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Review
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Phenotypic and molecular basis for genetic variation in jelly palms (*Butia* sp.): where are we now and where are we headed to?

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Abstract

We compiled studies that addressed morphological and physicochemical traits, as well as population genetic studies involving jelly palms, genus *Butia* (Arecaceae). First, we conducted a bibliometric study with selected articles, by revising the fundamental contributions to unraveling phenotypic traits that have been used for describing the phenotypic variation within and among populations. Moreover, we sought to comprehend the patterns of genetic diversity and structure that have been presented so far, based on molecular markers. Finally, we conducted a review of the gene sequences registered to NCBI for *Butia*. Overall, morphological descriptors have been proposed to depict population-level variability, but the most significant results are available from chemical properties and characterization of metabolites, revealing important traits to being explored. Yet, limited information is available to describe population variation and their genetic components. On the molecular level, almost all studies so far provided results with classical molecular markers. The literature of SNP markers for *Butia* species is virtually non-existent. Given the current endangered state of *Butia* species, it is urgent that researchers pursue updated genomic technologies to invest in in-depth characterizations of the genetic diversity and structure of jelly palms. The current state of population fragmentation urges effective measures toward their conservation.

Keywords: Genetic diversity, phenotypic variation, endangered species, palm trees, conservation genetics.

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Introduction

Butia (Becc.) Becc. is a genus of palm trees (Arecaceae) autochthonous to South America. Trees are popularly known as "butiás", pindo palms or jelly palms. The species are naturally distributed in southern and central Brazil, eastern Paraguay, northeastern Argentina and northwestern and southeastern Uruguay (Lorenzi *et al.*, 2010). Their occurrence in Brazil encompasses a few populations at the southeast of Bahia, east of Goiás and northern Minas Gerais, but most populations are found in the southern states, especially in Rio Grande do Sul and the south of Santa Catarina (Marcato, 2004; Soares and Longhi, 2011; Müller *et al.*, 2012; Soares *et al.*, 2014; dos Santos *et al.*, 2017). *Butia* species can also be found in São Paulo, Mato Grosso do Sul and Paraná (Reitz, 1974; Eslabão *et al.*, 2016; Barbieri *et al.*, 2017). Their occurrence encompasses the Pampa, Atlantic Forest and Cerrado biomes (Hoffmann *et al.*, 2017).

Jelly palms can reach 10 meters or more in height, with seasonal reproduction, characterized by monoecious, protandrous and allogamous plants, rarely showing geitonogamy (Mercadante-Simões *et al.*, 2006; Corrêa *et al.*, 2009; Beskow *et al.*, 2015; Sosinski *et al.*, 2019). The fruit clusters are composed of dozens or even more than a thousand fruits. Fruits vary in shape from ovoid to globose, fibrous, sweet, slightly acidic and are rich in phenolic compounds, carotenoids, vitamin C and potassium. Fruits turn yellow, orange or reddish when mature (Lorenzi *et al.*, 2010; Beskow *et al.*, 2015) and are quite versatile in usage by local communities, being employed in the manufacture of juices, liqueurs, ice cream, and jellies (Hoffmann *et al.*, 2014; dos Santos *et al.*, 2017). The pulp is composed of the exocarp and mesocarp, containing high concentrations of carbohydrates, fiber, pro vitamin A, vitamin C, carotenoids, and phenolic compounds, which offer potential for agroindustry expansion in the utilization of the fruit (Faria *et al.*, 2008a; Pereira *et al.*, 2013).

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The number of species counted within the genus *Butia* has changed considerably over frequent taxonomic debates based on morphological traits. The work by Noblick (2010) acknowledged 18 species, among them *Butia capitata* (Mart.) Becc., that was first identified in 1826 as *Cocos capitata*. Originally, Martius described the palm from their observations near the town of Montes Claros, in Minas Gerais state (Noblick, 2011). In general, this palm occurs in Cerrado areas, typically in sandy soils in Bahia, Goiás and Minas Gerais states (Noblick, 2010). A few authors, however, also attributed the name *Butia capitata* to a set of populations that occur in the coastal plain of Uruguay, Rio Grande do Sul and Santa Catarina states, in Brazil (Rosa *et al.*, 1998; Soares *et al.*, 2014). However, a recent reclassification was described for the populations of Uruguay and southern Brazil, and those located in Cerrado. *B. capitata* was then attributed only to the populations from Cerrado and *B. odorata* became the designated species for populations to the south of a small municipality called Osório, in Rio Grande do Sul state (approximately at latitude of 29ºS). All populations north from that and located by the coastal plain of the Atlantic are designated as *B. catarinensis* (Noblick, 2010; Noblick, 2011). Another study recognized *B. poni* as a novel species (Deble *et al.,* 2017) and, more recently, a new endemic and endangered species has been described in a narrow area from Brazilian Cerrado, *B. buenopolensis* (Noblick and Sant'anna-Santos, 2021).

The taxonomic delimitation of *Butia* species based on morphological diversity is a difficult task, given the full evolutionary activity of the species, which are still in the process of establishing morphological characters and the high degree of genetic variation in morphological, phenological and physicochemical traits (Soares 2013; Soares *et al.*, 2014; Beskow *et al.*, 2015).

In general, the species are threatened, and some are already at risk of extinction due to the fragmentation of their habitat by expansion of urban areas, agricultural activities that replace natural palm trees, removal and illegal commercialization of plants, reforestation with other tree species, and limited natural regeneration due to cattle grazing (Nazareno and dos Reis, 2014; Eslabão *et al*., 2016). This may have severe consequences, as habitat loss and fragmentation may reduce gene flow and genetic diversity, leading to inbreeding depression and reduced reproductive fitness (Reed and Frankham, 2003; Browne and Karubian, 2018).

Genetic diversity is one of the three components of biodiversity recognized by the World Conservation Union (IUCN) as worthy of conservation. The need to conserve genetic diversity within populations is based on two premises: (i) genetic diversity is a key factor for evolution to occur; (ii) and the expected relationship between heterozygosity and population fitness, that is, genetic variation an important factor for fitness (Reed and Frankham, 2003). Molecular genetic characterization is essential for the delineation of effective conservation measures, that is, the rational use of germplasm resources and conservation management of endangered species (Mable, 2019; Cao *et al.*, 2022; Aswathi *et al.*, 2023). To date, population genetic studies on jelly palms based on molecular markers are yet scarcely available. In this review, a compilation of the studies shows articles with traditional molecular markers such as RAPD (random amplified polymorphic DNA), AFLP (amplified fragment length polymorphism), ISSR (inter-simple sequence repeats) and SSR (simple sequence repeats).

Equally important for conservation, management and breeding of jelly palms is a deeper knowledge on phenological patterns as well as the reproductive biology of populations (Nazareno and dos Reis, 2014; Guilherme *et al.*, 2015). Morphometric characterization of fruits and seeds is important for taxonomic studies, allowing the identification of varieties with economic value, verification of the phenotypic and genetic variation occurrence and association with the environment, both within and between plant populations (Padilha *et al.*, 2016; Rios *et al.*, 2016). Fruit and seed size variability within and among populations are an important component for studying the adaptation and evolution of trees in tropical and subtropical ecosystems (Candido-Ribeiro *et al.*, 2019). For *Butia* palms, a wide phenotypic diversity is observed, which provides fruits varying for biometric, physicochemical and sensorial traits (Dal Magro *et al.*, 2006, Sganzerla, 2010).

This review was developed to address the current state of art of knowledge on phenotypic and genetic variation on *Butia* species, considering three fundamental categories: (i) plant morphology, (ii) physicochemical properties and nutrition, and (iii) population genetic studies and cytogenetics. Moreover, we searched the NCBI database to look into gene sequences that involved *Butia* palms. Our main goal is to provide a panorama of the fundamental knowledge acquired through the years and prospect their utility for novel endeavors toward conservation and breeding of jelly palms.

Material and Methods

Sistematic review

A bibliometric study and a systematic review of articles were employed to encompass the knowledge produced about the morphological, physicochemical and molecular variation of jelly palm species. Four main steps were conducted in our survey: (i) keyword search through bibliometric platform; (ii) article selection after analyzing title and abstract, avoiding irrelevant contents to our subjects as well as redundant publications; (iii) categorization of papers according to scope. For that, three main categories were pre-defined: plant morphology, physicochemical properties and nutrition and population genetic and cytogenetic studies; (iv) categorization according to the object of research, journal of publication, year, objectives, main results and species involved.

The review was conducted through the "Web of Science" data platform, using the keyword "Butia" to search for all the results published up to 2023. The choice of "Web of Science" was due to the feasibility of conducting the search on the platform and the full access to the published articles. Our search presented 227 results, which were analyzed for title, abstract, and keywords. After reading and manual filtering, 47 articles were excluded for not being related to the *Butia* genus (e.g. papers that mentioned a municipality that contains the word "Butia"; or the word was found in the text but from other contexts not related to our goals). One article was excluded for not being available on the platform and another was excluded for being written in German.

After this selection, 178 papers were analyzed concerning the three different categories here proposed:

1. Plant morphology: papers with phenology of the genus, biometric variables or anatomical and, eventually, even some physiological studies;
2. Physicochemical properties and nutrition: papers addressing chemical compounds in fruits, nutritional analyses and chemical composition of fruits and seeds;
3. Population genetics and cytogenetics: karyotype description, genetic diversity and structure.

After classification, 68 papers were selected. Of the total, 13 articles featured morphological analyses, 40 specifically dealt with physicochemical properties and nutrition, 11 referred to population genetic or cytogenetic studies, and 4 could be fitted into more than one category (e.g. morphological and physicochemical properties).

