

Research Article / Artículo de Investigación

Odonata (Insecta) in high-altitude fields and associated ecosystems in the Poços de Caldas Plateau, Brazil

Odonata (Insecta) en campos de gran altitud y ecosistemas asociados en la meseta de Poços de Caldas, Brasil

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ZooBank: urn:lsid:zoobank.org:pub:96538E88-F567-43F9-A08E-6AFBE035DCE0
<https://doi.org/10.35249/rche.49.4.23.18>

Abstract. The High Altitude Fields (HAF) are unique phytosociological features that occur only in certain regions of the Atlantic Forest. It is composed of herbaceous and shrubby vegetation and shallow soils that promote local water infiltration and recharge. Occurring on top of hills, the HAF are isolated units in the landscape, connecting with the matrix through associated ecosystems (springs with riparian forests and “capões de mata”, which are natural islands of arboreal vegetation, commonly associated with rural vegetation, such as high-altitude fields, located above 1,200 m in phytogeographic domains of the Atlantic Forest, Cerrado or Caatinga). These areas have great species endemism, and studies concerning the order Odonata are still scarce. Thus, we aimed to evaluate the ecological responses (richness, diversity, specificity) of adult odonates in these ecosystems. The study was conducted from November 2020 to March 2021 in three areas in the Poços de Caldas Plateau, Minas Gerais state, Brazil. A total of 45 species (247 specimens) were collected, with the highest total richness being recorded for Anisoptera. Among the sampled areas, there was no difference in Anisoptera communities, but there was a difference in Zygoptera species composition. In general, the most preserved remnant of HAF, the greater it presents greater richness of Odonata and harbors a regional pool of species.

Key words: Atlantic Forest; dragonfly; land uses; Minas Gerais state; species diversity.

Resumen. Los campos de gran altitud (HAF) son características fitosociológicas únicas que solo se encuentran en ciertas regiones de la Mata Atlántica. Están compuestos por vegetación herbácea y arbustiva, así como suelos poco profundos que favorecen la infiltración local de agua y su recarga. Situados en la cima de las colinas, los HAF son unidades aisladas en el paisaje, conectándose con la matriz a través de ecosistemas asociados (manantiales con bosques ribereños y “capões de mata”, que son islas naturales de vegetación arbórea, comúnmente asociadas con la vegetación rural, como los campos de gran altitud ubicados por encima de los 1.200 m en los dominios fitogeográficos de la Mata Atlántica, el Cerrado o la Caatinga). Estas áreas presentan un gran endemismo de especies, y los estudios sobre el orden Odonata aún son escasos. Por lo tanto, nuestro objetivo fue evaluar las

Received 30 September 2023 / Accepted 14 December 2023 / Published online 29 December 2023
Responsible Editor: José Mondaca E.



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respuestas ecológicas (riqueza, diversidad, especificidad) de odonatos adultos en estos ecosistemas. El estudio se llevó a cabo desde noviembre de 2020 hasta marzo de 2021 en tres áreas situadas en la meseta de Poços de Caldas, estado de Minas Gerais, Brasil. Se recolectó un total de 45 especies (247 ejemplares), siendo Anisoptera la que presentó mayor riqueza total. Entre las áreas muestreadas no hubo diferencia en las comunidades de Anisoptera, pero sí hubo diferencias en la composición de especies de Zygoptera. En general, cuanto más preservado esté el remanente de HAF, mayor será la riqueza de Odonata que alberga y más variado será el conjunto regional de especies.

Palabras clave: Bosque Atlántico; diversidad de especies; estado de Minas Gerais; libélula; usos del suelo.

Introduction

High Altitude Fields (HAF) are formations inserted in the Atlantic Forest that occur in high mountains areas of the Serra do Mar and Serra da Mantiqueira in the southern and southeastern states of Brazil (Martinelli 1989, 1996, 2007; Safford and Martinelli 2000; Safford 2007; Vasconcelos 2011). These environments have shallow soils, which support herbaceous and shrubby vegetation, that promote water recharge from the many springs occurring in these regions (Benites *et al.* 2003). Linked with the HAF and their springs, there are “capões de mata” and the “riparian forests”, which occur in the lowest surrounding topographic levels of the fields and the local headwater springs. They are very important ecosystems for local biodiversity because they are essential for the reproduction of aquatic species that inhabit the grasslands (*e.g.*, frogs, aquatic insects, etc.) (Magalhães *et al.* 2017; Mendes *et al.* 2022). They can still constitute natural vegetation islands, arboreal vegetation, located above 1,200 m in phytogeographic domains of the Atlantic Forest, Cerrado or Caatinga (Rizzini 1997), which promote connectivity between the high-altitude fields with which they are associated (Coelho *et al.* 2017, 2018).

The high rainfall rate in the regions where they are located promotes weathering and the formation of ravines in the relief along the slopes, which favor the formation of temporary and permanent pools, supporting diverse biological communities. The HAF occupy the top of mountains in regions of rugged topography, and they can function as islands, promoting isolation, and consequently the endemism of species (Alves *et al.* 2014; Jacobi *et al.* 2007; Marques Neto 2014; Martinelli 1996; Magalhães *et al.* 2017; Vasconcelos and Rodrigues 2010).

Due to their phytosociological characteristic, that is, vegetation predominantly composed of grasses, with some sparse shrubs and low woody yield, these ecosystems were for many decades confused with pasture areas and replaced in some regions by monocultures, agriculture, and mining (Ribeiro and Freitas 2010). Altitude fields have fragile soils for anthropogenic uses, despite that, usually have the surroundings removed (Vasconcelos 2014) and are targets of real estate expansion. In addition, they are regions isolated by relief with restricted geographic distribution within the Atlantic Forest (Vasconcelos 2011). This topographic isolation can be a determining factor for local endemism and constitute a geographic barrier for some species, especially those with more limited dispersive potential, such as some groups of aquatic insects (Finn and Poff 2005; Poff *et al.* 2006).

