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ORIGINAL PAPER

An assessment of the endemic spermatophytes, pteridophytes and bryophytes of the French Overseas Territories: towards a better conservation outlook

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Abstract
A broad range of climatic and biogeographical conditions are represented in the French Overseas Territories, from sub-polar to equatorial, resulting in a high diversity of endemic species. We mobilized data from herbaria, floras, checklists, literature, the expertise of botanists and plant ecologists to compile the most complete dataset on endemic vascular plants and bryophytes in the 15 French Overseas Territories. To date, 3748 spermatophytes (seed plants), 244 pteridophytes (ferns and lycophytes) and 448 bryophytes are strictly endemic to the overseas territories. New Caledonia, French Polynesia and Réunion harbour the highest numbers of strictly endemic species, yet French Guiana and the French Antilles harbour high numbers of regional endemic species due to their proximity with other territories. The endemic flora of these territories is highly threatened. In particular, 51% of strictly endemic spermatophytes are threatened and many species at risk belong to Rubiaceae and Orchidaceae families. Around 82% and 69% of strict and regional endemic spermatophytes and pteridophytes are found in the Paris herbaria. Only 34% of endemic bryophytes have their label information fully databased so that their total number in Paris herbaria is not known. Databasing the remaining specimens in the collection will greatly enhance future research and conservation projects. To facilitate the use of the information we compiled, we provide a publicly searchable dataset of the checklist. This study not only provides a picture of the flora of French overseas territories; it also identifies gaps in knowledge on which future research efforts in systematics, ecology and conservation could focus.

Keywords Bryophytes · Checklist · Endemism · French Overseas Territories · Islands · Orchidaceae · Pteridophytes · Rubiaceae · Spermatophytes

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Introduction

At the time of this writing, 20,798 bryophytes and 351,810 vascular plant species have been recorded on Earth (Roskov et al. 2019; Freiberg et al. 2020) with two in five of the latter potentially threatened with extinction (Nic Lughadha et al. 2020). Taxonomic information is obviously crucial for analyzing the distribution of organisms on Earth (Rouhan and Gaudeul 2021), and taxonomic data about plants is fundamental due to their key roles in ecosystem functioning and for human well-being (Isbell et al. 2011, 2015). Much knowledge is gained from local and regional studies which enrich our understanding of the world flora (WFO 2020). Some of the territories with high numbers of unique plant species and where recent and significant taxonomic and biogeographic advances have been made are the French Overseas Territories (hereafter FOTs) (Gargominy et al. 2020). We focus our study on the FOTs, showing how regional knowledge and collaborations can enhance understanding of plant diversity and alerting on the risks of extinctions of some unique species (Nic Lughadha et al. 2020; Pearce et al. 2020).

The biodiversity of the French Overseas Territories is remarkable in many ways. Notably, they harbour numerous species found nowhere else in the world leading to exceptionally high rates of endemism. Concerning plants, 95% of French endemic species occur in overseas territories, representing ca. 4000 species of tracheophytes (i.e. vascular plants grouping 'pteridophytes'-ferns and lycophytes- and seed plants) and bryophytes (i.e. non-vascular, free-sporing plants) (Gargominy et al. 2020). With the exception of French Guiana and Adélie Land, FOTs are islands (Table 1). Their isolation from the nearest continents or landmasses, their diverse environments across territories, the diversity of climatic conditions (from sub-polar to equatorial), as well as unique and diverse biomes in most of these territories, have resulted in numerous speciation events resulting in high rates of endemism. According to the latest studies, the territory that hosts the highest number of endemic plants is New Caledonia with about 2820 species and is the territory with the highest endemism richness, an index combining both endemism and species richness, in the world (Kier et al. 2009; Thouvenot et al. 2011; Morat et al. 2012; Gargominy et al. 2020; Munzinger et al. 2020). Approximately 62% of the vascular plants of French Polynesia have previously been identified as endemics, representing more than 550 species (Chevillotte et al. 2014). Réunion island harbours 237 endemic plants while 389 are endemic to the Mascarene archipelago (Boullet 2019). Other territories that harbour plants found nowhere else in the world are Martinique, Guadeloupe, Mayotte, French sub-Antarctic islands, Wallis and Futuna, French Guiana and Scattered Islands (Table 1). Yet, many endemic species are on the brink of extinctions and 10 out of 15 FOTs belong to the world biodiversity hotspots "*where exceptional concentrations of endemic species are undergoing exceptional loss of habitat*" (Myers et al. 2000). The main threats to biodiversity can be easily seen in these territories. New Caledonia, for example, is highly impacted by fire and mining activities, being the main threats to 68% and 43% of all the threatened plants of the territory (Endemia and RLA Flore NC 2019). In Réunion, deforestation, urbanization and agriculture are responsible for the loss of plant populations bringing species to the brink of extinction (UICN France et al. 2013b). In the West Indies, habitat loss or reduction is due to the export-oriented agricultural expansion (including sugar cane and banana cultivation) that followed European colonization and, more recently, due to residential and commercial tourism development (Hatzenberger 2001). Climate change, including sea level rise, is an additional threat to these ecosystems, which are already subject to major natural hazards such as hurricanes, volcanoes and seismic activity (Bernard et al. 2014). Invasive species

Table 1 Main features of French Overseas Territories

Territory	Main islands	Geographic coordinates (Google Earth)	Area (km²)	Maximum elevation (m)	Minimum distance to the mainland or very large islands (km)	Ontogeny (origin)	Hotspot (sensu Myers et al. 2000)	Area of regional endemism (= sub-endemism)
Pacific ocean								
New Caledonia	Grande-Terre, Loyauté, Belep, Chesterfield, Bellone	163°34′ E–168°09′ E; 19°32′ S–22°42′ S	16,483	1629 (Mt Panié)	1270	Continental	New Caledonia	
Wallis and Futuna	Wallis (Uvea and 19 islets), Futuna, Alofi	13°10′ S–14°23′ S; 176°07′ W–178°12′ W	142	524 (Mt Puke)	5000	Volcanic	Polynesia-Micronesia	Western Polynesia (Fiji, Niue, Samoa, Tonga)
Clipperton	Clipperton/La Passion	109°12′ W, 10°17′ N	9	29 (Le Rocher)	1080	Volcanic		
French Polynesia	120 islands in 5 archipelagoes: Gambier, Austral, Marquesas, Tuamotu, Society	7°47 ′S–23°15′ S; 134°46′ W–154°39′ W	3520	2241 (Mt Orohena—Tahiti)	> 5400 (Australia)	Volcanic	Polynesia-Micronesia	Southeastern Polynesia (French Polynesia, Cook Islands, Pitcairn islands)
Indian ocean								
Réunion	Réunion	21°24′ S, 55°55′ E	2512	3069 (Piton des Neiges)	700 (Madagascar)	Volcanic	Madagascar and the Indian ocean islands	Mascarene archipelago
Mayotte	Grande Terre, Petite Terre et petits îlots	12°50′ S, 45°08′ E	376	660 (Mt Bénara)	295 (Madagascar)	Volcanic	Madagascar and the Indian ocean islands	Comoro archipelago
Scattered Islands	Europa, Juan de Nova, Tromelin, Glorieuses, Bassas da India	11°29′S–22°24′S; 40°19′E–54°31′E	40	14	305	Volcanic	Madagascar and the Indian ocean islands	Scattered Islands, Seychelles, Madagascar*

