



Ballistochory in the herbaceous bamboo genus *Reitzia* (Poaceae, Bambusoideae, Olyreae): the second report of this dispersal syndrome in grasses

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Abstract

Seed dispersal is essential for the success of plants, allowing them to find advantageous areas to inhabit while avoiding inbreeding. Although predominantly anemochoric, grasses (Poaceae) have evolved other ways to disperse their diaspores, such as zoochory and also ballistochory (forcible dispersal), which is considered rare within this family. To date, ballistochory in grasses is only known for the sister genera *Raddia* and *Sucrea*, Neotropical herbaceous bamboos (tribe Olyreae). In this study, this dispersal syndrome is confirmed for *Reitzia*, a monospecific herbaceous bamboo genus and member of the *Piresia* clade, which is restricted to the Atlantic forest in southeastern and southern Brazil. We hypothesize that the pedicel of the pistillate spikelet, more than the glumes, may be responsible for the ballistic movement. We also provide an updated conservation assessment and a distribution map for the genus.

Keywords Atlantic forest · Conservation · Diaspores · Forcible dispersal · Seed shadow

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Seed dispersal and pollen transport are the most important factors in promoting gene flow in seed plant populations (van der Pijl 1982). Thus, seed dispersal is essential for the success of plant reproduction and adaptation (Lorts et al. 2008). Germination and growth away from the progenitor plant allow opportunities to find advantageous areas to inhabit, in addition to avoiding unfavorable conditions around the mother plant such as inbreeding and sibling competition (Willson and Traveset 2000). Seed plants have evolved a broad range of seed dispersal modes, relying on different dispersal vectors such as wind, water, or animals (Eriksson and Kiviniemi 2001). Plant structures that are dispersed are termed diaspores (van der Pijl 1982).

In Poaceae (the grass family), the fruit is a caryopsis, in which the seed coat is firmly attached to the inner wall of the uniovulate ovary (Kellogg 2015). The caryopsis is unique to this family, interpreted as a consistent morphological synapomorphy (GPWG 2001). However, the caryopsis alone is rarely the unit of dispersal in grasses (Clayton 1990; Gibson 2008). Their diaspores vary considerably, reflecting the many different plant tissues in which an abscission zone can form (Liljegren 2012; Estornell et al. 2013; Doust et al. 2014). In many cases, caryopses are released protected by lemmas and paleas (e.g. Olyrinae, many Pooideae), in others by glumes,

lemmas, and paleas (e.g. Paniceae and Paspaleae), and may even be dispersed in groups of spikelets surrounded by bristles (e.g. *Cenchrus* L.), whorls of spikelets (e.g. Parianinae), or pairs of spikelets, with one sessile and the other pedicellate (e.g. Andropogoneae) (Kellogg 2015; Ferreira et al. 2019; Welker et al. 2020; Gallaher et al. 2022). In summary, there is a plethora of dispersal strategies that vary among groups of grasses, reflecting the vectors involved and affecting the biology of dispersal (Howe and Smallwood 1982; Davidse 1987; Chapman 1996).

A remarkable dispersal mode in grasses is ballistochory (auto-ejection of the diaspores), reported to date only for the sister genera *Raddia* Bertol. and *Sucrea* Soderstr. (Sendulsky 1993). These and other herbaceous bamboos (subfamily Bambusoideae, tribe Olyreae) are important components of the Brazilian Atlantic forest, including many endemic genera such as *Reitzia* Swallen, distributed from the state of Espírito Santo (southeastern Brazil) to Santa Catarina (southern Brazil) (Soreng et al. 2022; Flora e Funga do Brasil 2023). Like *Olyra* L. and *Taquara* I.L.C.Oliveira & R.P.Oliveira, *Reitzia* has a distribution reaching the extra-tropical region (Soderstrom and Zuloaga 1985; Oliveira et al. 2020a).

