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Genomic characterization of repetitive DNA and transposable elements in *Dyckia* (Pitcairnioideae) species

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Abstract

Objective Repetitive DNA comprises the majority of nuclear genomes in eukaryotes and is critical for genome stability, gene regulation and evolutionary innovation. Yet, most genomic surveys focus on lowcopy regions, leaving repeats underexplored. Here, we assess how repetitive elements shape genomic diversity and rapid radiation in *Dyckia* (Bromeliaceae) by characterizing the abundance, composition and variability of major repeat families using lowcoverage whole-genome sequencing and the RepeatExplorer2 pipeline.

Results description A substantial proportion of *Dyckia* genome consists of repetitive DNA, reaching ~ 71% in *D. densiflora*, *D. elata*, and *D. consimilis*. Notable interspecific and intraspecific variation was observed, with *D. consimilis* ranging from 50.3 to 69.1%. Satellite DNA, though present in all species, varied in abundance (0.1–4.7%), indicating heterochromatin flexibility. Ty3/Gypsy and Ty1/Copia LTR retrotransposons dominate the repeatome, with lineage-specific expansions of Tekay and Ogre elements. Despite general conservation, population-level differences in repeat composition suggest a role in genome restructuring and phenotypic plasticity. These patterns point to repeat dynamics as a key driver of genome evolution, taxonomic complexity, and ecological adaptability in *Dyckia*.

Keywords Transposable DNA, Satellite DNA, Genomic radiation

Introduction

Repetitive motifs constitute the majority of nuclear DNA in eukaryotic organisms. However, most genomic characterization studies prioritize low-copy sequences, such as genes, while repetitive regions are often discarded due to the analytical challenges they pose. This exclusion limits our understanding of the origin, evolution, and functional roles of repetitive DNA in eukaryotic genomes [1].

In plants, repetitive DNA is remarkably structured. Tandem repeat regions consist of long sequence blocks that are typically found in the centromeric and heterochromatic regions of the genome. These blocks are composed of satellite DNA, mini- and microsatellites, as well as ribosomal genes. However, the majority of repetitive

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DNA is dispersed through the genome, primarily in the form of transposable elements [2].

Transposable elements (TEs) are DNA segments capable of moving throughout the genome, playing structural roles and contributing to chromosomal evolution, speciation, and genetic diversity [3]. TEs are classified into two major groups, Class I and Class II, based on their transposition mechanism. Class I elements, known as retrotransposons, are DNA sequences that replicate themselves through reverse transcription from an mRNA template. As a result, the original retrotransposon remains in place while its copy is inserted into a different part of the genome. In contrast, Class II elements, or DNA transposons, move directly within the genome without increasing their copy number [4].

Wicker et al. proposed a hierarchical classification based on transposition mechanism, sequence similarity, and TE structure. This classification includes two classes, nine orders and 29 superfamilies.

Class I elements comprise the orders LTR (Long Terminal Repeat), DIRS (Dictyostelium Intermediate Repeat Sequence), Penelope-like elements, LINEs (Long Interspersed Nuclear Elements), and SINEs (Short Interspersed Nuclear Elements [5]. Class II elements, also known as DNA transposons, are divided into subclasses based on the number of DNA strands cut during the transposition process and their transposition mechanism.

Subclass I includes TIR (Terminal Inverted Repeat) elements, where transposition typically involves a "cut-and-paste" mechanism requiring double-strand breaks. Subclass II, which includes Helitron-like elements, operates via a single-strand (rolling-circle) transposition mechanism, often associated with replicative amplification. It is important to note that while many Class II elements transpose conservatively, some families can increase their copy number through replicative pathways, contributing significantly to genome size variation and structural dynamics in plants [6].

Historically regarded as functionless "junk" sequences, TEs contribute to chromosomal architecture and can be highly mutagenic [7]. They contribute to gene regulation, drive the emergence of new evolutionary traits, and thus serve as key facilitators of genome evolution, local adaptation, and structural diversity, particularly in species with recent radiation [8]. Therefore, accurately identifying TEs and their abundance in recently radiated species can provide valuable insights into their role adapting to new habitats or physiological responses to different ecotypes without altering genomic sequence [9].