Following bibliometric approaches, further analyses of the articles were conducted to determine: (i) a list of publication sources and the distribution of articles among them; (ii) discrimination of journal impact factors; (iii) production per year from the first to last publication date; (iv) ratios of publications per period and the categories defined as per our study; (v) ratio of annual publications per number of citations of each article.

The qualitative analysis of the studies sought the validation and interpretation of scientific evidence relevant to the topics studied, and the identification of gaps in the literature, which may guide future studies. A few additional studies were also considered for the purpose of contextualization or discussion.

NCBI/Genbank search for sequences

We also searched the GenBank from NCBI (https://www.ncbi.nlm.nih.gov/popset/?term=butia) in order to find all the sequence information already available. Searching for the term "Butia", we found 54 results (on April 26, 2023) in population sets (PopSets). After manually filtering the results, excluding non-related subjects, 43 popsets were checked for the gene sequences and the species involved.

Resources available from GBIF and iNaturalist

Public databases on records for *Butia* species were also searched from GBIF (https://www.gbif.org/species/2736210) and iNaturalist (https://www.inaturalist.org/observations?place_id=any&taxon_id=180225) as of August 3rd, 2023.

Results

Bibliometric study and public records on databases

Among the 68 articles that matched the scope of this research, 39 papers were published each in different journals (Table S1). The remaining 29 articles are distributed among 10 journals: "Revista Brasileira de Fruticultura" (Number of papers = 8), "Food Research International" (N = 4), "Food Bioscience" (N = 3), "Food Analytical Methods" (N = 2), "Ciência Rural" (N = 2), "American Journal of Botany" (N = 2), "Biota Neotropica" (N = 2), "Journal of Heredity" (N = 2), "Brazilian Journal of Biology" (N = 2) and "Food Science and Technology" (N = 2). Table S1 shows the list with all journals, number of publications and corresponding impact factor.

The highest impact factor (JCR 2021 list; as on April 27th, 2023) among all journals was for "Energy Conversion and Management" (IF = 11.5) and the lowest was for "Revista Chilena de Nutricion" (IF = 0.1). The highest number of studies in frequency (N = 8) were published in a low impact journal (IF = 1.1) – "Revista Brasileira de Fruticultura". Other four publications (N = 4) are available from a journal with a high impact factor (IF = 7.4) – "Food Research International".

The average number of published papers per year was 2.42. Most of the articles (N = 40) were published in the last eight years, with the highest number (N = 7) in 2022, and 25% were published in the last three years. Figure 1a presents the distribution of publications per year according to the category of the paper. From the date of the first study (1995) to the second (2008), there were 13 years without any publication regarding morphology, physicochemical properties and nutrition or population genetics and cytogenetics. In the period from 2008 to 2022, publications were available over all consecutive years, with an average of 4 publications per year. From 1995 to 2022, articles dealing with jelly palm physicochemical properties and nutrition have been published in all years in that publications were available and retrieved from our survey (Figure 1a).

As per our categorization, most studies in the period were devoted to physicochemical and nutritional analyses (N = 39). Plant morphology was the object of 18 studies, while population genetics and cytogenetics involved 12 articles. Among all papers, four were placed into more than one category, as they dealt with both morphology and physicochemical properties of jelly palms. Based on the frequency per category, an increase in physicochemical and nutritional studies is notable for the last five years (N = 17).

The selected articles were cited 971 times throughout the entire period (updated up to April 2023), with the highest number of citations corresponding to studies of physicochemical properties and nutrition (N = 670), followed by population genetics and cytogenetics (N = 132) and plant morphology (N = 98) (Figure 1b). The articles that fitted into more than one category were classified as "Mixed" and cited 71 times in total. Figure 1c demonstrates the total number of citations and publications per year, considering all papers selected for this study. The highest number of published papers occurred in 2010, 2015 and 2022 (N = 7). The year 2008 received the highest number of citations (178 citations). The most cited paper was of Genovese *et al.* (2008) (125 citations), that characterized bioactive compounds contents and antioxidant capacity of Brazilian exotic fruits, one of them being *B. capitata*. The second most cited article (103 citations) was of Denardin *et al.* (2015), which also evaluated bioactive compounds and antioxidant properties for *B. eriospatha*. In total, 8 articles received no citations until the time of this research and have been published in journals with an impact factor from 0.9 to 7.4.

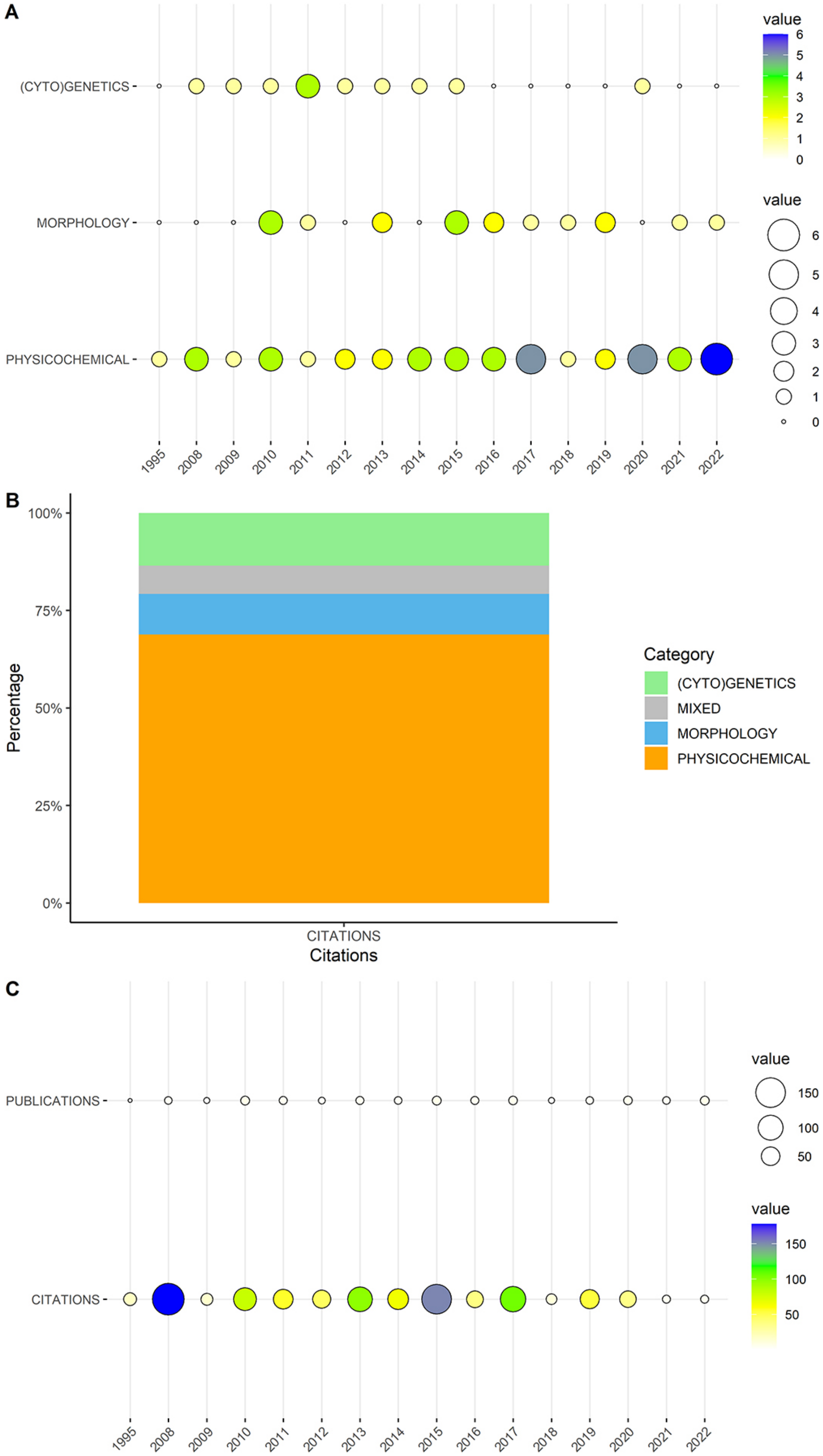

Figure 1 – Bibliometric analyses of papers related to *Butia* palm species available from Web of Science. a – Number of papers published per year that involved jelly palms, based on our categorization in three main types of articles: (i) population genetics and cytogenetics; (ii) plant morphology; and (iii) physicochemical properties and nutrition. b – Proportion of the total number of articles per category. c – Number of publications and citations in all years that had at least one publication since 1995.

As for the jelly palm species studied, Figure 2 shows that most of them (N = 29) were about *B. capitata*, followed by *B. eriospatha* (N = 17) and *B. odorata* (N = 16). In fact, the number of papers that actually studied *B. odorata* was higher. This is because before 2010, *B. capitata* encompassed both *B. capitata* and *B. odorata*. It was Noblick (2010) that redefined the scientific names, considering populations of Rio Grande do Sul and Uruguay as *B. odorata*, while those located in Cerrado and areas from Central Brazil remained as *B. capitata*. That taken into consideration, we counted the number of papers that studied *B. odorata* to 26 and that studied *B. capitata* to 19, as there were 10 articles which named *B. odorata* as *B. capitata* of samples from Rio Grande do Sul state. However, that may depend on the type of paper, especially for those that were more concerned with physicochemical analyses rather than the specifics of the sample origin. Other papers were dedicated to study *B. catarinensis* (N = 8), *B. yatay* (N = 8), *B. paraguayensis* (N = 7), *B. lallemantii* (N = 3), *B. purpurascens* (N = 3) and *B. witecki* (N = 2). *B. archeri, B. campicola, B. exospadix, B. leiospatha, B. leptospatha, B. lepidotispatha, B. marmorii, B. matogrossensis, B. microspadix* and *B. pubispatha* were involved in only one publication (Sant'anna-Santos *et al.*, 2018).

