The impact of taxonomic change on the Amazonian palm flora

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Abstract

Although species taxonomy is an ever-evolving discipline, taxonomic change is rarely accounted for in macroecological studies. By tracking the history of species description and synonymizations of more than 900 described names of Amazonian palms, we reveal shifts in species counts across space and time, the factors associated with taxonomic lumping, and the time needed to detect synonyms. The Amazonian palm flora results from a gradual accumulation of new descriptions, followed by decline due to the recognition of approximately 800 heterotypic synonyms. Most of these synonyms were detected in the mid-1990s, leading to a 4.5-fold decrease in species counts in ten years. The time to detect synonyms ranged from 3 to 227 years. Species with large populations, widespread distributions, early descriptions, also those that occur in Western Amazonia were more frequently lumped. The impact of taxonomic change on species counts is dependent on taxa, region, and time period considered. Biases in these counts are pronounced in the absence of taxonomic revisions, as undetected synonyms can inflate estimates of species richness. By quantifying the magnitude of such bias, this study offers conceptual and methodological insights on how incorporating taxonomic progress into macroecological analyses can provide a more accurate understanding of biodiversity patterns.

Keywords: Amazonia, Arecaceae, palms, species description, taxonomic lumping, time-to-event, species delimitation

Introduction

About four thousand new plants names are published each year. However, only half of these result from new field discoveries; the other half stems from the revision of already described species [1]. Taxonomic revisions often result in lumping, splitting, or reassigning species to a different taxon. When substantial, these taxonomic changes can alter species counts across taxa and ecosystems and reshape the geographic patterns of species richness [2]. Yet, their impact on biodiversity patterns remains largely unquantified. This knowledge gap is particularly problematic for hyper-diverse ecosystems like the Amazon rainforest, where new species discoveries and revisions are common [3–6] and may affect estimates of global species richness [7].

Taxonomic lumping is frequent for many plant groups [8]. Synonyms, that is, duplicated names for the same taxon, outnumber counts of plant species by a factor of 1.5 [9]. The number of synonyms across Angiosperms is not homogeneous but it varies by several orders of magnitude. Half of the Angiosperms are not associated with a single synonym, whereas a few Angiosperm species have been accumulating up to 300 synonyms [10]. The identification of synonyms may take only a few years or up to centuries after the first description of a name [11].

Yet, our understanding of the impacts of taxonomic change on plant species richness is mainly derived from theoretical models [12,13] or from other biological groups, such as birds or amphibians [14]. Complementing this theoretical work with empirical studies has long been hampered by limited data availability [15]. However, a growing volume of digital resources, including botanical taxonomic treatments (e.g., monographs, revisions, and synopses), and easy access to plant nomenclatural databases [e.g., 16,17] opens new opportunities to explore taxonomic change. Such data, to our knowledge, have not been used yet to explore how taxonomic change has shaped the current pattern of palnt richness at a broad temporal and spatial scales.

Here we analyse 200 years of taxonomic descriptions and lumping for all Amazonian palms and uncover temporal and spatial trends across taxa and regions to answer three questions: 1) How has the proportion of accepted species varied over space and time across Amazonia? 2) How long does it take to recognize a previously accepted taxon as a synonym? and 3) Which factors are associated with taxonomic lumping?

We chose Amazonian palms as a model group because they are among the best-studied groups of the tropical flora [18], with a wealth of botanical monographs and revisions published since the 18th century and contemporary field sampling, providing a rich baseline data for our analysis [18]. Moreover, a deeper understanding of taxonomic progress in Amazonia is needed. In times of global mass extinction and decreasing research budgets for addressing taxonomic questions and, we risk losing many species before they are adequately described or classified.

Materials and methods

Establishing a checklist of Amazonian palms and associated synonyms

We considered as Amazonian palms all palm species that occur within the biogeographic limits of Amazonia [as proposed by 19] at elevations below 500 m a.s.l.. A list of Amazonian palms (Arecaceae) was compiled based on species names provided in the following four checklists: Henderson (1995), dataset S1 in Cardoso et al. [20], appendix 1 in ter Steege *et al.* [3], and the dataset provided by Flora e Funga do Brasil [21]. This first compilation resulted in a checklist of 240 species, excluding hybrids, varieties, and subspecies that were present in any of the four checklists (Table S1). We then checked the taxonomic status of the 240 species names against four taxonomic data portals: Tropicos [22], Plants of the World Online (POWO), and World Flora Online (WFO). For all names identified as synonyms or unplaced in any of the data portals, we obtained the respective accepted name. This standardization of species names resulted in a checklist of 206 accepted species names.

Out of these 206 species, 73 were not included in Henderson [23], which is the most recent checklist of Amazonian palms compiled by a specialist of the group. We thus verified the geographical range of these 73 species in Flora do Brasil [21]; "Palms of the Americas" [24], and the website 'Palmweb' [25], or pertinent taxonomic literature. This cross-referencing identified 31 species that do not seem to occur below 500 m a.s.l within the biogeographic limit of the Amazonian rainforest. These species were excluded from our analyses. Therefore, our final checklist includes 175 accepted palm species. This list includes Amazonian palms described until 2012 (the last year with consolidated data in the checklists of Cardoso *et al.* [20] and ter Steege *et al.* [3]. Our list comprises species of different sizes and growth forms, e.g., large tall-stemmed palms, large to small acaulescent palms, small palms, and climbing palms [26].