Dyckia Schultz & Schultz f. are terrestrial bromeliads, predominantly xeromorphic and typically rupicolous, characterized by lateral inflorescences and rosette-shaped leaves. With approximately 160 described species, these tankless bromeliads are distributed across eastern South America, with the highest concentration of species in Brazil, often found in rocky outcrops (commonly referred to as "Campos Rupestres"), in small populations at high elevations [10].

The Espinhaço Mountain Range, spanning the states of Minas Gerais and Bahia, harbors the highest endemicity of *Dyckia* species. Isolated within this region, these species exhibit remarkable vegetative morphological variation as illustrated in Fig. 1, occurring in distinct lithological substrates of rocky outcrops, such as ferruginous and quartzitic formations [11].

Despite undergoing a recent and rapid radiation between 4.6 and 2.9 million years ago, the genomic mechanisms driving the diversification and wide ecological distribution of *Dyckia* remain poorly understood. Although the genus comprises over 160 recognized species with remarkable ecological breadth and morphological diversity, no reference genomes have been published to date for any *Dyckia* species, limiting our understanding of its genome architecture and evolutionary dynamics [12].

What role do repetitive DNA elements play in this evolutionary dynamic? To address this question, the aim of this study was to investigate the diversity, abundance, and composition of repetitive DNA sequences—particularly transposable elements and satellite DNAs—across different *Dyckia* species. We characterize these elements through low-pass whole-genome sequencing (WGS-low-pass) and graph-based clustering using the RepeatExplorer2 platform, which allows us to identify, quantify, and compare major repeat families without requiring a complete genome assembly. Our analyses reveal a high abundance of transposable elements (TEs), especially in microendemic species and those involved in recent radiations.

METHODS

Leaf samples were collected from *D. consimilis*, *D. densiflora*, *D. elata*, *D. rariflora*, and the yet taxonomically unestablished *D.* aff. *trichostachya* and *Dyckia* sp. These specimens were gathered at the base of the Espinhaço Range, specifically in the Sinclinal Moeda and Serra de Antônio Pereira Mountain ranges, located in the metropolitan region of Belo Horizonte, Minas Gerais, Brazil. The plant material was formally identified by Otavio Batista de Castro Ribeiro, a taxonomist specialized in Bromeliaceae. Voucher specimens, when available, are listed in Table S2 and have been deposited in publicly accessible herbaria.

One individual was sampled per taxon, with the exception of *Dyckia consimilis*, from which two individuals were collected from geographically distinct populations. This sampling strategy was motivated by the pronounced morphological heterogeneity exhibited by *D. consimilis*,