Table 1 (continued)

Territory	Main islands	Geographic coordinates (Google Earth)	Area (km^2)	Maximum elevation (m)	Minimum distance to the mainland or very large islands (km)	Ontogeny (origin)	Hotspot (sensu Myers et al. 2000)	Area of regional endemism (= sub-endemism)
French sub-Antarctic islands	Crozet, Kerguelen, Saint-Paul, Amsterdam	37°50′ S–50°00′ S; 50°15′ E–77°31′E	7616	1850 (Mt Ross)	2400	Volcanic		French sub-Antarctic islands, Marion and Prince Edward Islands, Heard and McDonald Islands
Adélie Land		65°00′ S, 138°00′ E	432,000			Mainland		
Atlantic ocean								
French Guiana		3°59′ N, 53°00′ W	83,856	851 (Bellevue de l'Inini)		Mainland		Guiana Shield
Guadeloupe	Basse Terre, Grande-Terre, Marie-Galante, Les Saintes, Désirade	16°16′ N, 61°33′ W	1628	1467 (La Soufrière)	580	Volcanic	Caribbean Islands	Lesser Antilles
Martinique	Martinique	14°39′ N, 61°01′ W	1128	1397 (Montagne Pelée)	410	Volcanic	Caribbean Islands	Lesser Antilles
Saint-Barthélemy	Saint-Barthélemy	17°54′ N, 52°50′ W	24	286	780	Volcanic	Caribbean Islands	Lesser Antilles
Saint-Martin	Saint Martin	18°04′ N, 63°02′ W	53	424 (Pic Paradis)	810	Volcanic	Caribbean Islands	Lesser Antilles
Saint-Pierre-et-Miquelon	Saint-Pierre, Miquelon, Langlade	56°19′ N, 46°53′ W	242	240 (Morne de la Grande Montagne)	20	Continental		Newfoundland and Saint-Pierre-et-Miquelon

*Juan de Nova, Europa and Glorieuses are considered to be part of the same Mozambique Channel coral complex, Tromelin is considered separate are also a serious threat in many of these territories, especially in tropical islands (Soubeyran et al. 2015; Meyer et al. 2018). To slow down the erosion of biodiversity worldwide, knowledge and conservation of the biodiversity of FOTs is of major importance. However, there are still many endemic plants for which very little or nothing is known, and new species are regularly described. This is particularly true for bryophytes as knowledge is regularly gained for this group (Söderström et al. 1992; Thouvenot et al. 2011). Bryophytes are the second largest group of land plants after flowering plants, and are central in our knowledge about early land plant evolution (von Konrat et al. 2010). They play important ecological roles in the diverse ecosystems they inhabit. Since they lack true vascular tissue and roots, they are closely tied to their environment, making them good indicators of environmental changes (Smith 2012; Leblond et al. 2004). Bryophytes are therefore more vulnerable to global changes than other plant groups (Hodgetts 2019). Yet, they are still less known than vascular plants and an important amount of research is necessary to get an accurate picture of their distribution, taxonomy and the threats they face (but see, Gradstein et al. 2001; Bernard and Schäfer-Verwimp 2011; Thouvenot et al. 2011; Ah-Peng et al. 2012).

Important knowledge for the conservation of plants have been gained from collecting, compiling, organizing, updating and sharing data, which can be tracked back to the eighteenth century. At the start of this period, overseas exploration and trade of natural resources, especially in tropical territories, dramatically increased the amount of plant material available for species descriptions by scientists. Among famous early explorers and naturalists were Joseph de Jussieu (1704–1779) who travelled to South America, Jean Baptiste Christian Fusée-Aublet (1720–1778) to what is now French Guiana, Joseph Dalton Hooker (1817–1911) to French sub-Antarctic islands, and Dumont d'Urville (1790–1842) and Philibert Commerson (1727–1773) who traversed the world. While the amount of scientific information (botanical or ecological) amassed by naturalists during the last three centuries is enormous, it is widely scattered. The highly valuable data for understanding and conserving biodiversity are contained in public or private biological collections, in voluminous and scattered literature, field notebooks, computer files, etc. In recent years, coordinated initiatives at the Paris National Museum of Natural History have been put in place to compile this wealth of data and to make information more accessible. These included the renovation of the herbarium building, digitization of the collections, incorporation of specimen data in the Museum's Sonnerat database (Le Bras et al. 2017), the creation of the RECOLNAT infrastructure to enhance the use of collection data (https://www.recolnat.org) as well as the creation in 2007 of the National taxonomic reference framework TAXREF (Gargominy et al. 2020). The urgency to collect and consolidate existing knowledge of biodiversity in order to protect it as best as possible is particularly relevant under the current sixth mass extinction of life on Earth, with extinction rates 1000 times greater than background rates (Pimm et al. 2014). Completing "*a widely accessible working list of all known plant species, as a step towards a complete world Flora*" is one of the targets of the Global Strategy for Plant Conservation and is fundamental in order to meet the different objectives for plant conservation it defined (https://www.cbd.int/decision/cop/?id=7183). Herbaria have a role to play in completing these objectives, as they can provide data such as species occurrences, new species descriptions, taxonomic reviews, endemic status, etc. (Bebber et al. 2010; Meineke et al. 2019). Many herbaria across the world have started digitizing and databasing their specimens in order to make the data more easily accessible to naturalists and researchers. This has enhanced the use of herbarium data in the improvement of knowledge about plants around the world. Essential contributions of herbarium data concern, for example, the assessment of species threat status and of their spatial distribution (Carrington et al. 2018), the testing of new hypotheses in biogeography, ecology and systematics, and the preparation of field expeditions (Lavoie 2013).

Herbaria data have been essential to improve our understanding of the biodiversity of the FOTs (Le Bras et al. 2017). They were key in supplying valuable information to TAXREF (Gargominy et al. 2020), and listing all species located in French mainland and the FOTs. TAXREF currently contains 17 plant phyla and more than 40,000 accepted names. It also contains information on the distribution, endemic status, and habitat of these species. However, work still remains to be done to reach a complete checklist of the flora of these territories.