Three studies are review articles, so they did not focus on a species to attend the classification, as well as one study by Paroul *et al.* (2009), about wax hydrocarbon fractions. The authors did not specify the species but only the location, which does not ensure to state which species was investigated. The description of the main results and defined category of the 68 selected articles were summarized in Table S2.

Besides research articles, we also checked GBIF and iNaturalist databases for occurrences that were registered. By searching "Butia" on GBIF, 2,731 occurences were found as of August 3rd 2023 for 27 species. Of the total, 1,437 records were georeferenced and 924 occurences are accompanied by photographs. For instance, the same search was conducted with iNaturalist, resulting in 853 observations for 14 species, frequently accompanied by photograps, at the same date of search that GBIF.

Phenotypic traits based on plant morphology

Plant morphological traits have been the object of several studies conducted with jelly palms. From our interpretation, the studies were frequently devoted to describing differences among populations, sometimes leading to the description of novel species. On the other hand, work had been done to unravel phenotypic differences for several traits in studies aimed at conservation and breeding strategies for jelly palms. For that purpose, morphological traits have frequently been compared among preserved and managed populations at distinct environments.

The distinction among species of *Butia* is frequently based on only a few morphological characteristics, such as between *B. catarinensis* and *B. odorata* (Figure 3). *B. odorata* can exceed 10m in adult individuals (Figure 3a). *B. catarinensis* individuals often do not exceed 2m in height (Figure 3b). Their distinction is also based on the spathe shape (Figure 3c). Although both species are monoecious, with male flowers more numerous than female flowers (Figure 3de), fruits o *B. odorata* are often round or slightly ovoid (Figure 3f), while

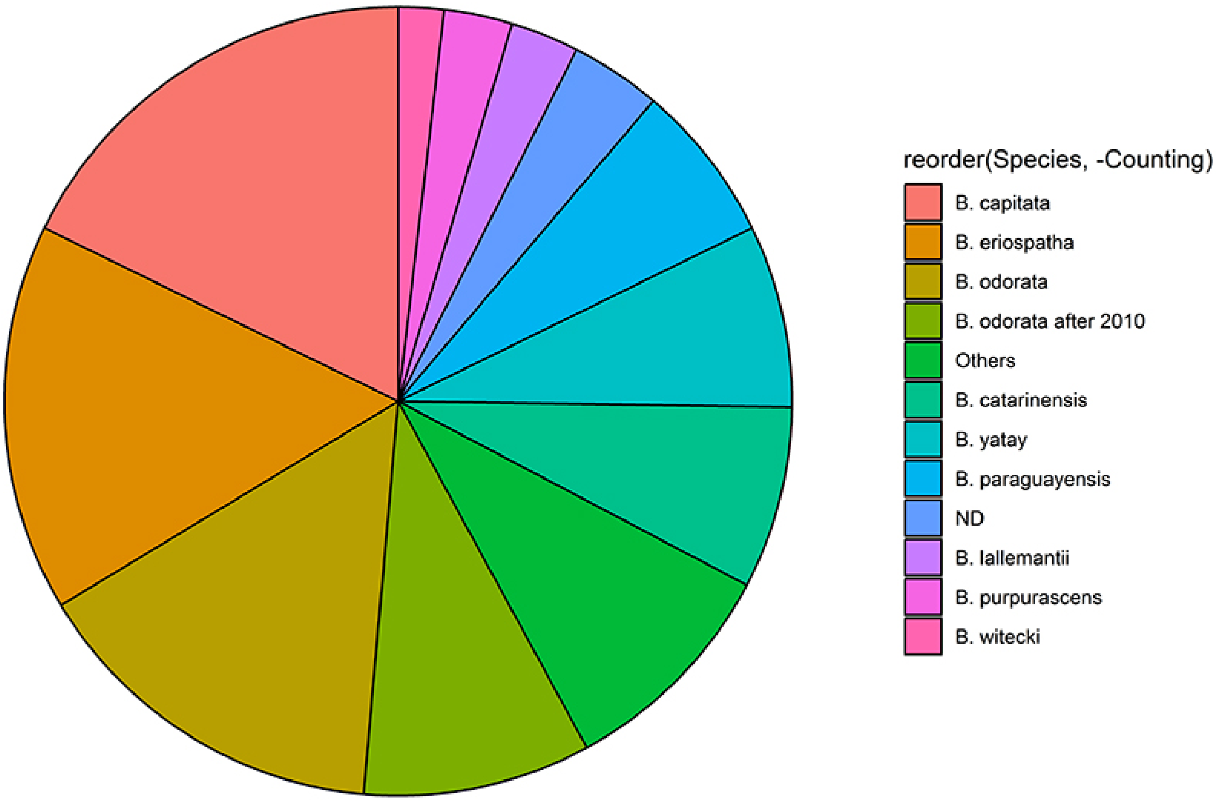

Figure 2 – Relative contribution of jelly palm species encompassed in our review. As per a change in taxonomical identification, 10 papers were indicated separately as they ID the studied species as *B. capitata*, but currently they should be identified as *B. odorata*.

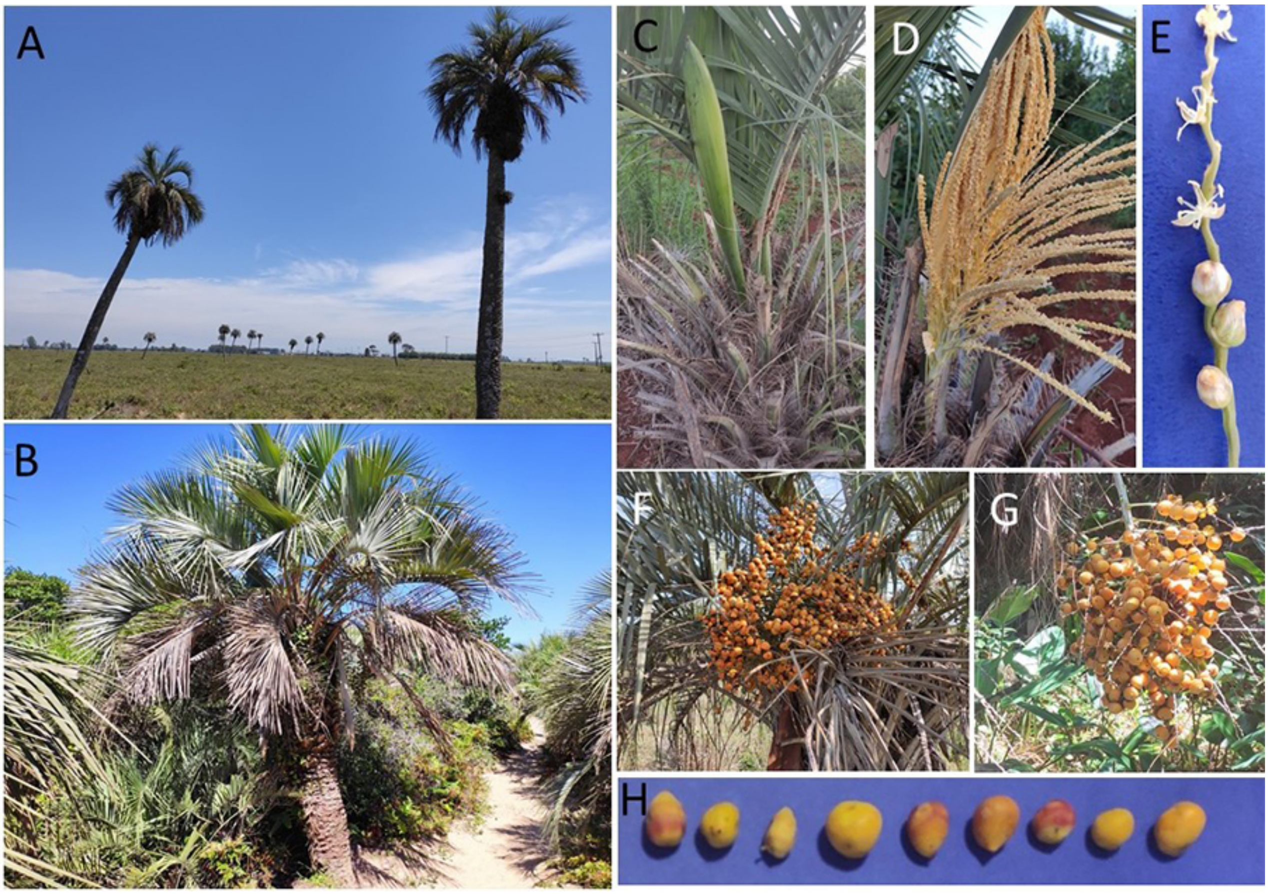

Figure 3 – Basic characteristics of *Butia odorata* and *B. catarinensis* a – *B. odorata* individuals *in situ.* b – *B. catarinensis* individual *in situ.* c – Spathe of an *B. odorata* individual. d – General aspect of an *B. odorata* inflorescence. e- Detail of opened male flowers (upper) and female flowers (bottom) in a raquile. f- Fruit bunch of *B. odorata*. g- Fruit bunch of *B. catarinensis*. h- Sample of size and color variation of *B. catarinensis* fruits.

B. catarinensis fruits are usually smaller and more elongated (Figure 3gh) (Soares *et al.*, 2014).

At the ultrastructural level, Sant'anna-Santos *et al.* (2015) compared the laminar anatomy between *B. capitata* and *B. odorata* and found some differences that they deemed useful for the distinction of the species. They observed that raphides were only found in *B. capitata* as well as small bundles of the midrib that fully surrounded the fibrous cylinder only in *B. odorata*.

