Eugen Warming’s *Florula Lagoensis* revisited: old lessons to new challenges

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Background and aims – We revisited *Florula Lagoensis*, the first floristic list of the Cerrado, published in 1892 by Eugen Warming. All flowering plants were nomenclaturally and taxonomically updated and associated with type material collected by him. We also analysed the contribution of new collections made in Lagoa Santa to assess how many species were recollected after his work.

Methods – We have used the list of phanerogams in Warming’s 1908 translation as primary data source and we performed a search on Brazilian virtual herbaria to retrieve all material collected at the locality of Lagoa Santa and surroundings.

Key results – Out of 2270 species collected by Warming, 560 (24.7%) have been recollected after 150 years, and only 242 species (9.6%) were new additions to the list. A total of 381 (14.4%) specific or infraspecific names from *Florula Lagoensis* have type specimens collected by Warming.

Conclusions – It is fair to recognize Eugen Warming as one of the pioneers of floristic studies in Brazil. We stress the completeness of his work and highlight the importance of following Warming’s footsteps, collecting intensively, exploring different environments, and working in a collaborative way.

Key words – Eugen Warming; floristic inventory; Lagoa Santa; type material.

INTRODUCTION

Eugen Warming (1841–1924), one of the fathers of ecology, started his work in the tropics between 1863 and 1866 (Goodland 1975; Klein 2002). He was the secretary of Peter Lund (1801–1880), a Danish paleontologist who lived in Lagoa Santa, a small village in the state of Minas Gerais, southeastern Brazil (Gomes 2006; Goodland 1975; Holten & Sterll 2011). As a researcher, he had a brilliant career. Back to Europe, he worked as a professor and published several works on morphology, taxonomy, ecology and phytogeography (Stafleu & Cowan 1988), linked with the data obtained in the short time he lived in Brazil.

Warming brought about 3000 exsiccates collected by him and 700 other exsiccates donated by Lund to Europe (Gomes 2006). The botanical material was distributed to the main specialists of that time and the results of this work were published in the series *Symbolae ad floram Brasiliensis Centralis cognoscendam* (Warming 1867–1893). Many specimens were cited in *Flora Brasiliensis* (Warming 1908; Goodland 1975), a comprehensive work (1840–1906) started by von Martius, composed of the description of about 22,000 species in 40 volumes with the contribution of more than 65 botanists and three editors (Nogueira 2000). In 1892 Warming also published “Lagoa Santa: Et Bidrag til den biologiske Plantegeografi: Med en Fortegnelse over Lagoa Santas
Hvirveldyr” (Warming 1892), translated only in 1908 to Portuguese, with the title “Lagoa Santa: contribuição para a geographia phytobiologica” (Warming 1908). This book is a quite complete regional ecological monograph (Goodland 1975), in which Warming described in detail soil conditions, vegetation physiognomies, climate, relief, and fire effects on the neotropical savanna, the Cerrado. Also, he presented the first floristic inventory of the Cerrado (Mendonça et al. 2008). The extensive list entitled *Florula Lagoensis*, covered a broad spectrum of organisms, from fungi to mosses and vascular plants, totalling 2593 species, of which 2488 were flowering plants (Warming 1908).

Warming’s work was pioneer in Brazil. Many species were described based on samples collected by him, resulting in nomenclatural types. Nowadays, type localities have received a renewed importance because of the increase in phylogenetic studies integrating molecular data with taxonomy (Tautz et al. 2003). The inclusion of DNA sequences obtained from the types or from specimens sampled from the same area where the type material was collected (for historical collections) serves as a standard for future taxonomic reference of species (Tautz et al. 2003). Similarly, it fulfils nomenclatural purposes, once studies are changing the circumscription of genera and species, sometimes splitting and renaming them (Meier 2008).