Another aggravating factor is the lack of research regarding HAF's biodiversity. Most of the existing studies focus on flora and its phytophysiognomies (Martinelli 1996; Jacobi *et al.* 2007; Martinelli 2007; Vasconcelos 2011; Matavelli and Monteiro 2012; Rezende *et al.* 2013; Alves *et al.* 2014). Added to this, the changes in these environments caused by climate

change (Wilson *et al.* 2021), which justifies carrying out studies to better understand the biodiversity of different taxa of invertebrates, such as the Odonata, an insect order that is sub-sampled in high altitude fields (Santos 1966, 1970).

The order Odonata constitutes an important component of the trophic food web of freshwater environments (Corbet 1999). Odonates spend part of their life cycle in the aquatic environment, being able to colonize from permanent and temporary pools to lakes and streams (Vilela *et al.* 2016). Compared to other aquatic insects, Odonata has a good dispersal potential and environmental tolerance, but some species have specific ecological demands of niches. For this reason, they are often used as bioindicators of forest ecosystems' degree of conservation (Corbet 1999; Corbet and May 2008; Oertli 2008; Hamada *et al.* 2019; Ribeiro *et al.* 2021).

Brazil has the greatest dragonfly richness in the world, with more than 870 species recorded (IUCN 2022), however, many ecosystems are still under-sampled. Despite that Minas Gerais state is considered well sampled, which has inventory studies in several physiognomies such as Cerrado (Vilela *et al.* 2020), Campo Rupestre (Bedê *et al.* 2015; Dos Anjos *et al.* 2020), and different Atlantic Forest phytophysiognomies such as Deciduous Forest (Souza *et al.* 2018; Gouvêa *et al.* 2022), Mixed Forest (Stefani-Santos *et al.* 2021) and Semideciduous Forest (Souza *et al.* 2017, 2018; Silva and Souza 2020; Stefani-Santos *et al.* 2021; Gouvêa *et al.* 2023), there are regions with few specific studies, such as the Poços de Caldas Plateau, in Minas Gerais state, which has only a list of species, dated to the 1960's (Santos 1966). This Plateau belongs to the Serra da Mantiqueira complex and is home to the remaining high-altitude fields with high potential for biological endemism that are still poorly known (Jacobi *et al.* 2007; Matavelli and Monteiro 2012; Rezende *et al.* 2013; Freitas *et al.* 2015; Souza *et al.* 2017). The plateau presents unique physiography that forms an annular dyke with raised edges formed approximately 80 million years ago (Moraes and Jiménez-Rueda 2008). This geomorphologic configuration confined internally the entire hydrographic network, and it is possible that biological specificities have evolved in the region. Indeed, some studies have shown that forested high altitude environments are rich with endemic species and play an important role in preserving the diversity of Odonata (Bota-Sierra *et al.* 2021, 2022).

Thus, we aimed to evaluate ecological responses (richness, abundance, diversity, specificity) of adult odonates present in remaining HAF fragments (*i.e.*, capões de mata) and riparian forests in the municipality of Poços de Caldas, south of the state of Minas Gerais, Brazil.

Materials and Methods

Study area

The study was carried out in three areas with different remaining proportions of natural HAF and associated ecosystems such as riparian forests and the capões de mata, which are islands of vegetation surrounded by natural fields, usually rounding temporary or permanent ponds, and the associated riparian forests, inserted between the mountains (Figs. 1A-C).

These regions are located inside the Poços de Caldas - MG Plateau (~1,180 masl) and are called in this study Moinhos (MO, 21°53'23"S, 46°32'53"W), Morro do Ferro (MF, 21°54'57"S, 46°33'56"W), and Jardim Botânico (JB, 21°47'4.57"S, 46°37'5.06"W), where lentic (marshes and temporary pools) - and lotic (streams and Ribeirão da Anta river) environments occur (Fig. 2).



Figure 1. Drone photographs from the highland field region “Morro do Ferro (MF)”. **a.** Image of the *stricto sensu* altitude field. **b.** Drainages ravines formed on the side of the hills by natural erosive processes, where there are temporary and permanent puddles. **c.** Riparian forest associated with springs that arise in the lower altimetric levels of the relief and “capões de mata” (island of vegetation) associated with the temporary and/or permanent ponds. / Fotografías aéreas tomadas con un dron desde la región de campos de altitud “Morro do Ferro (MF)”. **a.** Imagen del campo de gran altitud *stricto sensu*; **b.** Barrancos y drenajes formados en el costado de las colinas por procesos erosivos naturales, donde se encuentran charcos temporales y permanentes. **c.** Bosque ripario asociado a manantiales que surgen en los niveles altimétricos más bajos del relieve y “capão de mata” (isla de vegetación) asociado a charcos temporales y/o permanentes.