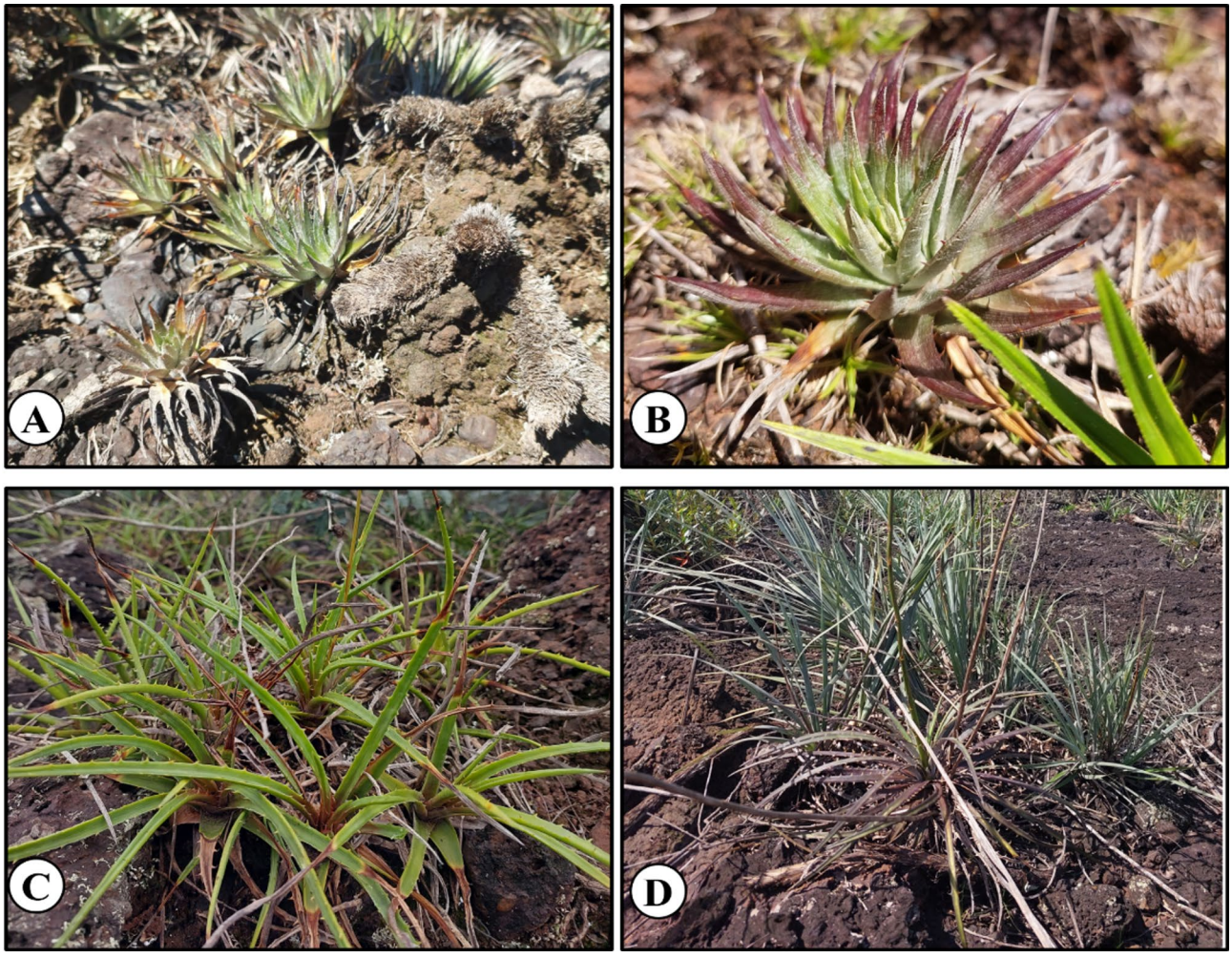

Fig. 1 Morphological diversity of *Dyckia* spp: (**A**) *D. consimilis* (Serra do Rola Moça, Nova Lima, MG); (**B**) *D. consimilis* (Serra da Moeda, Moeda, MG); (**C**) *D. rariflora* (Catas Altas, MG); (**D**) *D. rariflora* (Serra de Ouro Preto, Mariana, MG)

even among proximate populations, as well as the persistent taxonomic ambiguities associated with this species, which is frequently misidentified as *D. macedoi* or *D. schwackeana*.

The inclusion of two individuals aimed to more comprehensively capture the extent of intraspecific genetic variation, particularly regarding the repetitive DNA content, which may be inadequately represented by a single specimen. In contrast, a single representative per species was sampled for the other taxa, as they exhibit considerably lower morphological variability and taxonomic complexity. Leaf tissues from all sampled individuals were collected in situ under SISBIO license No. 71777-15 and subsequently processed for DNA extraction.

Genomic DNA was isolated from approximately 200 mg of young leaf tissue per sample. The leaf material was flash-frozen and pulverized using liquid nitrogen to ensure cell disruption and preserve DNA integrity. DNA extraction was performed following the manufacturer's protocol of the DNeasy Plant Maxi Kit (Qiagen). 2 µL of RNase A (10 mg/mL) was added to each sample to remove RNA contamination.