We also retrieved the following information from the four taxonomic portals: (1) a list of homotypic and heterotypic synonyms (see Box 1) associated with the 175 currently accepted palm species; and (2) ancillary bibliographical information (i.e., author, title of the taxonomic work, and year of publication) for the currently accepted species and their synonyms. We manually checked all names listed as synonyms (N = 1285) in the four taxonomic portals. We corrected obvious misspellings and flagged names that could not be assigned to a known taxon, as they were illegitimate or not validly published designations. We also flagged names that we could not associate with a publication or which were not available in the database of the International Plant Names Index [27]. Such manual checks were necessary because information on synonyms retrieved from the four taxonomic portals may be inconsistent.

We then selected only heterotypic synonyms, which result from synonymizing taxa that were once considered accepted species (Box 1). Heterotypic synonyms were identified by querying the Plants of the World database [16] with the R package ‘kewr’ [17] and by consulting taxonomic works, in which the currently accepted species have their synonyms (or unplaced names) often mentioned. Finally, we manually checked the earliest taxonomic work, including monographs, synopses, and revisions, to determine the year of synonymization for all heterotypic synonyms. These taxonomic works were identified through searches using main virtual botanical databases, such as POWO, TROPICOS, WFO. As our focus here is on temporal trends in the number of accepted palm species, we considered only heterotypic synonyms recognized at the species level. This is justified because species is the analytical unit for most (macro)ecological and conservation studies, we thus excluded subspecies and from our analyses. For simplicity, we refer to species-level heterotypic synonyms as synonyms.

BOX 1. Definition of taxonomic terms according to Turland [28]	
Accepted species	a taxon that is formaly recognized in the taxonomic literature as a unique biological entity (e.g., *Acrocomia aculeata* (Jacq.) Lodd. ex Mart.)
Heterotypic synonyms	two or more scientific names that were published based on different type specimens that are considered to belong to the same taxon; also known as taxonomic synonyms (e.g., *Acrocomia antiguana* L.H.Bailey)
Homotypic synonyms	two or more scientific names that were published based on the same type specimen; also known as nomenclatural synonyms (e.g., *Cocos aculeata* Jacq.)
Illegitimate name	a homonym or a scientific name that was nomenclaturally superfluous when published [for details and examples see Article 52 of the International Code of Nomenclature for algae, fungi, and plants; ,29] (e.g., *Bactris minor* Gaertn.)
Taxon *versus* Name	a taxon is a group of organisms, while a name is the label used to reference it. A taxon is described; a name is published and assigned to the taxon.
Nomen nudum (pl. *nomina nuda*)	a name without a validating description, diagnosis or reference (traslation: naked name) (e.g., *Acrocomia cubensis* Lodd. ex H.Wendl.)
Synonym	two or more scientific names that apply to the same taxon
Validly published name	a species name that is published in accordance with the rules of International Code of Nomenclature for algae, fungi, and plants [29] (e.g., *Acrocomia antiguana* L.H.Bailey; *Acrocomia antiguana* L.H.Bailey).

Herbarium records of Amazonian palms

We explored spatial variation on the proportion of accepted species across Amazonia based on based on the location of 15,446 herbarium records of all 175 species of Amazonian palms, which were retrieved from the Global Biodiversity Information Facility [30]. We screened all records and flagged those with uncertain geographical coordinates and/or missing taxonomic information at species level. This filtering led to a dataset containing 8249 herbarium records of 170 palm species. The 'rgbif ' package [31] was used to retrieve records, and the 'bdc' package [32] to flag records with potential errors.

Data analysis

Temporal trend in proportion of accepted species

To characterize the temporal trend in the proportion of accepted species among all described taxa, we followed [11] and calculated for each year the proportion of accepted species (*A*) in the total of all described taxa (i.e., accepted species plus heterotypic synonyms) as follows:

$$A_n = \frac{(\sum_{1769}^{n} d)}{(\sum_{1769}^{n} d) + (\sum_{1769}^{n} s)};$$

where *d* stands for the sum of accepted species, and *s* denotes the sum of synonyms, beginning in the year after its description and continuing up year *n*. To visualize the time needed to recognize a previously accepted taxon as a heterotypic synonym, we used Kaplan-Meier curves [33]. Kaplan-Meier curves are commonly used in medical research to visualize the probability of an event (e.g., death) over time for different treatment groups. Here, we considered the year of taxonomic description as the initial point in time of the observation period (t_0) and the year of synonymization as the point in time that an event is recorded (t_1), as this represents the year in which a name no longer corresponds to an accepted species. The Kaplan-Meier curves were established considering only heterotypic synonyms. Both the proportion of accepted species among all described taxa over time and the Kaplan-Meier curves were calculated for: (1) all taxa; (2) taxa grouped cohorts according to year of description (i.e., descriptions and synonymizations until 1900; between 1901 and 1950; between 1951 and 1980; and between 1991 until 2022); and (3) taxa belonging to the three most species-rich palm tribes (Cocoseae, Euterpeae, Geonomateae). Kaplan-Meier curves were established with the 'survival' [34] and 'survminer' [35] R packages.

Spatial trend in proportion of accepted species

Herbarium records were aggregated in a regular grid of 100 × 100 km projected to 'South America Albers Equal Area Conic' coordinate system (crs = "ESRI 102033") covering the biogeographic limit of

Amazonia [19]. Then, for each grid cell, we calculated the share of accepted species in the total of accepted species plus heterotypic synonyms. We also determined the average proportion of accepted species for latitudinal and longitudinal bins of 100 km. Proportion of accepted species were obtained for two distinct periods of time: (1) from 1768 and 1990; and (2) from 1768 until 2020. We chose these periods because they align with substantial changes in the total number of accepted palm species.