In a posterior study, the leaf anatomy of 18 species of *Butia* were evaluated. *B. marmorii* and *B. matogrossensis* showed unique characters: *B. marmorii* presented peculiar leaf anatomy represented by three exclusive anatomical characters, while discontinuity points within the fibrous ring of the midrib were exclusive to *B. matogrossensis*. The presence of raphides in *B. catarinensis* were deemed useful to distinguish it from *B. odorata* and *B. eriospatha* (Sant'anna-Santos *et al.*, 2018). Pollen morphology and viability was studied in only one paper, which analyzed *B. odorata, B. eriospatha, B. yatay* and *B. paraguayensis*. Mourelle *et al.* (2016) concluded that all species produced monosulcate pollen grains with perforated exine, and pollen viability among species was shown not to be a limiting factor for the continuity of the species.

A new species called *B. witeckii*, from the central of Rio Grande do Sul state, was identified only by the analysis of biometric and anatomical differences in comparison with the species *B. yatay* and *B. paraguayensis* (Soares and Longhi, 2011). In the study of the leaf anatomy of the species *B. paraguayensis, B. eriospatha, B. yatay* and *B. odorata*, Noblick and Sant'anna-Santos (2021) observed considerable variation in the characteristics evaluated among the species and suggested the revision of characters that have been used in the taxonomical keys used for species differentiation.

Morphological traits have also been used as diagnostic tools for conservation. As local human populations use jelly palms leaves for making brooms in Brazilian Cerrado, leaf extraction may damage the structure and dynamics of jelly palms populations. In fact, leaf harvesting sites produced significantly fewer leaves, spurs, inflorescences and infructescence than preserved sites (Guilherme *et al.*, 2015). In fragmented populations of *B. purpurascens*, morphometric differences among populations were notorious for fruit length, width, and weight. The authors suggested the possibility of deleterious genetic effects by interrupting gene flow between populations in fragmented ecosystems (Rocha *et al.,* 2022).

By phenotyping morphological characteristics of distinct *Butia* species, studies have revealed the influence of environments and genotypes on fruit clusters composition and their productivity. After comparing fruit productivity between forest and grassland habitats for *B. eriospatha* populations, lower average production of infructescence and lower proportion of pulp per fruit was identified in the forest environment. The transformation of one population located in an Araucaria Forest to an open grassland environment may have shifted phenotypic variation related to fruit morphology and reproduction. Changes in fruit production, seedling survival and seed dispersal could have occurred, affecting the dynamics of the local population (Candido-Ribeiro *et al.,* 2019). In a population of *B. capitata* in the Cerrado biome, fruit productivity differed among the sites evaluated and was directly related to the weight of the individuals and their leaf mass (da Silva and Scariot, 2013). In evaluating three different populations of *B. capitata* in Santa Vitória do Palmar – Rio Grande do Sul, researchers also found variations in fruit morphology, ratio of total soluble solids to total acidity and yield (Schwartz *et al.*, 2010). *B. odorata* also differed concerning morphological and physicochemical aspects between populations from Santa Rosa and Santa Maria, southern Brazil (Ferrão *et al.*, 2013). The nutritional characteristics of soils also appear to have direct implications in fruit productivity. In a study by Schlindwein *et al.* (2017) with *B. odorata*, more fertile soils were associated with higher productivity.

In the evaluation of 11 genotypes of *B. capitata*, Nunes *et al.* (2010) were successful in differentiating in relation to size, weight, number of fruits, firmness, color, acidity, and total soluble solids. Different characteristics in *B. capitata* were also recognized for follicles, nuts, drupes, berries, capsules and pyrens (Bobrov and Romanov, 2019). In a study with *B. odorata*, simultaneous analyses of yield and bioactive compounds were performed, however the most productive genotype did not coincide with the richest in bioactive compounds. Thus, fruit yield and bioactive phytochemical content appeared to be inversely proportional (Beskow *et al.*, 2015).

In *B. odorata* individuals preserved *in situ*, different morphological characters were identified based on leaf arrangement on the plant, stem circumference, leaf color, rachilla color, number of clusters, ripe fruit color, fruit shape, presence of fiber in the pulp, fruit diameter, flowering and fruiting time (Mistura *et al.*, 2016). The authors evaluated which traits were also considered by local farmers for selecting desirable individuals, providing important highlights on which traits could be useful in conservation and breeding programs of *Butia* palms.

Physicochemical properties and nutrition

Although we separated morphological and physicochemical characteristics, both provide important traits that may be phenotyped for conservation and breeding endeavors with jelly palms.

Butia species have been frequently studied for their physicochemical profile and antioxidant capacity. Studies have shown that jelly palms are rich in phenolic compounds, carotenoids, anthocyanins, tocopherols, minerals, vitamins, amino acids, and fatty acids (Faria *et al.*, 2008b; Pierezana *et al.*, 2015; Kobelnik *et al.*, 2016; Barbosa *et al.*, 2021; Morais *et al.*, 2022; Wagner *et al.*, 2022). In *B. capitata*, the distinct stages of ripening and storage conditions influenced compounds such as acetic acid, (E)- and (Z)-hex-2-enal, methoxyphenyloxyme, (E)-β-ocimene, α-fenchene and octyl methyl ether (Aguiar *et al.*, 2014). High lipid concentration, beta-carotene, vitamin C and E, phenolics and copper were found in the pulp (Barbosa *et al.*, 2021). High oil content and dietary fiber were also discovered (Faria *et al.*, 2008a).

In *B. odorata*, 86 phenolic compounds were identified, with hydroxycinnamic acids and flavonols being the most common. After quantification by liquid chromatography, 4-hydroxybenzoic acid and catechin were identified as prevalent (Ma *et al.*, 2019). The main volatile compound responsible for the fruit aroma was described as ethyl hexanoate (Bernardi *et al.*, 2014). Sinapic and ellagic acid, trans-reveratrol, naringenin and apigenin were reported for the first time (Boeing *et al.*, 2020). The fruits of *B. odorata* showed a rich composition in fiber, vitamin C, total carotenoids, and total phenolic content (Wagner *et al.*, 2022).

In *B. catarinensis* and *B. eriospatha*, high values of soluble solids were found, compared to other native fruits. High fiber values were also found, especially of the insoluble type (Rockett *et al.*, 2020a). In another study with the same species, the authors performed *in vitro* assays and found 18 phenolic compounds in *B. catarinensis* and 28 in *B. eriospatha*. The main groups of phenolic compounds were hydroxybenzoic acids and flavonoid oils (Rockett *et al.*, 2020b). For the species *B. eriospatha*, higher ascorbic acid content and high antioxidant capacity for the peroxyl radical were denoted (Denardin *et al.*, 2015). High carotenoid content, compared to other fruits, total flavonoid and phenolic content were also observed (Egea and Pereira-Netto, 2019). *B. witecki* and *B. lallemantii* seeds showed the presence of 25% fatty acids, high content of the phenolic compounds ferulic acid, luteolin, quercetin-3-rutinoside, isoquercetin and isorhamnetin (Rodrigues *et al.*, 2022).

Other studies have evaluated the composition of the oil present in *B. capitata*, as well as the characterization of the lipid content and fatty acid profile (Pierezana *et al.*, 2015; Kobelnik *et al.*, 2016). Kobelnik *et al.* (2016) demonstrated a predominance of saturated fatty acids at about 80% through chromatographic profiling. Oleic, palmitic and linolenic acids were also predominant, as well as unsaturated fatty acids. The main ester components from the transesterification of jelly palm oil were lauric acid (42.2%), capric acid (15.9%) and caprylic acid (14.6%) methyl and ethyl esters (Pierezana *et al.*, 2015; Teixeira *et al.*, 2022). Isolation of triterpene methyl ethers from epicuticular waxes demonstrated a large amount of ethers, including extensive alkanol and triterpene methyl ether fraction (García *et al.*, 1995). Regarding phenolic composition, variability was found in fruits after comparing genotypes of *B. catarinensis, B. odorata, B. paraguayensis* and *B. yatay* (Hoffmann *et al.*, 2017).

In a sensory evaluation of ripe fruit of *B. capitata*, yellow-orange, juicy, fibrous and soft appearance were denoted. The pulp of mature fruits showed carbohydrates, lipids, proteins, carotenoids and pronounced juice acidity. Pulp senescence was related to decreased acidity, increased soluble solids, reduced firmness, nutrient levels, and increased phenolic accumulation (Ventura *et al.*, 2022). Caproic acid methyl esters have indicated a link with fruit aroma perception (Lopes *et al.*, 2012). As a feedstock for the synthesis of fatty acid methyl esters, the seed oil from the fruit of *B. capitata* and *B. Yatay* has been shown to be a suitable feedstock for biofuel, in accordance with the requirements of Brazilian, American and European agencies, with typical characteristics for use with fossil fuels and application in diesel engines (Zanuttini *et al.*, 2014; Vieira *et al.*, 2016).

Studies have demonstrated antioxidant, anti-inflammatory and antimicrobial activity in *Butia*. The antioxidant potential seems to be related to the high concentration of carotenoids, being zeaxanthin the majority compound (Pereira *et al.*, 2013; Otero *et al.*, 2020; Teixeira *et al.*, 2022). In *B. catarinensis*, Cruz *et al.* (2017) obtained extracts with strong antioxidant performance and bactericidal inhibition, mainly for Gram – negative bacteria. The main compounds identified were cinnamic and caprylic acid. The antioxidant potential in *B. eriospatha* was tested using the *Caenorhabditis elegans* animal model. Tambara *et al.* (2020) observed that extracts of *Butia* palm were able to prolong nematode (*C. elegans*) life cycle by protecting and reversing hydrogen peroxide-induced oxidative damage. *B. capitata* species, on the other hand, demonstrated functionality as an inhibitor of colorectal cancer cells (HT-29) in an *in vitro* antitumor activity analysis (Lahlou *et al.*, 2022). *B. odorata* also demonstrated antitumor activity, this time on cervical cancer cell lines (SiHa and C33a) (Boeing *et al.*, 2020). In the study by Vinholes *et al.* (2017), the fruits of *B. odorata* were shown to be promising sources for alpha-glucosidase inhibition and antioxidants and could be used to control blood glucose in patients with type 2 Diabetes mellitus.