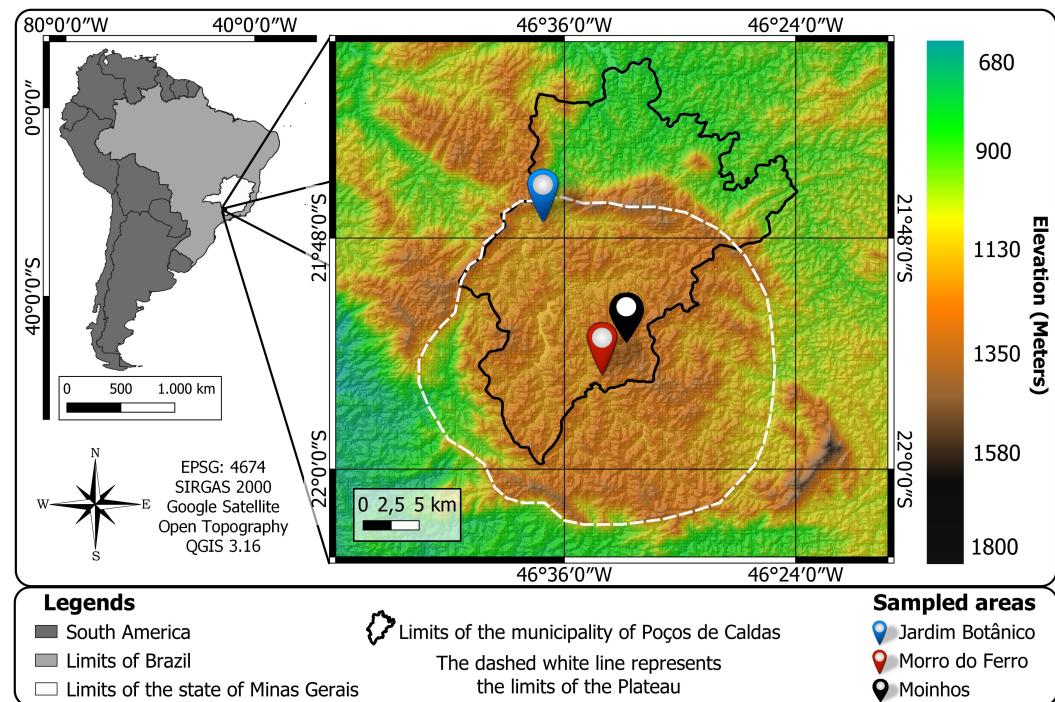


Figure 2. Study area at the Poços de Caldas Plateau in the state of Minas Gerais, Brazil, and its respective location within Brazil (grey) and Minas Gerais state (white). / Área de estudio en la meseta de Poços de Caldas en el estado de Minas Gerais, Brasil, y su respectiva ubicación dentro de Brasil (en gris) y en el estado de Minas Gerais (en blanco).

There is a maximum distance of 15 km and a minimum of four km among them. Within a 1200-meter buffer from a central point in the sampling area (surrounding lotic and lentic environments, such as rivers and ponds), land uses (*i.e.*, pasture, agriculture activities in areas of riparian forest and capões de mata) were quantified from high-resolution satellite images and digital elevation models (DEM) of the relief, by means of temporal comparison

with maps from the MapBiomas 6.0 collection. The respective areas in hectares were verified in the Q-GIS software (Fig. 3).

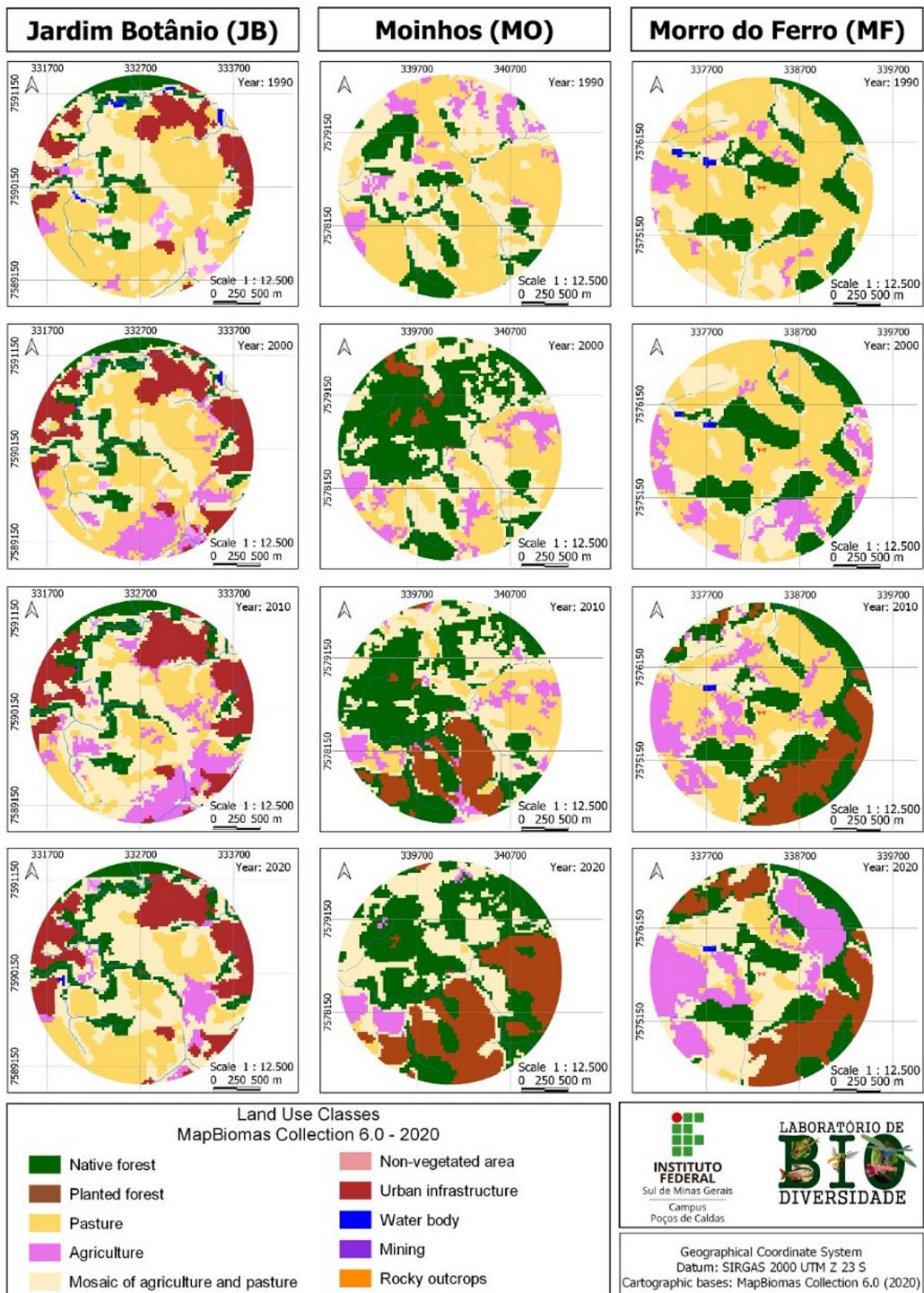


Figure 3. Land uses in the surroundings (buffer) of 1200 meters from a central point of the three sampled sites. / Usos del suelo en los alrededores (buffer) de 1200 metros desde un punto central de los tres sitios muestrados.