In order to provide a state of knowledge of plant endemism in the FOTs using the most recent information and data, through an update of the TAXREF register, we initiated a project entitled "Flore Endémique des Territoires d'Outre-Mer" (FEnTOM). We present here an analysis of all known endemic spermatophytes, pteridophytes and bryophytes present in the FOTs as well as information on the occurrences, taxonomy, floristic status, and regional and global IUCN threat statuses when available. We used TAXREF as a starting point for our work and we mobilized data from the Paris Herbarium (vascular plants in P and bryophytes in PC), floras and checklists of overseas territories, and the expertise of botanists around the world to obtain the most complete dataset possible. This study not only provides the most up-to-date picture of the flora of FOTs; it also identifies gaps in knowledge on which future research efforts in systematics, ecology and conservation could focus.

Methods

Geographic scope

The FEnTOM dataset has been built from TAXREF and covers all French Overseas Territories (Fig. 1 and Table 1):

- *Pacific Ocean*: New Caledonia, Wallis and Futuna, French Polynesia, Clipperton

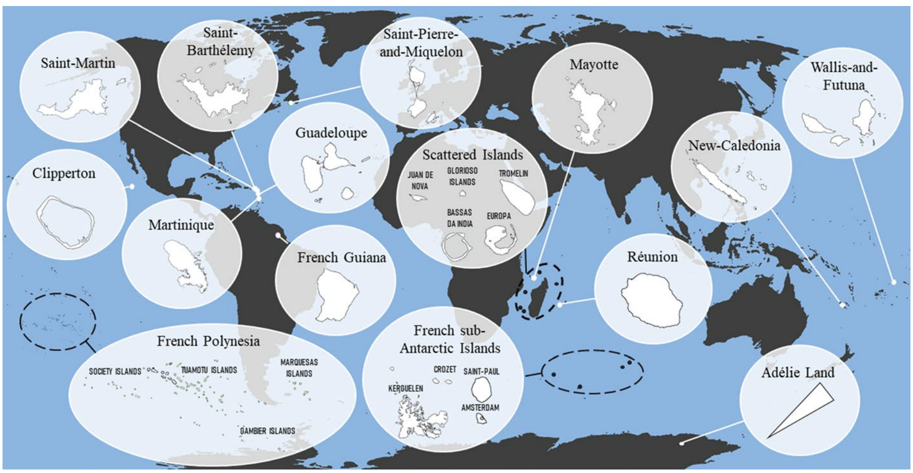


Fig. 1 Map of the French Overseas Territories (FOTs)

- *Indian Ocean*: Réunion, Mayotte, French sub-Antarctic islands, Scattered Islands,
- *Atlantic Ocean*: Guadeloupe, Martinique, Saint-Pierre-and-Miquelon, Saint-Martin, Saint-Barthélemy
- *Continental areas*: French Guiana (South America), Adélie Land (Antarctica)

The FEnTOM dataset compiles data for strict and regional endemism (also called subendemism in TAXREF and in this paper) for tracheophytes and bryophytes. Strict endemism to a territory refers to plants which are found only on this single territory and regional endemism is defined as the occurrence of species in a larger region corresponding to a well-defined ecological, environmental or geographic unit (e.g. an archipelago). Regional endemism for each territory is described in Table 1, following its definition in TAXREF. Endemism was assessed at the family, genus, species and infra-specific levels.

The TAXREF register

The TAXREF register is aimed at listing and classifying all species (bacteria, fungi, plants and animals) present in the French metropolitan and overseas territories (Gargominy et al. 2020). Data in TAXREF are presented as a scientific name associated to an identification, the name of the author, a taxonomic rank and validity (i.e. accepted name, basionym, and synonyms), the habitat in which the species occurs, as well as a biogeographical status. The TAXREF register is associated to a web-service with public access (API; https://taxref.mnhn.fr/taxref-web/api/doc) which provides the following information about each taxa: a detailed taxonomy, the conservation programs which include the taxa, the history of changes the taxa has undergone in TAXREF, literature references, traits, photos, protection status, and information about its ecology (phenology, interactions). These data are also freely accessible online from the website of the "Inventaire National du Patrimoine Naturel" (https://inpn.mnhn.fr/) and the Global Biodiversity Information Facility (GBIF, https://dx.doi.org/10.15468/vqueam). The taxonomic register can be downloaded in text format (https://inpn.mnhn.fr/telechargement/referentielEspece/referentielTaxo) as well as web-semantic triple store (http://agroportal.lirmm.fr/ontologies/TAXREF-LD). Three types of source data are used in TAXREF. The core dataset is compiled from local (e.g. Florical for plants of New Caledonia, http://publish.plantnet-project.org/project/florical_fr), regional (e.g. EuroMed for European and Mediterranean plants, https://www.emplantbase.org/home.html), global (Tropicos from the Missouri Botanical Garden, https://www.tropicos.org) databases (see also the main references used in Appendix 1). An accepted name or a synonym is included in TAXREF only on the basis of an accepted publication. For plants, 127,000 and 160,000 links exist between TAXREF and local flora and global plant databases, respectively. Second, some data are compiled directly from the scientific literature. Third, TAXREF uses data from groups of experts. Taxonomists work at improving taxonomy and classification, and bring their expertise about occurrences of the TAXREF data.

Revision of endemism in overseas territories

From TAXREF (version 13 accessed 12/2019), we downloaded the most recent data about endemic spermatophytes, pteridophytes and bryophytes in the French overseas territories in order to check, revise and update them. This work involved local and international participants from museums, research institutes, botanical conservatories and Non-Governmental

Organizations. First, we looked for specimen of overseas endemic species in Paris herbarium. Although herbaria are widespread (Thiers 2016), the Paris herbarium is one of the most important herbaria in the world in term of number of specimens. Around 8 million specimens have been gathered for more than three centuries and many belong to species endemic from overseas territories (Le Bras et al. 2017). Indeed, in addition to holding types from these territories, the Paris herbarium also keeps many other specimens collected by botanists either from the Museum or from the international community and sent to the Museum as duplicates. Ninety nine percent of the specimens are linked to one (the herbarium sheet) or more images (e.g. pictures of plants in nature, or microphotographies of organs), and 16% have field-collecting information available (Le Bras et al. 2017). Collection names for tracheophytes is titled “P” and collection name for bryophytes (as well as algae, lichens and fungi) is “PC”. These data are freely searchable online via a web interface linked to Sonnerat (https://science.mnhn.fr/institution/mnhn/item/search). Herbarium specimens enabled taxonomic checks and determination of endemic status of plants. For example, we identified species defined as endemic from a territory but for which we found an herbarium specimen outside this given territory. The endemic status of these species was then checked thanks to literature, expert knowledge and global biodiversity databases. For species of interest whose field-collecting information was missing in the Herbarium database, we (i) directly searched for them in the physical collections of Paris or (ii) used a participatory science program called “Les Herbonautes” from the RECOLNAT infrastructure that allows the databasing of herbarium sheets from images available online (Rouhan et al. 2016). This program was used to database data of endemic species in French Polynesia, the French Antilles (Guadeloupe, Martinique, Saint-Barthélemy, Saint-Martin), New Caledonia and Wallis and Futuna.