Lagoa Santa is inserted into the Cerrado, a biome that covers about 2 million km², representing around a quarter of the land surface of Brazil (Oliveira-Filho & Ratter 2002). Mostly distributed in the Brazilian central plateau and small areas of Bolivia and Paraguay, it is one of the 34 global biodiversity hotspots, with richness estimated to about 10 000 species of vascular plants, approximately 4400 being endemics. The remaining areas cover 21.3% of its original distribution (Mittermeier et al. 2004). As well as the biome, which is currently highly endangered (Françoso et al. 2015), the vegetation of Lagoa Santa, described so accurately by Warming, has faced different threats over time. The Cerrado has experienced a rapid decrease in recent years, mostly by the replacement with grasslands for cattle, but also agriculture and urbanization (Auler 2016). Consequently, the landscape has drastically changed. Habitats originally described to the area were strongly reduced, increasing the risk of the extinction of populations related to the type of many species.

Linking the past and the present, but worrying about the future, we revisited the *Florula Lagoensis*. We nomenclaturally and taxonomically updated all flowering plants listed by Warming, analysed the contribution of new collections over more than 150 years, and highlighted the type collections. After such a long time and because Lagoa Santa is located nearby important research centres in southeastern Brazil, we expected most species to have been recollected in the area.

**MATERIALS AND METHODS**

Lagoa Santa (19°37′38″S, 43°53′22″W) is situated in Southeastern Brazil, about 30 km far from Belo Horizonte, the capital of Minas Gerais state. It is inserted in a karstic region, with very important paleontological and archaeological samples for the reconstruction of the South American prehistory (Berbert-Born 2002). Within the Cerrado biome, distinct phytophysiognomies can be recognized in Lagoa Santa: Cerrado s. str., Cerradão, deciduous and semideciduous forests, wetlands, as well as cultivated areas and pasture lands (Herrmann et al. 1998).

We used the list of phanerogams in Warming (1908) as a primary data source. The names of native identified species have been transcribed and updated based on APG IV (2016), using as main reference Flora do Brasil 2020’s website (continuously updated), as well as other online databases (Tropicos continuely updated; The Plant List 2013), taxonomic monographs and the advice of specialists. To this list were added records from herbarium data derived from the

**Figure 1** – Number of species of flowering plants recorded from Lagoa Santa, Minas Gerais, Brazil, including Warming’s *Florula Lagoensis* (1908) revised list and herbarium data, separated per frequency of collection. From left to right: the first bar shows the number of species not collected by Warming; the second bar shows the total number of species only collected by Warming; the bars numbered from 1 to 16 representes the total number of species collected after Warming (bar 1), twice after Warming (bar 2), three times after Warming (bar 3), and so on.
area visited by Warming and retrieved from the INCT Virtual Herbarium (2014, including RB), as well as records from BHCB, PAMG and R (herbarium acronyms following Thiers continuously updated), visited in loco as to fill a gap related to herbaria with collections not yet completely on-line. We assumed that Warming collected most material around the village, usually not exceeding one league (almost 5 km) in all directions, as reported by him (Warming 1908: 11). All synonyms were also updated to the current correct name, in the same way as mentioned above. Duplicated records, with the same collection number by the same collector, were excluded, leaving only one record per species.

We accounted taxa richness, sampling frequency of the species and the proportion of life forms classified following Flora do Brasil 2020’s website (continuously updated). Besides, we recovered the type specimens collected by Warming in Lagoa Santa, using protologues, JSTOR-Global Plants (continuously updated), Tropicos (continuously updated) and Natural History Museum of Denmark type databases (herbarium C). Threatened species were checked in the Brazilian official list published by MMA/Brazil (2014).

RESULTS

The floristic list compiled from Warming’s *Florula Lagoensis* reported 2420 species of flowering plants. The nomenclatural updated list summed 2270 species. Herbarium specimen database retrieved 1439 records from Lagoa Santa, corresponding to 802 species, from this 560 (69.8%) species were in the *Florula Lagoensis*. Combining Warming’s revised list and the additional records from herbaria database, we have recorded 2512 species to the flora of Lagoa Santa. Out of the species of *Florula Lagoensis*, 1710 (75.3%) have not been recorded in the searched databases and herbaria, hence probably have not been collected again in the region after Warming (fig. 1). A total of 242 species (9.6%) were not collected by him in Lagoa Santa (supplementary file 2).

