) and also react more on stochastic events (Zhang *et al* 2015), further research on the role of common species in this

process would be interesting, as well at investigating the partitioning between effects caused by the habitat and landscape versus effects of species composition.

Initially, we see a need for conservation to focus on creating more heterogeneous landscapes, as odonate richness is affected by the different scales of land-use (Foster & Soluk 2006). Therefore, when looking at more original habitats, which could be considered potential conservation areas, we should prioritize localities with few common species, where rare species would be more abundant. Through providing this information derived from the distribution and occurrence of a freshwater group (the Odonata) in the Pampa biome, we expect to contribute for the maintenance and conservation of the aquatic environment a whole.

Authors contributions

SR collected the field data. SR, EP, MD and GS jointly developed the study concept and wrote the manuscript.

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CHAPTER 5

Ecoregions within the Brazilian Pampa biome reflected in Odonata species assemblies

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Abstract

Based on vegetation composition, previous studies of the Pampa biome in southern Brazil have defined seven ecoregions within the area. Here we test this ecoregion approach studying the semiaquatic insect group Odonata in five of these regions, aiming at comparing the ecoregions to the more traditional environmental predictors of water quality and land cover. Based on a dataset of occupancy comprising 99 species distributed between 131 localities, a one-way Permutational Multivariate Analysis of Variance (PERMANOVA) was used to compare differences in the species composition between the ecoregions, followed by a Principal Component Analysis (PCA) to visualize the variation. The composition varied significantly between all groups tested, and the ordination explained 61.8% of the variance. A partial redundancy analysis of ecoregions, land cover and water quality variables explained 71% of the variance in Odonata community structure. Ecoregion was the most important predictor, followed by water quality and land cover. Within these species assemblies, we could select certain species that were representative of a given ecoregion, to which their distribution within the Pampa biome was entirely or mainly confined. Out of 24 representative species 41.7% were rare, while the rest were more abundant and, hence, easier to detect. We suspect that the differences found between the Pampa ecoregions might be due to geology, since such factors may be strong determinants of biodiversity. Specific ecological requirements at the family and genus levels also seemed to act selectively on the species compositions within the ecoregions. Today, the Pampa is highly fragmented due to agricultural activities such as rice cultivation, extensive cattle farming, and forest plantations. We suggest that an ecoregion-based approach to the implementation of conservation measures may be the best way to help these distinct species assemblies survive.

Key words: species distribution, biodiversity, biogeography, ecology, Neotropics.

INTRODUCTION

The ability to target specific areas of the world with appropriate conservation strategies is constrained by the fact that our comprehension is not yet sufficiently complex to encompass the distribution of all natural communities on Earth (Olson *et al*. 2001). Measures to prevent further habitat loss, and subsequent loss of biodiversity, are initiated on priority areas, which are mainly selected based on human interests, rather than natural biodiversity/species distribution, or imminent threats (Myers *et al*. 2000). To deal with such matters, governments and conservation institutions have developed mapping systems based mainly on political borders, GIS data and biomes division *per se*. The biome concept gives a clear division pattern based on environmental properties, biodiversity distribution and landscape physiognomy, which is a very useful system/tool (Brown & Maurer 1989), especially when combined with comprehension of the relationships that affect the functioning of the ecosystems (Cardinale *et al*. 2012). However, considering the current levels of fragmentation (Ellis *et al*. 2010) and threats caused by human interference, the biome approach to nature still lacks information that is sufficiently detailed to enable us to identify many distinctive biota (Noss 1992). In all environments, it is therefore important to use the knowledge of biodiversity (measured as indices or in other ways) and abundance data for the organisms present (common species, rare species, vagrants), as they all contribute to the maintenance/stability of the ecosystems and the provision of ecosystem services (McNaughton 1978; Tilman & Downing 1994; Lehman & Tilman 2000). Today there is still a big inconsistency in the use of available data. It is therefore difficult to compare studies from different ecosystems, both with regard to ecosystem functioning and biodiversity patterns (Hooper *et al*. 2005).

The Brazilian Pampa lies within the South Temperate Zone (between 28°00' and 34°00'S and 49°30' and 58°00'W, encompassing areas with both a subtropical and a temperate climate (Streck *et al*. 2008). In terms of vegetation, most of the area was originally covered by grasslands and sparse shrub and tree formations (Overbeck *et al*. 2009). Human activity such as agriculture, cattle farming and silviculture has converted or degraded many areas within this biome (Baldi & Paruelo 2008; Overbeck *et al*. 2013). The main geological formations go back to the Gondwanan formation (Paraná basin), pre-Cambrian and Cenozoic sediments (IBGE 1990). Hence, the soil of the region consists mainly of sandy and sedimentary rock, sensitive to erosion. The process known as "sandification" (desertification) is getting increasingly common in some regions, due to the natural frailty of the soils, which are easily eroded by wind and water (Suertegaray 1995). The native grassland vegetation is highly sensitive to the introduction of exotic animal and plant species and, once lost, it is difficult to recover. This biome has been subdivided according to geographical or political borders, ecoregions and plant distribution as well as geological formations, but there is still plenty of room for discussion about biodiversity distribution and the known anthropogenic borders/divisions. The Pampa area is the least protected biome in Brazil. At present, only 0.8% of the Pampa region lies within nature reserves and other protected areas (Oliveira *et al*. 2017). When selecting priority areas for conservation of the Pampa, the fact that natural communities are already severely fragmented must always be taken into consideration (Santos & Silva 2007; Overbeck *et al*. 2009; Roesch *et al*. 2009), if possibly to a varying extent in different ecoregions. Knowledge of the historical development within each ecoregion is crucial to ecological science and conservation planning alike (Foster *et al*. 2003).

The species composition of a community always depends on the species present in the regional species pool (which in turn is dependent on the species pools of surrounding areas),

but also on large-scale biogeographical processes such as the dispersal possibilities of species, and the availability of suitable habitats over extended periods of time (Wiens & Donoghue 2004). For instance, the insect order Odonata has been widely used in ecological studies. It is a well-known group of organisms, which react rapidly to changes in landscape (Juen *et al.* 2007; Brasil *et al.* 2017) and climate (De Block & Stoks 2003). Hence, the Odonata are often used as bioindicators (Carle 1979; Sahlén & Ekestubbe 2001; Simaika & Samways 2009; Renner *et al.* 2015). Their life cycle involves both an aquatic larval stage and a terrestrial, aerial adult stage, for which different selection pressures apply. Hence, larvae and adults may have different preferences in terms of habitat choice (Hassall 2015; Villalobos-Jiménez *et al.* 2016). The occurrence of Odonata is related to forest structure, tree density and diversity (Paulson 2006), and they form distinct assemblages characteristic of forested and open landscapes, respectively (Renner *et al.* 2016; Brasil *et al.* 2017).

Evidence for the existence of such assemblies in the Pampa has been presented previously by Renner *et al.* (2018), where the authors demonstrated that waterbody type (lotic, lentic, temporary) and land cover (forest vs. grassland and agriculture), seemed to be particularly important factors determining the species composition of the Odonata communities. Bearing the different ecoregions of the Pampa in mind, we here aim at an increased understanding of the species assemblies at a regional level, asking the following questions: 1) Are the Odonata species assemblies distinctly separated by ecoregions? And, if so, is it possible to select a set of representative species for each ecoregion? 2) Are the ecoregions better predictors of species assemblies in the Pampa compared to variables related to land cover and water quality, which are frequently used? We expect ecoregions to have a large impact on the species distribution, but we also expect a combined approach (also including land cover and water quality variables) to be even better.

METHODS

Studied regions

We follow the division of Roesch *et al*. (2009) of the Pampa in southern Brazil into seven

ecoregions based on tree density and diversity, which we think are strongly connected to the

behaviour of odonates (cf., Paulson 2006). We sampled 131 localities situated within the five

largest regions: Steppe, Steppic-savanna, Savanna, Transition areas and the Coastal region,

ranging from 29°15' to 31°00' S and 49°40' to 56°30' W. Further information on each

ecoregion is presented below. The sampling localities were arranged in five clusters according

to Fig. 1. The climate of the area is Temperate (Cfb Köppen) with a mean annual temperature

of 18.3°C, mean precipitation varying between 1,200 to 1,600 mm and altitude ranging from 1

to 200 m.a.s.l. (INPE 2014).

The sampling localities included river sections, rivulets, streams, lakes, swamps and

temporary water bodies (e.g., small pools formed by rain and erosion), i.e. virtually all types

of water bodies suitable for Odonata that exist within the region. The size of the sampling

localities ranged from 100 m in diameter or length to larger areas (lakes and artificial ponds)

covering several hectares, but most of the sites were small.
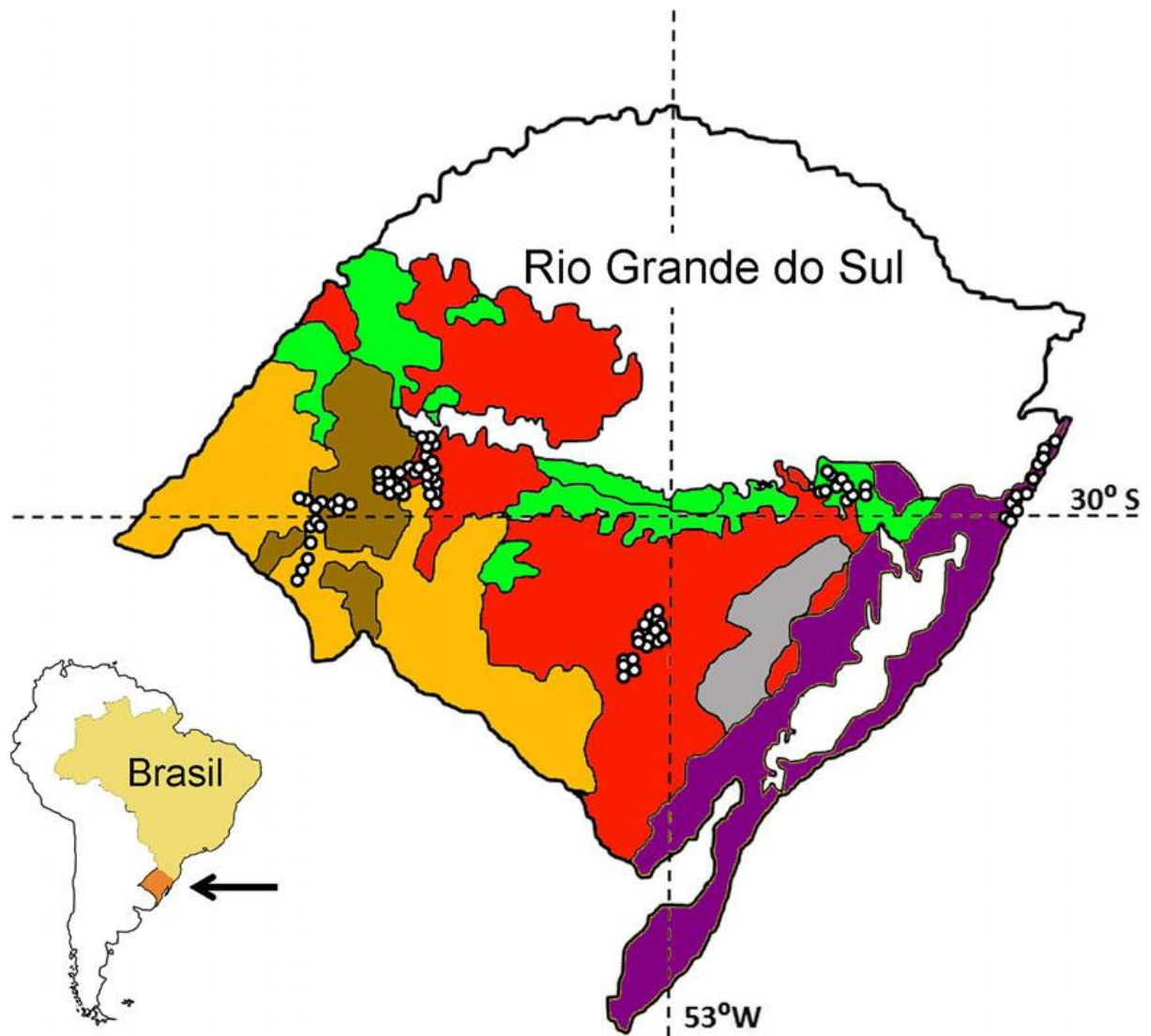
Fig. 1. South America map, highlighting the Rio Grande do Sul. Colours representing each of the ecoregions in the southern half of the state considered in our study: (1) Brown – Steppic-savanna; (2) Red – Savanna; (3) Orange – Steppe; (4) Green – Transition zone, including seasonal deciduous forest; and (5) Purple – Coastal areas. Small circles represent the location of the sampling sites, clustered within each region.