Confirming a hypothesis of a close relationship made by Swallen (1964), in a recent phylogenetic study (Carvalho et al. 2021) *Reitzia* was recovered in a clade with *Piresia* Swallen, which has a disjunct distribution between the Amazon and the Atlantic forest. Unlike *Piresia*, which has six species (Carvalho et al. 2021), *Reitzia* currently includes only *R. smithii* Swallen, a diminutive species with a terminal contracted racemose synflorescence, in which each branch bears 1–2 sessile staminate spikelets at the base and a single apical pistillate spikelet with a clavate pedicel (Fig. 1A–B) (Swallen 1956; Judziewicz et al. 1999; Silva et al. 2012).

During field work carried out in Espírito Santo state in 2009, a population of *R. smithii* was found in the municipality of Alegre, located in the south of the state. Since then, living plants kept in cultivation have allowed close monitoring of the reproductive phases of this species. As with Dr. Tatiana Sendulsky when cultivating species of *Raddia* and *Sucrea* (Sendulsky 1993), we noticed that some *Reitzia* plants were growing away from the mother plants (Fig. 1C–G). Thus, in order to confirm the possibility of dispersal by ballistochory in *Reitzia*, an experiment was conducted, as described below. Additionally, the conservation status of *R. smithii* was evaluated and an updated distribution map of the species was generated, which are herein presented.

1 Material and methods

Field work and cultivation – This study was based on collections made in 2009 in the municipality of Alegre, located in the southern region of Espírito Santo state, Brazil (Figs. 1A and 2). Vouchers were deposited in the HUEFS herbarium

(acronym according to Thiers 2023): *Ferreira et al. 2203* and *2204* (barcodes HUEFS 57416 and HUEFS 25642, respectively). During field work, three specimens of *R. smithii* were fully removed from the soil with a garden shovel. Then, aerial culms with leaves and roots were cut with a pruning shear, and the base of the plant containing the rhizome was kept inside a closed plastic bag for transportation. This procedure kept the plants alive until field work was completed, when they were put to grow in the backyard of a house in the municipality of Baependi, Minas Gerais, Brazil, in an area protected from direct sunlight and wind. The plants were grown in plastic pots (4.3 l) with a substrate composed of 70% organic compost (substrate for flower beds) and 30% inorganic compost (sand and gravel) (Fig. 3A).

Morphological data – Morphological data for *Reitzia smithii* was obtained from the original description (Swallen 1956), field observations, cultivated specimens, and herbarium sheets (BHZB, CEPEC, CESJ, FLOR, HBR, HUEFS, IAN, K, MBM, MO, NY, R, SP, UEC, US herbaria; acronyms according to Thiers 2023). Herbarium specimens were analyzed during visits to herbaria or from images available at online platforms [Tropicos (www.tropicos.org), Smithsonian National Museum of Natural History (www.collections.nmnh.si.edu/search/botany/), New York Virtual Herbarium (www.sweetgum.nybg.org/science/vh/), speciesLink system (www.splink.org.br/index), and Flora e Funga do Brasil (www.floradobrasil.jbrj.gov.br)]. We also used descriptions provided by Judziewicz et al. (1999), Delta Keys (Watson and Dallwitz 1992 onwards), GrassBase (Clayton et al. 2006 onwards), and Silva et al. (2012).

Experimental design – To determine whether seedlings growing away from parent plants developed from diaspores released by ballistochory and not by other factors (wind, rain, animals), a specimen was isolated in a room (ca. 9 m²) with controlled environmental conditions during the flowering period, from January to September of 2022 (Fig. 3). The number of diaspores was recorded, and the distances between them and the parent plant were measured using a plastic measuring tape (Fig. 3). These data were used to calculate the diaspore density at different distances (seed shadow) (Janzen 1971).

Conservation status – Assessment of the conservation status of *Reitzia smithii* was based on specimens examined in herbaria or online databases, following the criteria of the International Union for Conservation of Nature (IUCN Standards and Petitions Committee 2022). Both the extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the GeoCAT tool (Bachman et al. 2011), considering 2 km² grids, as recommended by IUCN Standards and Petitions Committee (2022). This information was used to prepare an updated distribution map of the species using SimpleMappr (Shorthouse 2010).