We registered just one species collected before Warming in Lagoa Santa, *Hyptis linarioides* Pohl ex Benth. (Lamiaceae). It was based on material collected by A.L. Riedel, in 1824 (NY 00857575) and cited in *Florula Lagoensis*. After Warming, several collectors visited Lagoa Santa, including…

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**Table 1** – Number of species and proportion of the richest flowering plant families recorded to Lagoa Santa, Minas Gerais, Brazil.

| Family           | Revised *Florula Lagoensis* & Herbaria data | Revised *Florula Lagoensis* | Herbaria data |
|------------------|---------------------------------------------|-----------------------------|---------------|
|                  | number of species | %                          | number of species | %                          | number of species | %                          |
| Asteraceae       | 286             | 11.4                        | 257             | 11.3                        | 101             | 12.6                        |
| Fabaceae         | 241             | 9.6                         | 211             | 9.3                         | 91              | 11.3                        |
| Poaceae          | 172             | 6.8                         | 156             | 6.9                         | 47              | 5.9                         |
| Orchidaceae      | 120             | 4.8                         | 118             | 5.2                         | 35              | 4.4                         |
| Euphorbiaceae    | 97              | 3.9                         | 88              | 3.9                         | 27              | 3.4                         |
| Rubiaceae        | 92              | 3.7                         | 85              | 3.7                         | 27              | 3.4                         |
| Cyperaceae       | 82              | 3.3                         | 76              | 3.3                         | 26              | 3.2                         |
| Apocynaceae      | 82              | 3.3                         | 74              | 3.3                         | 25              | 3.1                         |
| Melastomataceae  | 67              | 2.7                         | 64              | 2.8                         | 24              | 3.0                         |
| Malvaceae        | 67              | 2.7                         | 60              | 2.6                         | 22              | 2.7                         |
| Myrtaceae        | 67              | 2.7                         | 58              | 2.6                         | 21              | 2.6                         |
| Malpighiaceae    | 62              | 2.5                         | 55              | 2.4                         | 16              | 2.0                         |
| Lamiaceae        | 49              | 1.9                         | 46              | 2.0                         | 15              | 1.9                         |
| Solanaceae       | 49              | 1.9                         | 43              | 1.9                         | 15              | 1.9                         |
| Convolvulaceae   | 45              | 1.8                         | 41              | 1.8                         | 15              | 1.9                         |
| Bignoniaceae     | 44              | 1.8                         | 39              | 1.7                         | 13              | 1.6                         |
| Sapindaceae      | 38              | 1.5                         | 35              | 1.5                         | 11              | 1.4                         |
| Piperaceae       | 35              | 1.4                         | 35              | 1.5                         | 10              | 1.2                         |
| Acanthaceae      | 31              | 1.2                         | 29              | 1.3                         | 10              | 1.2                         |
| < 31 species     | 786             | 31.3                        | < 29 species    | 700                         | 30.8                        | 251             | 31.3                        |
| Total            | 2512            | 100.0                        | Total           | 2270                        | 100.0                        | Total           | 802             | 100.0                        |
H.L. Mello Barreto (from 1932 to 1942), who made 187 records for the municipality.

The richest families were Asteraceae (286/11.4%), Fabaceae (241/9.6%), Poaceae (172/6.8%) and Orchidaceae (120/4.8%) (table 1). This richness was very similar to Warming’s revised list alone – Asteraceae (257/11.3%), Fabaceae (211/9.3%), Poaceae (156/6.9%) and Orchidaceae (118/5.2%). On the other hand, herbarium records showed difference in the proportion of family richness: – Fabaceae (101/12.6%), Asteraceae (91/11.3%) and Poaceae (47/5.9%) were the richest ones, but Orchidaceae appeared with only 13 species (1.6%) (table 1). *Paspalum* L. (Poaceae) was the richest genus in all lists. The species more systematically sampled over the years was *Xylopia aromatic* (Lam.) Mart. (Annonaceae), with 16 records (supplementary file 1). Among the life forms, shrubs were predominant (874/35%), followed by herbs (824/33%), trees (503/20%) and vines (312/12%) (supplementary files 1 and 2).