The quantity and quality of the extracted genomic DNA were assessed using the Qubit Broad Range Assay Kit (Sigma-Aldrich), following the manufacturer's guidelines. Subsequently, genomic libraries were constructed for low-pass whole-genome sequencing (WGS-low-pass) using the Illumina DNA Prep Kit. Library preparation followed the manufacturer's standard protocol, incorporating dual indexing and size selection steps to ensure uniform fragment distribution.

Sequencing was performed on the Illumina NextSeq 2000 platform, employing a paired-end strategy with 2×100 bp read lengths and an average insert size of approximately 300 bp, providing sufficient resolution for graph-based clustering in RepeatExplorer2.

To identify repetitive elements, we utilized the BBMap ((https://github.com/BioInfoTools/BBMap)[13], FastX (http://hannonlab.cshl.edu/fastx_toolkit/), and Repea tExplorer2 platforms [13]. BBMap was initially used

to filter the quality of raw reads and convert the files from FASTQ to FASTA format. Next, the FastX program was employed to standardize sequence lengths and rename them in a uniform manner. Finally, paired-end reads (read 1 and read 2) were concatenated using BBMap's *reformat.sh* tool, which merges reads into a single file without attempting to overlap or merge them into contiguous sequences. While concatenation does not produce merged overlaps, this preprocessing step is recommended by RepeatExplorer2 to maximize cluster detection during downstream analyses.

The RepeatExplorer2 analysis requires samples with genome coverage ranging from 0.01× to 0.50×. Given the absence of genome size estimates for the species, an initial test was conducted using the RepeatExplorer2 clustering in basic mode to determine the optimal number of sequences to analyze (Table S1).

Repetitive elements were identified through sequence clustering. The annotation of repetitive elements was performed automatically based on the REXdb database (*Viridiplantae* v3.0) [14].

Clusters with low similarity to known repeat families or lacking domain signatures were classified as "Unknown_repeats". The total composition of repetitive elements in each population was estimated excluding clusters annotated as organellar DNA or contaminants. Annotated clusters were used to characterize and quantify repetitive elements. The genomic proportions of repetitive classes were determined based on the percentage of sequences associated with each annotated cluster [13].

Results and discussion

A substantial proportion of the genome estimated through low-coverage libraries of *Dyckia* species is composed of repetitive DNA, with *D. densiflora*, *D. elata*, and *D. consimilis* having the highest genomic proportions (70.97%, 70.72%, and 69.09%, respectively), while *D. sp.*, *D. rariflora*, and *D.* aff. *trichostachya* exhibit the lowest percentages (68.44%, 68.29%, and 67.87%). We observed variation between individuals in repetitive DNA content, as observed in *D. consimilis 2*, with only 50.33% (Table 1; Fig. 2).

Even though present in all samples, satellite DNA content shows variation among *Dyckia* species (Table S2). This DNA, primarily located in centromeric regions and characterized by extensive tandem repeats in heterochromatin, ranges from 4.68% in *D. rariflora* and 4.39% in *D. densiflora* to only 0.1% in *D. elata* (Table 1; Fig. 2). Such variation reflect increased genome flexibility and chromosomal rearrangements, influencing genomic architecture and adaptation [15].

