



Environmental constraints on germination and establishment of two endangered *Dimorphandra* species: the role of water availability, fire, and livestock

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Abstract

Dimorphandra exaltata and *D. wilsonii* are endangered species in the Atlantic Forest and Cerrado, biomes threatened by anthropogenic activities such as fire and livestock grazing. Also, in the areas where these species occur, annual rainfall tends to decrease due to climate change. Thus, this study investigated the influence of the bovine digestive tract, water, and fire on the germination and establishment of seeds from both species, to support future management and conservation plans. To address this question, we conducted experiments to assess the effects of seed passage through the bovine digestive tract, water availability (natural or irrigated), and exposure to fire on the germination and establishment of *Dimorphandra* species. Passage through the bovine digestive tract did not enhance germination. However, it did not impair the seeds' viability, favoring germination over time. Daily irrigation increased germination of the two species, suggesting that natural precipitation may be insufficient to establish them under field conditions. Fire did not stimulate germination in either species, indicating that recurrent fires in native areas could impair seedling establishment. Considering changes in precipitation and increased fire occurrence due to climatic changes, as well as livestock expansion, *D. exaltata* and *D. wilsonii* may have their regeneration compromised, threatening their persistence in natural habitats. We propose that, to increase the regeneration rate of the species studied, replanting young individuals at advanced stages of development would be a viable alternative, given environmental limitations, such as water deficit and fire occurrence, which are more detrimental to the natural regeneration of seedlings of these species.

Keywords Climate change · Environmental disturbance · Fecal plaque · Precipitation · Viability

Introduction

Ecosystem degradation is considered a global problem, with anthropogenic activities, ranging from urbanization to agricultural expansion, turning areas of continuous ecosystems into areas of fragmented vegetation (Lewis and Maslin 2015). The Cerrado and the Atlantic Forest are biomes considered biodiversity hotspots (Myers et al. 2000). The Atlantic Forest was one of the first biomes in Brazil to suffer

from anthropogenic impacts since European colonization, due to logging, illegal hunting, and fires (Salto 2006). By 2023, only 12.4% of the Atlantic Forest's original forest cover remained, consisting of fragments of mature vegetation larger than three hectares, characterized by a closed canopy and no degradation detectable by satellite images (SOS Mata Atlantic Foundation and National Institute for Space Research, 2024), which destroys habitats rich in biological resources. In the Cerrado, degradation was primarily due to the expansion of pastures, soybean cultivation (Dias et al. 2017), and anthropogenic fires (Santana 2018). The area deforested in the Cerrado by clear-cutting reached 49.9% by 2019 (Vieira et al. 2022), significantly decreasing natural vegetation.

Agricultural expansion leads to severe environmental degradation, causing physical and biological changes over time, altering landscapes, and compromising ecosystems

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(Campos et al. 2017). Inappropriate livestock management, especially in intensive pasture areas, contributes to the loss of native vegetation through deforestation, wildfires, and soil compaction from cattle trampling (Abadias et al. 2020). These factors favor erosion processes and the loss of organic matter, compromising the soil's ability to retain water (Bell et al. 2011). These physical impacts on the soil directly affect the structure and functionality of ecosystems and exacerbate the effects of climate change. According to the Intergovernmental Panel on Climate Change (IPCC 2023), extreme events are expected to intensify, including changes in rainfall patterns and prolonged dry periods. In this scenario, water restriction is a critical factor, reducing germination and seed bank diversity (Dias et al. 2024) and directly affecting the recruitment and establishment of plant species in degraded areas.

In addition to environmental changes, ruminant livestock can be responsible for seed dispersal (Carmona 1992; Abbas et al. 2018). Processes involved in endozoochory, such as the mechanical action of chewing, rumen microbial activity and acids, temperature, and pH changes throughout the gastrointestinal tract of cattle, can affect seed viability and, consequently, reduce germination of plant species (Schaedler et al. 2021). On the other hand, seeds of species in the Fabaceae family may exhibit increased germination following mechanical and chemical scarification, which suppresses seed dormancy (Milotić and Hoffmann 2016). According to Nakao and Cardoso (2010), the germination of *Cajanus cajan* (L.) Millsp. after passage through the digestive tract was strongly inhibited, while the germination of *Leucaena leucocephala* (Lam.) de Wit was not affected by passage through the digestive tract of cattle, which may be attributed to the hard, impermeable seed coat. Despite their low efficiency as legitimate dispersers, cattle can contribute to species dispersal. Thus, the viability of seeds after passing through the digestive tracts of ruminant animals depends on specific seed characteristics, such as size and tegument type (Whitacre and Call 2006).

Further to seed dispersal and viability after endozoochory, abiotic factors such as fire are fundamental for breaking dormancy and germination, especially in biomes where fire is a natural process (Pausas and Lamont 2022). Fire is a natural process that occurs in the Cerrado biome, mainly at the end of the dry season and the beginning of the rainy season, and is considered a determining factor in vegetation (Brasil 2016; Mistry 1998; Durigan 2020). In the Cerrado, plant species adapted to fire can be fire-tolerant or fire-dependent, unlike species found in forests, such as the Atlantic Forest, which present higher mortality when fire occurs (Hoffmann et al. 2009). However, anthropogenic actions have intensified fire occurrence, mainly due to pasture management and the opening of new areas for cultivation, where uncontrolled

fires can affect extensive areas (Nascimento 2001). Anthropogenic fires tend to have greater intensity and spread speed than natural fires, as they often start during dry periods with high temperatures, low humidity, and strong winds (Hantson et al. 2022). In Minas Gerais, the biomes most affected by anthropogenic fires are the Cerrado and the Atlantic Forest. Over 20 years, approximately 21.6% of the state's territory has experienced at least one natural or anthropogenic fire (Latuf et al. 2022).