Dragonfly collection

We sampled adult dragonflies from March 2011 to April 2017, visiting the localities from one (temporary waters) up to seven times during this period. We followed the method described by Renner *et al*. (2015), collecting dragonflies on sunny days during the peak period of

odonate activity (between 09:00 h to 16:00 h). Two persons using hand-held insect nets walked along the perimeter of the site, along the water edges and marginal zones. The average time spent at each sampling site was 45 min. Most specimens seen were collected, but some members of the family Aeshnidae, which are strong flyers and very difficult to catch, were recorded visually. This is possible since the number of species occurring in this area is limited, and all of them can be identified by visual cues when flying. At each site, we noted all species encountered.

The collected specimens were preserved in 96% ethanol and determined to species level according to Garrison *et al*. (2006; 2010), Heckman (2006; 2010) and Lencioni (2006), and in some cases compared to specimens in our own reference collection. The specimens were deposited in the MCNU (Museu de Ciências Naturais da Univates). ICMBio issued the collection authorization process, through the SISBio system under the number 50624-1. Part of the dataset used in this paper has been used in other publications by the authors (Renner *et al* 2015; 2018). For all analyses, the species were divided by ecoregion (below) and the sampling effort per region was checked by a rarefaction curve.

Ecoregions

Although the Pampa biome in southern Brazil is usually regarded as a relatively homogenous grassland habitat, it comprises several different physiographic formations. Following the division by Roesch *et al*. (2009), which is based on the distribution of tree species, our sampling sites fall into five of the seven ecoregions (Fig. 1). We did not sample in two of the forested regions, Seasonal deciduous and Seasonal semideciduous forest. Within each of the regions sampled, our sites are somewhat clustered. We therefore assume that a larger number of species would have been found if the sites had been more numerous and/or more evenly

dispersed. Our aim is therefore merely to make a first attempt at understanding differences in species composition and distribution between ecoregions. We use the following designation of the five ecoregions included in the study (Roesch *et al.* 2009):

- (1) Steppic-savanna ($N = 52$): Natural grasslands with sparse occurrence of low-density forest; small numbers of isolated trees and shrub formations along the rivers. This ecoregion is the one most affected by the current desertification processes.

- (2) Savanna ($N = 27$): Natural grasslands with sparse patches of gallery forests known as 'capões', appearing as 'islands' scattered in the fields. Patches of taller forest also occur along watercourses.

- (3) Steppe ($N = 15$): Natural grasslands extensively mixed with shrub vegetation consisting of xerophytes and other plants adapted to a very dry climate and characterized by hard leaves or reduced leaf area. In addition, this region is characterized by the 'espinilho' formation (sparse trees, mostly bushy and spiny species), which is very similar to the Chaco formation in Argentina.

- (4) Transition ($N = 22$): Transition zone between the Atlantic Forest and the Pampa biome, featuring remnant patches of dense deciduous and semi-deciduous forest, as well as denser forest formation along the river courses. The northern limits of this ecoregion consist of the slopes of the 'Serra Geral' basalt formation.

- (5) Coastal ($N = 15$): Coastal habitats, also known as 'restingas': sandy coastal plains with abundant swampy areas and lagoons connected to rivers. This peculiar habitat is also considered part of the Pampa biome.

As site numbers vary between ecoregions, we compared our sampling efficiency by rarefaction curves based on data from all sampling events, using Jackknife1 as the chosen estimator, through the software Estimates 9.1 (Colwell 2009).

Land cover

Within each ecoregion we expect regional features, mainly land cover, to be of importance to species occurrence. For each site we used (2011 - 2017 Landsat) satellite images available via the software Google Earth Pro™, and quantified seven environmental factors within a circular area of 1 km² with its centre at the midpoint of the sampling site (water bodies/marginal zones). No clouds, haze or other objects preventing analysis occurred in the images. In addition, we confirmed the landscape characterisation through observations during the fieldwork. Using the area-measuring tool of the software, we determined the coverage of each environmental factor (percentage) at the localities. The land cover was defined as:

- Grasslands: areas covered by open fields with the typical vegetation of this biome and 'natural' Pampa, characterised by patches of taller vegetation, including bushes and reeds. Also fields of exotic grasses used for cattle grazing;

- Agriculture: areas with plantations; the most common crops in the region being rice, soybeans and corn. Farming activities bring about drastic changes in the natural landscape, to a varying degree depending on crop and cultivation method used (Roesch *et al.* 2009);

- Forested areas: patches of native forest scattered as islands in fields, near water bodies (as riparian forest), or surrounding rock formations. The majority of the trees in these areas are similar to those in the semi-deciduous or lowland Atlantic forest;

- Forestry: areas with exotic tree plantations for commercial purposes. The most common species planted in the Pampa are *Eucalyptus* sp., *Pinus* sp. and *Acacia* sp.;

- Sand patches: areas of desertification characterized by loss of vegetation cover. These areas are subject to severe erosion.

- Buildings and urban: structures built by humans, mainly found in localities situated close to urban areas; roads, houses and other buildings.

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- Water: areas covered by open water surfaces; ponds, lakes, rivers, streams etc.

The average land cover measurements for each ecoregion are found in Table 1.

Water quality

Within each water body, we expected water chemistry and physical factors to be important determinants of the species composition. Water quality has a direct impact on odonate larvae, and is known to be a selective factor (Corbet, 1999). We therefore used a water probe (Horiba Multi-parameter Water Quality Meter – Horiba Ltd. Japan) to measure the following variables: Temperature, pH, Conductivity, Turbidity, Dissolved O_2, Total dissolved solids and Salinity. In some localities (mainly temporary waterbodies) we were not able to use the probe at any of the visits due to very low water levels (<1 cm). The average water quality measurements for each ecoregion are found in Table 2.

Ecoregion species composition

If ecoregions are important to odonate species distribution, each ecoregion should have a characteristic species composition. We therefore performed a one-way Permutational Multivariate Analysis of Variance (PERMANOVA) to compare differences in Odonata species composition between ecoregions. We used presence/absence data for each individual species at all localities as independent variables, and the five ecoregions as grouping variable. The analysis was performed using Jaccard dissimilarity index and 9999 permutations. We used pairwise comparisons between analyzed factors to visualize the main differences in Odonata composition. Although the PERMANOVA here had an unbalanced design, it is considered very robust and tolerant to this type

Table 1: Mean ± standard deviation of the land cover for each ecoregion.

Ecoregions	Forest	Forestry	Grassland	Crops	Water	Human	Sand
1. Steppic-savanna	12.4±14.7	0.56±1.2	40.1±30.9	35.7±39.8	7.26±10.8	1.73±1.69	2.02±3.8
2. Savanna	25.0±22.2	2.29±8.5	63.1±23.3	4.1±13.0	1.80±2.67	1.95±4.20	1.69±2.9
3. Steppe	2.90±9.20	0.17±0.49	72.8±25.7	7.6475±10.8	8.85±9.09	1.30±0.49	0±0
4. Transition	17.0±13.1	12.4±11.1	11.9±14.4	42.0±21.7	8.32±9.14	8.23±17.9	0±0
5. Coastal	4.2±6.4	9.60±7.8	70.1±20.0	0.67±1.79	3.29±2.22	9.37±8.87	0.12±0.3

Table 2: Mean ± standard deviation of water quality measurements taken at the sampling sites separated by ecoregion.

Ecoregions	Temperature	pH	Conductivity	Turbidity	OD	TDS	Salinity
1. Steppic-savanna	28.59±3.00	8.53±2.05	0.03±0.02	95.63±146.6	8.44±2.91	0.02±0.10	0±0
2. Savanna	25.50±3.01	8.57±2.56	0.05±0.04	136.7±136.1	3.96±11.9	0.07±0.03	0.007±0.03
3. Steppe	26.39±2.62	10.70±2.30	0.11±0.04	41.51±57.7	4.59±1.72	0.07±0.03	0.04±0.04
4. Transition	23.74±4.57	5.98±2.04	0.11±0.05	10.39±213.1	26.85±13.2	0.07±0.03	0±0
5. Coastal	31.55±2.84	9.07±0.62	0.09±0.01	224.5±252.9	3.43±1.80	0.05±0.009	0.02±0.001

of data (Anderson & Walsh 2013). We are aware that by using unequal group sizes, we might get slightly deviating results, but this test was the best choice available for our data. As a last step, we used a Principal Component Analysis (PCA) to visualize the variation in Odonata composition shown by the PERMANOVA. These two analyses were carried out in PAST 3.20 (Hammer, 2015).

The importance of predictors

To determine the importance of each set of variables (environmental, land cover and ecoregions) to the variance in species composition, we partitioned the total variation in the composition matrix into unique percentage values for environmental, land cover and ecoregion components, respectively, using a partial redundancy analysis, pRDA (Legendre & Legendre 2012). As local variables, we used the water quality parameters, and as landscape

variables we used the percentage of each land cover category, as explained above. For the

ecoregions, each site was classified into one according to its location, with a zero value for the

other categories. From these PCA results we selected three first axes (PCs) within each sets of

variables for the pRDA, which was using the varpart function in the Vegan Package (Oksanen

et al. 2017) of R project 3.24 (R Development Core Team 2017). The following components

were tested: total explained variation (water quality + land cover + ecoregion); individual

explained variation (each set alone), combined explained variation (water quality + land

cover, water quality + ecoregion, land cover + ecoregion) and unexplained variation (1 – sum

of all combinations). We used the resulting r square values as explanation percentage to

construction of the Venn Diagram. The script used for this calculation is available as

supplementary material.

Selection of representative species

To select a series of species representative of each ecoregion, we used four stepwise-arranged

criteria. The criteria are an adaptation of those used by Suhling *et al*. (2006), who selected

species indicative of environments in a dry region in Africa, based on a dataset of

presence/absence for all localities and a discriminant analysis. In order to be included, the

species must conform to all of the following criteria:

(1) A representative species should not occur regularly in all ecoregions, but be confined

mainly to the region in question (>66% of its locations).

(2) A representative species cannot be common within the entire region. Hence, it should be

recorded in no more than 25% of the localities surveyed. Nor can it be very rare. We therefore

excluded all singletons from the dataset in order to reduce stochasticity. As we have very few

common species, but many rare ones, in our dataset, we are aware that excluding singletons

will reduce rather than remove the noise. There will still be many species which are recorded

by chance, e.g. among those appearing only twice in the dataset. Therefore, the resulting species must be discussed with regard to the number of localities in which they appear.

The last two criteria are based on a discriminant analysis using the presence/absence of each species as linear variables, with the five ecoregions as grouping variable. The resulting discriminant functions have Eigenvalues corresponding to relative measurements of the efficiency of the resulting functions. Five groups will yield four discriminant functions. For each function a Wilks' lambda value will measure how well the function separates the variables into groups, a small value being indicative of a higher discriminatory ability of the function. An associated chi-square analysis tests if the means of the functions are equal across the categories used (if so, they are not discriminating between groups). The analysis was carried out in IBM SPSS statistics release 24. For our criteria to be valid, the discriminant functions must be significant.