From all species, 39 are in the Brazilian red list. Two of them, *Chusquea tenuiglumis* Döll and *Gymnopogon doellii* Boechat & Valls (Poaceae) have been classified as critically endangered. They have not been collected again in Lagoa Santa after Warming. Eighteen species were classified as endangered and 19 as vulnerable (supplementary file 3). Out of the 39 threatened species, only three (0.08%) have more than one record for Lagoa Santa.

A total of 381 (14.4%) names from *Florula Lagoensis* have nomenclatural type specimens collected by Warming. They are distributed in the following herbaria: C (291), P (41), G (23), F (18), W (16), BR (15), GDC (12), NY (9), K (7), M (4), S (3), GH (3), US (5), GOET (3), A (2), MO (2), B (1), BAB (1), BM (1) and HBG (1), (supplementary file 1).

**DISCUSSION**

The revisited *Florula Lagoensis* confirmed the great richness in Lagoa Santa reported by Warming (1908). The occurrence of 2512 species of flowering plants places this area as one of the richest inventoried sites of Minas Gerais. This is clear when compared to other nearby rich areas such as the megadiverse Espinhaço Range (Rapini et al. 2008), a mountain chain distributed along 1200 km from southeastern to northeastern Brazil, in the states of Minas Gerais and Bahia (Knauer 2007). Floristic inventories reported 2943 angiosperms to Serra do Cipó (Pirani et al. 2015), 1700 to Serra do Caraça (Augsten, Universidade Federal de Minas Gerais, Brazil, unpublished results) and 1032 to Grão-Mogol (Pirani et al. 2003).

**Figure 2** – Phytophysiognomies of Lagoa Santa, Minas Gerais, Brazil, where E. Warming during about three years (1863–1866) collected 2270 species of flowering plants for the *Florula Lagoensis*. A. Cerrado, a savannah-like vegetation. B. Seasonal dry forest, deciduous during the winter. C. Massifs (carbonate rocks), with saxicolous plants. D. Lake, during the dry season. Photographs by J.R. Stehmann (A, B); C.P. Schindwein (C) and C. Palhares (D).
The floristic richness reported to Lagoa Santa may be primarily explained by the great heterogeneity of environments, each one with its particular flora and contributing with a subset of species (see fig. 2). Warming (1908) when describing the vegetation, recognized four original types: forests, grasslands, swamps (called brejos, with helophytes) and aquatic environments (distinguished by the presence of limnophytes), as well as secondary (or successional) vegetation in deforested areas and represented by ferns and an invasive grass (*Melinis minutiflora* P.Beauv.). From the eleven main vegetation types described from the Cerrado based on physiognomy, soil and floristic composition (Ribeiro & Walter 2008), at least eight were reported from Lagoa Santa, representing forests (from mesophilous to dry forests, ciliary forests and Cerradão), savannas (Cerrado s. str. and vegetation dominated by palms), and grasslands (Campos Limpo, swamps, and carbonate rock outcrops) (Herrmann et al. 1998; Warming 1908). The assessment of the remaining vegetation cover, as well as the contribution of each vegetation type (beta diversity) to floristic richness are interesting tasks to be done in the future.

Endemic species are important components of the richness of Brazilian megadiverse biomes as Atlantic forest and Cerrado, having a special significance for biological conservation (Forzza et al. 2012). However, in Lagoa Santa few endemic species were registered: *Lessingianthus bakkerianus* Dematt. (Asteraceae) (Dematteis 2006) and *Homalolepis warmingiana* (Engl.) Devecchi & Pirani (Simaroubaceae) (Devecchi et al. 2018), both collected by Warming in areas of Cerrado s. str. *Solanum lagoense* Stehmann (Solanaceae) (Stehmann & Moreira 2016) was recently described from the understory of the seasonal forest associated with carbonate rocks. Efforts searching for new populations of these species are in need. These can be considered small contributions since during the last ten years more than 2000 species have been described in Brazil, mostly coming from Atlantic forest and Cerrado biomes, hotspots of biodiversity where the taxonomic research has been centred (Sobral & Stehmann 2009; Stehmann & Sobral 2017).