Industrial processing of jelly palms fruits, with subsequent pasteurization and freezing proved to degrade carotenoids and vitamin C. The bagasse, on the other hand, showed relative richness in total phenols and carotene. In terms of industrialization, juice pasteurization seems inadequate in the nutritional aspect, whereas the extraction of carotenoids and phenolic compounds proved relevant (Jachna *et al.*, 2016). In a similar study, bioactive compounds and antioxidant capacity of commercial frozen pulp and fruits *of B. capitata* were compared. A large amount of vitamin C, quercetin and kaempferol derivatives were found as the main flavonoids present in the fruits. On the other hand, the frozen commercial pulps showed lower contents of bioactive compounds and antioxidant capacity compared to the fresh fruit (Genovese *et al.*, 2008).

Population genetics and cytogenetics

Up to date, few molecular genetic studies with *Butia* species have been published. In a cytogenetic approach, the chromosomal characteristics of *Butia* species were investigated by Corrêa *et al.* (2009). All species (*B. capitata, B. eriospatha, B. odorata, B. paraguayensis* and *B. yatay*) had the same number of chromosomes (2n = 32). The species also have the same karyotypic formula: 14 metacentric, 12 submetacentric and 6 acrocentric chromosomes.

Population genetic studies are available, but very limited to the end of the years 2000 and the 2010s, using RAPD, AFLP, ISSR and SSR markers. Using ISSR markers, Gaiero *et al.* (2011) investigated the variability among four species – *B. paraguayensis, B. lallemantii, B. yatay* and *B. eriospatha*, and found high variability within populations of *B. paraguayensis*, *B. lallemantii* and *B. yatay*, possibly due to gene flow, past hybridization or life history traits.

Using RAPD markers, Nunes *et al.* (2008) detected considerable genetic variability among 22 genotypes of *B. odorata* (the name was updated from the original paper, considering the reclassification proposed by Noblick, 2010). Using AFLP markers, Buttow *et al.* (2010) performed a molecular analysis of variance in eight populations of *B. odorata* (species name updated) and found that 83.68% of the genetic variability was attributed to variation within populations and 13.67% to differences between populations within the regions investigated. The results suggest that the populations have a common origin and may have undergone selection, drift, geographic isolation and mutations that caused the differences between them, structuring them into subpopulations (Buttow *et al.*, 2010).

Using 14 newly developed SSR markers, Nazareno, Reis and collaborators studied the variability in *B. eriospatha*. They validated the use of SSR as an important marker for studying population genetics and evolution (Nazareno and dos Reis, 2011; Nazareno *et al.*, 2011). In another study, combining SSR data with reproductive biology data, they concluded that *B. eriospatha* was predominantly outcrossing, with a certain degree of biparental inbreeding. Self-compatibility and geitonogamy seemed to be present in isolated populations (Nazareno and dos Reis, 2012). By using nine microsatellite loci in four populations of *B. eriospatha* from Southern Brazil, high levels of genetic differentiation were found. The amount of observed heterozygosity differed significantly between small and large populations, indicating that small populations are more susceptible to genetic drift (Nazareno and dos Reis, 2013). In a comparison of the genetic diversity between wild and urban *B. eriospatha* populations, authors found greater variation in the urban species. The expected heterozygosity within wild populations was lower (H_E = 0.48) than in an urban population (H_E = 0.62) (Nazareno and dos Reis, 2014).

The SSR markers developed by Nazareno *et al.* (2011) were also transferable to *B. catarinensis*, with 86% of the markers successfully amplified. Moreover, the results indicated that there is a high potential for transfer of SSR markers between species of the same genus in the Arecaceae family. As for genome sequencing, we identified only one paper that characterized the plastidial genome of *B. eriospatha*. The complete sequence was 154,048 bp in length, with the typical quadripartite structure, consistent with other six species from tribe Cocoseae (Magnabosco *et al.*, 2020).

Butia nucleotide sequences

After searching GenBank for sequences available, at least one sequence has been registered for *B. capitata*, *B. eriopatha*, *B. paraguayensis*, *B. yatay*, *B. marmorii*, *B. lallemantii* and *B. odorata* (registered as *B. capitata* var *odorata*). Moreover, a few sequences were registered as *B.* aff *yatay* and *B.* aff. *paraguayensis*, probably due to difficulties in determining their classification. We also found sequenced registered at the genus level only, as *Butia* sp. (Table 1). Of the 37 genes located, 22 were plastidial and 15 were nuclear. Most of the genes were useful for phylogenetic inferences and cladistic studies (e.g. *phytochrome B (PHYB); trnQ-rps16 intergenic spacer; trnD-trnT intergenic spacer; ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit; NADH dehydrogenase subunit F (ndhF)*), and for population genetics and evolution (e.g. microsatellite *but10*).

Table 1 – GenBank sequences for *Butia* species (based on the search https://www.ncbi.nlm.nih.gov/popset/?term=butia) as of 29 April 2023. The accession numbers for all sequences are presented.

Gene	Species and accession numbers for sequences									
	B. capitata	*B. eriospatha*	*Butia sp.*	*B. paraguayensis*	*B. yatay*	*B. marmorii*	*B. lallemantii*	*B. capitata var. odorata*	*B. aff. yatay*	*B. aff. paraguayensis*
acetyl-CoA carboxylase beta subunit (accD) gene	MG437906.1									
ATP synthase beta subunit (atpB) gene	JX903942.1	AY044469.1								
chloroplast trnD gene, trnY and trnE genes and trnE-trnT intergenic spacer region		AY044516.1								
maturase K (matK) gene	MH551819.1									
	EU004870.1									
	JX903668.1									
microsatellite but10 sequence*		JF748782.1								
NADH dehydrogenase subunit F (ndhF) gene	EU004887.1	AY044565.1								
	MG647202.1									
	JX903522.1									
phosphoribulokinase-like protein (PRK) gene		JQ821972.1								
phosphoribulokinase-like protein 2 (PRK) gene	AY601252.1									
	AY601251.1	AY601254.1								
		AY601253.1								
photosystem II protein D1 (psbA) and psbA-trnH intergenic spacer	OL312423.1									
photosystem II protein D1 (psbA), psbA-trnH intergenic spacer and tRNA-His (trnH) gene	OK469471.1									
phytochrome B (PHYB) gene		JQ822073.1		MK102235.1						
ribosomal protein S16 (rps16) gene	MG647461.1									
ribulose-1,5-bisphosphate carboxylase/ oxygenase large subunit (rbcL) gene	KY627008.1	AY044632.1	MK753383.1							

Table 1 – Cont.

Gene	Species and accession numbers for sequences									
	B. capitata	*B. eriospatha*	*Butia sp.*	*B. paraguayensis*	*B. yatay*	*B. marmorii*	*B. lallemantii*	*B. capitata var. odorata*	*B. aff. yatay*	*B. aff. paraguayensis*
	MG437645.1	MK753958.1	MK753382.1							
	JX903252.1	MK753956.1	MK753381.1							
	MK753957.1		MK753380.1							
	MK753955.1		MK753379.1							
	MK753954.1		MK753378.1							
			MK753377.1							
			MK753376.1							
			MK753375.1							
RNA polymerase subunit C1 (rpoc1) gene	MG438159.1									
rps16 gene	EU004908.1									
serine/threonine protein kinase (CISP4) gene				MK102259.1						
serine/threonine protein kinase RLCKVII (CISP4) gene		JQ822034.1								
tRNA-Leu (trnL) gene, trnL-trnF intergenic spacer and tRNA-Phe (trnF) gene	EU004864.1									
trnD-trnT intergenic spacer				MK102099.1						
trnK gene and maturase K (matK) gene	MK704816.1	MK704817.1	MK704787.1							
	MK704814.1	MK704815.1	MK704784.1							
	MK704813.1		MK704783.1							
			MK704782.1							
			MK704781.1							
			MK704780.1							
			MK704779.1							
			MK704778.1							

Table 1 – Cont.

Gene	Species and accession numbers for sequences									
	B. capitata	*B. eriospatha*	*Butia sp.*	*B. paraguayensis*	*B. yatay*	*B. marmorii*	*B. lallemantii*	*B. capitata var. odorata*	*B. aff. yatay*	*B. aff. paraguayensis*
			MK704777.1							
trnQ-rps16 intergenic spacer		EF605537.1								
trnQ(UUG)-rps16 intergenic spacer and ribosomal protein S16 gene		AY044612.1								
WRKY transcription factor 2 (WRKY2) gene	FJ956951.1	FJ956954.1		FJ956956.1	FJ956958.1	FJ956955.1	FJ956957.1	FJ956953.1	FJ956950.1	
								FJ956952.1		
WRKY transcription factor 6 (WRKY6) gene	FJ957096.1	FJ957099.1		FJ957102.1	FJ957103.1	FJ957101.1	FJ957100.1	FJ957098.1	FJ957095.1	FJ957094.1
								FJ957097.1		
WRKY transcription factor 7 (WRKY7) gene	FJ957170.1	FJ957173.1		FJ957176.1	FJ957177.1	FJ957175.1	FJ957174.1	FJ957172.1	FJ957169.1	FJ957168.1
								FJ957171.1		
WRKY transcription factor 12 (WRKY12) gene	FJ957242.1	FJ957245.1		FJ957248.1	FJ957249.1	FJ957247.1	FJ957246.1	FJ957244.1	FJ957241.1	FJ957240.1
WRKY transcription factor 16 (WRKY16) gene	FJ957310.1	FJ957313.1		FJ957316.1	FJ957317.1	FJ957315.1	FJ957314.1	FJ957312.1	FJ957309.1	FJ957308.1
								FJ957311.1		
WRKY transcription factor 19 (WRKY19) gene	FJ957381.1	FJ957384.1		FJ957387.1	FJ957388.1	FJ957386.1	FJ957385.1	FJ957383.1	FJ957380.1	FJ957379.1
								FJ957382.1		
WRKY transcription factor 21 (WRKY21) gene	FJ957023.1	FJ957026.1		FJ957028.1	FJ957029.1		FJ957027.1	FJ957025.1	FJ957022.1	FJ957021.1
								FJ957024.1		

*This is the reference sequence for the microsatellite. Other sequences with their polymorphisms are available from NCBI.