The different land uses present in areas of riparian vegetation and capões de mata and its typologies were analyzed through supervised classification for the years 1990, 2000, 2010 and 2020, to quantify the matrix substitutions over the last decades (Fig. 4). This is necessary to discuss the potential impact of different anthropic activities (*i.e.*, land uses) on the native forests in the period from 1990 to 2020, and its effects on the Odonata community.

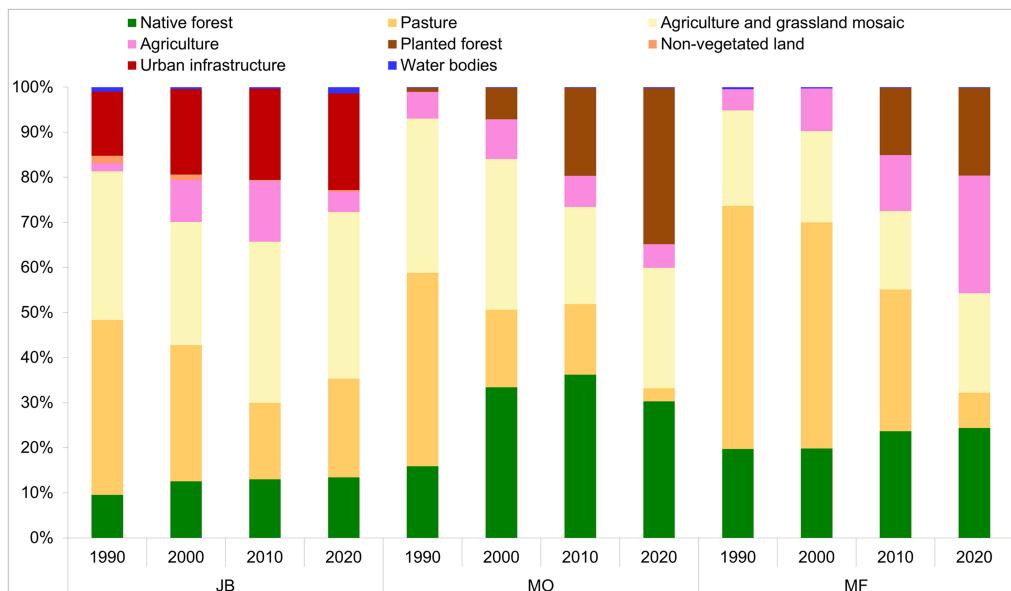


Figure 4. Land use quantification around 1200 meters from a central point at the collection sites. JB: Jardim Botânico (Botanical Garden); MO: Moinhos (Mills); MF: Morro do Ferro (Iron Hill). / Cuantificación del uso del suelo alrededor de 1200 metros desde un punto central en los sitios de recolección. JB: Jardim Botânico (Jardín Botánico); MO: Moinhos (Molinos); MF: Morro do Ferro (Colina de Hierro).

Samples

Collections were carried out between November/2020 to March/2021, the period of greatest regional rainfall index, with an average of 230 mm of precipitation in January. Temperatures in this period range from 16 °C to 25-26 °C on average (GMAO 2023). The total sampling effort consisted of four campaigns, each lasting three consecutive days, with 5 hours per day and four days per area, totaling 12 days and 60 hours per researcher. Entomological nets were used for collection in a standardized effort per hour/person, totaling five hours per day of sampling. Collections took place from 10:00 am to 3:00 pm, the period of highest dragonfly metabolic activity. To actively explore the greater heterogeneity and species richness of the ecosystem (Batista *et al.* 2021; Cezário *et al.* 2020), sampling was always carried out by three investigators who walked randomly within the boundaries of the HAF and its associated ecosystems (*i.e.*, the edges of forest capões and riparian forests), temporary and permanent puddles within drainage systems, and hilltops. All odonates sighted during the way were collected.

The collected specimens were kept in labeled and identified entomological envelopes (collector's name, date, and place). In the laboratory, the animals were fixed in acetone for 24 hours to remove the fatty tissues, maintain the color standard, and preserve the specimens (Lencioni 2005). The biological material was deposited at the Coleção Biológica

de Vespas Sociais (CBVS) of the IFSULDEMINAS, Campus Inconfidentes (<https://specieslink.net/col/CBVS>), Brazil. Taxonomic treatment at genus level was made using the keys of Garrison *et al.* (2006, 2010) and Lencioni (2005, 2006, 2017) for genus and species level. New occurrences were checked by comparing our list of species with the website Libelulas de Minas Gerais (libelulasdemg.com.br), that constantly updates the number of Odonata species in the state.

Dataset analysis

To compare the sampled areas, we used the following ecological indicators: Richness, Abundance, Shannon and Margalef Diversity Index total, and by suborders (Zygoptera and Anisoptera). One t-test was applied for diversity comparison with a significance level of 5%.

Taxonomic singularities were verified through species unique and shared among the sites. The occurrence of new species records for the municipality of Poços de Caldas, the state of Minas Gerais or Brazil was verified from another dataset research previously published in Brazil (Santos 1966). Due to the unique composition of HAF, we analyzed if any of the recorded species could potentially be an indicator species of replacing native vegetation with agricultural areas. An indicator species is defined as the most characteristic species of a typology, present in most of the sampling events (De Cáceres and Legendre 2009). They allow for a greater understanding of the current ecological relationships. We used the statistical package ‘indicspecies’ (De Cáceres and Legendre 2009) and Software R for data analysis.

To evaluate the sampling efforts, we build an accumulation curve from the observed richness with a confidence interval of 95%, using the species estimator Bootstrap 1, on the software EstimateS 9.1.0 (Cowell and Elsensonh 2014).

Results

In total, we collected 247 specimens belonging to 45 species, 31 genera, and nine families (Tab.1, Fig. 5).