Fig. 1 *Reitzia smithii*. **A** Habit (in Alegre, Espírito Santo, Brazil). **B** Detail of the contracted racemose synflorescence showing the pistillate spikelets (ps) with terete clavate pedicels (p), and the sessile staminate spikelets (ss). **C–D** *Reitzia smithii* in cultivation showing the distance reached by diaspores. **C** Diaspore (white arrow) about 1 m from the mother plant. **D** Detail of diaspore. **E–G** Seedlings growing out of the mother plant's pot. **E** Two seedlings (red arrows) growing about 30 cm from the mother plant's pot (yellow arrow). **F–G** Seedling (red arrow) growing about 70 cm from the mother plant's pot

2 Results

During the period of the experiment (nine months) 16 culms bloomed, each one with generally three terminal contracted synflorescences. Each synflorescence had five to seven pistillate spikelets. In total, 48 synflorescences and 288 pistillate spikelets were counted. Of these, 56 diaspores were dispersed in a distance between five to 190 cm

around the parent plant, most of them between 100 and 190 cm (Figs. 3 and 4). The other pistillate spikelets were not fertilized and fell out, landing next to the mother plant.

The diaspore of *Reitzia smithii* is the pistillate antherium, composed of the caryopsis with its lemma and palea that wrap tightly around it (Figs. 1D and 5). During anthesis, the antherium is cartilaginous, whitish, and slightly green towards the apex, but after fertilization and