We also checked literature, Global Species Database and biodiversity portals (GBIF, Tropicos, Plants of the World Online) and worked with a network of experts to consolidate the taxonomic and biogeographic status of endemic species. These data enriched the FEnTOM dataset, and conversely the FEnTOM dataset allowed information in existing checklists to be updated. In order to account for statistics closest to the actual endemic species diversity, we decided to include in our list some unpublished names that are however currently handled by taxonomists working on those taxa and that will be validly published later by these authors, and unpublished names that are included in databases dealing with the flora of the FOTs [e.g. "Nadeaud" for French Polynesia, (Chevillotte et al. 2014); Taxonomic Indexes of Réunion, Mayotte, Scattered Islands, (Boullet and Picot 2020; Boullet and Dimassi 2020)].

Results

The FEnTOM dataset

In total, 5039, 345 and 465 names of endemic spermatophyte, pteridophyte and bryophyte taxa are recorded in the FEnTOM dataset (https://doi.org/10.5061/dryad.xpnvx0kfd). We recorded data about the distribution of endemic taxa: the endemic status (regional or strict endemism), the name of the island and islets where each species occurs, as well as a degree of uncertainty about the endemic status. Threat status defined by the IUCN global and territory-specific Red Lists are compiled from the latest assessment available. The FEnTOM dataset presents some information about the taxonomy of each endemic taxon: order, family, genus, species, infra-specific taxa. Finally, we added a column stating whether each species has at least one specimen incorporated into the Paris herbarium. The FEnTOM dataset includes two excel files (one for tracheophytes and one for bryophytes) representing current knowledge about the endemic flora of FOTs at the time when this paper was published. Yet most information is available on TAXREF-web which is regularly updated and can be found via the "*groupe opérationnel*" called the "*Flore endémique d'Outre-mer*" ("Endemic flora of overseas territories").

How many endemic species are there in the French overseas territories?

The FOTs are home to between 3587 (validated endemic status) and 3748 (endemic status including species with doubt) strict endemic species and infra-specific taxa of extant spermatophytes, 239 and 244 strict endemic species and infra-specific taxa of pteridophytes, 204 and 448 strict endemic species and infra-specific taxa of bryophytes. Full lists of these taxa are available in a dryad repository (https://doi.org/10.5061/dryad.xpnvx0kfd). This represents 94.3%, 98.4% and 99.6% of the spermatophytes, pteridophytes and bryophytes endemic to the French territories, including taxa for which there is still some doubt. The reasons of doubt most often correspond to (1) suspicion of the species' presence outside the French overseas territories, (2) insufficient taxonomic knowledge about the taxon, (3) possible misidentification, (4) insufficient description, and (5) significant contradictions between bibliographic sources. Several sources of doubt are possible for the same taxon, and institutions in some territories have sometimes described uncertainties about endemism very precisely, for example the *Conservatoire Botanique National de Mascarin* in its Taxonomic Indexes of Réunion (Boullet and Picot 2020) and Mayotte (Boullet and Dimassi 2020).

Spermatophytes

The territories with the highest numbers of strict endemic spermatophytes are New Caledonia (between 2570 and 2647 species and infra-specific taxa without and with doubt), French Polynesia [n = (439–450)], Réunion [n = (265–302)] and French Guiana [n = (199–210)] (Fig. 2a). These are also the territories with the highest rates of endemic taxa.

The geography of French Guiana and its inclusion into the Guiana Shield, however, makes it the overseas territory with the highest number of regional endemic species (= subendemic species): between 511 and 524 species and infra-specific taxa have a regional endemic status, which represents between 10.9% and 11.2% of the territory's native spermatophytes (Fig. 2b). Réunion has the highest proportion of subendemic spermatophytes, 17.8%, which includes 135 species and infra-specific taxa at the scale of the Mascarene archipelago. In Mayotte, 63 species are subendemic (endemic to the Comoro archipelago). Martinique and Guadeloupe have 154 and 156 subendemic species (endemic to the Lesser Antilles), i.e. 10.7% and 10.1% of the spermatophytes native to these territories, respectively (Fig. 2b). However, the endemic or taxonomic status is dubious for 47 of them in Martinique and 43 of them in Guadeloupe.

At a higher taxonomic level, 116 strict endemic genera have been identified (96 in New Caledonia, 5 in French Guiana, 7 in French Polynesia, 7 in Réunion, 1 in French sub-Antarctic islands) as well as 33 subendemic genera (17 in French Guiana, 12 in Réunion, 2 in French Polynesia, 1 in Scattered Islands, 1 in French sub-Antarctic islands). There are 19 families for which 100% of the species present in the FOTs are endemic (e.g.