Table 1. Abundance and taxonomic composition of odonates sampled in the three high altitude field remnants and associated ecosystems from Poços de Caldas-MG. *Unidentified females, possibly belonging to already identified species. JB: Jardim Botânico (Botanical Garden); MO: Moinhos (Mills); MF: Morro do Ferro (Iron Hill), (T): species under some threatening category by the IUCN and/or ICMBio. / Abundancia y composición taxonómica de los odonatos muestreados en los tres remanentes de campos de gran altitud y los ecosistemas asociados de Poços de Caldas-MG. *Hembras no identificadas, posiblemente pertenecientes a especies ya identificadas. JB: Jardim Botânico (Jardín Botánico); MO: Moinhos (Molinos); MF: Morro do Ferro (Colina de Hierro), (T): especies bajo alguna categoría de amenaza según la UICN y/o ICMBio.

Species		JB	MF	MO	Total
<i>Castoraeschna januaria</i>	(Hagen, 1867)	0	1	0	1
<i>Castoraeschna longfieldae</i>	(Kimmings, 1929)	0	1	0	1
<i>Coryphaeschna</i> sp.*		1	0	0	1
<i>Coryphaeschna adnexa</i>	(Hagen, 1861)	1	0	0	1
<i>Rhionaeschna bonariensis</i>	Rambur, 1842	0	2	0	2
<i>Aphylla theodorina</i>	(Navás, 1933)	0	1	0	1
<i>Brechmorhogha nubecula</i>	(Rambur, 1842)	0	0	1	1

<i>Dasythemis mincki</i>	(Karsch, 1890)	0	5	5	10
<i>Elasmothemis constricta</i>	(Calvert, 1898)	1	0	0	1
<i>Erythemis attala</i>	(Selys in Sagra, 1857)	0	1	0	1
<i>Erythemis mithroides</i>	(Brauer, 1900)	1	0	0	1
<i>Erythemis plebeja</i>	(Burmeister, 1839)	1	0	0	1
<i>Erythrodiplax fusca</i>	(Rambur, 1842)	15	4	0	19
<i>Erythrodiplax media</i>	Borror, 1942	3	0	0	3
<i>Erythrodiplax paraguayensis</i>	(Förster, 1905)	0	1	0	1
<i>Erythrodiplax</i> sp.*		3	1	0	4
<i>Idiataphe longipes</i>	(Hagen, 1861)	0	2	0	2
<i>Macrothemis imitans</i>	Karsch, 1890	6	0	0	6
<i>Macrothemis</i> sp.*		1	1	2	4
<i>Macrothemis tenuis</i>	Hagen, 1868	0	0	17	17
<i>Micrathyria almeidai</i>	Santos, 1945	0	2	0	2
<i>Micrathyria stawiarskii</i>	Santos, 1953	0	0	1	1
<i>Micrathyria pirassunungae</i>	Santos, 1953	0	1	0	1
<i>Nephepeltia berlai</i>	Santos, 1950	0	1	0	1
<i>Orthemis aequilibris</i>	Calvert, 1909	1	0	0	1
<i>Orthemis discolor</i>	(Burmeister, 1839)	2	0	0	2
<i>Pantala flavescens</i>	(Fabricius, 1798)	1	0	0	1
<i>Perithemis tenera</i>	(Say, 1840)	5	5	0	10
<i>Tramea binotata</i>	(Rambur, 1842)	0	2	0	2
<i>Neocordulia setifera</i>	(Hagen in Selys, 1871)	0	1	0	1
<i>Neocordulia</i> sp.*		0	0	1	1
<i>Hetaerina hebe</i>	Selys, 1853	0	2	19	21
<i>Hetaerina rosea</i>	Selys, 1853	1	0	0	1
<i>Acanthagrion gracile</i>	(Rambur, 1842)	18	7	0	25
<i>Argia sordida</i>	Hagen in Selys, 1865	0	1	25	26
<i>Cyanallagma nigrinuchale</i>	(Selys, 1876)	0	7	0	7
<i>Forcepsioneura sancta</i>	(Hagen in Selys, 1860)	0	0	6	6
<i>Homeoura chelifera</i>	(Selys, 1876)	0	12	0	12
<i>Ischnura capreolus</i>	(Hagen, 1861)	0	1	0	1
<i>Ischnura fluviatilis</i>	Selys, 1876	0	1	0	1
<i>Oxyagrion microstigma</i>	Selys, 1876	1	6	1	8
<i>Oxyagrion terminale</i>	Selys, 1876	2	4	11	17
<i>Telebasis carmesina</i>	Calvert, 1909	0	2	0	2
<i>Tigriagrion aurantiinigrum</i>	Calvert, 1909	5	1	0	6
<i>Heteragrion cauei</i> (T)	Ávila Junior, Lencioni & Carneiro, 2017	1	0	0	1
<i>Heteragrion tiradentense</i>	Machado & Bedê, 2006	0	0	2	2
<i>Lestes paulistus</i>	Calvert, 1909	0	1	0	1
<i>Allopodagrion contortum</i>	(Hagen in Selys, 1862)	0	1	8	9
Abundance		70	78	99	247