Correlates of taxonomic lumping

We tested whether taxonomic lumping has been more frequent in taxa that occupy large areas, were described in early years, and have a large population. To do so, we correlations between: (1) number of heterotypic synonyms; (2) year of first taxonomic description; (3) size of the area of occupancy of accepted species; (4) number of individuals; and (5) estimated population size. Pearson correlation coefficients were calculated using the function *corphylo* in the ape R package [36]. The phylogenetic relationship among species was extracted from the Maximum Clade Credibility phylogenetic tree for palms proposed by Onstein *et al.* [37]. These correlations may entail self-reinforcing interaction between species characteristics and taxonomic history, by which taxa may achieve larger areas or population size as a consequence of taxonomic lumping.

The area of occupancy of a species was calculated based on the range maps for Amazonian palms, which were obtained with the function *BIEN_ranges_load_species* from the BIEN R package [38] and re-projected to South America based on Albers Equal Area Conic projection. Based on the re-projected range maps, we calculated the known area of occupancy (in km^2) for the 155 accepted species, which had range maps available in the BIEN database considering the entire geographic range of each species, including Amazonia and other biomes in the Neotropics. Observed and estimated population size were obtained from ter Steege et al. [39] for 57 accepted species.

Results

Our dataset contains 1470 unique names, including 175 accepted species and 1285 names that comprise homotypic and heterotypic synonyms, as well as unplaced names (e.g., *nomina nuda*, orthographic variants, or illegitimate names). Of the 175 accepted species, 68 had no synonyms or only homotypic synonyms, while 107 were associated with a total of 952 heterotypic synonyms. For 940 of these heterotypic synonyms, we were able to retrieve both the year of publication and the year of synonymization. Among the heterotypic synonyms, 136 represented varieties or subspecies, and 804 were species-level heterotypic synonyms linked to 102 accepted species (Appendix S2). We successfully obtained year of publication and year of synonymization for 798 of the 804 species-level heterotypic synonyms (Table S2). For brevity, we refer to these species-level heterotypic synonyms simply as heterotypic synonyms.

Changes in accepted species counts

Our results show that species counts can vary significantly depending on whether they are made before or after a major taxonomic revision. The current number of 175 accepted species for the Amazonian palm flora is comparable to the count in the 1850s (Fig 1a), with the difference that in 1850s there was not a single heterotypic synonym whereas now there are 804. This is surprising but indicates that the gradual accumulation of new species descriptions over centuries has been compensated by taxonomic lumping, most of which after 1990.

The number of Amazonian palm species increased steadily from the late 1700s until the mid-1960s and reached its maximum in 1966 when 854 taxa were recognized as distinct species. After nearly two centuries of almost continuous new descriptions, taxonomic lumping reversed this trend and led to an 82% decline in the overall number of accepted species in just three decades (Fig. 1b). The first significant drop, from 854 to 802 species, occurred in 1968 due to the work of Jan Gerard Wessels Boer [40]. The second drop was more substantial with the number of accepted palm species declining by 79% from 787 in 1990 to 206 in 1995. This reduction stemmed mainly from synonymizations proposed by Henderson [23] and Henderson *et al.* [24]. The third and most recent drop in the number of accepted species (from 206 to 175) occurred in 2020, and coincided with the lumping proposed for *Attalea* Kunth and *Bactris* Jacq. ex Scop. (Henderson, 2020). In brief, counting Amazonian palm species in 1990 and in 2000 would yield two very different totals, 787 and 175 respectively, which differ by a factor of 4.5 despite being only ten years apart (Fig. 1b). This striking observation underscores how critical taxonomic revisions are for obtaining species counts with significant knock-on effects on subsequent macroecological analyse.