Table 1 Repetitive DNA classes and their genomic proportions (%) identified in the individual analyses of *Dyckia* species using RepeatExplorer2

		Species						
		D. *consimilis*_1	*D. consimilis*_2	*D. densiflora*	D. elata	*D. rariflora*	*D.* sp	D. *trichostachya*
	Unknown_repeats	8,39	7,74	4,04	7,69	3,38	7,64	4,12
Class_I (Retrotransposons)	**LINE**	-	0,02	0,02	0,02	0,02	0,01	0,04
	LTR	0,10	0,15	0,46	0,16	0,39	0,15	0,46
Ty1_copia	**Ale**	-	-	-	0,02	-	-	0,04
	Angela	0,05	0,05	0,09	0,07	0,04	0,08	0,08
	Ikeros	0,17	0,35	0,39	0,24	0,28	0,35	0,39
	Ivana	-	-	-	-	0,01	-	-
	SIRE	3,38	5,01	5,29	5,52	5,89	5,71	5,51
	TAR	0,08	0,13	0,15	0,11	0,12	0,14	0,14
	Tork	0,47	0,72	0,67	0,64	0,67	0,72	0,70
Ty3_gypsy	**Chromovirus**	0,04	-	-	-	-	-	-
	Galadriel	0,32	0,16	0,31	0,24	0,11	0,48	0,17
	Reina	0,01	0,05	0,04	0,06	0,04	0,03	0,05
	Tekay	30,60	46,75	47,82	48,68	45,81	45,98	44,78
	Ogre	4,33	6,60	6,39	5,97	5,51	5,76	6,42
Class_II (DNA Transposons)	**MuDR_Mutator**	0,17	0,62	0,33	0,72	0,46	0,48	0,38
	PIF_Harbinger	0,09	0,03	0,10	0,12	0,14	0,11	0,10
	Helitron	0,20	-	0,03	-	0,01	0,03	0,02
rDNA	**18S_rDNA**	0,21	0,18	0,15	0,16	0,32	0,29	0,14
	25S_rDNA	0,30	0,24	0,19	0,21	0,42	0,37	0,19
	5S_rDNA	0,06	-	0,11	0,09	-	0,11	0,11
	Satellite	1,36	0,29	4,39	0,01	4,68	-	4,03
	TOTAL	**50,33**	**69,09**	**70,97**	**70,72**	**68,29**	**68,44**	**67,87**