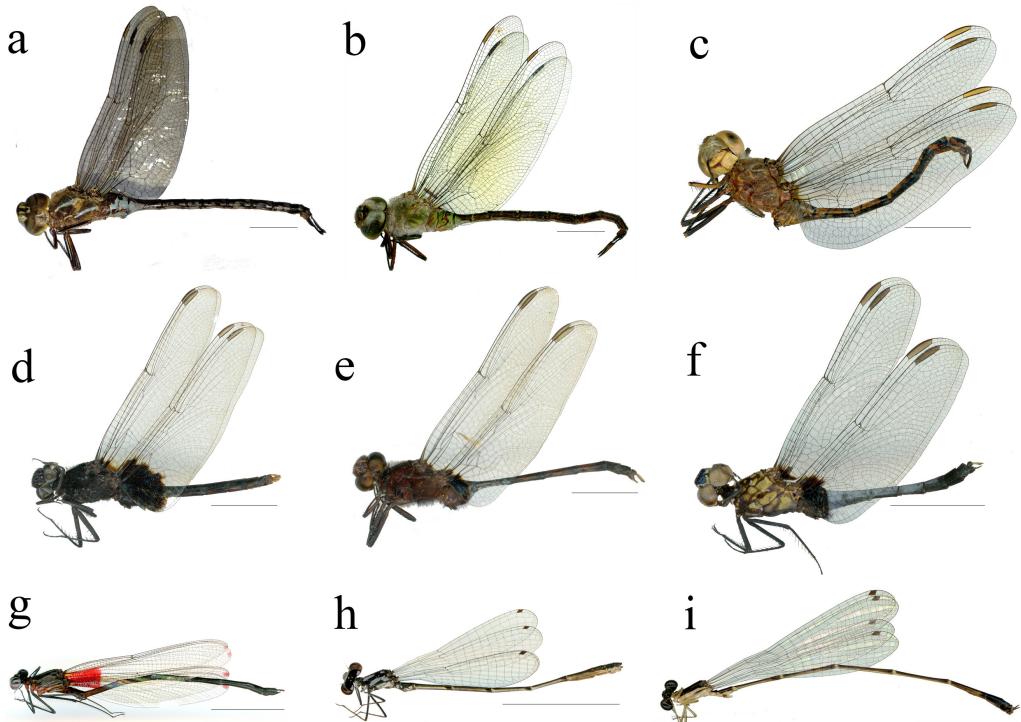


Figure 5. Some of the species sampled in the present study: **a.** *Rhionaeschna bonariensis*. **b.** *Coryphaeschna adnexa*. **c.** *Elasmothemis constricta*. **d.** *Erythemis attala*. **e.** *Erythemis plebeja*. **f.** *Erythrodiplax media*. **g.** *Hetaerina hebe*. **h.** *Cyanallagma nigrinuchale*. **i.** *Forcepsioneura sancta*. Scale bar: 10 mm. / Algunas de las especies muestreadas en el presente estudio: **a.** *Rhionaeschna bonariensis*. **b.** *Coryphaeschna adnexa*. **c.** *Elasmothemis constricta*. **d.** *Erythemis attala*. **e.** *Erythemis plebeja*. **f.** *Erythrodiplax media*. **g.** *Hetaerina hebe*. **h.** *Cyanallagma nigrinuchale*. **i.** *Forcepsioneura sancta*. Barra de escala: 10 mm.

Regarding the total community of sampled Odonata, the three areas are differentiated by richness and diversity, with Morro do Ferro (MF) being the most diverse region ($p<0.05$) (for both orders), followed by Jardim Botânico (JB) and Moinhos (MO), respectively (Tab. 2).

Table 2. Ecological indicators comparing the three study regions. JB: Jardim Botânico (Botanical Garden); MO: Moinhos (Mills); MF: Morro do Ferro (Iron Hill). / Indicadores ecológicos comparando las tres regiones de estudio. JB: Jardim Botânico (Jardín Botánico); MO: Moinhos (Molinos); MF: Morro do Ferro (Colina de Hierro).

Total diversity			p-value (pair-to-pair)			
	JB	MF	MO	JB-MF	JB-MO	MF-MO
Richness	18 <i>a</i>	28 <i>b</i>	11 <i>c</i>	0.005	0.059	0.0003
Shannon_H	2.29 <i>a</i>	2.97 <i>b</i>	1.98 <i>c</i>	0.003	0.039	0.0001
Margalef	4.06 <i>a</i>	6.23 <i>b</i>	2.19 <i>c</i>	0.009	0.005	0.0001
Anisoptera diversity			p-value (pair-to-pair)			
	JB	MF	MO	JB-MF	JB-MO	MF-MO
Richness	12 <i>a</i>	15 <i>a</i>	4 <i>b</i>	0.481	0.011	0.001
Shannon_H	1.95 <i>a</i>	2.49 <i>a</i>	0.83 <i>b</i>	0.076	0.001	0.001
Margalef	3.02 <i>a</i>	4.12 <i>a</i>	0.94 <i>b</i>	0.148	0.008	0.001

Zygoptera diversity			p-value (pair-to-pair)			
	JB	MF	MO	JB-MF	JB-MO	MF-MO
Richness	6 a	13 b	7 a	0.003	0.876	0.006
Shannon_H	1.14 a	2.17c	1.62 b	0.001	0.016	0.004
Margalef	1.50 a	3.13 b	1.40 a	0.004	0.736	0.001

The MF region, which contains the largest conserved remnants of Campos de Altitude, had greater richness and total diversity for Odonata and for the suborder Zygoptera, which showed equivalent diversity in JB and MO.

The bootstrap species estimator showed that the richness could reach 15.67 species in MO, 24.7 in JB and 28.89 in MF (Fig. 6).