As characteristic for the Cerrado biome and its main vegetation types, there was a dominance of shrubs and herbs among the life forms. Trees and vines, typical elements of forest environments appeared only secondarily. A very detailed description of the life forms and their distribution in Lagoa Santa vegetation was given by Warming (1908). The richest families listed by him correspond to those reported in the Iron Quadrangle in the centre of Minas Gerais (Biodiversitas 2007), mainly due to loss of habitat and overexploitation or suppression of the vegetation (Fleischer 2006; de Deus et al. 2012; Oliveira et al. 2016). Our revised lists were compatible too, except for Orchidaceae, whose richness in herbarium data was much lower than expected, probably evidencing a possible process of impoverishment of this family. The same way, Orchidaceae in the Minas Gerais red list has the highest number of endangered species (Biodiversitas 2007), mainly due to loss of habitat and overexploitation pressure for ornamental uses (Menini Neto 2012).

The only nearly nine per cent addition of new records to the list confirms the huge and comprehensive work Warming developed. This allows us to call him a "big hitting collector", borrowing an expression coined by Bebber et al. (2012). Warming's work was unique, in that he was one of the first naturalists to make an extensive sampling effort focused on a single area, resulting in a floristic inventory. The new additions to the list corresponded almost always to widespread species, such as *Emilia fosbergii* Nicolson (Asteraceae), *Desmodium tortuosum* (Sw.) DC. (Fabaceae) and *Andropogon leucostachyus* Kunth (Poaceae). Few exceptions were not generalist cases, such as *Vochysia pygmaea* Bong. (Vochysiaaceae), an endangered species considered nowadays limited to Serra do Cipó (Martinelli & Moraes 2013), a neighbour site to Lagoa Santa, collected in Lagoa Santa by Segadas-Vianna in 1953. Another example is *Brasilipuntia brasiliensis* (Willd.) A.Berger (Cactaceae), a very common species associated with rocky outcrops (limestones) but missing in Warming's list. It is hard to believe that Warming did not collect it; rather his material has probably been lost. In the prologue of Warming (1908), he indeed commented that some specimens of succulents such as Cactaceae, preserved in wine spirit, arrived in bad state in Copenhagen and were destroyed.

It is noteworthy that only about a quarter of the species sampled in three years by Warming have been recollected by botanists in Lagoa Santa over 150 years. In our understanding, this lack of collections results from a low-sampling effort after Warming's visit as well as a continuous process of landscape changing in Lagoa Santa. In the last decades, Brazilian botanists directed their interest to other nearby areas, such as Serra do Cipó and other sites of the Espinhaço Range, where dozens of new species have been described (Giulietti et al. 1987; Pirani et al. 2003, 2015). It is known, also, that Minas Gerais and the Brazilian territory have lack of collections in many areas, as indicates the low sufficiency rate of collection (Sobral & Stehmann 2009; Stehmann & Sobral 2009; Oliveira et al. 2016).

Besides, most of Lagoa Santa's natural habitats have been destroyed. A relatively recent study, from 2012, showed that every natural fragment has already been disturbed at some level; 49% of the area is covered by city or farms, 39.8% are Cerrado s. str. and deciduous forests, and only 10% corresponds to semideciduous forests (Ambiente Brasil, Brazil, unpublished report). Several areas of Cerrado s. str. have been converted into pasture and crop lands, the semideciduous forest has been fragmented along the Velhas river, and the deciduous forest usually associated with carbonate rocks is directly impacted by mining that causes disturbances or suppression of the vegetation (Fleischer 2006; de Deus et al. 2013; Auler & Piô 2015). There are also several lakes in the Karst region, harbouring many species of aquatic macrophytes. Most wetlands, however, are exposed to excessive exploitation or pollution (Calijuri et al. 2012; Auler 2016; Tayer & Velásquez 2017). All these threats put this huge biodiversity at risk.