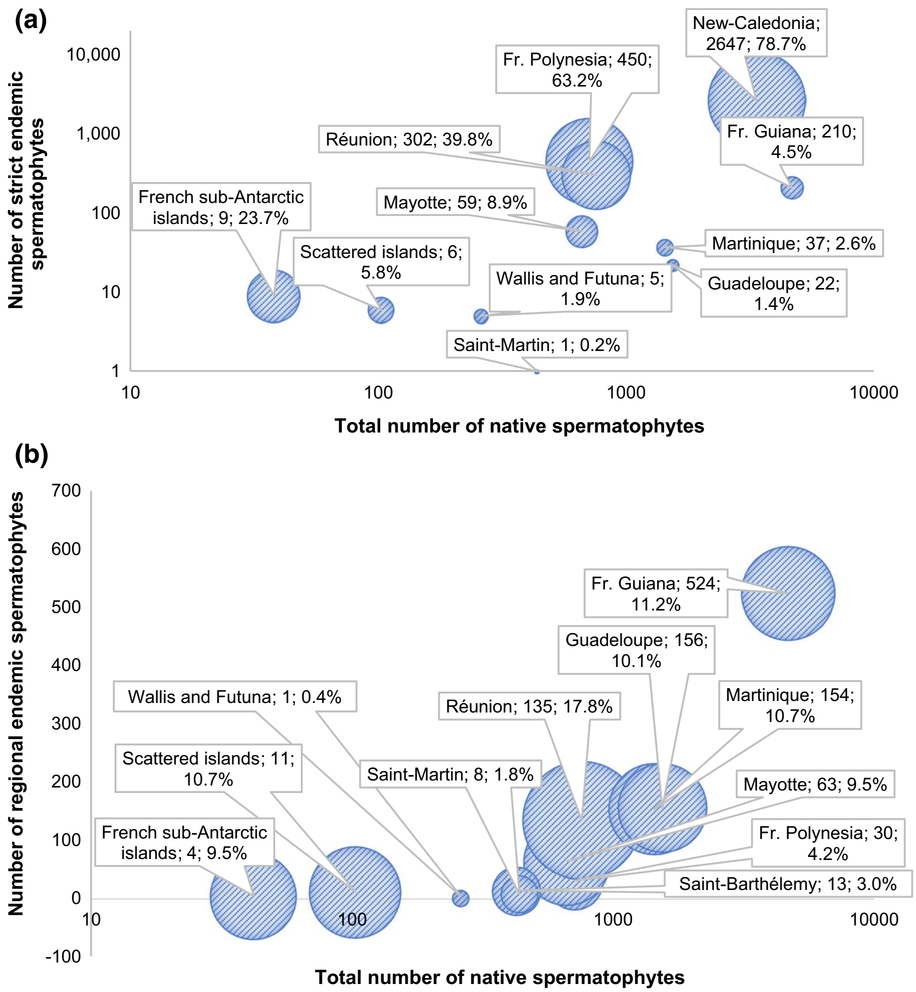


Fig. 2 Number and proportion of endemic taxa by territory for **a** strict endemic spermatophytes **b** regional endemic spermatophytes. These figures include specific and infra-specific levels. The number of endemics per territory is on the y-axis. The number of native species is on the x-axis. In Fig. 2a., these axes are represented in logarithmic scale for graphical purposes. The size of the circle is proportional to the percentage of endemic taxa per territory. In order to calculate this percentage, the number of native species in a territory was calculated as the sum of native but non-endemic species and infra-specific taxa present in the territory according to TAXREF and the number of endemic taxa (strict and regional) estimated from the FEnTOM dataset. The data tags represent the name of the territory, the number of endemic taxa and the proportion of endemic taxa per territory. Territories where no endemics are present are not represented (i.e. Clipperton, Saint-Pierre-et-Miquelon, Adélie Land)

Argophyllaceae, Phellinaceae, Winteraceae are among the most diverse of them). Most of these 19 families include species that occur outside the FOTs, with the exception of Amborellaceae, Oncothecaceae and Phellinaceae, which are endemic to New Caledonia.

The families of spermatophytes with the largest number of endemic species and infra-specific taxa are Rubiaceae, with 320 endemics out of 644 native species and infra-specific taxa (49.7%), Myrtaceae (300/437 species and infra-specific taxa; 68.9%), Orchidaceae (289/871 species and infra-specific taxa; 33.2%), Phyllanthaceae (196/271 species and infra-specific taxa; 72.3%) and Primulaceae (144/185 species and infra-specific taxa; 77.8%) (Fig. 3). The territories where Rubiaceae represent a high proportion of the endemic flora are New Caledonia (203 species and infra-specific taxa) and French Polynesia (79 species and infra-specific taxa). Many species of Myrtaceae are present in New Caledonia (276 species and infra-specific taxa), while the highest endemic species richness of Orchidaceae are found in New Caledonia (122 species and infra-specific taxa), Réunion (99 species and infra-specific taxa) and French Guiana (38 species and infra-specific taxa).

Pteridophytes

Seven territories are home to strictly endemic species and infra-specific taxa of Pteridophytes: New Caledonia (between 106 and 109 species—2 infra-specific taxa), French Polynesia (96 species), Réunion (21 species—4 infra-specific taxa), French Guiana (8 species), Guadeloupe (2 species), Mayotte (1 species) and the French sub-Antarctic islands (1 species) (Fig. 4a). There is a single genus of pteridophyte that is strictly endemic and found in New Caledonia (*Stromatopteris*, Gleicheniaceae). The highest species richness of regional endemic pteridophytes is found in Guadeloupe which hosts 34 species and 2 infra-specific taxa (Fig. 4b), Martinique (28 species and 1 infra-specific taxa), Réunion (24 species and 4 infra-specific taxa) and in French Guiana (20 species and 1 infra-specific taxa) (Fig. 4b). No genus of pteridophytes is regionally endemic. The family of pteridophytes with the most strictly endemic representatives are the Dryopteridaceae (41 species and infra-specific taxa) followed by the Polypodiaceae (34 species and infra-specific taxa) (Fig. 5).

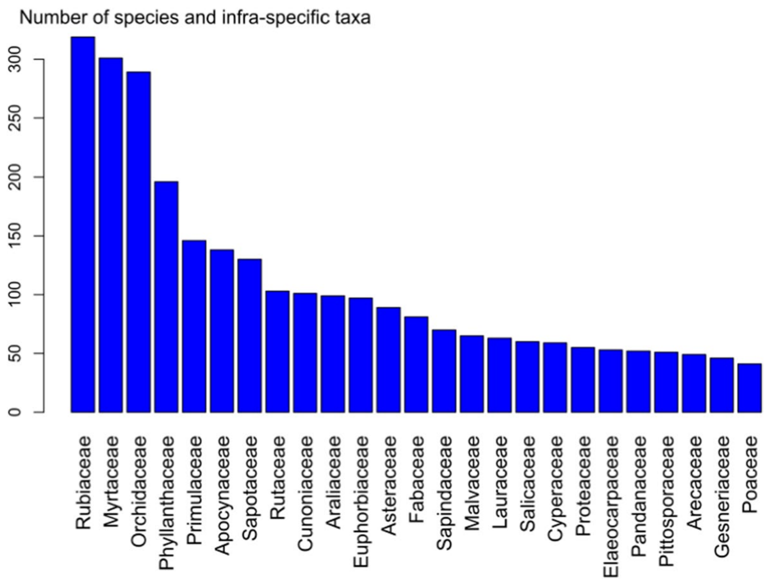


Fig. 3 Number of strict endemic species and infra-specific taxa per spermatophyte families (25 richest families)