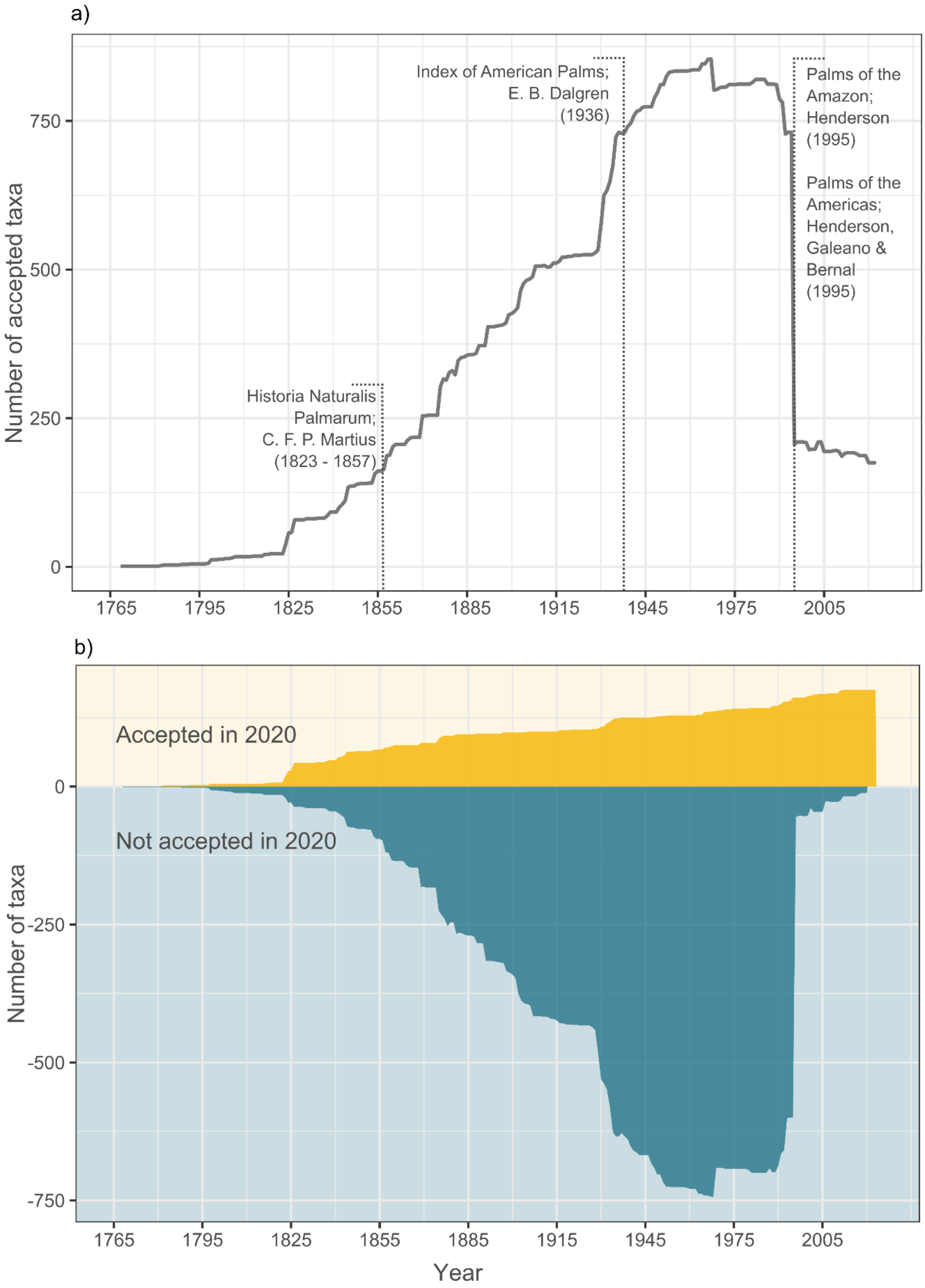

Figure 1. **Timeline of accepted species for the Amazonian palm flora**. a) Number of accepted taxa over time, dashed lines mark the year of major taxonomic works; b) Number of described taxa per year that are still accepted *versus* not accepted by 2020.

Of the 34 Amazonian palm genera, 11 reached their current species number in the 1990s and another 14 in the 2000s (Fig. 2a). *Attalea*, *Iriartella* H.Wendl. and *Syagrus* Mart. were the latest to reach their current number of accepted species, doing so in 2020. In contrast, *Raphia* P.Beauv. and *Wettinia* Poepp. ex Endl. were the earliest, reaching their current total before the 1900s. Because the abundance of genera can vary across geographic regions, different regions may reach their current number of accepted species at different times. We find that the current number of accepted species was reached relatively recently across Amazonia, with the exception of the central Amazon (Fig. 2b). Most genera that are frequently recorded in this region already reached the current number of accepted taxa around 1940.

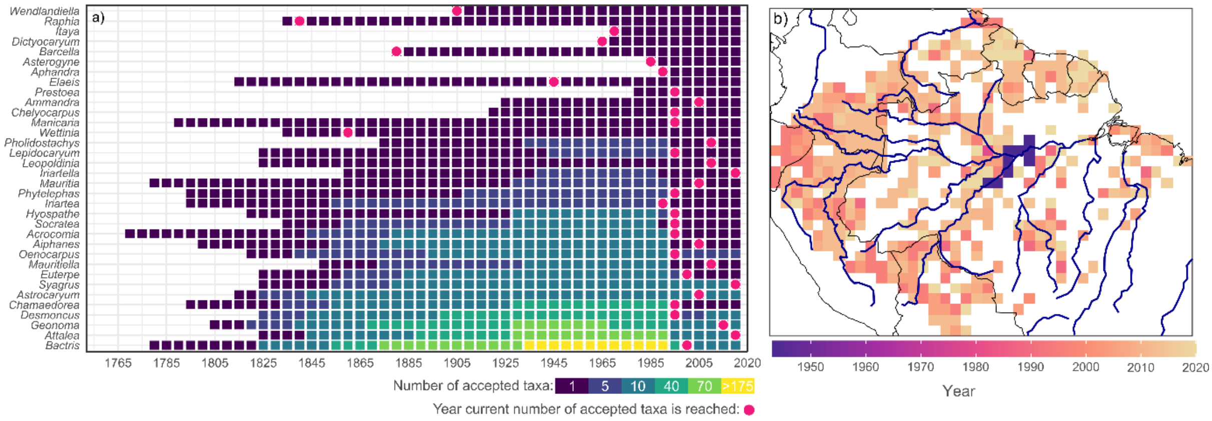

Figure 2. **Timeline of accepted species across genera in Amazonia**. a) Number of accepted taxa by genus over time; pink dots indicate the year in which the current number of accepted species was reached, yellow highlights periods exceeding. b) Map depicting the median year in which the genera recorded in each grid cell reached their current number of accepted species, with light colours indicating more recent years.

How has the proportion of accepted species varied over space and time across Amazonia?

The proportion of accepted species in all described taxa (i.e., all currently accepted species plus heterotypic synonyms) mirror the trend in taxonomic lumping described above. Overall, this proportion have remained relatively stable over 200 years and only started to decrease in the late 1960s. However, a more detailed examination suggests that lumping is less frequent in recently described than in older taxa (Fig. 3a and 3b). Nearly 80% of the species described after the 1990s are still considered accepted to date. This share is only 40% for taxa described between 1950 and 1980. Among the top three most species-rich tribes, Geonomateae have the highest share of species that remain accepted (Fig. 3c).