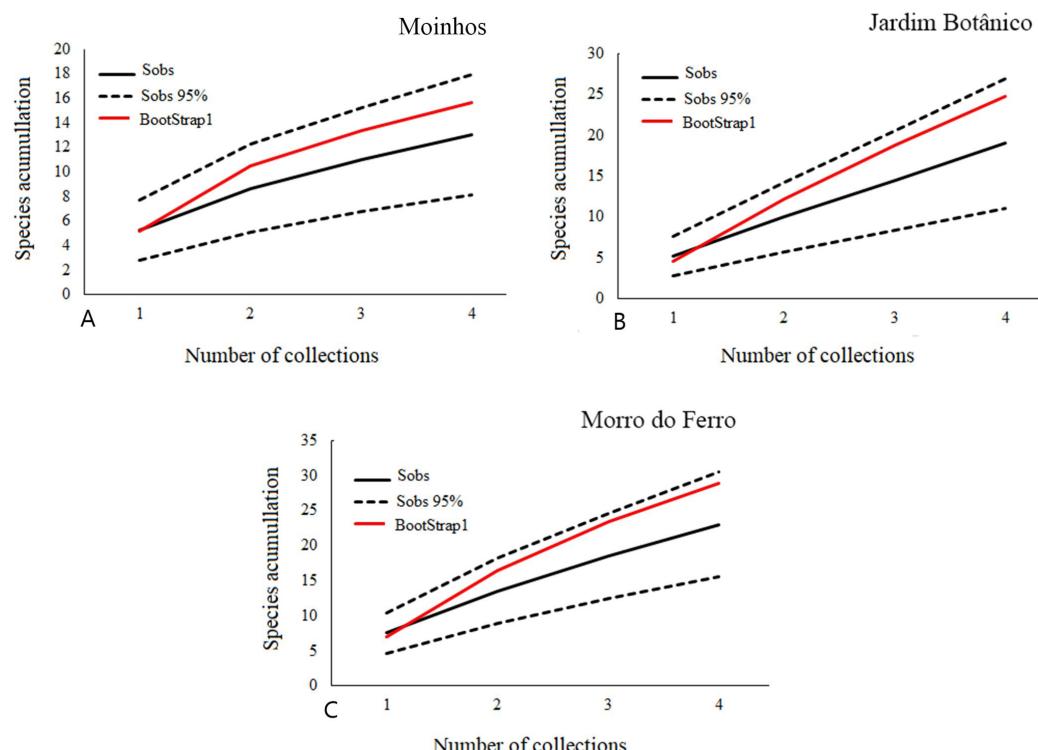


Figure 6. Accumulation curve of estimated (BootStrap1) and collected (Sobs) Odonata species in the Moinhos (Mills) area (A), Jardim Botânico (Botanical Garden) (B), and Morro do Ferro (Iron Hill) (C), with a confidence level of 95% (dotted lines). / Curva de acumulación de especies estimadas (BootStrap1) y recolectadas (Sobs) de Odonata en la zona de Moinhos (Molinos) (A), Jardim Botânico (Jardín Botánico) (B) y Morro do Ferro (Colina de Hierro) (C), con un nivel de confianza del 95% (líneas punteadas).

Seven species that occurred in MF also occurred in another area (JB or MO), but not in the three at the same time: Anisoptera: *Dasythemis mincki*, *Erythrodiplax fusca*, *Perithemis tenera*; Zygoptera: *Hetaerina hebe*, *Acanthagrion gracile*, *Argia sordida*, *Tigriagrion aurantinigrum*, *Allopodagrion contortum*. This demonstrates that MF can conserve the regional species pool.

Only the zygopterans *Oxyagrion microstigma* and *Oxyagrion terminale* were shared among three sites. The species *Argia sordida*, *Hetaerina hebe*, and *Macrothemis tenuis* were the most abundant in MO, while *Acanthagrion gracile* and *Erythrodiplax fusca* the most abundant in JB. *Homeoura chelifera* was the most abundant in MF. The MF region presented eighteen unique species, distributed in 15 genera; JB 11 unique species inserted in 10 genera, and MO five unique species in five genera.

Discussion

The HAF environments have been highly impacted with reduced original vegetation cover, as a result of intense changes in the landscape over the last few decades as demonstrated in land-use change (Figs. 3, 4). However, the richness observed in our study is similar to what was observed in some Conservation Units in the state of Minas Gerais (Souza *et al.* 2017; Stefani-Santos *et al.* 2021). Considering all the geographical extension of the Poços de Caldas Plateau (~750 km², inside which are the three sampled areas) and their physiographic particularities, it is possible that there are still many species to be sampled (as shown in Fig. 6). The species collector curve did not reach the asymptote (Fig. 6), therefore, the richness in the study area may be even greater, which is why more sampling is necessary to better understand the Odonata fauna in the region of the municipality of Poços de Caldas. For this reason, odonatological inventories should be extended to other remaining natural altitudes fields in the countryside of Plateau.

In our study, we have recorded greater general richness of Anisoptera than of Zygoptera. Zygopterans present physiological (*e.g.*, they are heliophiles to maintain energy metabolism and low flight potential) and ecological (*e.g.*, the need for more heterogeneous, forested habitats with pristine waters) demands which make them more sensitive to environmental changes, when compared to Anisoptera (Alves-Martins *et al.* 2018; Cezário *et al.* 2020; De Marco Jr. and Peixoto 2004; Kalkman *et al.* 2008). They may still have a lower dispersive potential as demonstrated by Alves-Martins *et al.* (2018) who realized greater spatial signatures acting on the diversity of Zygoptera in the Amazon biome. On the other hand, Veras *et al.* (2020) detected differences only in the composition (but not in the richness and diversity) of zygopterans and anisopterans from Cerrado regions with the replacement of specialists by generalist species associated with loss in environmental integrity. This highlights that the ecological responses of Zygoptera and Anisoptera can vary between different locations at different scales, from Biomes to specific phytosociological features such as an altitude field which present greater environmental amplitudes in temperature and rainfall index, similar to what we observed in this study (Benites *et al.* 2003; Gonçalves and Santos 2018). In addition, the altitude fields relief itself, associated with the natural disconnection of these remnants, may constitute a geographic barrier that isolates the taxa and promotes local richness, as reported by Stefani-Santos *et al.* (2021), in high altitude regions.

Elements of the ecophysiology of Odonata (such as those aforementioned) can affect these ecological parameters in response to environmental singularities at different scales and geographic locations and influence the species composition. For example, anisopterans are animals with higher energy metabolism, and consequently, good flight potential (Alves-Martins *et al.* 2018; Bilton *et al.* 2001; Padial *et al.* 2014; Petersen *et al.* 2004; Saito *et al.* 2015; Sarremejane *et al.* 2020). For this suborder, dispersing in the landscape matrix in the search for new oviposition sites constitutes a more “coherent” evolutionary trade-off relationship than for damselfly, when their environments are unsuitable (Alves-Martins *et al.* 2018; Santos *et al.* 2019). Considering the geographic scale of approach in this study (maximum distance of 15 km between areas), it is understandable the recorded greater general richness of Anisoptera than of Zygoptera.