Fire can stimulate the germination of some seeds in fire-prone environments, as high temperatures or smoke can break their dormancy (Pausas and Lamont 2022). Furthermore, post-fire environmental conditions generally favor the establishment of several species (Pausas and Lamont 2022). Conversely, fire can decrease germination, restrict seed production in forest species, affect seed dispersal agents, and cause the death of plant populations (Ribeiro and Borghetti 2014; Lamont 2022). In this context, Cerrado species such as *Dimorphandra mollis* Benth., *Erioteca pubescens* (Mart. & Zucc.) Schott & Endl., and *Qualea grandiflora* Mart. showed greater tolerance to thermal shock, with higher germination percentages than forest species at temperatures of 140 and 200 °C for up to two minutes; however, exposure to 200 °C for five minutes was lethal to all species studied (Ribeiro and Borghetti 2014). According to Daibes et al. (2019), when analyzing 46 legume species, only six showed increased germination when subjected to heat shocks, and half of the species became inviable after exposure to 200 °C for one minute, suggesting that fire may not be a determining factor in Fabaceae seed germination in tropical environments. Therefore, it is important to investigate the effects of fire on the germination and establishment of tree species in environments prone to fire and where it is absent, especially for endangered species.

Dimorphandra (Fabaceae) trees occur across Brazilian biomes, such as the Amazon, Cerrado, and Atlantic Forest (Muniz et al. 2019). Two notable species, *Dimorphandra exaltata* Schott and *Dimorphandra wilsonii* Rizzini, occur in sympatry and are classified as endangered by the International Union for Conservation of Nature (IUCN, Fernandez et al. 2021; Fernandez et al. 2025). *Dimorphandra exaltata* is endemic to the Atlantic Forest, with occurrences recorded mainly in Minas Gerais and Rio de Janeiro (Muniz et al. 2019). It can reach 30 m in height, has a straight trunk and thin bark, compound leaves with glabrous leaflets, and the fruits are rigid and flattened, measuring up to 15 centimeters (da Silva, 1986). *Dimorphandra wilsonii* occurs in ecotones between the Atlantic Forest and the Cerrado, especially in Minas Gerais (Fernandes and Rego 2014). These trees can reach up to 17 m in height, with reticulated bark and compound leaves bearing six to twelve leaflets, which are hairy and rigid, and flattened fruits up to 25 cm long (Martins et

al. 2014). Both species exhibit physical dormancy that can be broken by higher temperatures, leading to germination during the rainy season (Matheus et al. 2017). Most known individuals of these two species are located on private properties, mainly in pasture areas, where cattle consume their fruits (Fernandes and Rego 2014; Martins et al. 2014).

Given that *D. exaltata* and *D. wilsonii* occur on private farms with degraded environments that include ruminant livestock and fires, both anthropogenic and non-anthropogenic, these factors may influence the germination and establishment of these species, potentially impacting future management and conservation plans. Therefore, this study aimed to investigate the influence of cattle (*Bos taurus* Linnaeus), water, and fire on the germination and establishment of *D. exaltata* and *D. wilsonii*. Our primary hypothesis is that the environmental factors, such as the passage of seeds through the bovine digestive tract, water, and fire, influence the germination and establishment of *D. exaltata* and *D. wilsonii*. Our predictions are: (1) Passage of the fruit through the bovine digestive tract will benefit germination, resulting in greater establishment of the studied species; (2) After passing through the digestive tract, seeds in fecal plaques watered daily will show higher germination and establishment rates in both studied species; and (3) Fire may benefit the germination of *D. wilsonii* seeds by breaking seed dormancy, as this species occurs in ecotones between the Cerrado and the Atlantic Forest subject to fire, but it may harm the germination of *D. exaltata* seeds, as it is a forest species, where fire does not occur naturally.

Materials and methods

Collection of materials for setting up the experiments

The experiment was conducted at the Federal University of Viçosa - Florestal campus (19°52'35.15" S, 44°24'48.44" W), Minas Gerais, Brazil. We collected fruit from the two studied species in natural vegetation remnants on private farms in Florestal, Juatuba, and Mateus Leme, Minas Gerais (Figure S.1), between August and September 2023. During the same period, we collected bovine feces (fecal plaques) containing seeds of both species from pasture areas near the mother plants. To compare the effect of feces on the germination and establishment of the studied species, we collected bovine feces without seeds of the studied species at the Federal University of Viçosa – campus Florestal.

Precipitation in the study area was analyzed using data collected from the automatic meteorological station in Florestal, MG (A535) of the National Institute of Meteorology (INMET). During the entire experiment (130 days), only

four days had precipitation greater than 40 mm, and only 60 days had precipitation of 10.4 mm (Figure S.2).

Experiment on the effect of passage through the bovine digestive tract on the germination and establishment of *D. exaltata* and *D. wilsonii*

To investigate the influence of the bovine digestive tract and fecal plaques on the germination and establishment of the studied species, we collected 15 fecal plaques containing *D. exaltata* seeds in Florestal (MG) and 18 fecal plaques containing *D. wilsonii* seeds in Mateus Leme (MG). We also collected thirty-three seedless fecal plaques of the studied species at the Federal University of Viçosa (UFV/CAF). Immediately after collecting the plaques at the UFV/CAF, five manually scarified seeds (with wood sandpaper) were placed on each of the seedless plaques, totaling 15 fecal plaques containing *D. exaltata* seeds and 18 *D. wilsonii* seeds.

These fecal plaques were deposited on the ground in an experimental area at the UFV campus, and monitored daily for 105 days to assess seed germination, emergence, and seedling establishment of the two studied species. The experiment was conducted at the beginning of the rainy season, allowing for natural irrigation due to rainfall (as occurs in the species' ranges). To analyze the influence of artificial irrigation on fecal plaques, we irrigated six additional fecal plaques per species daily with seeds that had passed through the bovine digestive tract, collected from private farms.

To verify seed viability 105 days after the start of the experiment, we conducted another experiment called post-fecal plaque, in which the fecal plaques were sorted to separate the remaining seeds from the fecal content. These seeds were cleaned and placed in Petri dishes with germination paper in a B.O.D.-type incubator. (EL202/4E, ELETROLab, Brazil). The incubator was configured with a photoperiod of 12 h of light and 12 h of darkness at a constant temperature of 25 °C. The seeds were monitored daily for 15 days and moistened with deionized water.

To analyze the influence of passage through the bovine digestive tract, without the interference of fecal plaques and under ideal germination conditions, we conducted a control experiment using a B.O.D. incubator configured with the same conditions as in the post-fecal plaque experiment for two months. We used 90 seeds per species, divided into 30 seeds that passed through the digestive tract, 30 that were manually scarified, and 30 that were not scarified, totaling 180 seeds.

The germination rate for all treatments was calculated as proposed by Maguire (1962), using the formula:

($GR = \Sigma (\frac{G_i}{T_i})$), where G_i is the number of seeds germinated on day i and T_i is the number of days elapsed from sowing to day i .