(3) We selected species the distribution of which was correlated to one of the significant discriminant functions according to the canonical correlation analyses we derived from the discriminant analysis (above). Correlations needed to be stronger than 0.05, which is a very low value, but many rare species in the dataset will *per se* generate few strong correlations. Hence, we believe 0.05 to be a good compromise.

(4) Finally, we used univariate ANOVAs to test for the distribution equality of each species; this analysis was also part of the discriminant analysis, where it was used to test the potential of each independent variable in the analysis. We selected only species with a significantly non-random distribution.

RESULTS

Species numbers and regional diversity

Our dataset comprised 99 species, distributed between the 131 localities. They predominantly belonged to three families: Libellulidae (51.5%, 51 species), Coenagrionidae (24.2%, 24 species) and Gomphidae (9.1%, 9 species). The total number of specimens collected was 3,242. From these, seven specimens were removed from further analyses, as they could only be identified to genus level (cf., supplementary material). The number of species per site varied from 2 to 20, with an average of 9.06 ± 4.03 (SD). The number of sites per ecoregion varied: 15 (Steppe [3] and Coastal [5]; γ diversity 42 and 22 respectively), 22 (Transition [4]; γ 42), 27 (Savanna [2]; γ 59) and 52 Steppic-savanna [1]; γ 80). The dataset contained very few common species. Most species (73%) occurred in 10 or fewer localities, while only 7 species occurred in more than 50 of the 131 surveyed localities.

Species variation between ecoregions

The species composition varied significantly between ecoregions (pseudo-$F_{4,126} = 5.39$; p = 0.0001). The Pairwise comparison showed that the odonate composition differed between all groups tested. The similarity in odonate community composition was represented by two axes in the ordination analysis, which explained 61.8% of the variance (Fig. 2).
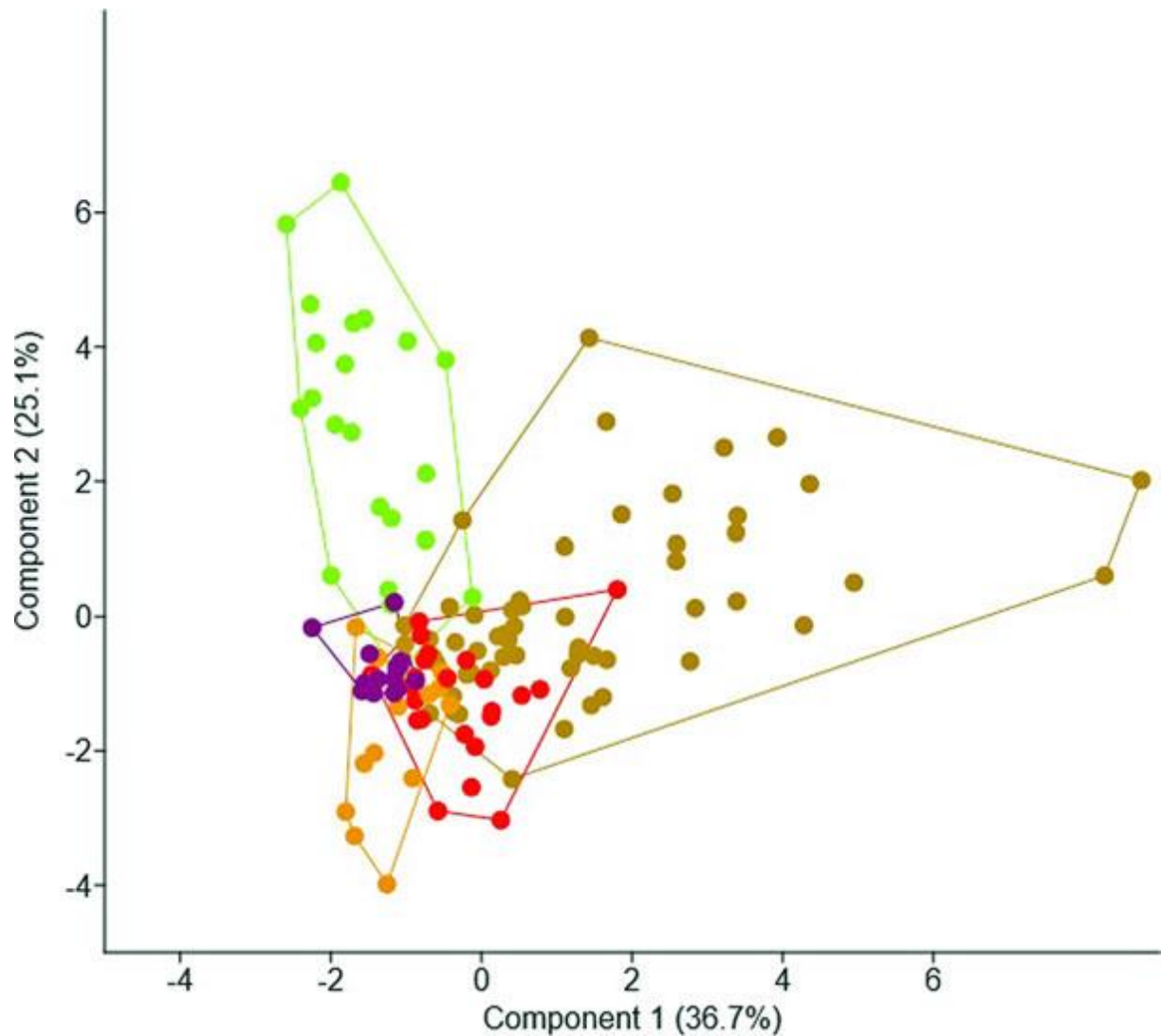
Fig. 2. PCA plot of species assembly variation between the five ecoregions. 1) brown circles, Steppic-savanna; 2) red circles, Savanna; 3) orange circles, Steppe; 4) green circles, Transition zone; and 5) Purple circles, Coastal area. Region 1 and 4 are most distinct, followed by 3. Savanna (2) and Coastal (5) are to a great extent overlapping with the others, indicating a less distinct species assembly.

Some sites have identical or very similar species composition (many overlapping dots) but the Steppic-savanna (brown; 1) and Transition area (green; 4) are well separated, as is part of the Steppe (orange; 3) region. Savanna (red; 2) and Coastal (purple; 5) are to a large part overlapping, but there are still many of the sites which differ strongly also between these

regions. Comparing the rarefaction curves (Fig. 3); we note that two of the curves (ecoregion 1 and 5) reach the asymptote, whereas the rest do not, which indicates that the actual species pool was larger than the one we recorded.
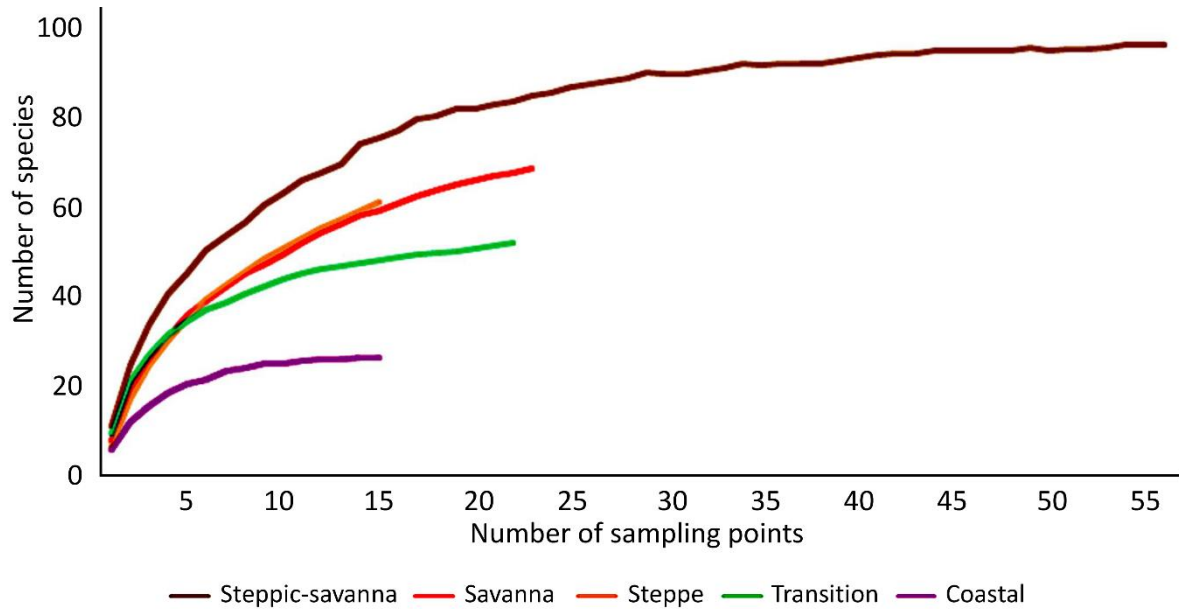
Fig. 3. Rarefaction curves showing the sampling effectiveness for each ecoregion: brown, Steppic-savanna [1]; red, Savanna [2]; orange, Steppe [3]; green, Transition zone [4]; and purple, Coastal area [5].

The resulting three PC axes explained 77.3% of the variance with regard to ecoregion, 71.4% with regard to water quality and 62.8% with regard to land cover. The PCA in the pRDA explained 71% of the variance in the Odonata community structure for the Pampa biome (Fig. 4). Comparing the selected variables, we found that ecoregion was the most important predictor of community structure (10%; $p = 0.0001$), followed by water quality (5%; $p = 0.003$) and land cover (4%; $p = 0.0001$). When combined, the three predictors yielded a stronger influence (17%; $p = 0.003$); combining them two by two gave the following results: ecoregion + land cover (13%; $p = 0.0001$), ecoregion + water quality (13%; $p = 0.003$) and land cover + water quality (9%; $p = 0.003$).
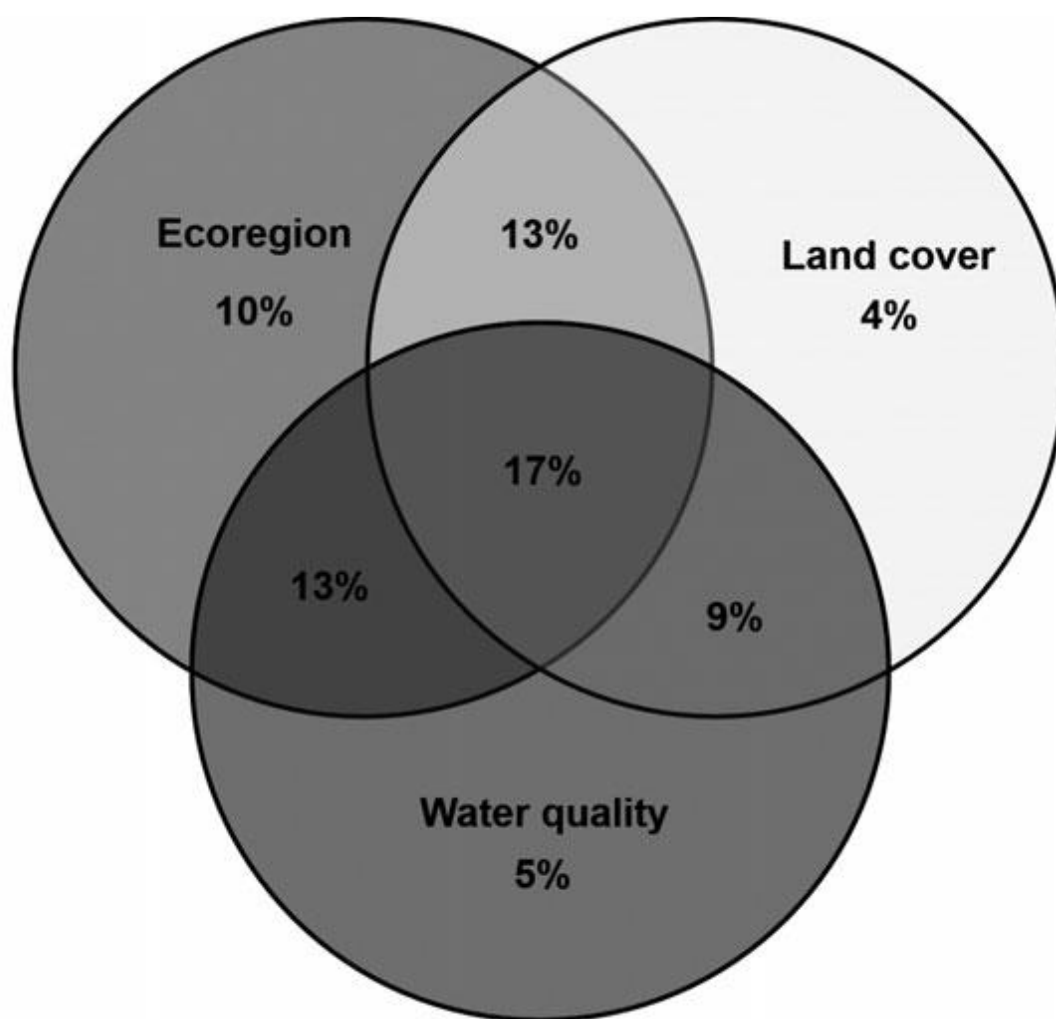
Fig. 4. Venn diagram resulting from the pRDA model analyses among predictor variables that may affect community structure. In total the predictor variables explained 71% of the model. Ecoregion was the most influential predictor (10%).