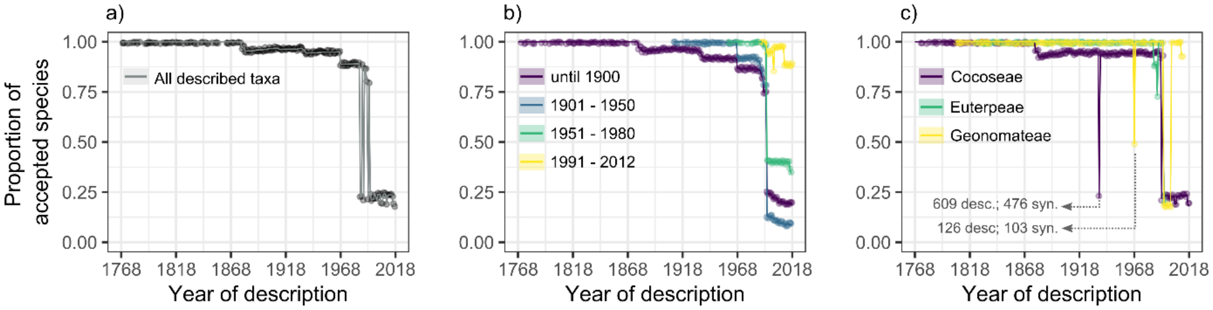

Figure 3. Temporal decay in the proportion of accepted species. Proportion of accepted species per year among all described taxa over time: (a) all taxa, i.e., 175 accepted species and 798 heterotypic synonyms; (b) all taxa grouped into cohorts based on the year they were described; (c) taxa belonging to one of the three most species-rich palm tribe (Cocoseae, Euterpeae, or Geonomateae)

In 1990, the share of accepted species among all described taxa was rather homogeneous and close to 1 across the entire Amazon. However, in the 2020s, this share dropped to 0.1-0.4 throughout the entire region (compare Fig. 4a and 4b). A comparison of two maps for 1990 and 2020 (Fig. 4) reveals that the species that are typically found in Western Amazonia are associated with a particularly high number of heterotypic synonyms. Relevant genera include *Attalea*, *Bactris* and *Geonoma* Willd., which reached a particularly high number of synonyms after the 1990s (Fig 4c and 4d). These results show that taxonomic revisions follow certain patterns across space, time, and taxonomic groups; rather than random, their impact on species richness can be substantial.

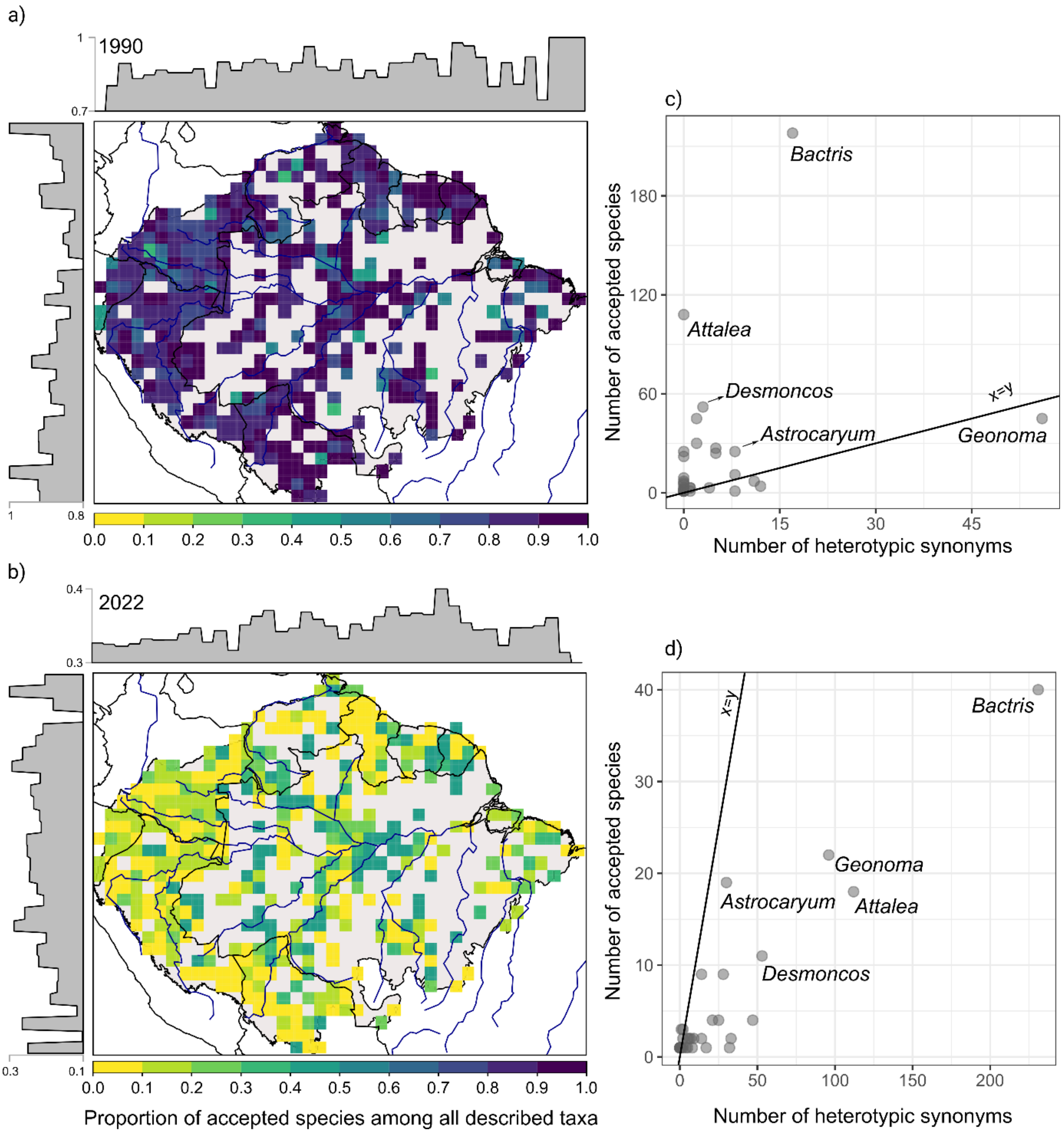

Figure 4. Proportion of accepted species among all described taxa (i.e., currently accepted and heterotypic synonyms)**.** Maps depict shares for 1990 (a) and 2022 (b). Lighter shades represent a lower proportion of accepted species (i.e., more heterotypic synonyms per accepted species), while darker shades represent a higher share (fewer synonyms per species). Histograms next to the maps show average share per longitudinal and latitudinal band of 0.9 degrees (100 km). Scatterplots show the number of accepted species as a function of the number of heterotypic synonyms recognized in 1990 (c) and in 2022 (d); black line indicate 1:1 ratio.