The germination percentage ($G = \frac{\text{Germinated seeds}}{\text{Total seeds}} \times 100$) and the germination interval (GI =days the seeds took to germinate from the beginning of the experiment) were determined after the end of the experiment by screening the seeds remaining on the fecal plaques.

After the seeds from the experiment with fecal plaques germinated, we analyzed the percentage of establishment of

the emerged seedlings ($EP = \frac{\text{established seedlings}}{\text{Total seeds}} \times 100$), seedling lifespan (SLS), and time to eophyll production (TEP). Analyses were performed with seedlings from all fecal plaques.

Experiment on the effect of fire on seed germination of *D. exaltata* and *D. wilsonii*

To verify the effect of fire on seed germination, an experiment was set up in the same experimental area at UFV/CAF. We used 120 seeds for the fire treatment, 60 for each species, divided into 30 scarified and 30 unscarified seeds. The seeds not exposed to fire were divided similarly, totaling 240 seeds.

Five hundred liters of dry leaves and five liters of alcohol were used as fuel for the fire, and firebreaks were created to prevent fire spread. The seeds were deposited on the soil in a 0.9×1.35 m plot and covered with leaves to allow the fire to pass through. During the fire event, we measured the height with a ruler, the temperature with a digital infrared thermometer, and the duration of the flames with a stopwatch.

The fire lasted 18 min and reached a maximum height of 60 centimeters. Eight minutes after starting, it reached its maximum temperature of 674 °C. The fire temperature equaled the ambient temperature 75 min after the start of the experiment (Figure S.3).

After the fire, the seeds were placed in Petri dishes and monitored for germination in a B.O.D. incubator under the same conditions used in the post-fecal plaque experiment for 2 months. At the end of the experiment, we calculated the same germination variables as in the first experiment.

Statistical analysis

To compare the germination and establishment of each species influenced by passage through the bovine digestive tract, a generalized linear model (GLM) was used. To analyze the germination interval, establishment percentage, and seedling lifespan, we used a GLM with the digestive tract

factor at two levels (seeds that passed through the digestive tract and seeds that did not pass through the digestive tract and were deposited in feces), the irrigation factor at two levels (daily irrigation and natural precipitation), and the species factor at two levels (*D. exaltata* and *D. wilsonii*).

To verify the significant differences between the fecal plaque experiment and the control, we used a GLM for the germination variables: interval, speed, and percentage, in which the species factor had two levels (*D. exaltata* and *D. wilsonii*), the seed protection factor had three levels (non-scarified seed, scarified seed and seed that passed through the digestive tract), the experiment factor had two levels (control and fecal plaque), and the irrigation factor had two levels (daily irrigation and natural precipitation).

A GLM tested significant differences between the post-fecal plaque experiment and the control for the variables: interval, speed, and germination percentage, in which the species factor had two levels (*D. exaltata* and *D. wilsonii*), the seed protection factor had three levels (non-scarified seed, scarified seed, and seed that passed through the digestive tract), the experiment factor had two levels (control and post-fecal plaque), and the irrigation factor had two levels (daily irrigation and natural precipitation).

The germination interval, speed, and percentage of the species after the fire experiment were analyzed using a GLM with two levels of fire (fire presence and absence), two levels of seed protection (unscarified seed and scarified seed), and two levels of species (*D. exaltata* and *D. wilsonii*). For all GLM analyses, we used a Gaussian distribution, and AIC values were used to select models. We used the Dharma package to test the GLM assumptions and the emmeans package to test post-hoc differences. Percentage data and data that did not meet the Dharma conditions were transformed to log10, arcsine, or Box-Cox. For all statistical analyses, we used the R program (R CORE TEAM, 2015). Graphs were created using the results of the statistical analyses in OriginPro (ORIGINLAB CORPORATION, 2016).

Results

Effect of passage through the bovine digestive tract on the germination and establishment of *D. exaltata* and *D. wilsonii*

The results of statistical analysis can be found in Table 1 and S.1. Germination rate (GR) did not differ between species in the control versus post-fecal plaque experiment ($DF=42$; $p=0.200$; $ES=-0.01$) nor in the control versus fecal plaque experiment ($DF=42$; $p=0.096$; $ES=-0.04$). Germination interval (GI) also showed no differences between species in the control versus fecal plaque

Table 1 Germination and eophyll production variables in seedlings of *Dimorphandra exaltata* (DE) and *D. wilsonii* (DW) that showed no significant differences in the performed analyses.

Analysis	Traits		Factors		Experiment													
			Protection						Irrigation									
			DE	DW	ES	Std.	t	Sig	DF	Control	Pos Fecal Plaque	Fecal Plaque	ES	Std.	t	Sig	DF	
Analysis	Control vs. Pos Fecal Plaque	GR	0.83±0.61	1.40±1.35	-0.01	0.01	-1.304	0.20	42	-	-	-	-	-	-	-	-	
		G	-	-	-	-	-	-	-	43.87±33.19	68.99±21.52	-	0.32	0.23	1.37	0.21	9	
	Control vs. Fecal Plaque	GI	14.65±12.12	26.35±26.78	0.20	0.10	2.007	0.05	44	-	-	-	-	-	-	-	-	
		GR	0.38±0.53	0.24±0.32	-0.00	0.10	-0.04	0.96	42	-	0.49±0.50	0.07±0.05	-0.24	0.15	-1.55	0.12	42	
	Fecal Plaque	G	-	-	-	-	-	-	-	43.87±33.19	-	10.10±20.80	-0.05	0.23	-0.25	0.80	11	
		GI	17.46±17.83	39.2±36.6	-0.75	16.78	-0.04	0.96	36	-	-	-	-	-	-	-	-	
		EP	3.88±17.11	1.34±4.94	-32.77	11.345	-2.88	0.21	3	-	-	-	-	-	-	-	-	
		DEP	4.8±1.64	6.33±5.85	-0.20	0.46	-0.43	0.68	7	-	-	-	-	-	-	-	-	
Analysis	Control vs. Pos Fecal Plaque	GR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		G	-	-	-	-	-	-	-	63.43±11.11	51.54±34.37	-0.067	0.28	-0.23	0.82	9	-	
	Control vs. Fecal Plaque	GI	-	-	-	-	-	-	-	16.41±23.80	24.38±21.98	-0.27	0.14	-1.86	869	0.06	44	
		GR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	Fecal Plaque	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		GI	16±2.13	39.06±37.64	57.15	33.01	1.73	0.09	36	16.44±23.09	44.5±32.22	50.65	28.19	1.79	0.08	36	-	
		EP	-	-	-	-	-	-	-	1.12±4.80	9.72±28.83	11.34	11.34	1.0	0.50	3	-	
		DEP	3.5±1.91	7.25±3.86	0.42	0.42	1.00	0.37	7	-	-	-	-	-	-	-	-	
	Generalized Linear Models (GLM) followed by Tukey's post hoc test were applied																	