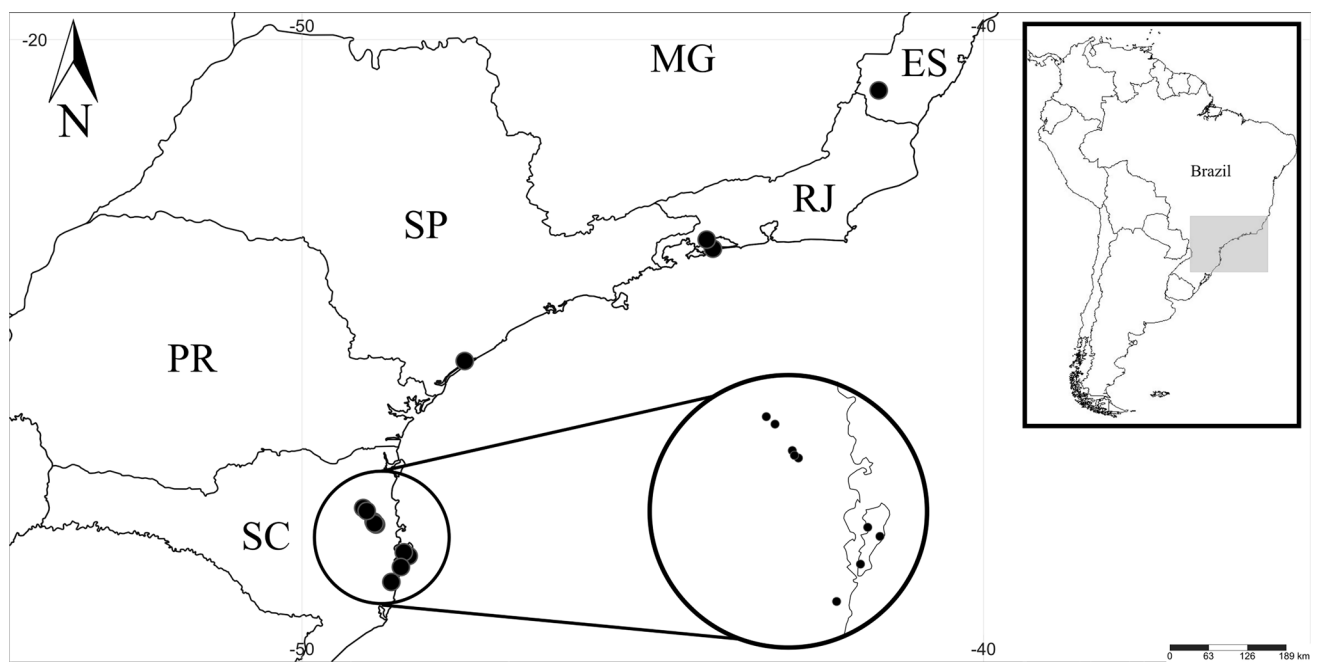


Fig. 2 Geographical distribution of *Reitzia smithii*. Brazilian state abbreviations: ES=Espírito Santo; MG=Minas Gerais; PR=Paraná; RJ=Rio de Janeiro; SC=Santa Catarina; SP=São Paulo



Fig. 3 A–C Experimental design. **A** *Reitzia smithii* in cultivation growing in a plastic pot. **B** Room with controlled environmental conditions where the specimen was kept in order to determine the occurrence of ballistochory. **C** Detail of a diaspore about 67 cm from the mother plant's pot

development of the caryopsis, it becomes very rigid and smooth, shiny, and dark, with the nerves and margins of the lemma light brown (Figs. 1D and 5A, B, D). When not fertilized, the whole pistillate spikelet becomes stramineous and falls off (Fig. 5A).

The abscission zone in *Reitzia smithii* is above the glumes, which remain attached to the pedicel for a while after release of the antherium (Fig. 5B), being tardily caducous (Fig. 5C, D). The pedicels are green, terete, and clavate, however, during the ripening of the pistillate antherium they progressively become flattened by dehydration (Fig. 5C), forcing the opening of the glumes, which may trigger ballistic movement. After dispersal, it is possible to observe a slight retraction of the outermost tissue of the pedicel of the pistillate spikelet (Fig. 5A, D).

3 Discussion

Dispersal in grasses is assumed to be predominantly anemochorous, in which diaspores fall from synflorescences and are spread by wind (Kellogg 2015). However, there is little or no wind in the understory of tropical forests (Richards 1996). According to van der Pijl (1982), anemochory is not an ideal dispersal mechanism in a dense habitat without strong wind. Thus, many forest grasses have replaced wind dispersal by zoochory (endo- and epizoochory) or, less commonly, by ballistochory (i.e. ejection of the diaspore by the plant itself) (Davidse and Morton 1973; Davidse 1987; Sendulsky 1993; Kellogg 2015). As we here confirm, this

is the case in *Reitzia*, which inhabits the understory of the Atlantic forest in eastern Brazil.

Ballistochory is not common in grasses and previously had been reported only for *Raddia* and *Sucrea* by Sendulsky (1993). According to this author, it is associated with different anatomical aspects of the two sides of the glumes, so when they dry out cells on their adaxial side abruptly lose turgor, then their margins roll up and eject the diaspore, composed of the pistillate antherium (i.e., lemma + palea) plus the caryopsis (Sendulsky 1993; Kellogg 2015). Oliveira et al. (2014) considered this mode of dispersal as a synapomorphy for the clade *Raddia* + *Sucrea* because it is absent in *Brasilochloa* R.P.Oliveira & L.G.Clark, the sister group of this clade (Oliveira et al. 2020b).

As in *Raddia* and *Sucrea*, the mature diaspores of *Reitzia* are very sensitive to the lightest touch. Besides our observations, we found a previous indication of this phenomenon in the label data of *Reitzia 5939* (US, barcode 00143757): “Striped fruit is expelled away when dry”. Although the abscission zone of *Reitzia* is above the glumes, as in *Raddia* and *Sucrea* (Sendulsky 1993), the glumes are probably not responsible for the catapult phenomenon. Instead, the clavate pedicel of the pistillate spikelet may be responsible (Fig. 1B). The pedicel is terete, slightly cupulate at the top, and becomes flat during the anthesis (Figs. 1B, and 5C). When the pedicel dehydrates, it could help the opening of the spikelet, which can trigger the ballistic movement (Fig. 5A–D). In old synflorescences, it is possible to observe a slight retraction of the outermost tissue layer of the pedicel (Fig. 5A, D). This may represent a spongier tissue that, when dehydrated, could act in the ballistic mechanism. It