In general, phylogenetic studies were not devoted to clarifying differences specifically for genus *Butia*, but rather to comprehend the relationships among palms in general. Two of the most important molecular phylogenetic studies used *WRKY* genes (Table 1), transcription factors involved in abiotic stresses. The comparison of sequences of a few paralogs among *Butia* species indicate that the genus constitutes a monophyletic group (Meerow *et al.*, 2009; Meerow *et al.*, 2015).

Discussion

This review provided a panorama of the phenotypic and genetic diversity studied so far for jelly palms. As per the bibliometric analysis, limited to our categorization, most studies were dedicated to physicochemical properties and nutrition facts of *Butia* species. A wide phenotypic variation for *Butia* palms, as revealed from the characterization of fruits with very different biometric, physicochemical and sensory properties is available from the literature. The indication of important traits that should be considered in the characterization of jelly palms (Mistura *et al.*, 2016), as well as the vulnerability of each species (Eslabão *et al.*, 2016), provide foundations for establishing conservation and breeding programs for these unique species.

With regards to species delimitation, the literature available is pretty much based on morphological traits, whether they can be screened from a naked eye or evaluated from ultrastructural profiles (anatomical analyses). By searching GBIF, the number of registered species is higher that what we found on Web of Science. The database provided records for 27 distinct species, that can be explained mainly by older publications and registered observations that can be found on the database, as well as hybrid taxa. In fact, there are substantial morphological differences among species, such as *B. odorata* and *B. capitata*. However, at the molecular level, a few phylogenetic markers provided nuanced differences among the proposed species, but not enough to actually prove them to be distinct at the nucleotide level. The debate on whether they are distinct species could go to the biological concept, stated by Mayr, that defines species as a group of potential interbreeding populations that are reproductively isolated from other groups. That stated, it is necessary to further explore whether the taxonomic delimitations based on morphological characters are consistent with molecular analyses. Moreover, there are reports of hybrids between *Butia* and *Syagrus* species (Engels *et al.*, 2021; Silveira *et al.*, 2022).

As for traits related to chemical compounds and nutritional facts, *Butia* species demonstrate to be great sources of bioactive compounds and antioxidants, with potential as functional food for the treatment of cancer cells and glycemic control in patients with diabetes (Vinholes *et al.*, 2017; Boeing *et al.*, 2020, Lahlou *et al.*, 2022). In this regard, further studies are needed to investigate the antitumor potential in different cancer cells, expanding the evidence so far demonstrated in *in vitro* studies.

The phenolic composition varied among the *Butia* species evaluated (Hoffmann *et al.*, 2018; Rockett *et al.*, 2020a; Rodrigues *et al.*, 2022) but in all, fruits have proved to hold excellent functional, nutritional, antioxidant, antimicrobial and antitumor properties. The broad functional potential for the cosmetic, pharmaceutical, industrial and food industries demonstrated in the reviewed studies, makes *Butia* a certainly rich product and still little or poorly explored.

The molecular genetic studies so far developed have proven to be scarce and with important gaps. Usually, studies are limited to a few populations. Broader analyses and using single nucleotide polymorphisms (SNP) should be the goal of novel endeavors toward unraveling more specific as well as a broader context of range of distribution of jelly palms, so that a detailed panorama of their genetic conservation status might be described. Whole genome sequences of *Butia* taxa also need to be obtained, considering that only a few short sequences are available for conserved phylogenetic markers, as revealed by our search on NCBI.

Another line of studies that has been increasingly employed among plant species is epigenetics or epigenomics. Since epigenetics deals with changes in gene expression due to modifications of DNA that do not alter the nucleotide sequence, such as DNA methylation, histone acetylation and other mechanisms, the environment is an important component to affect cellular mechanisms beyond genetic determination. As per our review, jelly palms have a broad phenotypic variation and populations are usually separated by considerable distances and in distinct climates and soils. Therefore, we believe that not only genetic adaptive mechanisms, such as Candido-Ribeiro *et al.* (2019) reported, but also epigenetic(epigenomic) processes are adaptive among the distinct populations.

The prominent morphological differences among jelly palms led taxonomists to distinguish more than 20 species to this date. In fact, the differences are remarkable when we compare *Butia* taxa. At the genomic level, we have little information available for conducting phylogenomic analyses to further determine the levels of differentiation among the taxa. Either ways or both ways together, we need rapid and increasing studies toward conservation of jelly palms. Population viability analyses should be conducted coupling genomic resources as well as an in-depth characterization of the phenotypic variation available, as the literature showed that individuals of several populations are frequently old and no regeneration is occurring. This will ultimately lead to much more damage that could be repaired, so urgent measures need to be pursued for conservation of the genetic resources of these important and unique habitats that butiás compose, the palm groves.

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Conflict of Interest

The authors declare that they have no conflicts of interest.

Author Contributions

CFC and ERK conceived the main ideas for the review; ACTZ, MMB e MIZ contributed with literature review and the methodology applied for analyses. All authors have contributed for the written manuscript. All authors read and approved the final version.

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Supplementary material

The following online material is available for this article:

Table S1 – Journals, number of papers involving *Butia* species in the subjects addressed in this review and impact factors (2021) at the time they were searched.

Table S2 – List of papers selected: category, *Butia* species and main findings.

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Genetics and Molecular Biology
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Supplementary Material to "Phenotypic and molecular basis for genetic variation in jelly palms (*Butia* sp.): where are we now and where are we headed to?"

Table S1 - Journals, number of papers involving *Butia* species in the subjects addressed in this review and impact factors (2021) at the time they were searched.

Journal	Nº	Impact Factor
Revista Brasileira de Fruticultura	8	1,1
Food Research International	4	7,4
Food Bioscience	3	5,3
Food Analytical Methods	2	3,4
Ciência Rural	2	0,9
American Journal of Botany	2	3,3
Biota Neotropica	2	1,4
Journal of Heredity	2	2,6
Brazilian Journal of Biology	2	1,6
Food Science and Technology	2	2,6
Journal of Food Biochemistry	1	3,6
Conservation Genetics	1	3,0
Journal of Supercritical Fluids	1	4,5
Energy Conversion and Management	1	11,5
Acta Botânica Brasilica	1	1,3
Botany Letters	1	1,5
Journal of Food Processing and Preservation	1	2,6
Aob Plants	1	3,1
Journal of Thermal Analysis and Calorimetry	1	4,7
Food Chemistry	1	9,2
Semina-Ciências Agrárias	1	0,5
Ciência Florestal	1	0,6
Acta Oecologica - International Journal of Ecology	1	1,9
Nutrients	1	6,7
Journal of Food Composition and Analysis	1	4,5
Pakistan Journal of Botany	1	1,1
Antioxidants	1	7,6
Phytochemistry	1	4,0
Journal of the Science of Food and Agriculture	1	4,1
Phytotherapy Research	1	6,3
Molecules	1	4,9
Plant Systematics and Evolution	1	1,6
Revista Chilena de Nutricion	1	0,1

Journal	Nº	Impact Factor
Palynology	1	1,9
Food Science and Technology International	1	2,6
Phytokeys	1	1,3
Food Science and Technology Research	1	0,7
Plant Genetic Resources - Characterization and Utilization	1	1,2
Fruits	1	0,5
Allelopathy Journal	1	0,9
Química Nova	1	1,1
Fuel	1	8,0
Scientia Horticulturae	1	4,3
Genetics and Molecular Biology	1	2,0
Anais da Academia Brasileira de Ciências	1	1,8
Interciencia	1	0,3
European Food Research and Technology	1	3,4
Journal of Agricultural and Food Chemistry	1	5,8
Journal of Food and Drug Analysis	1	6,1

Genetics and Molecular Biology
https://doi.org/10.1590/1678-4685-GMB-2023-0145

Supplementary Material to "Phenotypic and molecular basis for genetic variation in jelly palms (*Butia* sp.): where are we now and where are we headed to?"

Table S2 – List of papers selected: category, *Butia* species and main findings.

Category	Authors	Journal	Butia Species	Findings
Physicochemical properties and nutrition	Aguiar *et al*. (2014)	Food Research International	*B. capitata*	Volatile compounds were influenced by stages of its maturation and storage times. Ethyl hexanoate is indicated to be involved with the aroma of fruits over their maturation.
	Barbosa *et al*. (2021)	Food Science and Technology	*B. capitata*	Pulp yield was considerably high (68.59%). Pulp has high lipid content and total energy. Pulp contains beta-carotene, vitamin E, and high concentrations of vitamin C, phenolics and copper. The pulp is a source of carotenoids, vitamin C, copper and total phenolics, both natural antioxidants.
	Barcia *et al*. (2010)	Semina Ciências Agrárias	*B. capitata*	Fruits are good sources of bioactive compounds. All fruits showed concentrations of L-dehydroascorbic acid higher than L-ascorbic acid.
	Bernardi *et al*. (2014)	Food Analytical Methods	*B. odorata*	The principal volatile compounds identified as responsible for the characteristic aroma of jelly palm are ethyl hexanoate (positively) and hexanoic acid (negatively).
	Boeing *et al*. (2020)	Food Analytical Methods	*B. odorata*	Sinapic and ellagic acids, trans-resveratrol, naringenin, and apigenin were reported in *B. odarata* fruits for the first time. *B. odorata* fruits showed antitumor activity against cervical cancer cell lines (SiHa and C33a).
	Cruz *et al*. (2017)	Journal of Supercritical Fluids	*B. catarinensis*	The extracts presented antioxidant performance and were considered strong bacterial inhibitors. The main compounds were cinnamic acid and caprylic acid. In general, extracts were more effective against Gram-negative bacteria.