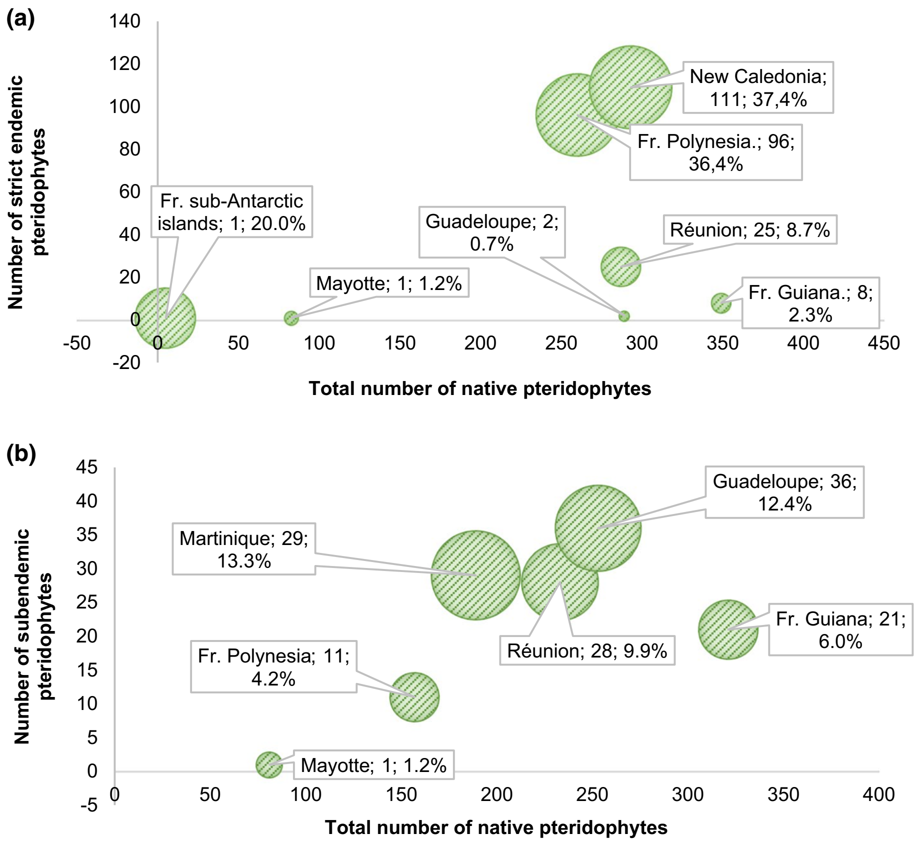


Fig. 4 Number and proportion of endemic taxa by territory for **a** strict endemic pteridophytes **b** regional endemic pteridophytes. These figures include specific and infra-specific levels. The number of endemics per territory is on the y-axis. The number of natives per territory is on the x-axis. The size of the circle is proportional to the percentage endemic taxa per territory. In order to calculate this percentage, the number of native species in a territory was calculated as the sum of native but non-endemic species and infra-specific taxa present in the territory according to TAXREF and the number of endemic taxa (strict and regional) estimated from the FEnTOM dataset. The data tags represent the name of the territory, the number of endemic taxa and the proportion of endemic taxa per territory. Only territories where endemics are present are represented

Bryophytes

New Caledonia has the highest endemic richness of bryophytes, i.e. 347 endemic species and infra-specific taxa although only 154 have a confirmed endemic status (Fig. 6). Réunion is home to 74 endemic species and infra-specific taxa (28 have a confirmed status), the French sub-Antarctic islands hosts 15 endemic species (14 confirmed), Mayotte has a richness of 7 strict endemic species (2 confirmed), Guadeloupe 3 species (all confirmed, Gradstein and Lavocat Bernard 2020), Martinique 1 species (confirmed), French Polynesia hosts 1 single strict endemic species but its endemic status remains to be confirmed (ref dryad). Finally, no strict endemic species have been recorded in French Guiana, Wallis and Futuna, Martinique, Adélie Land, Clipperton, Saint-Pierre-et-Miquelon, Scattered Islands. Regional endemism is complex to study because of the high dispersal capacity of

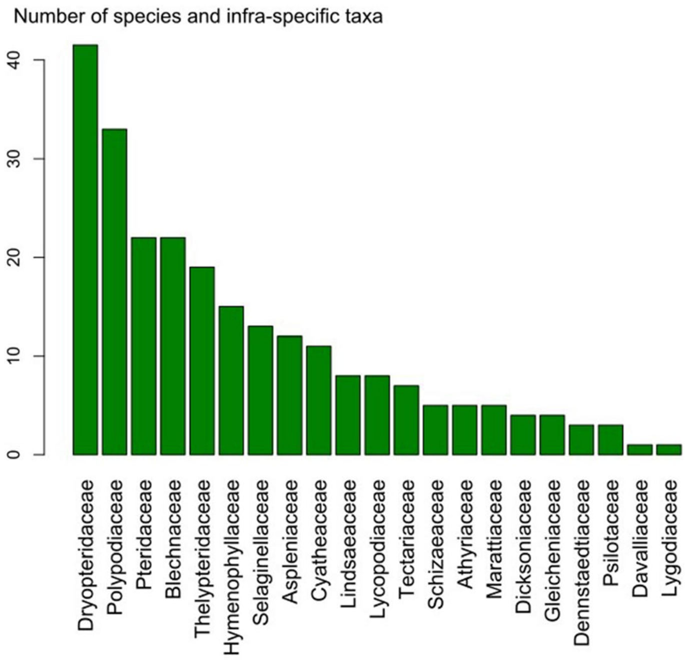


Fig. 5 Number of strict endemic species and infra-specific taxa per pteridophytes families

bryophytes, and only 1 species in Martinique and Guadeloupe, and 5 species in the French sub-Antarctic Islands would be possible regional endemics. Among bryophytes, strict endemic species belong to 68 different families, the most represented being Lejeunaceae (43 species), Dicranaceae (42 species), Lepidoziaceae (38 species), Lophocoleaceae (35 species) Frullaniaceae (32 species), Sematophyllaceae (23 species) (Fig. 7). This richness by family is mainly due to endemic species found in New Caledonia; since they make 90% of all the endemic Lejeuneaceae species of the TOM, 79% of the Dicranaceae, 97% of the Lepidoziaceae, 97% of the Frullaniaceae, 87% of the Sematophyllacieae. The dominant families in Réunion are Dicranaceae (9 species), Pterobryaceae (5 species), Pylaisiaceae (5 species) while the French sub-Antactic islands are home to a majority of Sphagnaceae (5 species), and the family most represented in Mayotte is Hypnaceae (2 species).

Ilustrations of some endemic spermatophytes, pteridophytes and bryophytes are provided in Fig. 8.

Threatened endemic species

Currently, only a few FOTs have a IUCN territory-specific Red List for vascular plants: Martinique (UICN France et al. 2013a), Guadeloupe (UICN France et al. 2019), French Polynesia (UICN France et al. 2015), New Caledonia (Endemia and RLA Flore NC 2019), Réunion (UICN France et al. 2013b), Mayotte (UICN France et al. 2014). Concerning endemic spermatophytes, 886 are threatened with extinction Critically Endangered (CR), Endangered (EN), Vulnerable (VU)] representing 51.6% of the species