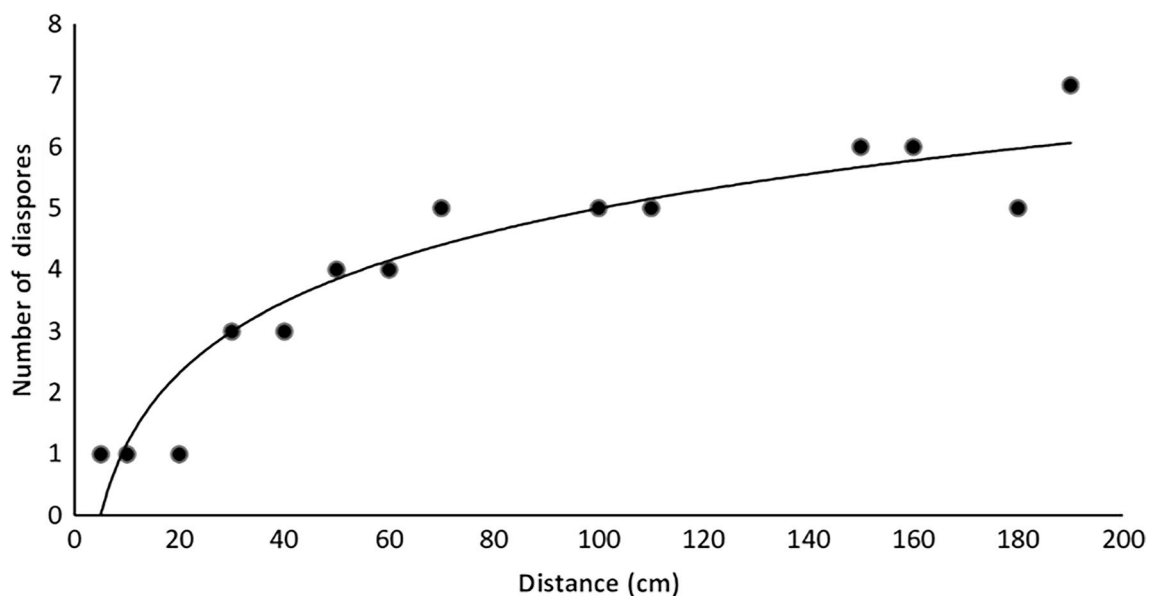


Fig. 4 Dispersal distance of diaspores (seed shadow) of a *Reitzia smithii* specimen in cultivation in a room with controlled environmental conditions