Species representative of the five ecoregions

25 species appeared predominantly in only one of the ecoregions and were therefore specific enough for inclusion among the candidates. One of these was too common to be included. The discriminant analysis used four discriminant functions, all of which were highly significant (p < 0.0005). In total, 99.6% of all habitats could be classified according to the species occurring at the site, and therefore criteria 3 and 4 could be used. All candidate

species were correlated (r ≥ 0.05) to at least one of the functions. The resulting 24 species (Table 3) were also unequally distributed (p < 0.05) between ecoregions, with 6 species representative of ecoregion 1 (Steppic-savanna), 6 species of region 2 (Savanna), 4 species of region 3 (Steppe), 6 species of region 4 (Transition), and only 2 species of region 5 (Coastal). Some of the selected species were relatively rare, occurring at only 2-4 sites (41.7%), whereas others occurred at more than 10 (29.2%) sites, mainly within the specific ecoregion (Table 3).

Table 3. Representative species for five ecoregions of the Pampa biome in Rio Grande do Sul, selected by the four-step process. Eco = ecoregion of which the species is representative; N = the number of sites in which the species was encountered; % = percent of sites within the ecoregion; p = significance of the F-test (df = 4, 221); 1-4 = strength of the correlation of each species with the four discriminant functions, correlations <0.05 were excluded.

Species	Eco	N	%	p	1	2	3	4
Acanthagrion ascendens Calvert, 1909	4	4	100	<0.0005	-0.064	-	-0.096	0.066
Anax concolor Brauer, 1865	4	2	100	0.002	-	-	-0.064	
Aphylla producta Selys, 1854	4	3	100	<0.0005	-0.054	-	-0.081	0.056
Argia lilacina Selys, 1865	1	14	100	<0.0005	-	-	0.128	0.096
Erythemis credula Hagen, 1861	5	5	100	<0.0005	0.099	-0.112	-0.129	-
Erythrodiplax avittata Borror, 1842	5	2	100	<0.0005	0.055	-0.062	-0.072	-
Erythrodiplax hyalina Förster, 1907	1	25	68	0.002	-0.050	-	-	-
Erythrodiplax umbrata Linnaeus, 1758	3	4	75	<0.0005	0.07	0.086	-	-
Macrothemis heteronycha Calvert, 1909	1	11	90.9	<0.0005	-	-	0.113	0.081

Species								
Macrothemis imitans Karsch, 1890	2	14	78.6	<0.0005	-	-	-	-0.214
Macrothemis marmorata Hagen, 1868	1	9	88.9	<0.0005	-	-	0.095	
Mnesarete lencionii Garrison, 2006	2	4	75	0.003	-	-		-0.097
Mnesarete pudica (Hagen *in* Selys, 1853)	1	8	100	<0.0005	-	-	0.102	0.076
Oligoclada laetitia Ris, 1911	4	11	100	<0.0005	-0.135	0.084	-0.204	0.14
Orthemis ambinigra Calvert, 1909	1	10	80	0.007	-	-	0.086	-
Oxyagrion hempeli Calvert, 1909	2	7	100	<0.0005	-	-	-	-0.191
Oxyagrion rubidum Rambur, 1842	3	9	88.9	<0.0005	0.155	0.195		-
Peristicta aeneoviridis Calvert, 1909	2	3	100	<0.0005	-	-	-	-0.114
Perithemis icteroptera (Selys *in* Sagra, 1857)	4	17	82.4	<0.0005	-0.139	0.107	-0.209	0.136
Planiplax erythropyga (Karsch, 1891)	3	6	100	<0.0005	0.127	0.161	-	-
Progomphus complicatus (Selys, 1854)	2	2	100	0.011	-	-	-	-0.091
Progomphus lepidus Ris, 1911	3	3	66.7	0.001	-	0.073	-	-
Telebasis willinki Fraser, 1948	4	6	83.3	<0.0005	-0.07	-	-0.095	0.079
Tholymis citrina Hagen, 1867	2	4	100	0.006	-	-	0.072	0.054

Highlighted in Table 3 are the most representative species according to our selection method: *Argia lilacina* Selys, 1865 and *Erythrodiplax hyalina* Förster, 1907 for ecoregion 1 (Steppic-savanna), *Macrothemis imitans* Karsh, 1890 and *Oxyagrion hempeli* Calvert, 1909 for ecoregion 2 (Savanna), *Oxyagrion rubidum* Rambur, 1842 and *Erythrodiplax umbrata* Linnaeus, 1758 for ecoregion 3 (Steppe), *Perithemis icteroptera* (Selys *in* Sagra, 1857) for ecoregion 4 (Transition), and *Erythrodiplax avittata* Borror, 1842 for ecoregion 5 (Coastal).

Although representative, most of these species require careful examination for accurate identification.

DISCUSSION

By comparing the species assemblies found in the five surveyed ecoregions of the Brazilian Pampa, we were able to show that ecoregion was, indeed, the most influential predictor (Roesch *et al*. 2009). Further, we could confirm that each ecoregion possessed a distinct assembly of odonate species, a small number of which could be regarded as representative of the ecoregion in question. The presence of characteristic species assemblies, comprising species which are representative of their respective ecoregions, is common among plants and animals alike (Sarkar *et al*. 2009; Figueiredo *et al*. 2017; Wang *et al*. 2017). In the case of Odonata, also specific habitats can sometimes harbour special species assemblies, as shown by Suhling *et al*. (2006) for spring brooks and lakes in Namibia. There are also cases where ecoregions fail to associate with any species assemblies, as demonstrated by e.g., Kusbach *et al*. (2015) for plants in western United States. In the latter case, the authors concluded that the traditional ecoregion division did not seem to represent the basic ecological units of the area. In our case, the ecoregion division by Roesch *et al*. (2009), based on tree species, was highly applicable also to the occurrence of species belonging to a semiaquatic insect order.

It has been clearly stated that it is often problematic to treat diversity and ecology on different geographic scales (Whittaker *et al*. 2001). Combining different scales in our pRDA, we could see that ecoregions were more important than both local (water quality) and regional (land cover) variables, but also that combining all these predictors explained 71% of the variation between species assemblies. Treating the Pampa (or any other biome) as a single,

homogenous area therefore seems to be a less suitable approach. This has been shown in earlier studies in other regions: worldwide, Olson *et al*. (2001), North America, Gering and Crist (2002). The high level of explanation in the pRDA suggests that in the Pampa, the ecoregion division is central to the development of species assemblies and can be regarded as a major driver of differences in diversity. Other studies (e.g., Brasil *et al*. 2017) noted a lower explanatory degree (29%) using the same method in the Amazon forest biome in Brazil.

The distinctiveness of the Pampa ecoregions may be due to geological events in a distant past, as the main geological formations of the Pampa date back to the Gondwanan formation (IBGE 1990). Today, these major events are mirrored in the many features and general differences between the ecoregions, including the amount and quality of water, soil, bedrock and, subsequently, the vegetation formations therein. The influence of ecological features on macroinvertebrate communities is known to be great, sometimes even greater than the impact of stream specific anthropogenic features (Richards *et al.* 1996). Most of the new world grasslands started to form at around 35 MYA, reaching their modern structure at around 15 MYA (Graham 2011). The exact age of the Pampa ecoregions is unknown to us, but it has been pointed out that only the coastal region has topsoil of recent origin (Roesch *et al.* 2009). Water and climate fluctuates over time, with subsequent changes in biota, but factors such as soil, bedrock and geography take very long to change. We might speculate that such factors may be strong determinants of the biodiversity of the Pampa, just as they are in the case of North American rivers, as pointed out by Richards *et al.* (1996).

Looking into the separate ecoregions, we noted that in terms of species assemblies, the most distinct ones were Steppe and Coast (Fig. 2). Distinctive species assemblies may develop due to a wide range of causes, mainly related to physical and biological environmental variables

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(Morton & Law 1997; Dickie *et al*. 2010; Pavoine & Bonsall 2011). We know that the Steppe is an area with relatively little urbanization, but where a large part of the original vegetation has been converted to cattle pastures (Baldi & Paruelo 2008; Overbeck *et al*. 2013). Along this, the damming of small rivers and temporary waters in order to provide drinking water for the cattle is commonplace. The situation in the Coastal ecoregion is similar, but also different. This region is under pressure from urbanization and, as in the Steppe, many new water bodies have been created - often for storm water, but also ornamental ones. Many result from changed hydrology due to the construction of roads and buildings, but there are also many natural swamps in the region. According to the Brazilian government statistics, around 24% of the state's population lives in this ecoregion (MMA 2017).

We noted the presence of a number of species that were representative of each surveyed ecoregion (Table 3). Using our selection methods, the number varied from 2 to 7 representative species per region. Although these species are representative of their respective ecoregions, appearing predominantly in a single ecoregion in southern Brazil, the knowledge of their ecology is not sufficient to make any detailed analyses (Lewinsohn *et al*. 2005; Clausnitzer *et al*. 2009; Garrison *et al*. 2010). At the genus level, we can, for instance, tentatively attribute the preference of *Erythrodiplax* for the coastal areas to the dominance of lentic habitats in this ecoregion, although the variation within this genus is considerable - males of several species defending territories in swamps, rivers and lakes alike (Resende 2010). Some species within this genus have been shown to prefer open, sunny areas (Calvão et al. 2013), while others are forest dwellers in grassland areas (von Ellenreider 2000). In our area, the mix of riparian forest and grassland would constitute a suitable blend of habitats, enabling several members of this genus to occur specifically in single ecoregions. The genus *Argia* contains both tolerant generalist species and habitat specialists (Monteiro Júnior 2015).