experiment (DF=44; $p=0.050$; ES=0.20) and in the fecal plaque treatment (DF=36; $p=0.960$; ES=-0.75). Germination percentage (G) did not differ in the control versus post-fecal plaque experiment (DF=9; $p=0.210$; ES=0.32) or in the control versus fecal plaque treatment (DF=11; $p=0.800$; ES=0.05). Seed protection did not influence GI (DF=36; $p=0.173$; ES=0.57) or days to eophyll production (DEP) (DF=7; $p=0.370$; ES=11.34) in fecal plaques. Irrigation regime did not affect germination percentage (DF=9; $p=0.820$; ES=-0.06), germination interval in the control versus fecal plaque comparison (DF=44; $p=0.869$; ES=-2.72) or in the fecal plaque treatment (DF=36; $p=0.179$; ES=50.65), nor establishment percentage (EP) (DF=3; $p=0.500$; ES=11.34). Additionally, establishment percentage did not differ between species in fecal plaques (DF=3; $p=0.212$; ES=-32.77), and days to eophyll production showed no significant differences between species (DF=7; $p=0.686$; ES=0.35). For germination rate and germination percentage, effect sizes were negligible, indicating minimal biological differences between treatments. In contrast, germination interval and establishment percentage showed larger raw mean differences in some comparisons. However, these effects were accompanied by high variability and low degrees of freedom, resulting in non-significant statistical tests.

The germination interval of seeds in fecal plates was 1.8 times greater than under control conditions ($p<0.05$; simple effect of experiment; ES=0.44, Fig. 1a). Regardless of species, germination percentage and germination rate were 8.0 and 5.9 times greater, respectively, in seeds under daily irrigation than in those under natural precipitation ($p<0.05$; simple effect of irrigation; ES=0.05, Fig. 1b

and d). Germination rate was higher in scarified seeds than in non-scarified seeds and in seeds that passed through the digestive tract ($p<0.05$; simple effect of protection; ES=0.40, Fig. 1c).

When analyzing the viability of seeds remaining in feces after 105 days compared to seeds germinated under control conditions, the germination interval was highest in non-scarified seeds, followed by seeds that passed through the digestive tract and scarified seeds ($p<0.05$; simple effect of protection; ES=0.94, Fig. 2a). When comparing germination intervals between treatments, seeds under control conditions showed values 3.2 times those in the post-fecal plate experiment ($p<0.05$; simple effect of experiment; ES=0.42; Fig. 2b). Germination rate was higher for *D. wilsonii* seeds in the post-fecal plate experiment compared to the control ($p<0.05$; interaction between species and experiment; ES=0.04, Fig. 2c). Additionally, in the post-fecal plate experiment, *D. wilsonii* exhibited a higher germination rate than *D. exaltata* ($p<0.05$; interaction between species and experiment; ES=0.04, Fig. 2c).

Seedlings of both studied species lived longer under daily irrigation than under natural precipitation ($p<0.05$; simple effect of irrigation; ES=-0.64; Fig. 3a), with longevity 196.7% higher under daily irrigation than under natural precipitation. In addition, *D. exaltata* seedlings had a longer lifespan than *D. wilsonii* seedlings ($p<0.05$; simple effect of species; ES=-0.27, Fig. 3b), with lifespan being 198.9% higher in *D. exaltata* compared to *D. wilsonii*.

Fig. 1 (a) Germination interval and (b) germination percentage of *D. exaltata* and *D. wilsonii* under control conditions or in fecal plaques over 105 days. (c, d) Germination rate of *D. exaltata* and *D. wilsonii* under control conditions or on fecal plaques for 105 days. Black bars represent the standard error for each treatment. Lowercase letters indicate significant differences between (a) experiments and (c) protection treatments. Uppercase letters indicate significant differences among irrigation treatments. Asterisks indicate significant differences between experiments

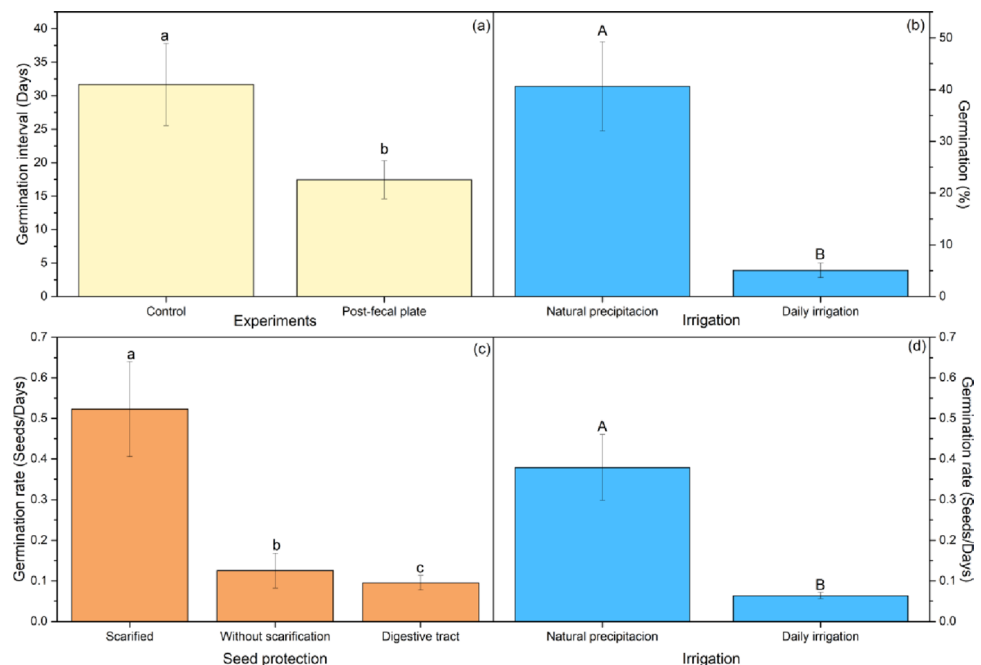


Fig. 2 (a, b) Germination interval of *D. exaltata* and *D. wilsonii* grown under control conditions for 105 days or seeds left 105 days on fecal plaques (post-fecal plaque). The black bars represent the standard error for each treatment. (c) Germination rate of *D. exaltata* and *D. wilsonii* under control conditions or post-fecal plaque. Black bars represent the standard error for each treatment. Lowercase letters indicate significant differences between (a) protection treatments and (c) experiments within the same species. Uppercase letters indicate significant differences between (b) experiments and (c) species within the same experiment