How long does it take to recognize a previously accepted taxon as a synonym?

For Amazonian palms, it took anything from 3 to 227 years to detect a heterotypic synonym (median = 79 years; upper and lower confidence limits = 66 and 89 years, respectively). The time required depends on the age of the taxonomic description and the tribe to which the species belongs to. It has taken an average of 81 years to detect about half of all currently recognized heterotypic synonyms.

The remaining half required an additional 147 years to be detected (Table 1; Fig. 5a). For taxa described before the 1900s, it has taken on average 114 years to identify half of them as synonyms and a total 220 years to detect all synonyms (Figure 5b). This detection time is shorter for more recently described taxa. For example, it only took an average of 26 years to detect synonyms among palms described between 1951 and 1980, and 18 years for those described between 1991 and 2012. The time lag between the first taxonomic description and synonymization also varies depending on the palm tribe. Among the top three tribes, Euterpeae and Geonomateae had half of their synonyms detected approximately 60 years after description. In contrast, Cocoseae had half of the synonyms detected on average 90 years after description (Figure 5c). The average time to detect heterotypic synonyms within each tribe ranged from 60 (Lepidocaryeae) to 164 years (Leopoldinieae). This result shows that during prolonged periods without taxonomic revisions species counts can be highly uncertain, as potential heterotypic synonyms can remain "hidden" among the accepted species.

Table 1. Summary statistics of Kaplan-Meir curves, indicating time lag between taxonomic description and detection of heterotypic synonyms of Amazonian palms.

	N heterotypic synonyms	**Median detection time (years)**	**Lower confidence limit (years)**	**Upper confidence limit (years)**
All heterotypic synonyms	798	79	66	89
Taxa described until 1900	422	114	110	117
Taxa described between 1901 and 1950	327	61	60	61
Taxa described between 1951 and 1980	34	26	14	32
Taxa described between 1981 and 2012	15	18	10	18
Cocoseae	505	90	76	93
Euterpae	56	63	60	67
Geonomateae	101	65	62	92

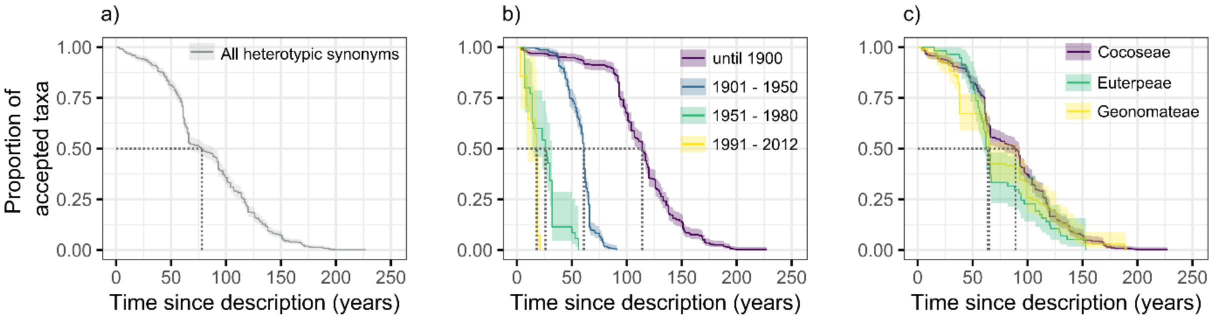

Figure 5. Time-lag between species description and synonymization. Kaplan-Meier curves for (a) all heterotypic synonyms, (b) heterotypic synonyms grouped in cohorts according to year of taxonomic description, and (c) heterotypic synonyms associated with accepted species belonging Cocoseae, Euterpeae, or Geonomateae. The proportion of accepted taxa (y-axis) reaches zero because the Kaplan-Meier curves were performed considering only heterotypic synonyms.

Which factors are associated with taxonomic lumping?

Species described in earlier years, that occupy a larger area, and comprise a large population tend to have a higher number of heterotypic synonyms, according to Pearson correlations (Table2). This indicates either that such taxa are more subject to taxonomic or that they reach a large area of occupancy (and consequently larger total population size) as a result of recurrent taxonomic lumping. Additionally, we found that species with a larger area of occupancy tend to be described earlier (Table 2).

Table 2. Pearson correlation coefficients and significance levels (***$p < 2.2e\text{-}16$; **$p < 0.001$).

Parameter	Number of heterotypic synonyms	Size of area of occupancy	Year of description	Number of individuals	Population size
Number of heterotypic synonyms	1				
Size of area of occupancy	0.6***	1			
Year of description	-0.2***	-0.5***	1		
Number of individuals	0.4**	-	-	1	
Population size	0.4**	-	-		1

Discussion

Our study shows that the impact of taxonomic progress on species richness is substantial but not homogeneous across palm taxa. This variation depends very much on the taxa, region, and the period considered. Over the past two and a half centuries, species descriptions have steadily accumulated, while taxonomic lumping occurred in three distinct waves, mostly after 1990. As a result, more than 800 heterotypic synonyms remained unrecognized for periods ranging from a few years to over two centuries. Lumping has been recurrent for taxa that were earlier described, that occupy a large area and that have a large population. Moreover, species that typically occur in Western Amazonia were subject to more lumping than species that occur elsewhere in Amazonia. Currently, accepted species represent only 12% of all described names, likely because palms are one of the best-studied groups within tropical flora [18].