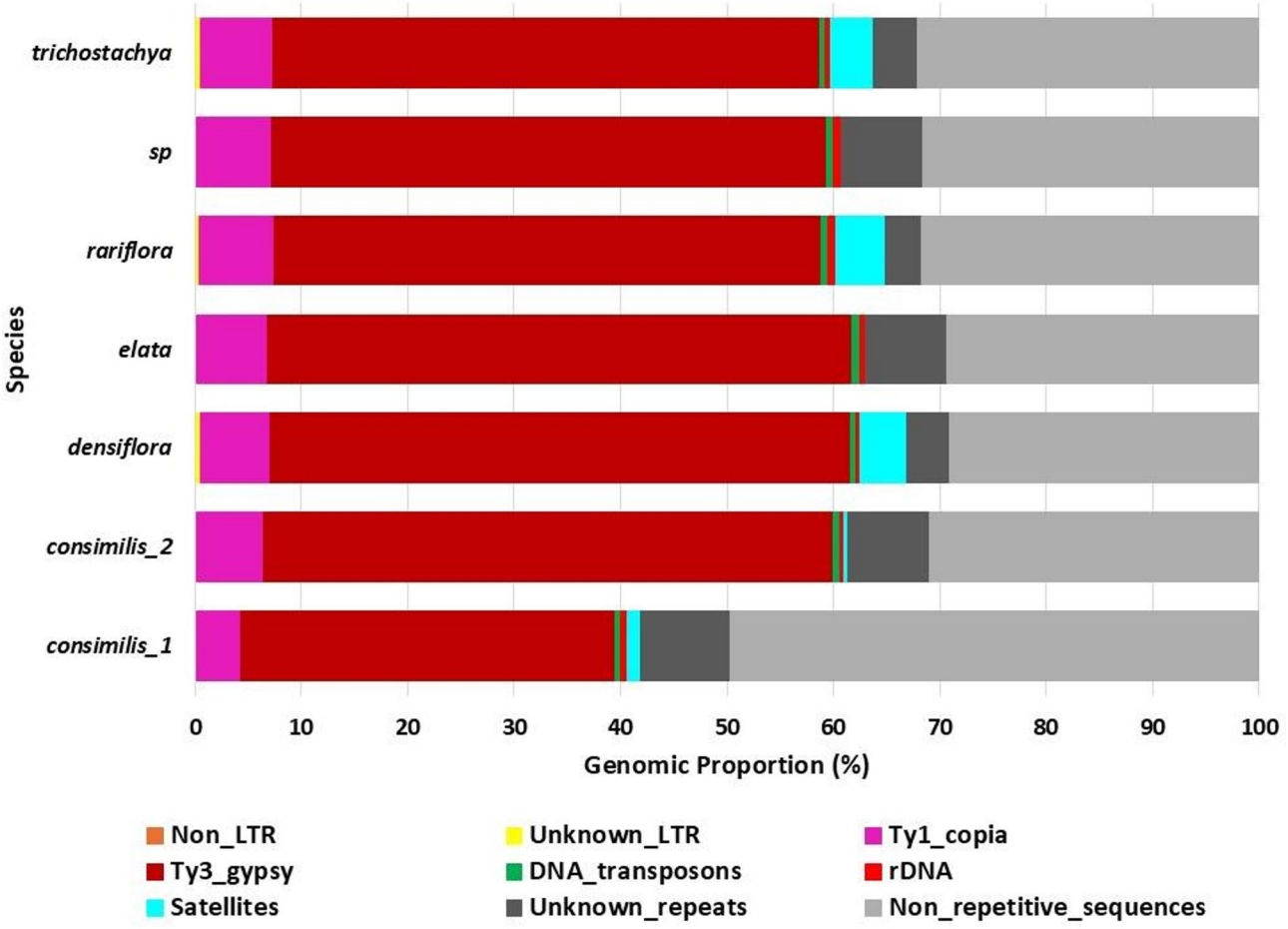

Fig. 2 Genomic proportion (%) of the main classes of repetitive elements identified in the individual analyses of *Dyckia* species using RepeatExplorer2

Among the repetitive elements that compose the *Dyckia* genome, the Ty3/Gypsy family (Class I Retrotransposons) is the most abundant across the analyzed species (Fig. 2). Although these elements are frequently silenced by epigenetic mechanisms, they can function as promoters, modulators, or silencers of gene expression, depending on their genomic location [16].

The Ty1/Copia family, the second most abundant repetitive element in *Dyckia*, is widely identified in eukaryotic genomes. It is transposed via an RNA intermediate and reintegrated into the genome through the action of reverse transcriptase. By inserting into different regions of the genome, this family can promote increased intra-specific diversity, as observed between *Dyckia consimilis* 1 and *Dyckia consimilis* 2 (Fig. 2).

The Ty3/Gypsy/Tekay and Ty3/Gypsy/Ogre retrotransposons showed the highest frequencies across species, especially in D. densiflora and D. elata, indicating possible lineage-specific amplification (Fig. S1). We hypothesize that their proliferation in heterochromatic regions of recently radiated species may drive rapid genomic divergence. Additionally, transposable element activity can affect gene expression via epigenetic mechanisms, such as DNA methylation spreading to nearby gene-rich regions [17].

Mata-Sucre et al. (2020) proposed that a significant portion of species diversity within *Caesalpinia* (Fabaceae) is modulated by genomic modifications in heterochromatic regions rich in LTR-RT Ty3/Gypsy-Tekay elements [18]. The high species richness of *Dyckia*, even under edaphic constraints, may be influenced by the abundance of the repetitive elements identified in this study.

The taxonomic identification of *Dyckia*, particularly for species associated with the potential center of origin of the genus, has historically been problematic [10, 19]. This has led to the formation of several taxonomic complexes comprising morphologically similar, sympatric species, or species described from anomalous materials deposited in herbaria [20, 21].