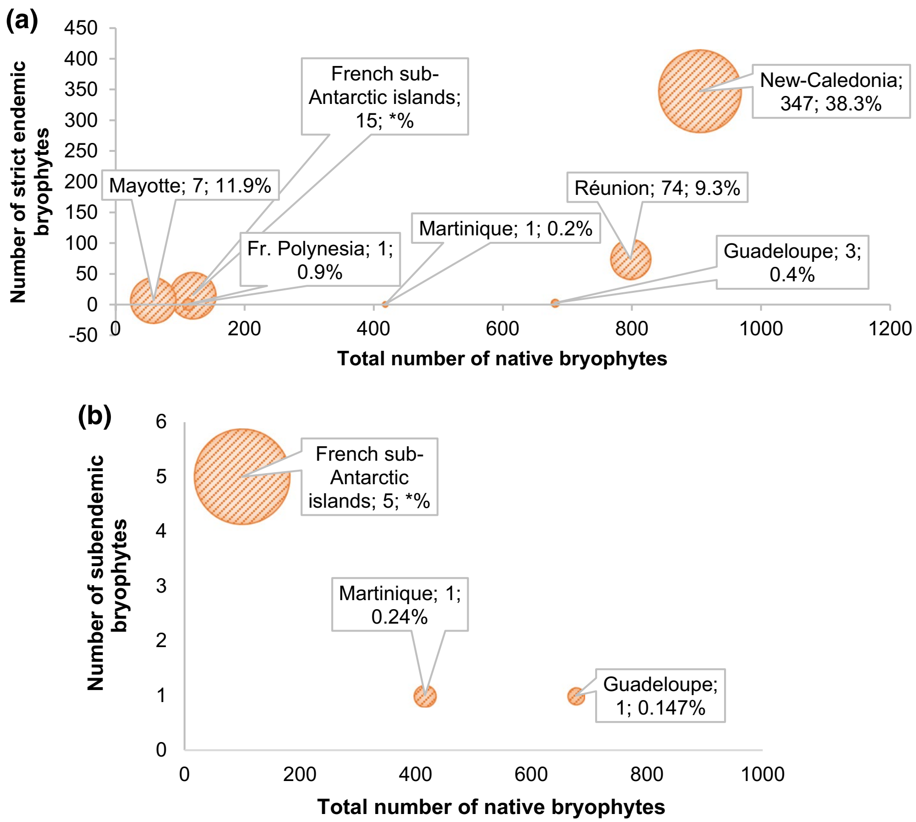


Fig. 6 Number and proportion of endemic taxa by territory for **a** strict endemic bryophytes **b** regional endemic bryophytes. These figures include specific and infra-specific levels. The number of endemics per territory is on the y-axis. The size of the circle is proportional to the percentage of strict endemic taxa per territory. In order to calculate this percentage, the number of native species in a territory was calculated as the sum of native but non-endemic species and infra-specific taxa present in the territory according to TAXREF and the number of endemic taxa (strict and regional) estimated from the FEnTOM dataset. The data tags represent the name of the territory, the number of endemic taxa and the proportion of endemic taxa per territory. Only territories where endemics are present are represented.*data on native moss of French sub-Antarctic islands and French Polynesia have not been compiled into TAXREF so far

assessed, and among which 267 are Critically Endangered (Fig. 9). Ten strict endemic spermatophytes are extinct and one is extinct in the wild, moreover three additional species in New Caledonia have been assessed as EX by the global Red List but not by territory specific Red Lists. The highest number of strictly endemic species under threat was observed in New Caledonia (446 spermatophytes and 4 pteridophytes). Other regions with a large number of endemic threatened species are French Polynesia (302 spermatophytes and 26 pteridophytes) and Réunion (87 spermatophytes and 3 pteridophytes). The highest proportion of endemic spermatophytes and pteridophytes under threat was observed in Mayotte (73.8%) but the highest number and proportion of critically endangered strictly endemic spermatophytes is in French Polynesia (122; 28.2%). Moreover, 100% of the endemic spermatophyte species found in the Red List of Martinique are threatened, although this proportion is probably due to the age of the IUCN assessments

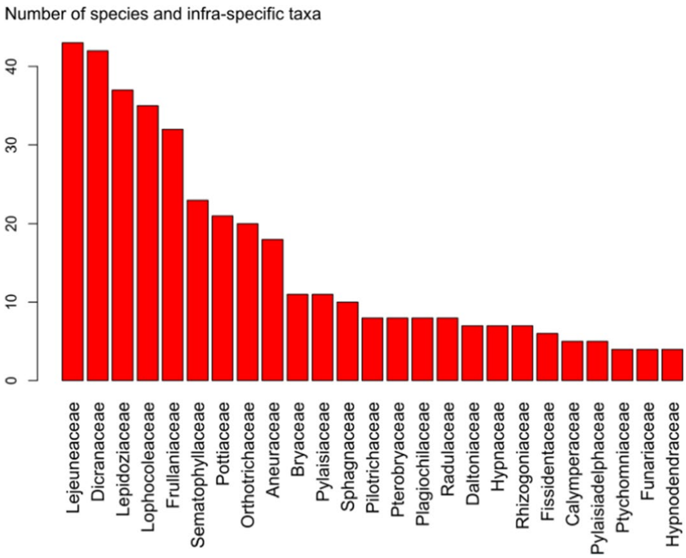


Fig. 7 Number of strict endemic species and infra-specific taxa per bryophytes families

Fig. 8 Some endemic plant species from the FOTs. **a** *Pseudocentrum guadalupense*; **b** *Macromitrium cardotii* **c** *Heterochaenia fragrans*; **d** *Sclerotheca raiateensis* **e** *Dicnemon planifolium* **f** *Megalastrum taafense*

and the low number of endemic species assessed (8 species). One hundred and thirteen endemic spermatophytes at the regional level are also threatened, which represents about 33.1% of the subendemic species assessed). Among them 30.2% are Critically Endangered (34 species). In Réunion island 1 subendemic spermatophyte is extinct, 5 are regionally extinct and 1 pteridophyte is regionally extinct. This is the only territory in which subendemic species have been recorded as extinct.

According to territory-specific Red List estimates, Rubiaceae strict endemic species are the most threatened, i.e. 112 species (61% of all Rubiaceae endemic species assessed), including 49 critically endangered (CR), 47 endangered (EN) and 16

Fig. 9 Number and proportion of species and infra-specific taxa in each threat status category for **a** strict endemic spermatophytes **b** regional endemic spermatophytes **c** strict endemic pteridophytes **d** regional endemic pteridophytes. Territories without endemic taxa assessed in IUCN Red Lists are not represented. *Extinction of *Galactia nummularia* in Saint-Martin was reported in Humphreys et al. (2019)

vulnerable (VU). The second family with the highest number of threatened species is Orchidaceae, of which 55 representatives are threatened (30.1% of strictly endemic orchids assessed). Besides, 36 endemic orchids are Data Deficient (DD), making it the family with the highest number of strictly endemic DD species.