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A. lilacina, which was characteristic of ecoregion 1 (Steppic-savanna), occurred mainly in rivers, which is the dominant type of water in ecoregion 1. Looking at *Perithemis,* characteristic of the transition zone (4), the genus is common in Atlantic forest aquatic systems and even regarded as a generalist in that type of biome (Renner *et al.* 2016). At the family level, we noted that only few representatives of Calopterygidae and Heteragrionidae were present in running water habitats in all regions dominated by open or sparsely forested grasslands. In ecoregion 4, however, where forest patches are predominant, they are much more numerous and abundant (Renner *et al.* 2016). We also note that representative species of the genera *Mnesarete*, *Tholymis*, *Argia* and *Orthemis* were confined to ecoregion 1 and 2, the regions with a high percentage of both forest and grassland (Table 1). Carvalho *et al.* (2018) showed that other members of the first two genera prefer forest covered streams, while members of the last two were characteristic of open streams. The ecology of species thus seem to be species and habitat specific, and it is difficult to draw any firm conclusions from the data available to us. Our point is that we see an ecoregion specific species distribution, the use of which might in the future add more information on the ecology and habitat preferences of the species involved. The grassland-dominated ecoregions of the Pampa seem to harbour a rather unique species composition, with many rare species and only a small number of widespread ones. How specific these rare species are to their respective aquatic environments within the ecoregions is, however, still unknown. It is apparent that these species assemblages need to be further investigated, possibly from an indicator perspective and in the light of the ongoing red listing of Neotropical insects.

As mentioned above, we noted that rare species are dominant in the Pampa. This has interesting implications, as the proportion of rare vs. common species is important to the shape of the community structure (Magurran & Henderson 2003). The biome as a whole

displays a relatively high level of human disturbance, manifested by vast areas that are converted to pastures, rice fields, *Eucalyptus* plantations etc. (Overbeck *et al*. 2013; Roesch *et al*. 2009). This applies to all five ecoregions investigated. Many studies have shown that disturbed habitats are often colonised by widespread generalist species (Sahlén & Ekestubbe 2001; Hendrickx *et al*. 2007; Monteiro-Júnior *et al*. 2014; Renner *et al.* 2015) but we do not see this pattern in the Pampa region. One possible explanation to this might be the stabilising effect of geology on the macroinvertebrate communities discussed above (Richards *et al.* 1996), but this needs to be further investigated. Generalist species were uncommon, and 73% of the species occurred only in a total of up to 10 localities. In their review of species dispersal patterns in South America, Turchetto-Zolet *et al*. (2013) showed that species associated with open vegetation displayed a somewhat unclear population expansion during glacial cycles, followed by fragmentation during interglacial periods. Increasing species diversity within a region can be achieved either through the dispersal of species from adjacent regions or via *in situ* speciation (Wiens & Donoghue 2004). If we assume that the ancient species composition of the Pampa was dominated by rare species, with few (if any) generalist species, the pattern observed today would be expected. In addition, the test of our sampling effectiveness (Fig. 3) shows that Steppic-savanna and Coastal are the best-sampled regions in our study, indicating a much lower total species number in the coastal area compared to the other regions, which is interesting when discussing diversity patterns in this part of the world. Of the other regions, Transition almost reaches the asymptote while the others do not; but all have a varying number of sampling sites, which points to a highly unequal number of species between these five ecoregions. Based on that, we can assume that the differing number of sites per ecoregion did not, to a great extent, affect the sampling completeness although there should still be more species to discover in all regions.

Morton and Law (1997) predicted that a large number of consumer species at a site would reduce the total number of species, but that a larger number of species at lower trophic levels would be present if the consumers were specialized. We did not account for lower trophic levels in our study, but this also merits further investigation. It is otherwise often assumed that a rich Odonata community corresponds to a high diversity also at other trophic levels (Sahlén & Ekestubbe 2001), implying that most localities in the Pampa would be species poor. We might also speculate that there may be a set of unknown factors in the Pampa environment, which promote diversity between sites, or that it might be a remnant of the natural diversity in the area prior to human colonization.

For most areas, in the Pampa biome or elsewhere, a trade-off between conservation of freshwater biodiversity and the use of ecosystem services by humans is necessary (Dudgeon *et al*. 2006). In the same publication, it was concluded that in order to protect aquatic diversity one must consider the upstream areas, the surrounding land and the riparian zone. For the frequently migratory Odonata, surrounding water bodies are also of interest, as is the impact of geology and the prehistoric development of the Pampa ecoregions on the maintenance of factors important to the current community structure. In the Pampa and its ecoregions, all areas are already to a high extent converted by humans, with only 36% of the area remaining in something resembling an original state (MMA 2009), but the data is old. We hence recommend that studies such as ours be expanded to other taxa, to provide better underpinning for decision makers when implementing new conservation measures. We believe that actions on an ecoregion level is ideal for protecting a full range of representative areas (Olson *et al*. 2001). This is especially important in this part of the world (the Neotropics), as the threats to Nature are greatest in developing countries, where the conservation resources are scarce (Oliveira *et al*. 2017). In terms of natural reserves and

conservation measures, the Pampa is the least protected biome in Brazil (Oliveira *et al*. 2017), a fact that justifies all effort towards increased knowledge of this biome and, consequently, its conservation.

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CHAPTER 6

A preliminary selection of biodiversity indicators among dragonflies (Odonata) in the Pampa biome, Rio Grande do Sul, Brazil: a methods evaluation

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Running title: Odonata as indicators in the Pampa

Manuscript in development

Abstract

We surveyed adult dragonflies and damselflies (Odonata) in 131 bodies of water among several regions on the Pampa biome in southern Brazil aiming to test for the first time, whether a combination of selection methods for diversity indicators could be applied in such ecosystem, where limited ecological knowledge on species level is available. In this study we followed an ecoregion approach which defines environmental divisions, based on vegetation cover, for the Pampa biome. The chosen combination of selection methods to be tested in this biome was based on a nestedness and discriminant analysis with the almost classical method IndVal. The number of species per site varied from 2 to 20, with an average of 9.06 ± 4.03 (SD). From the combination of the two methodologies, we were able to select nine indicator species from a species pool of 99. The species selected as indicators demonstrated high specificity in relation to the ecoregions where they occur.

Keywords: Community, ecology, neotropics, ecoregions.

Introduction

In order to prioritize areas under consideration for conservation, biologists and decision makers need concise information on species diversity, especially in threatened habitats (Kerr et al., 2000). There are critical issues associated to the development of environmental monitoring and programs aiming to restore the ecological integrity of an ecosystem (Carignan & Villard, 2001). Information on biodiversity becomes more relevant every day, as the knowledge on the distribution of extant species richness can provide powerful tools to put focus on human impact on the more sensitive environments (Lewis 2006; Cardinale et al., 2012).

In the Neotropics, the dominant landscape mosaic is constituted by different kinds of anthropogenically transformed systems with various levels of disturbance and intensity of human occupation, mixed with pristine habitats sheltering the small remains of undisturbed biodiversity (Collins & Thomas, 1989). Although the general picture of this region is known, there are many gaps remaining to be filled. Numerous studies describing the diverse fauna and flora in the Neotropics are published, but there is still much to be unveiled (May 1998, Scotland & Wortley 2003, Oliveira et al., 2017). The scientific knowledge of the biodiversity in this region of the world is reserves great potential for discoveries (Calvo-Alvarado et al., 2013), and a major question towards its conservation consists in the comprehension of the functioning of such rich nature (Sánchez-Azofeifa & Portillo-Quintero, 2011).

Since several decades, studies have proposed indicators for species richness and habitat quality. In the Neotropics several such studies with the indicator approach are in use for the forested biomes, or at least suggested, focusing mostly on taxonomic groups like bats (Cunto & Bernard, 2012), forest mammals (Sebastião & Grelle, 2009), plants in general or specific

groups of species (Kessler & Bach 1999). Among invertebrates e.g., butterflies (Beccaloni & Garton, 1995) and benthic macro invertebrates (Fenoglio et al., 2002) are widely used. There are some studies such as Moritz et al., (2001) suggesting that invertebrates perform better than vertebrates for indicative purposes, probably because of faster adaptation and shorter generation times.

In spite of this, there is a need for more studies regarding the distribution of species among the ecological domains, as well the understanding of the effects produced by human development over those communities (Brooks et al., 2006). In Brazil, most of the forested biomes (Amazon and Atlantic Forest), already have well developed protection systems but in other biomes, such systems are rare or lacking. One such understudied biome in the Neotropics is the Pampa (Oliveira et al., 2017).

Only 2% of the Brazilian territory is covered by the Pampa biome, but in the state of Rio Grande do Sul it covers more than 63% of the area (IBGE, 2016). The Pampa changes from small and scattered, partly tree covered patches near the Atlantic Forest into the proper grasslands, covering more than the half of the southern part of the state, south of 29° S. Outside of Brazil, these grasslands extend southwards throughout the Uruguay, and in Argentina reaching as far as the Temperate Patagonian steppes at 39º S (Roig & Flores, 2001). Pressure from human activities such as agriculture, extensive cattle farming and commercial forestry has grown at alarming rates in the last 60 years (Overbeck et al., 2009; Roesch et al., 2009; Mazia et al., 2010), causing habitat loss mostly through fragmentation. Also, the increasing introduction of non-native species pushes these landscapes to an even worse situation (Medeiros & Focht, 2007). Exotic species such as *Acacia* sp., *Eucalytpus* sp. and *Pinus* sp. are the most common species used for commercial forestry, and African grass species such as *Eragrostis plana* (Poaceae) are in use aiming to improve the cattle grazing. Another problem consists in the intriguing desertification process observed locally in several

places among the fields and grasslands. The expansion of these sand patches are also assumed to be one of the consequences of unsustainable land-use and extensive cattle farming, as aforementioned (Overbeck et al., 2013).

In Brazil, little has been done in terms of grassland protection and restoration, and historically, the priority has been given to forest biomes (Oliveira et al., 2017). Data from 2008 demonstrated that only 36% of the original Pampa vegetation was still untouched, and that it was pictured in a highly fragmented mosaic (MMA, 2009). According to the Brazilian Ministry of Environment (MMA), only 0.5% of the biome is inserted in protection areas. Only recently, diversity indicators for aquatic environments (e.g. Pérez et al., 2013) have been tested for some taxa, in the Atlantic Forest and Amazon Forest (Campos et al., 2014; Graça et al., 2015; Renner et al., 2015), but not yet in the Pampa biome.

According to Legendre & Legendre (2012), the selection of indicator species is a classical problem in the studies of communities and biogeography. Indicator species can be a useful tool for conservation measures, for the demarcation of protection areas, and has frequently been incorporated into policies and regulations in order to monitor the environment (Carignan & Villard, 2002; Nobrega & De Marco, 2011). The selection of specific target taxa is a well-known method to improve data on environmental conditions, including species diversity as they provide a cost- and time-efficient mean to access the general status of the ecosystems (Carignan & Villard, 2002; Valente-Neto et al., 2018).

Studies have shown, at least on other Brazilian biomes such as Atlantic Forest (Renner et al., 2015), Amazon (Valente-Neto, et al., 2018) and Cerrado (Calvão, et al., 2018), that the presence of dragonflies in the environment reflects the general species richness. The dragonflies in general are some of the most visible creatures in the aquatic systems, they have

since long time been used as model organisms by conservationists (Carle 1979, Samways et al., 1996, Simaika & Samways 2009, Koch et al., 2014), are sensitive to human disturbance, such as forestry (Sahlén 1999, Flenner & Sahlén, 2008), have been used as indicators of species richness and, to monitor restored habitats (e.g. Clausnitzer 2003, D'Amico et al., 2004, Suhling et al., 2006). They react to general local/regional conditions, and certain species are better indicators than others, considering their dispersal abilities, life cycle constraints and intrinsic ecological requirements (Gall et al., 2017). Dragonflies also demonstrate high niche specificity in aquatic environments (Nessimian et al., 2008), which increases their reliability as bioindicators. Particularly in the Neotropics, some dragonflies can inhabit only ponds situated in particularly well preserved landscapes (Renner et al., 2018a), as well, many observed patterns of neotropical dragonflies, reflects landscape variations on the aquatic environments of their occurrence (De Marco et al., 2015, Gall et al., 2017). Many observed patterns of neotropical dragonflies, reflects landscape variations on the aquatic environments of their occurrence (De Marco et al., 2015).