Dyckia elata and *D. rariflora*, taxa that were historically included in the *Dyckia saxatilis* complex due to their considerable morphological similarity, have recently been synonymized (Reflora Virtual Herbarium, available at: ht

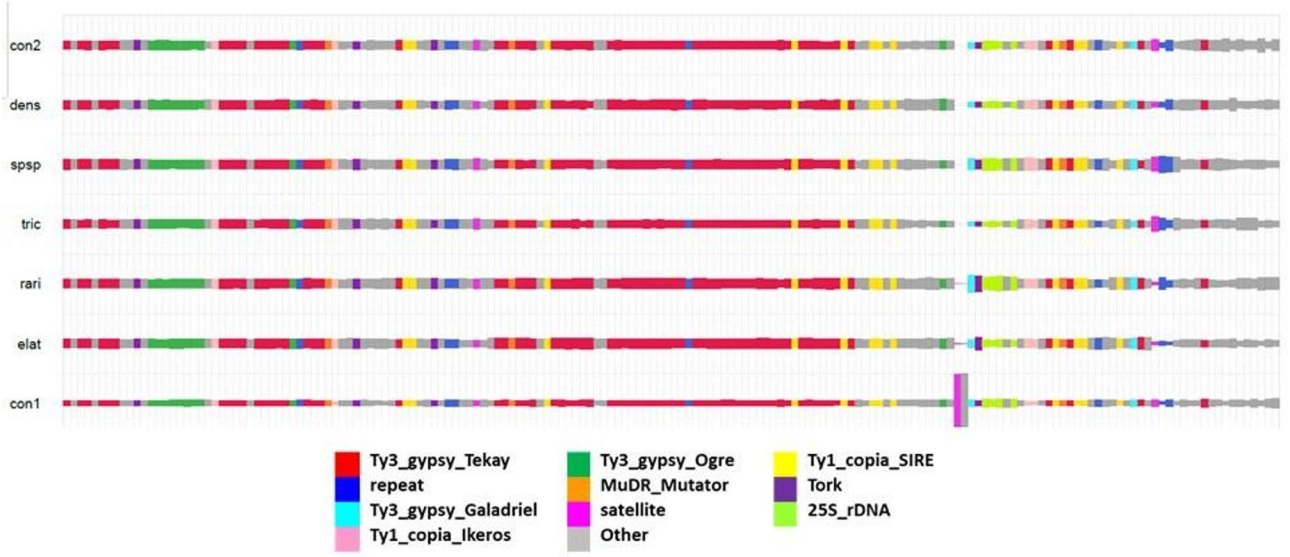

Fig. 3 Comparative analysis of the composition of repetitive elements between *Dyckia* species inferred in RepeatExplorer2. The columns represent different clusters, the colours represent different repeats, and the size of the rectangles is proportional to the number of reads in a cluster for each species. (con2 – *Dyckia consimilis_2*; dens – *D. densiflora*; spsp – *D. sp*; tric – *D.* aff. *trichostachya*; rari – *D. rariflora*; elat – *D. elata*; con1 – *D. consimilis_1)*

tps://reflora.jbrj.gov.br/reflora/herbarioVirtual/, accessed on: Mar. 2025). However, this hypothesis, grounded in morphological characteristics, has yet to be published and continues to face resistance within the academic community.

Although repetitive DNA data lack strong species-specific signatures, the overall similarity in repeatome profiles between these taxa underscores their close genomic affinity, especially compared to greater divergence among other congeneric species. The dynamic activity of transposable elements may influence gene expression, contributing to phenotypic plasticity and subtle morphological variation, which can complicate species delimitation based solely on morphology.

However, a comparative analysis of geographically close populations of *D. consimilis* revealed substantial variation in repetitive DNA content, not only in the total proportion but also in the composition of microsatellites and TE classes. This highlights the genomic variability among individuals of the same species (Table 1; Fig. 2). Such variation is likely to contribute to reproductive isolation or morphological differences, potentially explaining the species' phenotypic plasticity [22].