Although Anisoptera had reflected less the direct loss of regional diversity, Zygoptera showed taxonomic depletion between the different analyzed sites (Kalkman *et al.* 2008). This addresses the direct vulnerability of the Zygoptera to the replacement of natural matrices in the Poços de Caldas Plateau, as we detected differences both in structure (richness and diversity) and in the composition of the taxa from suborder. Furthermore, Anisoptera can be a strong indicator of ecosystem function loss in these studied altitude fields, from the changing of more specialist species to more generalist ones after the loss of environmental integrity, as also demonstrated by Veras *et al.* (2020). The persistence of Anisoptera in the analyzed landscapes is also not fully guaranteed, since their populations may be indirectly affected by the decrease in abundance, as demonstrated by Alves-Martins *et al.* (2018).

It is also important to highlight that over 50 years ago, in the same geographic region of our study (*i.e.*, Poços de Caldas Plateau), although in different phytophysiognomic features, a study with greater territorial extension and sampling effort recorded 58 species, with greater richness for Zygoptera than Anisoptera, opposite pattern to that registered in this study (Santos 1966). Ferraz *et al.* (2019) state that large *Eucalyptus* plantations have high water consumption, which directly affects the flow of the water table and, consequently, the flow of springs, streams and rivers, negatively impacting the biodiversity of these ecosystems and adjacent environments. This factor helps to understand the reason for the lower richness recorded in this study in relation to that carried out by Santos (1966).

In the same study, Santos (1966) reported the occurrence of *Minagrion caldense* Santos, 1965, that has Poços de Caldas as its type locality. This species is currently considered as threatened by both the IUCN and ICMBio lists of threatened species (De Marco Jr. *et al.* 2023; Guillermo-Ferreira and Vilela 2020; ICMBio 2018), due to its restricted distribution area and lack of recent records in the type locality and its vicinities. Our results corroborate the status of conservation that mentions its absence in Poços de Caldas since the 60's (Guillermo-Ferreira and Vilela 2020), as our collections also failed to record this species in that area.

We emphasize that zygopterans recorded in the three sampling sites are species with a wide distribution and occupy different phytophysiognomies in different biomes (Ávila Junior *et al.* 2020; Bedê *et al.* 2015; Lencioni 2017; Souza *et al.* 2017; Vilela *et al.* 2016), justifying both its higher frequency of occurrence and abundance in the sampled sites. On the other hand, we have also recorded singletons, that seem to be rare species in inventories and collections. This is the case for *Heteragrion cauei* Ávila Junior, Lencioni & Carneiro, 2017. This species was collected only in JB and is likely that this species is associated with forest fragments close to remaining altitude fields, such as the "capões de mata" or even riparian forest. Currently, this species is known only in two localities, in the municipality of Ouro Preto, within the Atlantic Forest biome (Ávila Junior *et al.* 2017) and from this biome in transition to the Cerrado in the municipality of Barroso (Gouvêa *et al.* 2023), both regions of the state of Minas Gerais. In addition, it is categorized as VU (vulnerable) on the Red List of Threatened Species (IUCN 2022). Our record of this species enlarges its distributional range and provides new data for further conservation assessments.

Among the Anisoptera, we have also recorded some singletons in our samples. For instance, *Aphylla theodorina* (Navás, 1933) was previously recorded in the Serra de São José in features of Campo Rupestre associated with semideciduous forest (Bedê *et al.* 2015). In our study area, it occurred uniquely in MF, the better feature altitude field among three areas. *Neocordulia setifera* (Hagen in Selys, 1871) occurs from the Caatinga area in northeastern Brazil (Takiya *et al.* 2016), to the state of São Paulo (Costa *et al.* 2008). Up to now, their occurrence biome in the state of Minas Gerais was undetermined (Costa *et al.* 2000). Nevertheless, it was suspected that it may also occupy an Atlantic Forest zone.

Although the MO region had the lowest exclusive richness (*i.e.*, taxa that only occurred in this location), we highlight the presence of the species *Heteragrion tiradentense* Machado & Bedê, 2006, which was previously recorded only in regions of deciduous forest, in the municipalities of Tiradentes (Bedê *et al.* 2015) and Barroso (Souza *et al.* 2013), both of Minas Gerais state, and in some Atlantic Forest areas in São Paulo state (Lencioni 2013). This site (MO) is largely occupied by eucalyptus monocultures, being the region that has suffered the most expansion of this monoculture in recent decades (Fig. 3). However, it is possible that the riparian forest fragments and the “capões de mata” present in the area are still supporting these populations. According to Coelho *et al.* (2017), these “capões de mata” function as natural islands and are very important for the biodiversity of the rural environments in which they are associated, although little studied. Considering the lower dispersive potential of *H. tiradentense* and their ecophysiological demands it is predictable that their dispersive processes are compromised through the isolation promoted by the monoculture of eucalyptus in the region.

The studied region is undergoing the replacement of its matrixes of natural altitude fields in a more accentuated way in the last decades, mainly by the large-scale cultivation of *Eucalyptus*, however, we still recorded a high richness compared to other ecotypes. The absence of some species previously recorded by Santos (1966), such as *Minagrion caldense*, *Heteragrion triangulare* Selys, 1862, *Macrothemis capitata* Calvert, 1909, and *Progomphus reticarinatus* Calvert, 1909, evidences this habitat homogenization. As for the remaining species, they all are classified as data deficient (DD) by the IUCN assessments, indicating that not much is known about its distribution and ecological preferences, thus hampering a proper conservation assessment. The fact that these species were not collected again in that area reinforces their DD status, and more collections are needed in search of these rare and possible endangered taxa. Despite the observed habitat homogenization, the regional altitude fields and their associated ecosystems are unique and contain a considerable odonatan diversity, which was demonstrated by the gradient of the environmental integrity of the sampled areas.

Acknowledgments

We would like to thank: the Biodiversity Laboratory of IFSULDEMINAS – Campus Poços de Caldas for logistical and financial support; the Rufford Foundation for funding the acquisition of the drone used for imaging and field work (Grant 32714-2). To the Laboratory of Zoology of the IFSULDEMINAS, Campus Inconfidentes; Walter Ávila Junior for the Zygoptera identification; Laboratory of Aquatic Biology, Department of Biological Sciences, Faculty of Sciences and Letters of Assis, Universidade Estadual and. DSV thanks Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for a postdoctoral fellowship grant (Proc. 2019/26438-9).

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