Exploring the indicative potential of dragonflies here, we attempt to select indicators, in this case representative species for the Pampa region in southern Brasil. Indicators will occur foremost in species rich habitats and will mirror diversity in lower levels. Further, they should not be distributed randomly in the landscape but be selective in their choice of habitats. We ask the question whether there are some combination of potential biodiversity indicators among the Odonata of the Pampa biome, and if yes: is the ecological knowledge of the species in the region good enough to allow for a meaningful evaluation? Finally, if any indicators can be identified, could they be used in ongoing conservation prospects in the region? To answer these questions we surveyed the species composition along the ecoregions

of this biome, and analyzed the patterns of occupancy, and from there, determined which species are suitable as regional indicators of species richness.

Material and Methods

Field work

We sampled adult dragonflies in 131 aquatic habitats; lakes, swamps and streams, with the goal of getting a general overview of the regional Odonata species richness. The sites were clustered in five main regions: Alegrete / Quaraí / Uruguaiana (N = 26); Manoel Viana / São Francisco de Assis (N = 44); Santana da Boa Vista / Caçapava do Sul (N = 23), Vale do Taquari (N = 23) and Litoral zones (N = 15), ranging from 29°24' to 30°55' S and 53°07' to 56°29' W (Fig. 1). The areas have mean annual temperatures between 13°C and 17°C, altitudes ranging from 0 to 200 m.a.s.l. and mean precipitation between 1,200 to 1,600 mm annually (INPE, 2014) corresponding to temperate climate (Cfb Köppen).
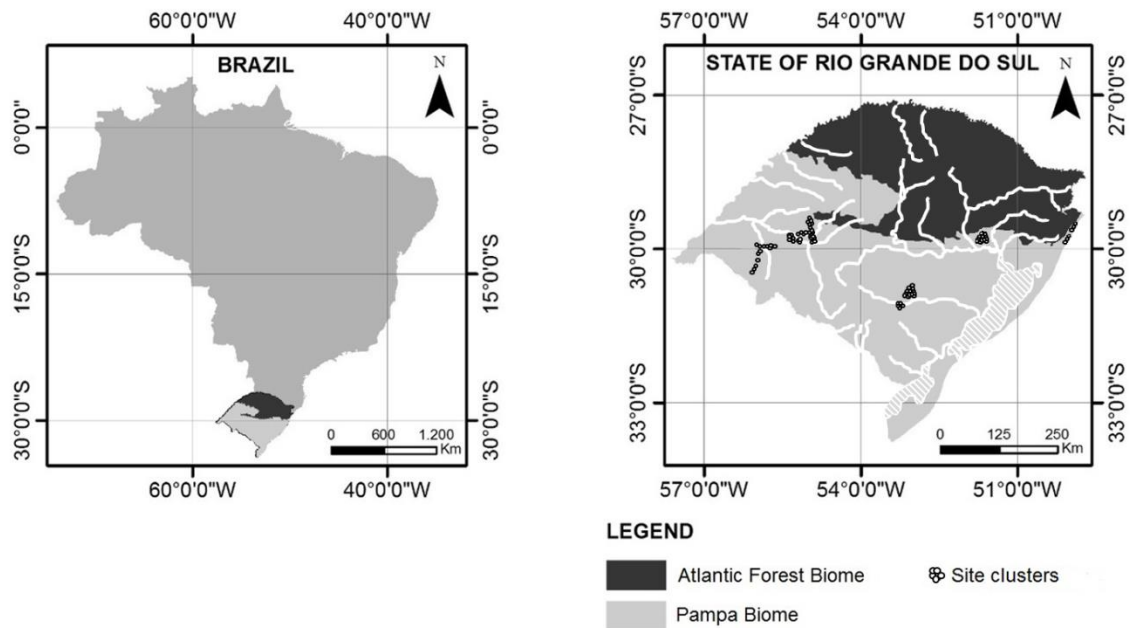

Fig. 1 – Small circles represent the clusters of sampling sites along the chosen regions of the Pampa.

Collections were made from March 2012 to January 2017, visiting sampling sites 1-5 times during this period, often once per season excluding winter months (June-August). We choose to sample only adults since Odonates are known to respond to environmental conditions/changes in congruence at both larval and adult stages (Mendes et al., 2017), also due the easier identification. Our sampling efforts were concentrated on adults, since the larvae can present great difficulties to the determination work, as only scarce information is available for the Neotropical region (Garrison et al., 2006). Temporary sites were, with some exceptions, visited only once. We used the method described by Renner et al., (2015): hand-held insect nets by a team of two people in sunny days during the peak activity of Odonata (09:00 h to 16:00 h). We collected along the edges and marginal zones of waterbodies; distances varying in length according to the size and shape of the water; the average time spent per site at each occasion was 30 minutes. For each site we noted the species present and the number collected. The sampling sites included a whole range of different waterbodies in the region that are suitable to maintain Odonata: from large river shoreline sections, to man-made lakes and temporary water. Our sites were mostly small in size, often around 100 m in length (for lotic environments) or diameter (for lentic water bodies) up to bigger lakes with surface area of many hectares.

The specimens were determined to species level according to Garrison et al., (2006, 2010), Heckman (2006, 2010) and Lencioni (2006); consulting original species descriptions and external experts when needed. Afterwards the specimens were deposited in the MCNU (Museu de Ciências Naturais da Univates). The sampling permit was issued by ICMBio, through the SISBio system under the number 50624-1.

Ecoregions

In a previous paper we have shown that the Odonata of the Pampa differ between ecoregions (Renner et al., 2018b). Ecoregions may therefore serve as subgroups for the biome, separating the surveyed localities and the species found between them. We use ecoregions as the unit for species distribution with the assumption that species are not randomly distributed among ecoregions. A high specificity to regions mean a better structures species community which will enable us to select indicators (cf. Suhling et al., 2006). Here we follow the ecoregion division proposed by Roesch et al., (2009), which is based on the distribution of tree species. Our sampling sites fall into five regions which were analyzed individually in addition to the complete dataset. Ecoregions used are presented in Table 1 along with the number of sampling sites.

Selecting indicators: Nestedness and IndVal

Relying on a single selecting method to find indicators may result in biased results. As the Pampa has never been analyzed for indicators before and we have observed an unusually high amount of rare species in combination with a surprisingly few common species (Renner et al., *submitted*), we decided to use two different methods and combining their results. We will use the combined nestedness and discriminant analysis used by Suhling et al., (2006) and the almost classical method IndVal (Dufrêne & Legendre, 1997; Legendre & Legendre, 2012). While the latter method calculates the significance of each indicator species using a site randomization procedure (McGeoch & Chown, 1998), while the former method uses no randomization, only a sorting.

The use of nestedness as a tool for analyzing species composition controversial (Simberloff, 1998; Suhling et al., 2006), and the last decade has seen a modification of the analysis to

better quantify the metrics (Almeida-Neto et al., 2008). As we have not previously used the modified calculations in a selecting process for indicators of diversity, we decided to use the method to which we are familiar, the Nestedness Temperature Calculator, NTC (Atmar & Patterson, 1995) as in e. g. Sahlén & Ekestubbe, (2006) and Suhling et al., (2006). All species and localities were included in a presence–absence matrix for which an analysis of nestedness was performed. We then made separate presence-absence matrices for each ecoregion and analyzed them separately. A nested distribution of Odonata in the Pampa or in the separate ecoregion implies that species are not distributed in random and that diversity indicators can be selected from the moderately common species in the matrix.

The next step was to perform a discriminant function analysis using SPSS 24 to determine if the five ecoregions were distinct with regard to the odonate assemblages of the localities. A discriminant analysis uses a set of independent variables (here we assume all species are distributed independently; each species constitute one variable) to find linear combinations (discriminant functions, based on the original variables) that the groups of cases (in our case the ecoregions). The calculation results in Eigenvalues, explaining how strong each discriminant function is, and Wilks' lambda values which explain how well the functions separate cases (observation data) into groups (ecoregions). The Wilks' lambda is equal to the proportion of the total variance in the discriminant scores which is not explained by the differences between groups; smaller values mean a higher discriminatory ability of the function. Chi-square tests explain if the means of the discriminant functions are equal across groups and canonical correlations explain which variables (species) correlate best with the respective functions. The r-test is summarized in a classification table which shows how well-defined the species assemblies are in each ecoregion.

The selection of indicative species are based on the nestedness and the discriminant analyses following the criteria suggested by Suhling et al., (2006) and already applied on the Pampa dataset by Renner et al., (2018b):

(1) Species must be ecoregion specific. We compared the number of sites per ecoregion for each species. A vagrant/generalist species will occur in most ecoregions while indicative species would occur foremost in a single region (with some scattered localities elsewhere).
(2) Species must be 'moderately common' as an indicator must have a chance to be discovered at a site but cannot occur in too great a proportion of the sites (Sahlén & Ekestubbe, 2001). We set the limits to occurring in <20% and >3% of the localities surveyed.
(3) As another criterion of ecoregion specificity, we used the univariate ANOVA analyses in the discriminant calculation, which is used as a test of the explanatory potential of each independent variable in the discriminant analysis. Significant ANOVAs would mean that the species are not randomly distributed among ecoregions.
(4) We selected species the distribution of which were correlated with one of the significant discriminant functions in the discriminant analysis.

The IndVal method follows Dufrêne & Legendre (1997). The method consists of a classification procedure of species among sites or groups of sites, sampled in one or several events. Species with a high specificity and high fidelity within a habitat are considered to achieve the highest indicator value. Only taxa with IndVal >0,25 were proposed as the finalist indicators (Dufrêne & Legendre, 1997). To apply this method we used the R 3.2.4 program (R Core Team, 2013) through the *Indicspecies* package 1.7.5 (De Caceres & Jansen, 2015) with 9999 permutations, using data for dragonfly occurrences.

Each of the above methods will present a list of potential indicator species, Nestedness a list of species occurring together with many other species, and IndVal instead, present species which are characteristic for each ecoregion.

Results

Field survey

Our dataset comprised 99 species distributed among 131 localities. The total number of specimens collected was 3,242 (Anisoptera: 1,822; Zygoptera: 1,420). Species were predominantly belonging to three families: Libellulidae (51,5%, 51 species), Coenagrionidae (24.2%, 24 species), Gomphidae (9,1%, 9 species), also Aeshnidae, Calopterygidae, Lestidae, Heteragrionidae, with lower numbers. From these we omitted seven specimens as they could be identified to genus level only. The number of species per site varied from 2 to 20, with an average of 9.06 ± 4.03 (SD). The number of sites per ecoregion varied: 15 (Steppe (3) and Coastal (5); γ diversity 42 and 22 respectively), 22 (Transition (4); γ 42), 27 (Savanna (2); γ 59) and 52 (Steppic-savanna (1); γ 80). The data set contained very few common species. Most species (73%) occurred in 10 or fewer localities, while only 7 species occurred in more than 50 of the 131 surveyed localities.

The NTC results showed that the temperature of all matrices except the one for the Steppe ecoregion was significantly lower than the random temperature (1000 permutations), meaning that species are non-randomly distributed among sites (Table 1). The discriminant analysis used four discriminant functions of which all were significant. The first function (Eigenvalue = 13.37, Wilks' lambda = 0.00011, Chi-square = 1715.10, df = 382, p<0.0001) explained 36.2% of the variance. Function 2 (Eigenvalue = 10.91, Wilks' lambda = 0.002, Chi-square = 505.87, df = 291, p<0.0001) explained 29.59%; function 3 (Eigenvalue = 7.41, Wilks' lambda

= 0.019, Chi-square = 311.37, df = 192, p<0.0001) explained 20.0%; and function 4

(Eigenvalue = 5.28, Wilks' lambda = 0.159, Chi-square = 144.23, df = 95, p = 0.001)

explained 14.34%. The separation in this analysis was 100% meaning that all ecoregions were

distinct according to their species composition.