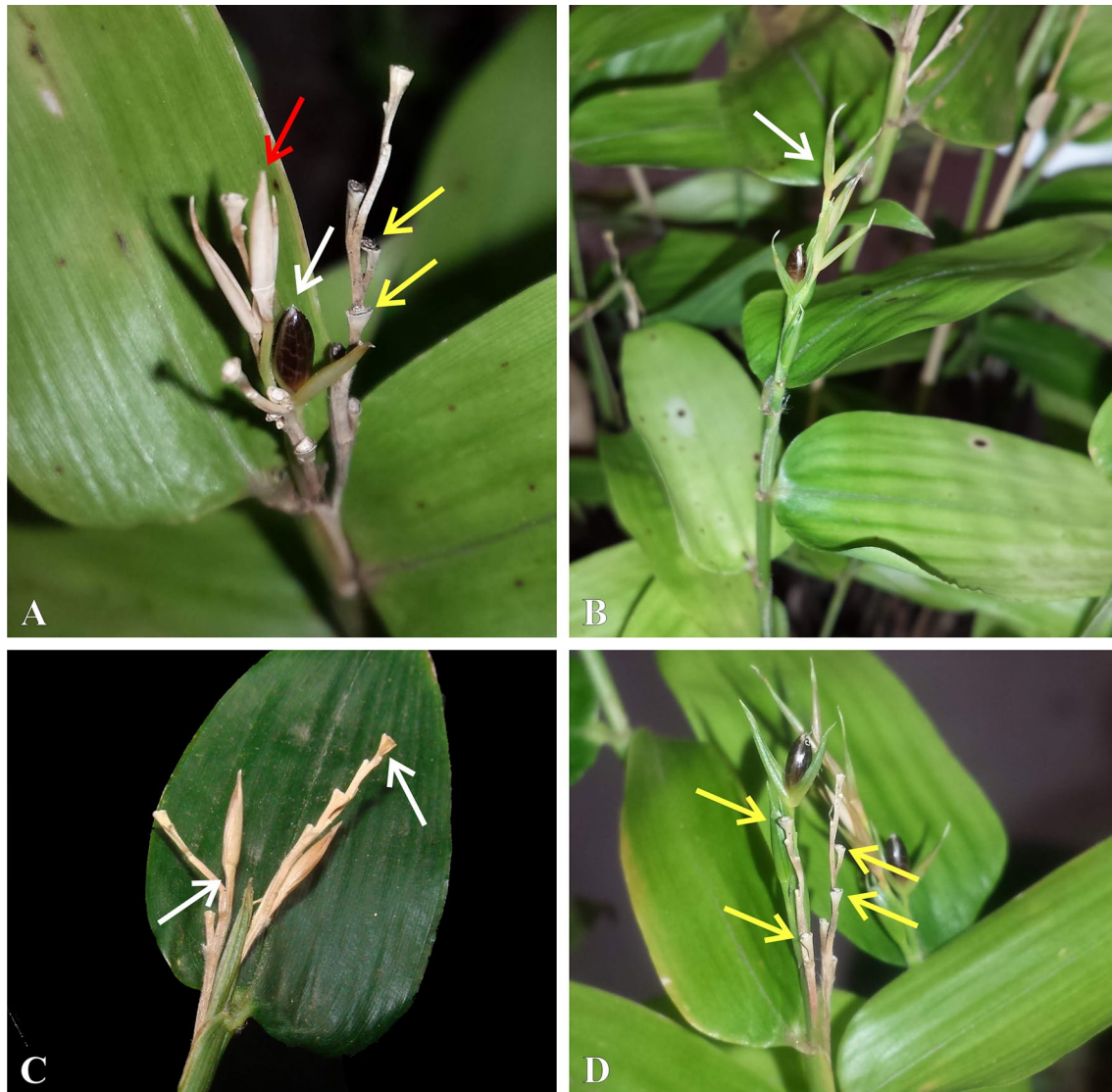


Fig. 5 *Reitzia smithii*. **A** Synflorescences showing a mature diaspore characteristically smooth, shiny, and strongly marbled with dark spots (white arrow). In the same synflorescence, it is possible to observe an unfertilized stramineous pistillate spikelet (red arrow). Beside it, there is an old synflorescence where it is possible to observe the slight retraction of the pedicel tissue of the pistillate spikelet (yellow arrows). **B** Synflorescence showing the empty glumes attached to the pedicel indicating that the abscission zone in *Reitzia smithii* is above the glumes (white arrow). **C** Old synflorescences showing the flat pedicels of the pistillate spikelets (white arrows). **D** Old synflorescences with retraction of the pedicel tissue of the pistillate spikelets (yellow arrows)

is noteworthy that clavate pedicels are also present in other genera within Olyrinae, such as *Arberella* Soderstr. & C.E. Calderón, *Cryptochloa* Swallen, *Diandrolyra* Stapf, *Olyra*, *Maclurolyra* C.E. Calderón & Soderstr., *Piresia*, and *Rehia* Fijten (Stapf 1906; Swallen 1964; Soderstrom and Calderón 1974; Soderstrom and Zuloaga 1985; Clayton and Renvoize 1986; Watson & Dallwitz 1992 onwards; Judziewicz et al. 1999; Clayton et al. 2006 onwards; Clark and Oliveira 2018). Thus, it is possible that ballistochory is more common in Olyreae than we currently know.