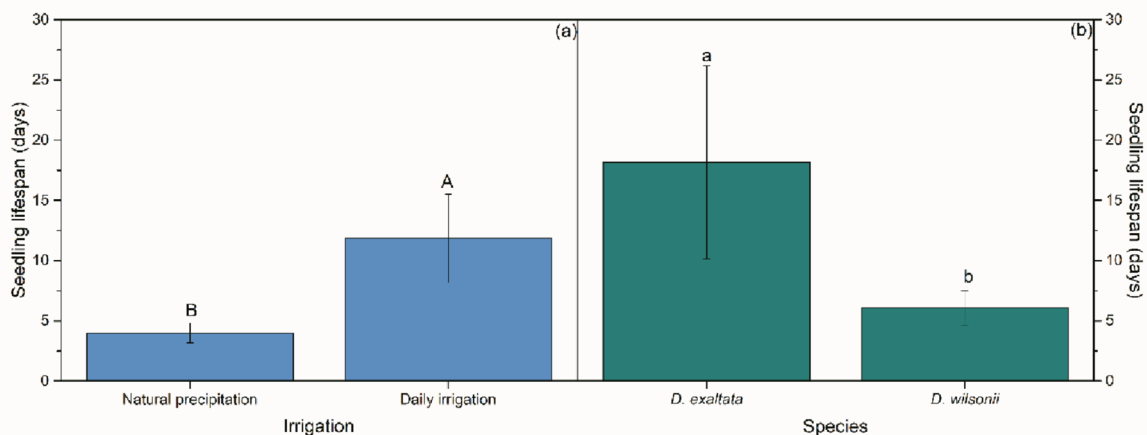
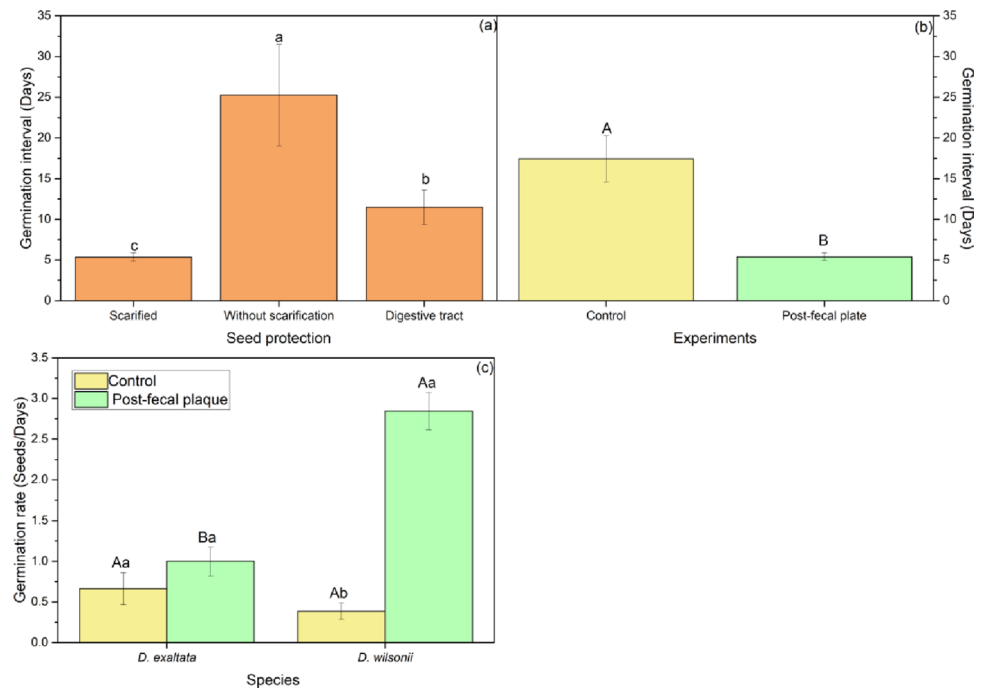


Fig. 3 (a, b) Lifespan of *D. exaltata* and *D. wilsonii* seedlings grown on fecal plaques for 105 days. Black bars represent the standard error for each treatment. Lowercase letters compare significant differences

between species. Uppercase letters indicate significant differences between irrigation treatments

Effect of fire on seed germination in *D. exaltata* and *D. wilsonii*

The results of the statistical analysis are presented in Table 2 and S2. Germination interval (GI) did not differ between species ($DF=17$; $p=0.082$; $ES=0.211$) nor between fire treatments (presence vs. absence) ($DF=17$; $p=0.300$; $ES=-0.19$). Similarly, germination percentage (G) showed no significant differences between species ($DF=39$; $p=0.090$; $ES=-0.24$). Effect sizes were generally small,

particularly for germination percentage and fire effects. However, the germination interval between species showed a moderate mean difference, although associated with high variability and marginal statistical significance.

Overall, both species exhibited similar responses to fire treatments, and fire presence did not significantly affect germination parameters. Seeds not exposed to fire exhibited germination rates approximately 2.0 times greater than those exposed to fire ($p<0.05$; simple effect of fire; $ES=0.91$, Fig. 4a). Seeds of *D. exaltata* showed germination

Table 2 Germination traits of *Dimorphandra exaltata* (DE) and *Dimorphandra wilsonii* (DW) did not show significant differences in the analyses performed

Traits	DE	Factors									
		Species					Fire				
		DW	Effect size	Std.	t	Sig.	DF	Presence	Absence	Effect size	Std.