Table 1. Results from analyses of nestedness using the Nestedness Temperature Calculator (Atmar & Patterson, 1995). All regions and the total matrix have a low fill (implying lower temperatures in the calculations, i.e too many rare species). Matrix temperatures significantly lower than the randomised temperatures (1000 permutations) for all matrices but Steppe.

Region	No. species	No. localities	fill	matrix temperature	random temperature	significance
Total Pampa	99	130	9.2 %	12.71°	38.19 ± 1.1°	p < 0.0005
Steppic-savanna	80	56	13.3 %	17.29°	46.44 ± 1.96°	p < 0.0005
Savanna	50	23	15.5 %	26.63°	42.08 ± 3.88°	p < 0.0005
Steppe	42	15	17.3 %	32.69°	40.55 ± 5.0°	p = 0.058
Tansition	42	22	23.5 %	29.4°	56.18 ± 4.42°	p < 0.0005
Coastal	22	15	28.4 %	32.74°	50.69 ± 6.62°	p = 0.0031

In total 17 potential indicators of diversity fulfilled the criteria set up (Table 2). Out of these,

2 were indicative for Steppic-savanna, 5 for Savanna, 3 for Steppe, 5 for Transition and 2 for

Coastal.

Table 2. Moderately common species selected by the analysis of nestedness and the following discriminant analysis. N: number of sites in total, F-value and p-value from discriminant equations cnfirming non-random distribution btw. ecoregions. Numbers 1 to 5 corresponding to ecoregions; showing the number of sites per ecoregion.

N	Species	F-value	p-value	1	2	3	4	5
17	*Perithemis icteroptera*	8.50	< 0.0005	2	0	1	14	0
16	*Micrathyria tibialis*	6.37	< 0.0005	3	3	1	9	0
14	*Argia lilacina*	5.79	< 0.0005	14	0	0	0	0
14	*Macrothemis imitans*	10.98	< 0.0005	2	10	1	1	0
14	*Telebasis corallina*	9.84	< 0.0005	2	5	0	0	7
11	*Macrothemis heteronycha*	3.08	0.019	10	0	1	0	0
11	*Oligoclada laetitita*	26.21	< 0.0005	0	0	0	11	0
10	*Tramea binotata*	2.67	0.035	4	5	0	0	1
9	*Oxyagrion rubidum*	24.49	< 0.0005	1	0	8	0	0
7	*Oxyagrion hempeli*	12.23	< 0.0005	0	7	0	0	0
6	*Telebasis willinki*	5.71	< 0.0005	1	0	0	5	0
6	*Planiplax erythropyga*	27.09	< 0.0005	0	0	6	0	0
5	*Erythemis credula*	13.95	< 0.0005	0	0	0	0	5
5	*Tauriphila argo*	18.60	< 0.0005	3	0	0	2	0
4	*Acanthagrion ascendens*	5.82	< 0.0005	0	0	0	4	0
4	*Argia sp.*	2.95	0.023	0	1	0	3	0
4	*Erythrodiplax umbrata*	4.61	0.002	1	0	3	0	0

The IndVal method selected 20 potential representative species for the five ecoregions. The number of species selected per region varied between 2 and 8 (Table 3).

Table 3. Species selected by IndVal listed per ecoregion. 1 - 5 Ecoregions of occurrence. IndVal values >0,25 selected as indicators.

Species	Ecoregion	IndVal	p-value
Argia lilacina	1	0,5	0,005
Mnesarete pudica	1	0,378	0,05
Macrothemis imitans	2	0,57	0,005
Oxyagrion hempeli	2	0,552	0,005
Oxyagrion rubidum	3	0,718	0,005
Planiplax erythropyga	3	0,632	0,005
Erythrodiplax umbrata	3	0,428	0,015
Rhionaeschna bonariensis	3	0,367	0,035
Perithemis icteroptera	4	0,74	0,005
Oligoclada letitia	4	0,707	0,005
Acanthagrion lancea	4	0,597	0,005
Micrathyria tibialis	4	0,504	0,005
Telebasis willinki	4	0,459	0,005
Acanthagrion ascendens	4	0,426	0,005
Aphylla producta	4	0,369	0,02
Rhionaeschna planaltica	4	0,361	0,05
Erythrodiplax paraguayensis	5	0,748	0,005
Erythemis credula	5	0,577	0,005
Erythemis sp.	5	0,384	0,03
Erythrodiplax avittata	5	0,365	0,04

Notable is the fairly big overlap, where 10 species are selected by both methods. These ten species occur in all ecoregions, but only a few species in each region. These are: *Perithemis icteroptera,* by both methods selected for transition zone; *Argia lilacina*, by both methods selected for Steppic-savanna; *Oligoclada laetitita*, by both methods selected for Transition

zone; *Oxyagrion rubidum*, by Nestedness selected for Steppe (n.s.), by IndVal selected for Savanna; *Oxyagrion hempeli*, by both methods selected for Savanna; *Telebasis willinki*, by both methods selected for Transition zone; *Planiplax erythropyga*, by both methods selected for steppe (n.s. for nestedness); *Erythemis credula*, by both methods selected for coastal; *Acanthagrion ascendens*, by both methods selected for transition zone; and *Erythrodiplax umbrata*, by both methods selected for steppe (n.s. for nestedness).

Discussion

Pampa regional diversity

Contrary to our expectations there was a big overlap in the indicator species selected by the combined nestedness-discriminant method and the IndVal method. Nine species were selected by both methods from lists of 17 (nestedness) and 20 (IndVal) respectively. This gives at hand that the nine species demarked by two methods should be explored further regarding their ecology. The straightforward sorting of species should be sufficient for this type of comparison. Further, using the indicator power system as proposed by Halme et al., (2009) would only work on single species indicating a set of species, but in our case we have a set of species indicating a strong specificity to the features of each ecoregion, which in turn, is believed to be a good assumption for regional indicative purposes.

Interestingly, our analysis suggested 9 species as indicators, out of 99, which is a big species pool if compared to other regions, demonstrating the overall dragonfly richness of the Pampa. The size of regional species pools for dragonflies has been studied widely in other regions of the world. In temperate regions of northern Europe, specifically southern and central Sweden, several studies have reported a regional species pool of 24-30 species (Wittwer et al., 2010, Flenner & Sahlén, 2008). In the Neotropics, Pires et al., (2013) surveying mainly river sections and a few ponds along the Jacuí River basin, in Rio Grande do Sul, Brazil, found 30

genera of dragonfly larvae, indicating the occurrence of a big regional species pool. De Marco et al., (2014), sampling 71 lakes in central Brazil, listed a species pool of 56, while Monteiro et al., (2013), sampling eight rivers in tropical Amazonas (Manaus, Brazil), reached 32 species. Corresponding numbers for river basins in Namibia (Suhling et al., 2010), varied from single species in arid areas to 78 in the border areas of the humid tropics.

It is apparent that with the few species selected for each ecoregion, their use as indicators for species diversity and/or the ecoregion itself are limited. Each of the ecoregions have shown differences in their species compositions, denoting that variation on the density and quality of vegetation cover, affects directly the organization and occupation of the aquatic habitats by the dragonflies, as shown in Renner et al., (2018a; 2018b). Using indicators require that they can be found during a survey (McGeoch & Chown, 1998), making a single or a few, rather rare species, difficult tools. Better in such case to use the full set of selected species for the whole Pampa. There is a big chance that a small subset of the selected species can be found during a survey and this would then indicate a diverse environment typical for the "best" spots in the biome. Such an approach has been tested by Sahlén & Ekestubbe (2001) and found to work well in separating protected areas of high habitat integrity, from general areas with no special features.

Indicators

Among our indicators, for the Steppic-savanna solely, both methods selected *Argia lilacina*, which is a genus specialized in running waters (Garrison et al., 2010). We speculate that this result could demonstrate that, at regional level and in terms of aquatic environments, this region has better preserved rivers/streams than the lakes/impoundments located there. Also, from our field perceptions we could reach the same results, as most of the environments

where we recorded this species, were springs with clear and cold water, possibly streamed from clean groundwater.

For the Savanna ecoregion, both methods pointed out *Oxyagrion hempeli*, which has being collected mostly into well vegetated river sections and sometimes in the proximities of standing waters. This species has been found in our studies performed in Atlantic Forest (Renner et al., 2015; 2016), fact that could denote its preference for denser vegetation or even forest, instead of open field areas.

In the Steppe, an environment with less dense vegetation, our analyses pointed to *Oxyagrion rubidum* by Nestedness and *Planiplax erythropyga* and *Erythroduplax umbrata* by both methods. From these first two species, we can speculate that they have strong specificity in relation to this ecoregion, since all its records from the Pampa belong to this ecoregion. *Erythrodiplax umbrata* was also selected for the indicators pool, but we suppose that it could be treated as a weaker indicator since this genus is known as widespread generalist, inhabiting mostly environments that are under anthropogenic pressure (Machado, 2001).

For the Transition zone, our methods selected four species in total: *Acanthagrion ascendens*, *Telebasis willinki*, *Oligoclada letitita* and *Perithemis icteroptera*. From those, we conclude that *P. icteroptera* may be also considered a weak indicator since its abundant records in very disturbed fragments of Atlantic Forest. The other three species, corroborate our study performed in 2015 (Renner et al., 2015), as indicators of species richness in fragments of Atlantic forest.

Finally in the Coastal zone, our analyses have found one species as potential indicator: *Erythemis credula.* This genus is known to be widespread in the Neotropical region (Machado, 2001; Garrison et al., 2006). But we regard *E. credula* as a potential indicator

since this species was recorded in well preserved areas both in our studies as in previous ones (Machado et al., 2001; Dalzochio et al., 2018).

Evaluation

Among a vast diversity of animal groups, some groups of organisms seem to be more suitable than others as bioindicators, and Odonata seem to be among such groups (Sahlén & Ekestubbe 2001; Renner et al., 2015; Valente-Neto et al., 2018). In this study we conclude that it is possible to select indicators for species richness in highly fragmented landscapes of Brazil's Pampa biome, by using an analysis of nestedness combined to the IndVal method. As aforementioned, the main problem is still being the lack of the ecological supportive knowledge needed to evaluate all species used and patterns seen. However, the method allows to select indicator species *in blanco* from groups that little is known.

Another factor to consider is the 'noise' of random occurrences in the dataset, as adult Odonata are known to disperse well, fact that is explained by the large number of rare species in our dataset. Conrad et al., (1999) found dispersal between ponds 0.8 km apart relatively common. In our areas, our clusters of sampling sites are located at similar distances in some cases, implying that many species in our study would be able to disperse between them. Nevertheless, this was not the case between the ecoregions, indicating that adult dragonflies display high regional habitat specificity, which has been proposed as the most important factor affecting the regional distribution of dragonflies (Harabis & Dolný, 2010).

In Brazil, the macro invertebrates are commonly used as the focus group in aquatic environments (Buss & Borges 2008; Valente-Neto et al., 2018), in some cases combined with other taxonomic groups, e.g. fishes (Pompeu et al., 2003). However, it is also common the need to use a higher taxonomic level than species, as there is a lack species descriptions and taxonomic keys, not to mention the shortage on ecological knowledge on the species. We

assume that the adults of Odonata, as a taxonomic group, can already be incorporated in monitoring programs, which would eventually contribute to the ecological knowledge on the species.