Taxonomic progress and its impact on the Amazonian palm flora

The current Amazonian palm flora, comprising 175 accepted species, resulted from a gradual accumulation of species descriptions and distinct events of taxonomic lumping through which *ca.* 800

heterotypic synonyms were detected. Thus, this palm flora did not grow continuously as a result of new descriptions over the past century. Our results show that progress in taxonomy is not a 'zero-sum game' through which reductions in species numbers by taxonomic lumping are compensated by increases in species numbers by taxonomic splitting (Fig 1b). Instead, new descriptions were added, and previously accepted descriptions were refuted unevenly across taxa, geographic regions, and time.

Changes in species taxonomy arise from evolving taxonomic practices, data sources and criteria [41]. After the 1950s, taxonomy moved away from the use of subjective species concepts and reliance solely on morphological characters for justifying species boundaries towards the adoption of more stringent concepts and the application of different sources of data and analysis to delimit species [41,42]. For Amazonian palms, the impact of these changes is reflected in the large number of synonymizations proposed for taxa described in the 1940s, for example, by Maximilian Burret, who has been criticized for considering a very narrow morphological variation within a single taxon [40]. Most of the synonymizations of taxa described by Burret were justified by the use of a morphometric quantitative analysis and the adoption of the phylogenetic concept to define species limits [43].

The recent lumping resulting from progress in taxonomy is not restricted to Amazonian palms. *Guatteria* Ruiz & Pav. (Annonaceae), for example, lost the status of the most species-rich genus of woody Neotropical trees after significant taxonomic lumping in 2015 [44]. Sapotaceae, a pan-tropical family that today encompasses 65 to 70 genera, with 11 of them in the Neotropics, has been thought to have 125 genera, with 45 occurring in the Neotropics [45]. Other groups of tropical plants experienced similar lumping, including Euphorbiaceae and *Miconia* Ruiz & Pav. [46,47]. In this context, it is interesting that globally, the overall number of accepted plant species has been increasing continuously [48]. This increase is well-documented and results mostly from the accumulation of new species descriptions [49,50]. However, the extent to which lumping offsets this growth remains challenging to quantify, as the proposal of heterotypic synonyms is not a nomenclatural act [51].

For seed plants, it is estimated that accepted species account for 34% [52] to 40% [9] of all taxonomic descriptions, indicating that more than half of the described taxa are at a later point recognized as synonyms. These numbers are a factor 2 higher than the 21% (considering only heterotypic synonyms) observed here for Amazonian palms. Multi-taxa comparisons of synonym rates, however, typically not distinguish between homotypic and heterotypic synonyms [51,53,54]. While homotypic synonyms arise when a taxon is reassigned to another genus, tribe, or family, heterotypic synonyms result from changes in the delimitation of given a taxon. By explicitly distinguishing between these two types of synonyms when calculating synonym rates, we can better understand how changes in taxonomy, whether due to changes in delimitation or reassignments, affect species counts.

Taxonomic lumping across taxa and regions

Taxonomic lumping has been more frequent for palm taxa that were described earlier and that occupy larger areas. This finding is expectable because taxa covering larger areas tend to have higher morphological variation due to a higher diversity of environmental conditions [55]. Particularly, flower morphology within species can substantially vary with climate, soil, and pollinator communities [56]. The resulting morphological plasticity can lead to independent taxonomic descriptions, which were likely prevalent in times when the exchange of botanical information was limited or restricted. However, both large phenotypic variation and broad range size could themselves be the consequence of taxonomic lumping. This leads to ambiguity regarding the actual causes and effects of taxonomic lumping. A species that were subject to multiple taxonomic lumping may display high phenotypic variation and occupy a larger area than its original, more narrowly defined boundaries.

Our data also show that western Amazonia harbours taxa that were subject to recurrent taxonomic lumping. One possible explanation for this is that Western Amazonia comprises several young lineages that diversified relatively recently within the region's mosaic of habitat and fertile soils [57,58]. These lineages, initially described as distinct species, underscore the difficulty of defining species boundaries for closely related groups [41,59]. This observation suggests that the higher than expected species richness of palms in Western Amazonia [60] might need to be re-evaluated using post-2007 taxonomic revisions—such as updates for *Attalea* [43], *Bactris* [61], *Desmoncus* [62], and *Geonoma* [63]. Such research could determine whether the excess palm richness in Western Amazonia is caused by ecological and evolutionary processes or to some extend by taxonomic artefact.

If taxonomic lumping is not random across taxa and regions – as we observe for Amazonian palms – and taxa show strong spatial phylogenetic structure [64], then regions may have reached their current number of accepted species at different points in times. We find that genera that typically occur in central Amazonia have reached their current number of species 50 years earlier than those occurring in other Amazonian regions. This result may be influenced by the higher frequency of *Elaeis oleifera* (Kunth) Cortés recorded in central Amazonia than elsewhere. *Elaeis* Jacq. is a genus with a single accepted species in the Americas (Henderson et al. 1995) that is typically recorded in central Amazonia [65]. By contrast, *Geonoma* and *Bactris*, which are recorded relatively more frequently in Western Amazonia are among the most species-rich genera of Amazonian palms and have a high number of heterotypic synonyms. It is important to note that our map depicting when genera reaches its current number of species is draw from digital herbarium specimens and thus it is subject to incompleteness and biases [66,67]. Moreover, both palm inventories and taxonomic studies have been particularly abundant in western Amazonia in the last 30 years [68], which may have led to more species description and detection synonyms over time. These observations highlight the importance of considering the historical and spatial context of taxonomic research when interpreting broad-scale pattern of species richness, as uneven taxonomic effort may introduce bias in estimates of species richness [69].