GI 6.96±4.61 13.70±11.77 0.21 0.11 1.87 0.082 17 8±5.65 10.62±9.79 -0.19 0.18 0.30 17

G 28.33±39.47 26.66±34.72 -0.24 0.14 -1.71 0.09 39 - - - - - -

Seedlings were subjected to different fire treatments (with or without fire). The analyzed variables were germination interval (GI, days) and germination percentage (G, %). Values are presented as mean ± standard deviation for each factor level. SD = standard deviation; Sig. = p-value; df = degrees of freedom; ES = effect size. Generalized Linear Models (GLM), followed by Tukey's post hoc test, were applied. 00

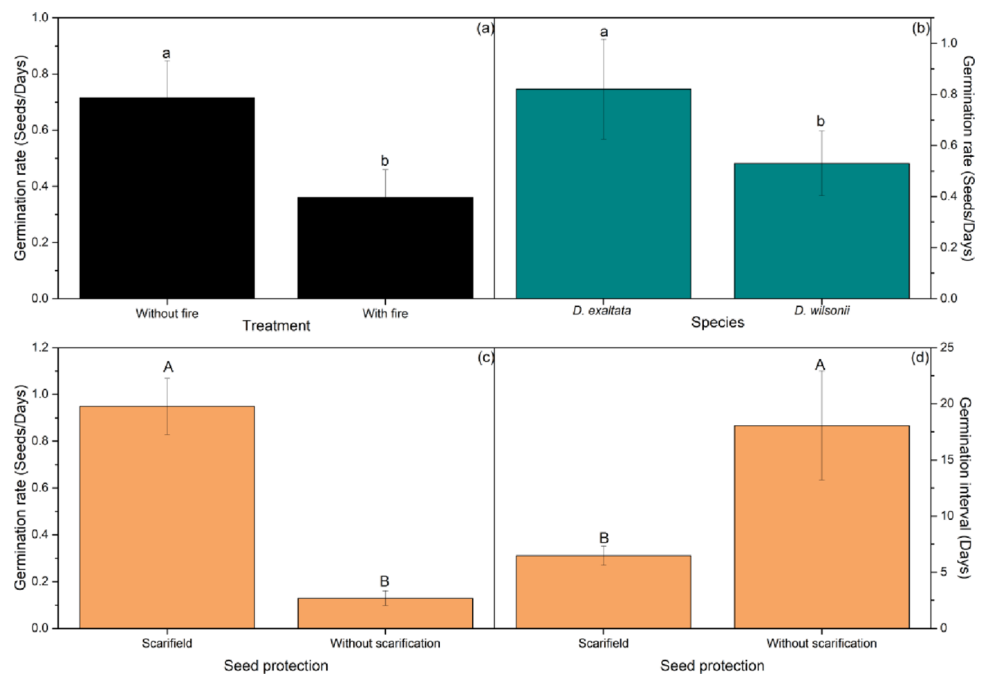
rates approximately 1.5 times greater than those of *D. wilsonii* ($p < 0.05$; simple effect of species; $ES = -4.29$, Fig. 4b). Regardless of fire, scarified seeds exhibited germination rates approximately 7.4 times greater than non-scarified seeds ($p < 0.05$; simple effect of protection; $ES = -1.15$, Fig. 4c). Additionally, regardless of fire, non-scarified seeds showed germination interval values approximately 2.8 times those of scarified seeds ($p < 0.05$; simple effect of protection; $ES = 0.38$; Fig. 4d).

Scarified seeds, regardless of fire, exhibited germination percentages approximately 7.5 times greater than non-scarified seeds ($p < 0.05$; interaction between protection and fire; $ES = -1.03$, Fig. 5). Seeds not exposed to fire exhibited germination percentages approximately 3.1 times greater than those exposed to fire ($p < 0.05$; interaction between protection and fire; $ES = 1.20$, Fig. 5).

Discussion

Contrary to our initial hypothesis, passing seeds through the ruminant digestive tract did not benefit germination rates. Effect sizes associated with digestive passage were small ($ES < 0.3$), reinforcing the limited biological magnitude of this treatment. Regardless of whether the seeds passed through the bovine digestive tract or were subjected to fire, scarified *D. exaltata* and *D. wilsonii* seeds showed higher germination rates, indicating that a resistant seed coat hinders germination. This morphological characteristic may be linked to a strategy for propagating the plant species over time, allowing viable seeds to persist after unfavorable environmental conditions (Willis et al. 2014). Although predominantly heritable, environmental factors can also influence physical dormancy during seed development (Jaganathan 2016). Furthermore, it is associated with seasonality (Rubio de Casas et al., 2017), being more frequent in seeds matured under high temperatures and low precipitation than in those developed under more favorable environmental conditions (Jaganathan 2016). When linked to adaptation to unfavorable environments, diversification tends to be limited and associated with high extinction rates (Willis et al. 2014), as lineages specialized to specific environmental conditions exhibit lower phenotypic plasticity and greater vulnerability to environmental change (Lavergne et al. 2010; Liu et al. 2022). In previous studies, young *D. exaltata* plants showed low phenotypic plasticity in response to water and light availability (Costa et al. 2025), whereas *D. wilsonii* showed low plasticity in relation to temperature (Gonçalves 2024), which limits the species' ability to adjust to climate change. Furthermore, the hard seed coat of *D. exaltata* and *D. wilsonii* can act as a barrier to imbibition, resulting in low germination of unscarified seeds. This dormancy, combined

Fig. 4 (a, b, c) Germination rate of *D. exaltata* and *D. wilsonii* grown in B.O.D. for 60 days after fire. (d) Germination interval of *D. exaltata* and *D. wilsonii* grown in B.O.D. for 60 days after fire. Black bars represent the standard error for each treatment. Lowercase letters indicate significant differences (a) in the fire treatment and (b) between species. Uppercase letters indicate significant differences among seed protection treatments



with the decrease in predicted precipitation patterns due to climate change in the areas where the studied species occur, tends to reduce the likelihood that the species will establish itself in its natural environment (Arroyo-Vargas et al. 2019).

Effect of passage through the digestive tract of cattle on the germination and establishment of *D. exaltata* and *D. wilsonii*

In our experiments, water was the factor that most benefited the germination percentage and germination rate of the studied species. Daily irrigation increased germination percentage, germination rate, and seedling lifespan in both species, with moderate-to-large effect sizes, indicating strong biological magnitude. This reinforces the second prediction and suggests that the natural water regime within the species' distribution range may be insufficient to promote high germination performance, given the requirement for a specific rainfall frequency for germination (Iralu et al. 2019). According to predictions from the Intergovernmental Panel on Climate Change (IPCC 2023), precipitation is expected to decrease in the coming years across the species' distribution, intensifying drought events. Given the strong effect sizes observed for irrigation, reductions in rainfall are likely to limit germination and establishment substantially. Reduced seedling recruitment leads to fewer individuals reaching maturity, decreasing population size, and increasing extinction risk (Aronne 2017).