Two emblematic threatened species, *Gymnopogon doellii* Boechat & Valls (Poaceae) and *Dimorphandra wilsonii* Rizzini (Fabaceae), were recorded from Cerrado s. str. in Lagoa Santa. The first species was collected by Warming in Lagoa Santa; recently it was assessed (Martinelli & Moraes 2013) as Critically Endangered because of the small known populations, considered restricted to the Federal District of central Brazil. Nevertheless, since 2013 new records have been registered in the Iron Quadrangle in the centre of Minas Gerais.
Lagoa Santa was classified as a priority area for conservation in Minas Gerais because it harbours threatened, endemic and rare animal species and is under high human degradation pressure (Drummond et al. 2005). The north of the metropolitan region of Belo Horizonte, where it is located, is under intensive urban sprawl, given the presence of the state capital’s international airport, the state’s administrative centre and a plan of economic expansion (Pereira & Caldeira 2013; Sampaio et al. 2014). In view of all this, a system of conservation units (UCs) is gradually being implemented. Some important places where Warming collected are already in UCs of integral protection, as the Parque Estadual do Sumidouro (IEF-MG 2019), but others, such as Lapa do Baú and Lapa Vermelha (Warming 1908), are in UCs of sustainable use and in private areas dealing with the threats from economic activities (Herrman et al. 1998; de Deus et al. 2013). Recently, the region was included in the Ramsar Convention, as a wetland of international importance, due to the expressive presence of endemic species and migratory birds (Ramsar Convention 2017).

Brazil has some challenges to reach the Global Strategy for Plant Conservation 2011–2020 targets (CBD 2010). The first one is a complete national inventory of its flora. In this regard, it would be important to overcome some gaps in sampling, particularly, in the Northern part of the country (Stehmann & Sobral 2009; BFG 2015; Morim & Lughadha 2015). To achieve this goal, Warming’s work can be taken as an example of a wide-ranging inventory with marked sampling sufficiency in Brazil. Other examples are Ducke reserve project (Hopkins 2005), São Paulo’s flora project (Wanderley 2011), the Floristic and Forest Inventory of Santa Catarina (Gasper et al. 2014) and Carajás (Viana et al. 2016), all cases of medium- or long-term research with great collection effort, concerning many specialists and with important input of knowledge. In this context, to improve collections and at the same pace develop information about taxonomy, distribution and conservation of species, more financial investments in human resources, fieldwork and infrastructure will be necessary (Sobral & Stehmann 2009; BFG 2015; Canhos et al. 2015; Teixido et al. 2017).

**Florula Lagoensis** can be considered one of the most important floristic studies made in Brazil during the XIXth century, comparable to A.F. Regnell’s work developed in Caldas, Minas Gerais (Dahlgren 1962; Concha-Quezada 2011; Santos 2016). We highlight the completeness of the work considering the number of species registered to this small area and how Warming dealt with the identification process, sending samples to specialists of different families. Currently, we use the same methods and the accuracy of the determinations depends on the collaborative work. We would like to stress the importance of following Warming’s footsteps and lessons, collecting intensively, exploring different environments and working in a collaborative way. It would be fair, therefore, to call him a pioneer of floristic studies in Brazil.

**SUPPLEMENTARY FILES**

Three supplementary files are associated to this paper:

1. **List of taxa studied by Warming (1892, 1908: names and authors in his spelling), corresponding correct name, nomenclatural types, life form and the number of recollections:**
   - https://doi.org/10.5091/plecevo.2020.1527.2063

2. **List of species representing new records for Lagoa Santa based on herbarium data retrieved, a voucher, herbarium number and acronyms, and life form:**
   - https://doi.org/10.5091/plecevo.2020.1527.2065

3. **List of endangered species with their IUCN category indicated:**
   - https://doi.org/10.5091/plecevo.2020.1527.2067

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