Timing of taxonomic lumping

Our results show a large variation in the time heterotypic synonyms remain undetected, with recently described taxa being recognized as heterotypic synonyms more quickly. This may reflect either insufficient time for the synonymization of younger taxa or that younger taxa are taxonomically more robust, as their delimitations are often justified by multiple sources of evidence [70]. Moreover, taxa belonging to the tribes Euterpae or Geonomateae are recognized as heterotypic synonyms on average 100 years earlier than those belonging to the Cocoseae, which includes some of the most species-rich genera of Amazonian palms, such as *Attalea* and *Bactris*. This temporal variation arises because species descriptions have steadily accumulated over nearly two centuries, while most synonyms of these species-rich genera were proposed in a few recent taxonomic revisions during a relatively short time span. Although taxonomic revisions for species-rich genera such as *Bactris*, *Geonoma,* and *Attalea* have been published 10 years a part [43,61,71].

These results show that heterotypic synonyms can remain hidden for periods ranging from a few years to centuries due to the time lag of taxonomic revisions across different groups. Given the limited taxonomic coverage in botanical monographs [72], many heterotypic synonyms remain unrecognized across other plant taxa. Yet, a detailed understanding of temporal trends in synonym detection is lacking for a broader range of taxa. A comparative analysis, particularly across tropical plants, could provide valuable insights into uncertainty on species counts that may arise from the lack of revisionary work.

Taxonomic lumping and hyperdominance of the Amazonian palm flora

Palms are among the most dominant species in the Amazonian tree flora [39]. The extent to which changes in species delimitation affect dominance patterns is the subject of ongoing discussions [12,73]. If an accepted species resulted from the lumping of several species, it may have a larger population size than it would have if was recognized as different species. Such a species could then be considered as hyperdominant. Palms partially support this expectation, as we observed a moderate correlation (r = 0.4) between the number of heterotypic synonyms and estimated population size, suggesting that taxonomic lumping, to some degree, may have influenced the current pattern of species dominance. Given the substantial lumping proposed for Amazonian palms, we anticipate that further lumping is unlikely to happen in the near future. Consequently, changes in species dominance may arise if future research uncovers cryptic species within large populations. Recent molecular evidence suggests that *Astrocaryum murumuru* Mart., with four heterotypic synonyms and an estimated population of 2.4 billion individuals [39], could potentially include cryptic species [74]. This could justify a re-evaluation of species boundaries within this group. It is important to note that generalizations about the relationship between hyperdominant species and taxonomic lumping or cryptic diversity are not applicable, as both lumping and description of cryptic species depend on taxonomic practices that vary across taxonomic groups and geographic regions [75]. For example, *Eschweilera coriacea* (DC.) S.A.Mori (Lecythidaceae), another hyperdominant species, has undergone frequent taxonomic lumping but recent molecular analysis indicates that *E. coriacea* is indeed a single taxon [12,76].

Way forward: bridging taxonomy and macroecology

Many plant taxa lack taxonomic revision [72], and a relatively small proportion of new species descriptions are supported by molecular data [42,77]. As species descriptions, revisions, and changes in delimitation depend on factors that vary substantially across taxonomic groups and regions [72], cryptic species and hidden synonyms will continue to bias broad-scale, multi-species ecological studies. This bias cannot be completely eliminated but, as we show here, it can be measured, thereby providing a baseline reference to quantify this source of uncertainty in biogeographical, evolutionary, and macroecological analyses. An increasing number of data infrastructure supports handling complex taxonomic data [77,78] and plant ecologists can now to navigate in the complexities of data ontologies and taxonomic terminology to map when and how often species limits have been re-evaluated and redefined [79,80]. A significant challenge is that recognizing a heterotypic synonym—unlike describing a new species or designating a homotypic synonym—is not a mandatory nomenclatural act. This means that the way and extent to which it is documented in taxonomic literature vary depending on the taxonomist's choice [51]. Consequently, quantifying the reduction in accepted species due to taxonomic lumping in many plant groups is not straightforward. To address this, ecologists, taxonomists, and data scientists may work together to ensure that advancements in these three disciplines are fully integrated.

Concluding remarks

We have analysed the temporal and spatial trend of taxonomic descriptions and lumping for the Amazonian palm flora. Our findings challenge the view of zero-sum game, where lumping offsets the addition of newly described species. Strikingly, counting Amazonian palm species in 1990 and in 2000 would yield two different totals, 787 and 175, respectively, a 4.5-fold decrease in just ten years. We also demonstrate that the impact of new species descriptions and lumping on total counts vary significantly across taxa, regions, and time periods considered. Lumping has been more prevalent among widespread, abundant, and earlier-described species, particularly those occurring in western Amazonia. However, disentangling the drivers and effects of taxonomic lumping is complex, as lumped species may appear more widespread and abundant if they were treated as distinct taxa. Our analyses also show that synonym detection can span from just a few years to more than two centuries. We suggest that the general lack recent taxonomic accounts for several plant groups [72], particularly in the tropics, leaves many heterotypic synonyms undetected, potentially inflating estimates of species richness at local, regional, and global scales. Identifying where these inaccuracies are most pronounced requires embedding taxonomic progress within macroecological analyses.

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