Despite irregular rainfall during the experimental period, high germination rates were observed in the fecal plaque experiments. However, seedling survival was low, mainly

due to predation by birds and ants on seeds and seedlings (personal observation). Species with restricted distributions and small, isolated populations are often more susceptible to seed and seedling predators than widespread, abundant species (Combs et al. 2013). The presence of herbivores may further intensify the adverse effects of unfavorable environmental conditions, reducing individual survival and population size (Ancheta and Heard 2011).

Passage through the cattle digestive tract was ineffective in promoting germination, contrary to our initial prediction. Effect sizes associated with digestive passage were small, reinforcing the limited biological relevance of this treatment. Despite low germination efficiency, cattle may function primarily as dispersal agents rather than germination enhancers, contributing to fruit breakdown and seed release without damaging the seed coat or reducing viability (Xu et al. 2022). The viability of *D. exaltata* and *D. wilsonii* seeds after passage through the digestive tract was maintained, enabling future germination. A longer germination interval may represent an adaptive advantage in unpredictable environments, as spreading germination over time functions as a risk-minimization strategy (Gianella et al. 2021; Pausas et al. 2022). However, under increasingly irregular rainfall regimes intensified by climate change (Zhang et al. 2021), faster germination, as observed in our study and associated with larger effect sizes under irrigation, may be more advantageous by promoting synchronized establishment and enhancing recruitment (Vacchiano et al. 2021).

When testing seed viability after 105 days on fecal plaques under field conditions, seeds that passed through the digestive tract and were exposed only to natural

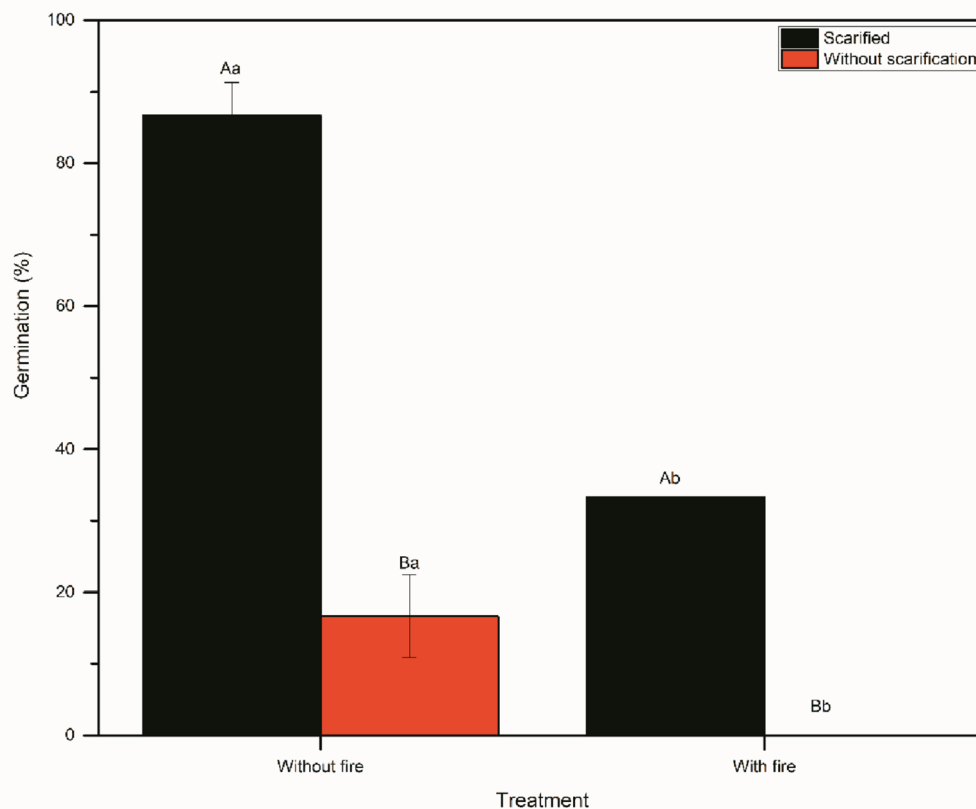


Fig. 5 Germination percentage of *D. exaltata* and *D. wilsonii* grown in B.O.D. for 60 days after fire. Black bars represent the standard error for each treatment. Capital letters compare differences in seed protec-

tion within the same fire treatment. Lowercase letters compare significant differences between fires within the same seed protection

precipitation showed higher germination rates than control seeds. Although this interaction was statistically significant, its effect size was moderate, indicating a context-dependent response rather than a generalized enhancement of germination. High seed recovery after digestive passage is related to chewing particle size and seed structural resistance (Martz and Belyea 1986), as hard, impermeable seed coats allow seeds to withstand rumination and microbial activity in the rumen (D'hondt and Hoffmann 2011). The absence of strong effect sizes on germination percentage across treatments suggests that fecal plaques may help maintain seed viability rather than actively stimulating germination. Regarding interspecific comparisons, *D. wilsonii* seeds germinated faster than *D. exaltata* after 105 days in fecal plaques, with moderate effect sizes indicating meaningful differences in germination dynamics. As a hybrid between *D. exaltata* and *D. mollis* (Muniz et al. 2020), *D. wilsonii* may exhibit enhanced germination performance relative to one of its

parental species. Hybrid taxa often show increased fitness in ecotonal environments (Abbott 2017). However, evidence of inbreeding depression in *D. wilsonii* suggests that conserving this species, along with its parental taxa, may be necessary to maintain genetic diversity (Rego and Mesquita 2025). Despite high germination rates, both species present small natural populations (IUCN; Fernandez et al. 2021). Combined with low genetic diversity (Muniz et al. 2020), limited phenotypic plasticity (Costa et al. 2025; Gonçalves 2024), and the strong dependence on water availability, as indicated by the observed effect sizes, these factors increase their vulnerability to climate change and raise concerns about long-term persistence.