Category	Authors	Journal	Butia Species	Findings
	Denardin *et al*. (2015)	Journal of Food and Drug Analysis	*B. eriospatha*	*Butia* had the highest content of ascorbic acid, although its antioxidant activity in the DPPH and FRAP assays were the lowest. In the TRAP assay, purple-fleshed pitanga, cherokee blackberry, and butiá showed the highest capacity to scavenge the peroxyl radical.
	do Vale *et al*. (2021)	Biota Neotropica	*B. capitata*	After analyzing yeast species in native trees from Cerrado, the fruits of *B. capitata* presented the highest species richness. *Candida* and *Meyerozyma* were the most frequent genera.
	Egea and Pereira-Netto (2019)	Europeand Food Research and Technology	*B. eriospatha*	Total carotenoid content was significantly higher in jelly palm fruits. Total flavonoid content was significantly higher.
	Faria *et al*. (2008a)	Revista Brasileira de Fruticultura	*B. capitata*	*Butia* pulp presented high content of oil, dietetic fiber, pro-vitamin, vitamin C, phenolic compounds and potassium. *Butia* shows high potential for food enrichment in a local community. Results showed the high value of products supplied by small farmers, presenting the cultural importance of *B. capitata*.
	Faria *et al*. (2008b)	Revista Brasileira de Fruticultura	*B. capitata*	*Butia* nut presented 9,9% of moisture, 57,8% of total lipid, 25,8% of neutral detergent fiber, 17,6% of acid detergent fiber and 1,6% of ash. The fat from *Butia* nut presented high content of lauric acid (42,1%), followed by oleic acid (16,9%). The saturated fatty acids predominated (78,9%), mainly the medium chain length fatty acids (58,3%).
	Faria *et al*. (2011)	Revista Brasileira de Fruticultura	*B. capitata*	Results suggested that *B. capitata* pulp may be a good source of β-carotene and provitamin A.
	Ferrão et al. (2017)	Food Science and Technology Research	*B. odorata*	The water activity of the dried pulp ranged from 0.43 to 0.51. The best results were obtained using MW at 60°C, because this presented no significant sensory differences and required a shorter drying time than MW at 50°C.
	García *et al*. (1995)	Phytochemistry	*B. capitata*	*B. capitata* contain large amounts of ethers. In *Butia* species, the alkanol plus triterpene methyl ether fractions represent 60-80%.
	Genovese *et al*. (2008)	Food Science and Technology International	*B. capitata*	*B. capitata* showed a significant vitamin C content. Quercetin and kaempferol derivatives were the main flavonoids present in all samples. All commercial frozen pulps presented lower contents of bioactive compounds and antioxidant capacity than their respective fruits.
	Hoffmann *et al*. (2017)	Journal of Agricultural and Food Chemistry	*B. catarinensis, B. odorata, B. paraguayensis* and *B. yatay*	Liquid chromatography–mass spectrometry based metabolic profiling coupled with chemometric analysis can be used to discriminate among *Butia* species and between geographical origins of *B. odorata* and to identify primary and specialized metabolites responsible for their discrimination.

Category	Authors	Journal	Butia Species	Findings
	Hoffmann *et al*. (2018)	Fruits	*B. catarinensis, B. odorata, B. paraguayensis and B. yatay*	The phenolic composition varied among four species evaluated and was dependent on the collection site for *B. odorata*. The abundant phenolics make butia fruit an excellent source of natural antioxidants for food and pharmaceutical applications.
	Jachna *et al*. (2016)	Journal of the Science of Food and Agriculture	*B. capitata*	The evaluation of *Butia* pomace showed that it is relatively rich in total phenols and in-carotene. From the nutrition viewpoint, pasteurized juice does not seem adequate. On the other hand, extraction of carotenoids and phenolic compounds from the pomace appears to be a relevant process.
	Kobelnik *et al*. (2016)	Journal of Thermal Analysis and Calorimetry	*B. capitata*	A chromatographic profile of *B. capitata* oil revealed a predominance of saturated fatty acids. The results of gas chromatographic analysis showed that this oil has a high amount of saturated fatty acids, which corresponds to around 80%.
	Lahlou *et al*. (2022)	Food Bioscience	*B. capitata*	*B. capitata* contains high amounts of medium-chain saturated fatty acids, a good source of lauric acid. The methanol:water extracts of fruits induced dose-and time-dependent inhibitory effects on HT-29 cancer cells. Overall, the fruits of Arecaceae taxa evaluated constitute suitable candidates to be used as functional foods.
	Lopes *et al*. (2012)	Revista Brasileira de Fruticultura	*B. capitata*	Oleic and palmitic acids predominated in *B. capitata* and other species; all presented prevalence of unsaturated fatty acids.
	Ma *et al*. (2019)	Antioxidants	*B. odorata*	This study indicated that *B. odorata* fruits are a good source of polyphenols and has strong antioxidant potential for health promotion.
	Magalhães *et al*. (2012)	Allelopathy Journal	*B. capitata*	Methanol extracts of endosperm and endocarp did not affect germination, germination speed, fresh and dry weights of radicle and hypocotyl, but decreased the hypocotyl and radicle lengths. The principal allelopathic substances identified were: esters methyl (Z)-octadec-9-enoate, methylhexadecanoate and lauric, myristic, oleic, palmitic and linoleic acid.
	Morais *et al*. (2022)	Nutrients	Na	Arecaceae palm tree fruits have high nutritional value and are rich in bioactive compounds. Fruits also have potential for uses in food, pharmaceutical, biotechnology, and cosmetic industries.
	Otero *et al*. (2020)	Revista Chilena de Nutrición	*B. capitata*	*Butia* had a high concentration of carotenoids. *Butia* and the pupunha were those that presented the highest content of carotenoids. Among the fruits analyzed, those with the highest potential antioxidants were guava, java plum and butia.

Category	Authors	Journal	Butia Species	Findings
	Paroul *et al.* (2009)	Brazilian Journal of Biology	*Butia* sp.	The comparison of the means for the total crude wax yields showed significant differences among *Butia* and *Syagrus* samples.
	Pereira *et al.* (2013)	Journal of Food Composition and Analysis	*B. capitata*	*Butia* palm fruit showed elevated carotenoid content and greater antioxidant capacity. By the DPPH (2,2-dipheny1-1-picrylhydrazyl) method, *Butia* palm fruit and mandacaru-de-tres-quinas fruit were considered to have the same antioxidant potential with no difference between them.
	Pierezana *et al.* (2015)	Quimica Nova	*B. capitata*	Lauric acid (42.2%), capric acid (15.9%) and caprylic acid (14.6%) methyl and ethyl esters were the main ester components of transesterification of the oil from *B. capitata*.
	Rockett et al. (2020a)	Food Research International	*B. catarinensis and B. eriospatha*	Phenolic compounds were identified in *B. catarinensis*, *B. eriospatha* and *Arumbeva*. The main groups of phenolic compounds found in the fruits were hydroxybenzoic acids, flavan-3-ols and flavonols. In hydroethanolic extracts of *B. catarinensis* and *Arumbeva*, the total phenolic content increased by around 67% and 35%, respectively.
	Rockett *et al.* (2020b)	Journal of Food Processing and Preservation	*B. catarinensis and B. eriospatha*	The value obtained for soluble solids of *B. catarinensis* was higher. *B. eriospatha* exhibited the highest and lowest values for magnesium. In general, the fruits evaluated presented high moisture content, low lipid content, and a good amount of fiber.
	Rockett *et al.* (2021)	Food Bioscience	*B. catarinensis*	The use of packing was able to increase softness, maintain carotenoid levels, the antioxidant capacity of the fruit, and suffer less significant ascorbic acid losses. The use of packages combined with cooling (5 degrees C) was sufficient to prolong the shelf life for up to 25 days.
	Rodrigues *et al.* (2022)	Food Research International	*B. catarinensis, B. lallemantii, B. odorata, B. witecki*	25% of the fatty acids in the seeds of *B. lallemantii*, *B. odorata*, *B. witeckii*, and *Syagrus romanzoffiana* were found to be unsaturated. A high content of the phenolic compounds ferulic acid, luteolin, quercetin-3-rutinoside, isoquercetin, and isorhamnetin were found in *B. odorata*, *B. catarinensis*, and *B. witeckii*.
	Schneider *et al.* (2017)	Phytotherapy Research	Na	*Butia* showed some antioxidant, anti-inflammatory, and antimicrobial activity. Clinical studies must be conducted to confirm the effectiveness of *Butia* sp.
	Tambara *et al.* (2020)	Journal of Food Biochemistry	*B. eriospatha*	*Butia* extract increased *C. elegans* lifespan under stress. The *Butia* is able to extend the lifespan of the nematode *C. elegans* and this effect may be mediated by an induced resistance to oxidative stress.