Comparative synteny analysis of repetitive elements in *Dyckia* reveals a high degree of conservation in the order and composition of these structures (Fig. 3). However, two exclusive repetitive elements were identified in *Dyckia consimilis* 1, corresponding to blocks formed by satellite DNA and an abundant unidentified element, which are absent in the other analyzed species, including the second *Dyckia consimilis* individual.

Despite the fact that no statistical tests were conducted, the RepeatExplorer2 pipeline is a widely validated and robust tool for comparative repeats analyses. It employs graph-based clustering to estimate the relative abundance of repetitive elements, generating reliable and semi-quantitative results even from low-coverage datasets and in the absence of a genome assembly [13, 23]. Never the last, while RepeatExplorer2 allows estimation of repeat abundance from low-pass data, some biases may arise due to stochastic sampling or variation in genome size.

Although high-coverage genome assemblies are not yet available for *Dyckia* and other Pitcairnioideae species, our results suggest that TE's dynamics may play a critical role in shaping genome architecture and driving phenotypic changes in Bromeliaceae.

This hypothesis is supported by recent findings in the subgenus *Tillandsia*, where a highly dynamic TE landscape, in combination with large-scale chromosomal rearrangements and regulatory rewiring, has been associated with shifts in key physiological traits, such as the repeated evolution of Crassulacean Acid Metabolism (CAM). These findings highlight the potential of TEs to influence phenotypic diversification by modulating the expression of genes linked to adaptive traits [24].

This finding suggests that, despite overall conservation of repetitive element organization in *Dyckia*, certain *D. consimilis* populations display unique structural patterns absent in other individuals. These exclusive blocks of satellite DNA and unidentified elements reflect genomic variability that may influence genome structure or regulation. Although direct evidence of chromosomal

rearrangements or gene expression effects is lacking, these observations highlight the potential role of repetitive DNA in promoting intra-specific genomic diversity.

Conclusion

The characterization of *Dyckia* repetitive DNA shows overall conservation, though occasional individual differences reveal genomic complexity and variability even within populations. These results suggest that rearrangements of repetitive regions may contribute to adaptation, phenotypic plasticity, and the genus' wide distribution. Further studies using fluorescence in situ hybridization (FISH) and long-read sequencing are needed to clarify the functional roles of these elements. Understanding whether unique repeats represent mobile elements, structural variants, or adaptive features will shed light on the evolutionary forces shaping *Dyckia* genomic diversity.

Limitations

Limitations of this study include the small number of sampled species due to their limited population sizes and threatened status. The lack of reference genomes restricts detailed interpretation of the genomic distribution and function of repetitive elements. The low-pass sequencing approach, while suitable for comparative analyses, underrepresents low-copy elements and biases toward high-copy transposable elements, increasing the proportion of unclassified repeats. Future work with deeper sequencing and population-level replicates is needed to enhance TE classification and evaluate intra-specific variation.

Abbreviations

TE	Transposable elements
LTR	Long Terminal Repeat
DIRS	Dictyostelium Intermediate Repeat Sequence
LINEs	Long Interspersed Nuclear Elements
SINEs	Short Interspersed Nuclear Elements
TIRs	Terminal Inverted Repeats

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13104-025-07359-0.

Supplementary Material 1

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Author contributions

Designed research: J.V.S.R.A, A.C.S.A.N, M.I.Z; Performed research: J.V.S.R.A, A.F.F, C.B.G; Z.P.C; O.B.C.R; Analyzed Data: J.V.S.R.A, A.F.F, Z.P.C; Wrote the paper: J.V.S.R.A; A.F.F, Z.P.C.

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Data availability

The consensus satellite DNA sequences have been deposited in the NCBI GenBank database under accession numbers PV390229-PV390236 and PV442150-PV442158.

Declarations

Ethics approval and consent to participate

All necessary permits for plant collection were obtained from the appropriate authorities (SISBIO license No. 71777-15). The genetic material of the analyzed species was handled with the appropriate authorization from SISGEN (Registration: A1B8713).

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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