Most ballistochorous plants are small in stature (Willson and Traveset 2000), as is *Reitzia*, with the whole plant no

taller than 10–30 cm (Watson and Dallwitz 1992 onwards; Clayton et al. 2006 onwards). In these plants, diaspores with adaptations that enhance dispersal are to be expected (van der Pijl 1982). As indicated by Sendulsky (1993), the combination of a heavy weight and the smooth surface of the diaspores in *Raddia* and *Sucrea* allow them to reach greater speeds and greater distances. In *Reitzia*, the mature anthercium is also heavy and smooth (Fig. 5A), however, in these three bamboo genera, as well as in other ballistochoric plants, the seed shadow is usually small (Willson 1993). In fact, in the present study, the maximum range of *Reitzia* diaspores was 190 cm away from the parent plant.

However, *Reitzia* has a relatively wide distribution in the Atlantic forest of eastern Brazil (Fig. 2), so in addition to ballistochory, other forms of secondary dispersal may occur in the genus. Davidse (1987) indicated that some Olyreae, including *Reitzia*, have significantly modified pistillate spikelets, showing adaptations for endozoochory. According to the author, granivorous birds could be the major dispersal agents. However, the indurate, smooth, shiny, and dark mottled fertilized antheria are much more similar to a bug than a berry (Figs. 1D and 5A). The understory avifauna of tropical forests is composed mainly of insectivorous birds that search for food in different microhabitats, such as litter, trunks, and foliage (Develey and Peres 2000). In Brazil, the Atlantic forest has a large number of such bird species (Aleixo 1999), which can act as secondary dispersers. This could explain the distribution of *Reitzia* and other small herbaceous bamboos.

Therefore, ballistochory is here confirmed in *Reitzia smithii*. We hypothesize that the pedicel of the pistillate spikelet, more than the glumes, may be responsible for the ballistic movement. Although *Reitzia* presents a small seed shadow, it is relatively widely distributed in the Atlantic forest, which could be explained by dispersal by insectivorous birds or a combination of dispersal strategies.

Conservation status – *Reitzia smithii* is endemic to the Atlantic forest, occurring along the southern and southeastern regions of Brazil (Fig. 2). Thirteen localities of occurrence were confirmed, one in Espírito Santo state, two in Rio de Janeiro, one in São Paulo, and nine in Santa Catarina (Fig. 2). According to CNCFlora (2012) and Flora e Funga do Brasil (2023), *R. smithii* is considered vulnerable (VU), based on criterion D2. However, the populations of Espírito Santo and Rio de Janeiro were not included in this assessment. Thus, after updating distribution data, we calculated the extent of occurrence (EOO) as 99,445 km², which fits the species in the category least concern (LC). Nonetheless, based on the area of occupancy (AOO) calculated as 52 km², severely fragmented populations, and continuing decline in area, extent and/or quality of habitat and number of subpopulations [criteria B2ab(iii, iv)], *R. smithii* is here indicated as Endangered (EN). At least one of its known localities is within a Conservation Unit (Área de Proteção Ambiental de Mangaratiba in Ilha da Marambaia, Rio de Janeiro, Brazil; INEA 2015). However, the Atlantic forest is one of the most endangered biodiversity hotspots, and even protected areas have been impacted by ongoing human activities (Ribeiro et al. 2009; Rezende et al. 2018). In addition, in Santa Catarina *R. smithii* occurs near urban centers, such as Blumenau, Brusque, and Florianópolis (Fig. 2), which are impacted by poorly-controlled tourism and city expansion, threatening its survival in those areas.

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Author contributions FMF reviewed herbaria, performed the experiment, wrote the manuscript, and prepared the illustrations and maps. RPO reviewed herbaria and reviewed the manuscript. CADW, CS, and LGC contributed to the interpretation during the writing of the manuscript and reviewed it.

Declarations

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

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