We see the logical next step to include more environmental factors in combination to other taxa (e.g. amphibians and other macroinvertebrates) to broaden the scope of research when dragonflies are studied. For the of environmental variables to the communities, we suggest the application of methods such as the DBI (Dragonfly Biotic Index) as proposed by Simaika and Samways (2009), and the HII (Habitat Integrity Index) as proposed by Nessimian et al., (2008). Such combinations would possibly provide accurate results for the selection of priority areas for conservation.

Using the analysis of nestedness combined with other approaches we can determine a wide range of indicator species in all taxa and even in less well-known groups of organisms, finding valuable indicators in a cost and time efficient way. We expect that our results, combined to other studies, would provide further information towards, the so needed, conservation efforts for the Pampa biome.

Acknowledgements

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CHAPTER 7

General discussion and key findings

This study can be classified as pioneer in the Pampa, one of the less known biomes of Brazil, providing a first insight on the structure of the Odonata communities in this area. Prior to this study, it was unknown how agriculture, forestry and other disturbances impacted on the freshwater habitats/ecosystems and the odonate assemblages of this region. Such studies have great importance to attract attention of the general public and to highlight the biodiversity encountered.

The main objective of this thesis was to investigate the relations of the landscape variables to the Odonata communities in the Pampa biome. From this main objective, several secondary ones were achieved, bringing further knowledge on the Odonata ecology, habitat preferences, distribution, occurrence patterns and potential indicators of species richness. Furthermore, we expect that our results could be of use for future conservation measures, which are on high demand for the Pampa biome.

In general, each of the chapters, in its own way, had demonstrated that the Odonata can be used to evaluate environmental conditions of the dominant aquatic habitats/ecosystems in the studied region. Therefore, they are considered a step forward in supporting decision-making and possibly robust ecosystem management/recovery in the context of the need for quick, standardized, and cost-effective assessment methodologies (CLAUSNITZER 2003; SUHLING et al., 2006; RENNER et al., 2018).

First of all, the initial steps of this thesis were done by the compilation of literary information on the biome and the chosen sampling regions, and by acquiring environmental data on the sites planned to be visited. This data was the very first proof of the richness in terms of Odonata for the Pampa biome: a biome which is surprisingly rich. In comparison to other biomes, to get an overview, we can cite De Marco et al., (2014), sampling 71 lakes in central Brazil, listed a species pool of 56, while Monteiro et al., (2013), sampling eight rivers in tropical Amazonas (Manaus, Brazil), reached 32 species. From this initial steps, the first inventory was

developed, which was still being fed even after its publication (RENNER et al., 2017) increasing the data for the subsequent studies.

As the second study, we investigated where, how and when the landscape features of the Pampa could shape the Odonata communities. The chosen variables where selected based on previous studies that used dragonflies as model organisms to test whether the communities are affected by human development (SAMWAYS, STEYTLER, 1995; CUNNINGHAM et al., 2007; STOKS; CÓRDOBA-AGUILAR, 2012). From these comparisons, we detected some of the species choices and inhabiting preferences in terms of environment, as land cover and type of aquatic system. Similar studies have been developed on other biomes showing similar results (MONTEIRO-JÚNIOR et al., 2013; RENNER et al., 2016). The result of this was a manuscript published in Journal of Insect Conservation (RENNER et al., 2018), also a pioneer study for the Brazilian Pampa odonates.

In a more specific study of the Odonata in the Pampa, we explored how the species are distributed along the communities, which ones could be considered rare or common, based on the species records of our sampling sites. We also tested if the distribution of common species are somehow affecting the distribution of the rare ones. In conclusion, we got to an interesting relation of common and rare species: the anthropogenic changes in the environment has increased the number of common species, which in turn, have shown to be negative for the survival of rare species in the same locations. These results corroborate other studies on several animal groups such as butterflies (THOMAS; MALLORIE, 1985), ants (KUNIN; GASTON, 1993), and also among vertebrates (MAGURAN; HENDERSON, 2003).

Following a similar approach of our second study, we investigated if the odonatan assemblies have also specific preferences regarding the density and type of vegetation cover. For that we selected an ecoregion division proposed by ROESCH et al., (2009), for the Pampa biome in Brazil. Studies like KIETZKA et al., (2015), developed in South Africa, have demonstrated similar results: the vegetational features are of great influence on the Odonata communities. Our study has shown that the communities follow strictly such environment variables which brought us to another level of comprehension of the Pampa ecology. Such studies should definitely be expanded for other animal groups aiming to a better comprehension of the overall functioning of the Pampa. Nevertheless, the development of this study has inspired us to investgate further how the actual protected areas are distributed in the Pampa, in

relation to the ecoregions (Table 1). This gaves us an overview of the regions which need the most further protection, that in turn, can be backgrounded by studies such as ours.

Table 1 - Amount of protected areas already established within the five ecoregions studied.

Ecoregion	Approx. area (km^2)	Reserve area (km^2)	Proportion protected
1	36424	950.00	0.026
2	16089	36.45	0.0023
3	63561	2777.99	0.044
4	38489	228.26	0.0059
5	44971	30.00	0.00067

Reserves taken into account are: APA Ibirapuitã, APA Banhado Grande, APA Delta do Jacuí, PE Itapuã, PE Espinilho, PE Camaquã, PE Itapeva, PE Podocarpus, RVS Banhado dos Pachecos, REBIO São Donato and REBIO Banhado do Maçarico.

As dragonflies are popular among conservation studies as reliable indicators of environmental quality (VALENTE-NETO et al., 2016; CALVÃO et al., 2018). For a final chapter for this thesis, we developed a study testing for the first time a combination of two popular selection methods for bio indicators using dragonflies as model organisms. We reserved this study for the end of the thesis, aiming to analyse the biggest dataset we could get. In this study we detected potential indicators among dragonflies using a nestedness and discriminant analyses combined to the newer IndVal methodology. Our results have brought a set of species, pointed out by both methods, which could be used as thermometers of environmental quality in the Pampa: using an easy and cheap survey method we can get to a general status of environment conditions. We therefore hope that studies like this could be of help in the suggestion of future conservation areas, so needed in the Pampa.

The main results of this thesis corroborated the findings of several other studies that demonstrated the composition and structure of communities of dragonflies are affected prove dragonflies are directly affected by human actions, as shown in biomes as the Cerrado (VALENTE-NETO et al., 2016), Amazon (MONTEIRO-JÚNIOR et al., 2013) and Atlantic Forest (RENNER et al., 2016). The Pampa biome is being subjected to great human interference by three major activities: agriculture, cattle farming and forestry. These activities have all its own effects over the landscape, but in common it all result in habitat fragmentation and isolation (OVERBECK et al., 2009; ROESCH et al., 2009; MAZIA et al., 2010; DOBROVOLSKI et al., 2011). The main actions towards conservation in Brazil are taken in forested biomes (OLIVEIRA et al., 2017) denoting some negligence towards the Pampa, a proven rich biome. Nowadays only 0.8% of the Pampa area is inside preservation areas (OLIVEIRA et al., 2017), being the least protected biome in Brazil. Also, the suggestion of priority areas for conservation in the Pampa must take into consideration the fact that natural communities are already severely fragmented (SANTOS; SILVA 2007; OVERBECK et al., 2009; ROESCH et al., 2009).

Challenges and limitations

From the outcomes of this thesis, besides the results here presented, three major challenges were found, which will probably be still limiting the development of such studies: the interest/attention to such biome, the funding and the taxonomic challenges.

As pointed out along all the chapters of this thesis, the Pampa biome has been neglected by the Brazilians, not only government authorities but also by the research community and the general people. Several authors have shown that priority have been given mostly to forested biomes resulting in the less protected one among seven Brazilian biomes (OVERBECK et al., 2015; OLIVEIRA et al., 2017). Also it is worth to mention the international interest which usually prioritizes forest biomes in a biased and selective way, always pursuing potential for new products and monetary outcomes, as if the Pampa wasn't a rich biome. There are great potential in the Pampa (SANTOS; SILVA 2007; OVERBECK et al., 2009; ROESCH et al., 2009), as it is in all other Brazilian biomes.

Funding in Brazil follows the same rule above mentioned, as Brazilian forested biomes have been historically prioritized over the other biomes as the Pampa, the Caatinga and the Cerrado, all with great biodiversity and potential for discoveries (OLIVEIRA et al., 2017). Not to mention the economic problems Brazil have been facing since several years: escalating corruption, state inefficiency and ineffective policies towards the environment can be remarked, among other problems. Funding for research has been decreased steadily in the last years as consequence of these problems.

Third, and specifically related to the Odonata order, is the lack of taxonomic knowledge in the region. According to GARRISON et al., (2010) there are potential for new species among most of the Neotropical genera, not to mention the larvae descriptions, which covers as much as 25% of the known species. Also, several genera need urgent taxonomic revisions, such as those developed by Dr. Rosser Garrison and Dra. Natalia von Ellenrieder, as the review of the genus *Argia* (Coenagrionidae). Faunal surveys are still on high demand in Brazil and are more relevant every day, given the rate of habitat loss Brazil is facing. Besides all that, it is worth to mention that inventories can provide and improve ongoing and future management efforts (LEWIS, 2006).

Priorities for future work

In terms of general knowledge of the Pampa or specific knowledge of the Odonata, we suggest the development of more supportive material, including identification field guides for a broader public, as well the accumulation of supplementary material and the preservation of the existing collections as reference for future research.

Regarding conservation efforts, we suggest that it should be focused on the original habitat types, as we would also like to stress that there are still many questions regarding which factors are essential to the occurrence of the original species. For that, it is necessary an expansion of the sampling areas, aiming to achieve an even thorough picture of the biome, which may support more general conclusions. Hence, further research, accumulating data on a range of target taxa is necessary, as larval sampling would be a complement as well. In doing

so, we should be able to determine more accurately priority areas for conservation of the biome as a whole.

Through developing and making public all the information derived from our studies regarding the diversity, distribution and ecology of dragonflies in the Pampa biome, we expect to contribute for the maintenance and conservation of this biome as a whole.

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APPENDICES

Published article prints

Biota Neotropica (Capes A2)

Preliminary dragonfly (Odonata) species list from the Pampa biome in Rio Grande do Sul, Brazil, with ecological notes for 19 new records for the State

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Journal of Insect Conservation (Capes A2)

ORIGINAL PAPER

CrossMark

Water body type and land cover shape the dragonfly communities (Odonata) in the Pampa biome, Rio Grande do Sul, Brazil

Samuel Renner[1] · Eduardo Périco[1] · Marina Schmidt Dalzochio[1] · Göran Sahlén[2]

Austral Ecology (Capes A2)

Ecoregions within the Brazilian Pampa biome reflected in Odonata species assemblies

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Co-authored papers published during the doctoral period

Hydrobiologia (Capes A2)

PRIMARY RESEARCH PAPER

Effect of tree plantations on the functional composition of Odonata species in the highlands of southern Brazil

Marina Schmidt Dalzochio ⓘ · Eduardo Périco · Samuel Renner · Göran Sahlén

International Journal of Odonatology (Capes B1)

Taylor & Francis
Taylor & Francis Group

Check for updates

Description of the final stadium larva of *Erythrodiplax media* (Odonata: Libellulidae) with preliminary key to known South American larvae in the genus

Marina Schmidt Dalzochio [a]*, Eduardo Périco [a], Samuel Renner [a] and Göran Sahlén [b]

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Journal of Insect Conservation (Capes A2)

ORIGINAL PAPER

CrossMark

Predicting the effects of future climate change on the distribution of an endemic damselfly (Odonata, Coenagrionidae) in subtropical South American grasslands

Mateus Marques Pires[1] · Eduardo Périco[1] · Samuel Renner[1] · Göran Sahlén[2]

Biota Neotropica (Capes A2)

Checklist of Odonata (Insecta) in the state of Rio Grande do Sul, Brazil with seven new records

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Paper submissions

Neotropical Entomology (Capes B1)