Effect of fire on seed germination in *D. exaltata* and *D. wilsonii*

The third prediction was partially corroborated, as fire did not promote germination in any of the species evaluated (Fichino et al. 2016). Effect sizes associated with fire were moderate to large, indicating that the negative impact of fire on germination parameters was not only statistically significant but also biologically meaningful. This result is observed even considering that *D. exaltata* occurs in the Atlantic Forest and *D. wilsonii* in ecotones, both of which have evolutionary links with the Cerrado, an environment naturally susceptible to fire (Rocha et al. 2024; Daibes et al. 2019). Our results corroborate those of Ribeiro and Borghetti (2014), who found that *Dimorphandra mollis* showed no decrease in germination percentage or time to germination after seeds were exposed to temperatures up to 140 °C. However, this species did not germinate after exposure to 200 °C for 5 min. In general, Cerrado species may tolerate temperatures between 140 °C and 200 °C (Ribeiro and Borghetti 2014), which fall within the range recorded during natural fires in Cerrado areas (Miranda et al. 1993). Nevertheless, the maximum temperature reached in our experiment exceeded those typically observed in native fire regimes and was closer to values reported for human-induced fires, which tend to be more intense and potentially more harmful to native vegetation (Pivello et al. 2021). Similar results were reported in another study for *Dimorphandra mollis*, in which fire did not break seed dormancy and caused 75% seed mortality (Borghetti et al. 2019).

Natural and anthropogenic fires in these areas can result in significant losses for *D. exaltata* and *D. wilsonii*, as fire reduces both species' germination rate and speed (Ribeiro and Souza 2025). The large effect sizes observed for germination rate and germination percentage reinforce that fire acts as a strong limiting factor for recruitment. Fire may explain the low recruitment observed, especially given that these species occur exclusively on private properties, often lack effective fire prevention and control plans, and sometimes are subject to intentional burning. Continued exposure to fire events can lead to population declines in these sensitive species, increasing their risk of extinction (Machida et al. 2021). Furthermore, projections indicate that wildfires are likely to become more frequent and intense in the coming decades (Oliveira et al. 2022), further increasing the risk to the natural regeneration of these species in their habitats. Furthermore, seeds not exposed to fire germinated more than those that were, with effect sizes indicating a substantial reduction in germination performance after fire exposure, suggesting that fire may damage the embryo even in seeds with intact seed coats (Fichino et al. 2016). Similar results were found by Borghetti et al. (2019), who investigated the

effect of an experimental fire on seeds inside intact fruits and found that seed viability of *D. mollis* decreased after fire. However, it is also important to note that seed viability may not be homogeneous, and some seeds may be non-viable even without perturbation (Ursulino et al. 2025).

When comparing species, *D. exaltata* exhibited a higher germination rate, indicating greater synchrony than *D. wilsonii*. This difference was associated with a moderate effect size, suggesting meaningful interspecific variation in germination dynamics. Greater synchrony may represent an evolutionary strategy for reproductive protection in disturbed environments (Vacchiano et al. 2021). *Dimorphandra exaltata* likely originated from a Cerrado lineage and is considered a species of recent origin that specialized in closed forest areas (Rocha et al. 2024), suggesting that its ecological niche shift from fire-prone open areas to forest environments may still be ongoing. Thus, some ecological characteristics of the Cerrado may still be preserved in *D. exaltata*. In this context, it has been shown that *D. exaltata* has a broader thermal niche during germination than *D. mollis*, indicating that the species may be less affected by rising temperatures and more tolerant of high-temperature conditions (Buss et al. 2025). Furthermore, *D. wilsonii*, probably derived from *D. exaltata* and of even more recent origin (Muniz et al. 2020), appears to be undergoing adaptive adjustment to establish itself in its environment.

The fire regime has been constantly altered by anthropogenic actions, making it more intense than under natural conditions, such as lightning-induced fires at the beginning of the rainy season, since the most intense human-caused fires occur during dry periods (Pivello et al. 2021). Natural fires are heterogeneous, and their temperature and duration depend on vegetation cover acting as fuel (Daibes et al. 2018). In dry climates, fires spread faster and are more intense due to accumulated dry biomass, causing greater ecosystem damage than natural fires occurring at the onset of the wet season (Hantson et al. 2022). Fire temperatures can range from 80 °C to over 600 °C near the ground surface in the Cerrado (Miranda et al. 1993; Rissi et al. 2017). Thus, the temperature reached in our study simulates high-intensity fires capable of causing mortality in tree species (Hood et al. 2018), which is consistent with the strong negative effect sizes observed in germination performance after fire exposure.

Conclusions, conservation actions, and practical applications

Our results allowed us to evaluate the effects of endozoochory by cattle, water, and fire on the germination and establishment of *D. exaltata* and *D. wilsonii*. Contrary to

our hypothesis, we observed that passage of seeds through the ruminant digestive tract did not improve germination rates. The first prediction was partially confirmed, as the passage of fruits through the digestive tract of cattle did not favor germination. However, it did not impair the seeds, favoring germination over time. The second prediction was confirmed, as daily irrigation favored the germination and establishment of both species. However, this indicates that current and future natural precipitation is often insufficient for germination and establishment of the species. The third prediction was partially corroborated: the germination of both species was impaired by fire, not only that of *D. exaltata*, as expected. Thus, recurrent fires can be detrimental to both species. Thus, given changes in land use, habitat fragmentation, and climate change, which impact precipitation patterns, *D. exaltata* and *D. wilsonii* may be unable to establish and maintain viable populations in their habitats over time.

Based on the results of this study, it is possible to propose strategies that contribute to the conservation of the studied species. Given the identified challenges, such as low natural regeneration and anthropogenic impacts in the areas where *D. exaltata* and *D. wilsonii* occur, some strategies prove relevant to mitigate these threats and promote the long-term persistence of populations. A viable alternative is replanting seedlings at more advanced stages of development, since larger individuals tend to have higher survival rates in the field, especially in environments with limited natural regeneration. Furthermore, increased fire prevention and control measures on rural properties that harbor natural populations are essential, considering that fire poses a significant threat to the integrity of these areas. Another important point is raising awareness and engaging the owners of farms where the species occur. Dialogue with these stakeholders and promoting environmental education initiatives can foster more sustainable land-use practices, protect remaining populations, and support appropriate landscape management. These combined actions can strengthen conservation efforts and promote the restoration of the ecosystems where these species are found.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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