Category	Authors	Journal	Butia Species	Findings
	Teixeira *et al.* (2022)	Molecules	Na	Myristic, caprylic, capric, and lauric acids are the main saturated fatty acids, while oleic acid is the main unsaturated. Carotenoids and phenolic compounds are the main bioactive compounds, contributing to high oxidative stability.
	Ventura *et al.* (2022)	Scientia Horticulturae	*B. capitata*	The fruits had a yellow-orange, succulent, fibrous, and soft aspect, with reduced phenolic contents in the vacuoles and high levels of soluble solids. Pulp senescence is related to a decline in acidity, reduction in firmness, in nutrient levels, and increased phenolic accumulations.
	Vieira *et al.* (2016)	Fuel	*B. capitata*	*B. capitata* proved to be suitable starting material for biofuel according to the requirements of Brazilian, American and European agencies and has the typical characteristics for use with fossil fuel and the possibility of application in diesel-based engines without drastic performance changes.
	Vinholes *et al.* (2017)	Food Bioscience	*B. odorata*	All fruits were rich in total phenolic compounds; jelly palms were the richest ones in non-reducing sugars. Native fruits are promising sources of alpha-glucosidase inhibitors and antioxidants that can be used to control glycemia in patients with type 2 Diabetes mellitus.
	Zanuttini *et al.* (2014)	Energy Conversion and Management	*B. yatay*	*B. Yatay* coconut oil had acid values between 109 and 140 mg KOH/g, and phosphorus content in the order of 600 ppm. The kinetic constant for the esterification reaction rapidly decreased as a function of time, due to the consumption of the catalyst by the alkyl-sulphate formation reaction.
	Wagner *et al.* (2022)	Food Science and Technology	*B. odorata*	Fruits showed a rich composition in fibers, vitamin C, total carotenoids, and total phenolic content, which contribute to health maintenance. *Butia* fruits represent a potential product for nutritional enrichment in diets.
Plant morphology	Bobrov and Romanov (2019)	Botany Letters	*B. capitata*	Twenty-seven morphogenetic fruit types are recognized in the research and their probable modes of transformations are described based on original data and earlier studies.
	Candido-Ribeiro *et al.* (2019)	Acta Oecologica - International Journal of Ecology	*B. eriospatha*	Greater variation was observed within the forest population. The grassland population showed a greater proportion of pulp per fruit, but smaller seeds, which may suggest plasticity, local adaptation, or both. The average production of infructescence per individual is lower in the forest environment.
	da Silva and Scariot. (2013)	Acta Botanica Brasilica	*B. capitata*	Fruit biometric variables differ between the populations of *B. capitata* in Cerrado. The productivity of fruits also differs between study sites sampled and is related to the height of individuals and to their foliar biomass.
	de Moura *et al.* (2010)	Biota Neotropica	*B. capitata*	The fruit pulp represents approximately 80% of the fruit. The mass and diameter of the fruit showed significant and positive correlations, suggesting that fruits of bigger size and mass have heavier pulp and pyrene and more seeds per fruit.
	Guilherme *et al.* (2015)	Brazilian Journal of Biology	*B. purpurascens*	The harvested sites produced significantly fewer leaves, spathes, inflorescences and infructescence than the non-harvested sites. The supply of resources to the local fauna is possibly reduced in sites

Category	Authors	Journal	Butia Species	Findings
				under leaf exploitation, which in the long term can represent damage to the palm tree population structure and dynamics.
	Mistura *et al*. (2016)	Plant Genetic Resources	*B. odorata*	Research developed a list of descriptors for *B. odorata*. Interactions with farmers led to the identification of only five descriptors: fruit size, number of bunches per plant, presence of fibers in the pulp, fruit flavor and color of mature fruit.
	Mourelle *et al*. (2016)	Palynology	*B. eriospatha*, *B. odorata*, *B. paraguayensis*, *B. yatay*	Results showed that pollen viability of all species of *Butia* analyzed was high enough to ensure good pollination. Therefore, pollen viability is not the limiting factor for population continuity.
	Noblick and Santanna-Santos (2021)	Phytokeys	*B. eriospatha*, *B. odorata*, *B. paraguayensis*, *B. yatay*	The importance of a broader sampling exercise when studying leaf anatomy, due to possible ecological and developmental variations that may occur in some species, was emphasized.
	Rocha *et al*. (2022)	Ciência Rural	*B. purpurascens*	Yellow morph showed larger and heavier fruits than magenta morph. Morphometric differences were also evident among the populations, suggesting that ecosystems fragmentation can cause deleterious genetic effects in *B. purpurascens* in long-term.
	Sant'anna-Santos *et al*. (2015)	Anais da Academia Brasileira de Ciencias	*B. capitata and B. odorata*	Leaf anatomy showed exclusive characters for *B. marmorii* and *B. matogrossensis*, reliable anatomical characters, especially the raphides, were valuable in species distinction.
	Sant'anna-Santos *et al*. (2018)	AOB Plants	*B. archeri*, *B. campicola*, *B. capitata*, *B. catarinensis*, *B. eriospatha*, *B. exospadix*, *B. lallemantii*, *B. leiospatha*, *B. leptospatha*, *B. lepidotispatha*, *B. marmorii*, *B. matogrossensis*, *B. microspadix*, *B. paraguayensis*, *B. pubispatha*, *B. purpurascens e B. yatay*.	Anatomical keys presented relevant characters that allow the identification of the recognized species of *Butia*. Reliable anatomical characters of easy observation, especially the raphides, are valuable in species distinction.

Category	Authors	Journal	Butia Species	Findings
Plant morphology, Physiochemistry and nutrition	Schlindwein *et al*. (2017)	Ciência Rural	*B. odorata*	Data analysis revealed a strong correlation between the edaphic conditions and the yield from the *Butia* palms. Tapes *Butia* palms exhibited higher fruit yield. The lowest fruit yields were linked to nutrient-poor soils in Brachiaria pastures, as well as sandy plains containing high levels of sodium.
	Soares and Longhi (2011)	Ciência Florestal	*B. witeckii*	*B. witeckii* was close to *B. paraguayensis* e *B. yatay*, differing from these two species by the size and weight of the fruit, size, weight and shape of the endocarp/pyrene, and by the number of pinnae (leaflets) on each side of rachis.
	Beskow *et al*. (2015)	Food Chemistry	*B. odorata*	Genotype 117 was the highest yielding, with an estimated fruit yield of 22,000 kg ha and pulp yield of 12,000 kg ha. None of the genotypes evaluated showed high levels of fruit yield and bioactive phytochemical content.
	Ferrão *et al*. (2013)	Food Research International	*B. odorata*	It was possible to discriminated samples from different regions mainly due to different total lipid content, fatty acids profile and color parameters.
	Nunes *et al*. (2010)	Interciencia	*B. capitata*	It was possible to differentiate butia palm genotypes in relation to size, weight, number of fruits, firmness, color, acidity, and total soluble solids in a population of 121 plants.
	Schwartz *et al*. (2010)	Revista Brasileira de Fruticultura	*B. capitata*	Properties and/or genetic variations among the populations of *B. capitata* provided variability for the duration of the cycle, color of the epidermis of the fruits, volume of juice produced, relation between total soluble solids and titratable acidity, biometric characteristics of fruit and annual productivity.
Population genetics and cytogenetics	Buttow *et al*. (2010)	Revista Brasileira de Fruticultura	*B. capitata*	83.68% of the genetic variability is attributed to variation within populations and 13.67% attributed to differences between populations within regions. There is presence of genetic variability among all populations, without subdivision due to geographic isolation.
	Corrêa *et al*. (2009)	Revista Brasileira de Fruticultura	*B. capitata, B. eriospatha, B. odorata, B. paraguayensis and B. yatay*	All species studied had the same chromosome number, 2n = 2x = 32, also having the same karyotypic formula. The karyotypes of all species are symmetrical, showing two pairs of satellite chromosomes, a pair of satellite metacentric chromosomes and a pair of satellite acrocentric chromosomes.
	Gaiero *et al*. (2011)	Plant Systematics and Evolution	*B. lallemantii, B. paraguayensis and B. yatay*	Genetic distance analyses indicate the existence of low variability among *Butia* species. Variability within populations was high, possibly due to gene flow, past hybridisation or life history traits.
	Magnabosco *et al*. (2020)	Genetics and Molecular Biology	*B. eriospatha*	The complete plastome sequence of B. eriospatha is 154,048 bp in length, with the typical quadripartite structure. This plastome encodes 113 unique genes, being 79 protein-code genes, 30 tRNA genes and four rRNA genes.
	Nazareno and dos Reis (2011)	American Journal of Botany	*B. eriospatha*	Study highlights that microsatellite molecular marker class can be a useful tool for population genetics and evolutionary studies for many plant species.

Category	Authors	Journal	Butia Species	Findings
	Nazareno and dos Reis (2012)	Journal of Heredity	*B. eriospatha*	*B. eriospatha* is a predominantly outcrossing species and certain degree of biparental inbreeding does occur. The species is self-compatible, and reproduction may also occur by geitonogamy. The effective population size was lower than that expected for panmictic populations.
	Nazareno and dos Reis (2013)	Journal of Heredity	*B. eriospatha*	Populations of *B. eriospatha* showed high levels of genetic differentiation. Populations investigated would be at an extremely high risk of local extinction, with a greater than 50% reduction in the effective population size, in the next 40 years.
	Nazareno and dos Reis (2014)	Conservation Genetics	*B. eriospatha*	The illegally traded *B. eriospatha* individuals had more genetic variation than all of the studied wild *B. eriospatha* populations. Urban *B. eriospatha* individuals came from a variety of different populations, with 46 % coming from other populations.
	Nazareno *et al*. (2011)	American Journal of Botany	*B. eriospatha*	New microsatellite markers were developed and described for *B. eriospatha*, and they have been shown to be applicable for other species from the *Butia* genus.
	Nunes *et al*. (2008)	Revista Brasileira de Fruticultura	*B. capitata*	A total of 136 fragments were obtained, 77 of which were polymorphic. With RAPD markers, it was possible to obtain a unique molecular profile and estimate of the existing variability between the evaluated genotypes.

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