Contribution of Paris herbarium to knowledge on endemism

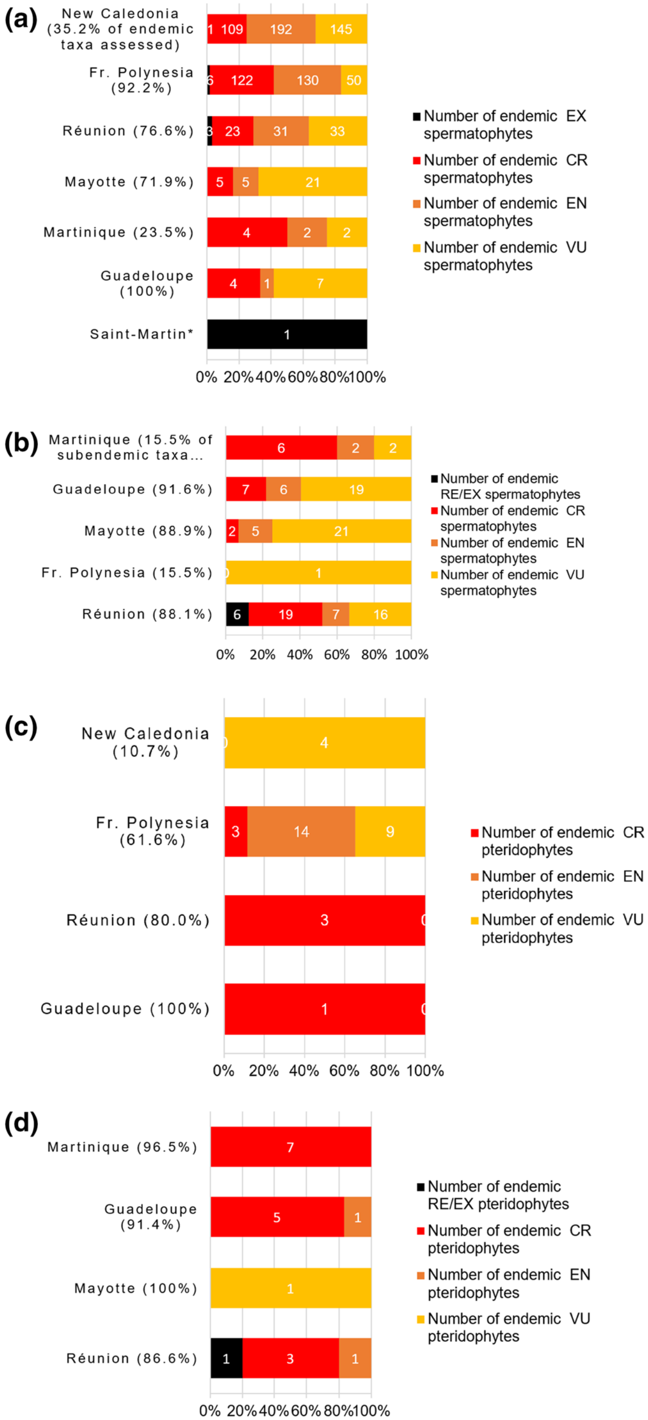
Among the strict endemic species of FOTs spermatophytes, 3126 taxa, or 83.2%, have at least one specimen in the Paris herbarium (including species of doubtful endemic status and extinct species but not synonyms). The largest proportion of strict endemic spermatophyte specimens are from New Caledonia, i.e. 83,302 specimens representing 81.8% of all strict endemic spermatophyte specimens from the FOTs. The Paris herbarium also hosts specimens of threatened species and 787 out of 886 (88.7%) threatened strict endemic spermatophytes are represented at least by one specimen in P, while 135 out of 188 (71.8%) DD species and 6 out of 11 (54.5%) extinct or extinct in the wild species are represented in P. Finally, 796 out of 987 (80.6%) subendemic spermatophytes have at least one specimen in P. For regionally endemic spermatophytes the proportions are 92.7%, 71.4% and 83.3% for specimens of threatened, data-deficient and extinct/regionally extinct species respectively. Most of these species present in P belong to the families Rubiaceae, Myrtaceae and Orchidaceae. An expected result since these are also the families with the highest number of endemic species in the overseas territories. Concerning pteridophytes, 153 out of 244 strict endemic species have a specimen in P (i.e. 62.7%), while this proportion is 95 out of 126 species for regional endemics (i.e. 75.4%). The territory with the best representation of endemic species in P are Wallis and Futuna and the Scattered Islands since, in the absence of endemic pteridophytes, all endemic spermatophytes have a specimen in P (Fig. 10). The other territories whose endemic flora is well represented in P are Réunion and the French sub-Antarctic Islands. On the contrary, French Polynesia and French Guiana for pteridophytes and Martinique, Saint-Martin, Saint-Barthélemy and French Guiana for spermatophytes have a lower proportion of endemic species and infra-specific taxa that are present in P (Fig. 10).

Bryophyte collections (collection PC) still have a high proportion of specimens to be digitized and databased, but a majority of types are already available in Sonnerat (34,770 specimens have been identified as types). The proportion of endemic species that have been located in PC and that have been databased is 34.8%, indicating the important effort of databasing of the collections that remains to be done.

Discussion

The flora of the French Overseas Territories

FOTs are home to the vast majority of the French endemic tracheophytes and bryophytes. As a result of this study, 3748 strict endemic spermatophytes, 244 strict endemic


(a)
New Caledonia (35.2% of endemic taxa assessed)
Fr. Polynesia (92.2%)
Réunion (76.6%)
Mayotte (71.9%)
Martinique (23.5%)
Guadeloupe (100%)
Saint-Martin*
1 109 192 145
6 122 130 50
3 23 31 33
5 5 21
4 2 2
4 1 7
1
0% 20% 40% 60% 80% 100%
Number of endemic EX spermatophytes
Number of endemic CR spermatophytes
Number of endemic EN spermatophytes
Number of endemic VU spermatophytes
(b)
Martinique (15.5% of subendemic taxa...
Guadeloupe (91.6%)
Mayotte (88.9%)
Fr. Polynesia (15.5%)
Réunion (88.1%)
6 2 2
7 6 19
2 5 21
1
6 19 7 16
0% 20% 40% 60% 80% 100%
Number of endemic RE/EX spermatophytes
Number of endemic CR spermatophytes
Number of endemic EN spermatophytes
Number of endemic VU spermatophytes
(c)
New Caledonia (10.7%)
Fr. Polynesia (61.6%)
Réunion (80.0%)
Guadeloupe (100%)
4
3 14 9
3
1
0% 20% 40% 60% 80% 100%
Number of endemic CR pteridophytes
Number of endemic EN pteridophytes
Number of endemic VU pteridophytes
(d)
Martinique (96.5%)
Guadeloupe (91.4%)
Mayotte (100%)
Réunion (86.6%)
7
5 1
1
1 3 1
0% 20% 40% 60% 80% 100%
Number of endemic RE/EX pteridophytes
Number of endemic CR pteridophytes
Number of endemic EN pteridophytes
Number of endemic VU pteridophytes

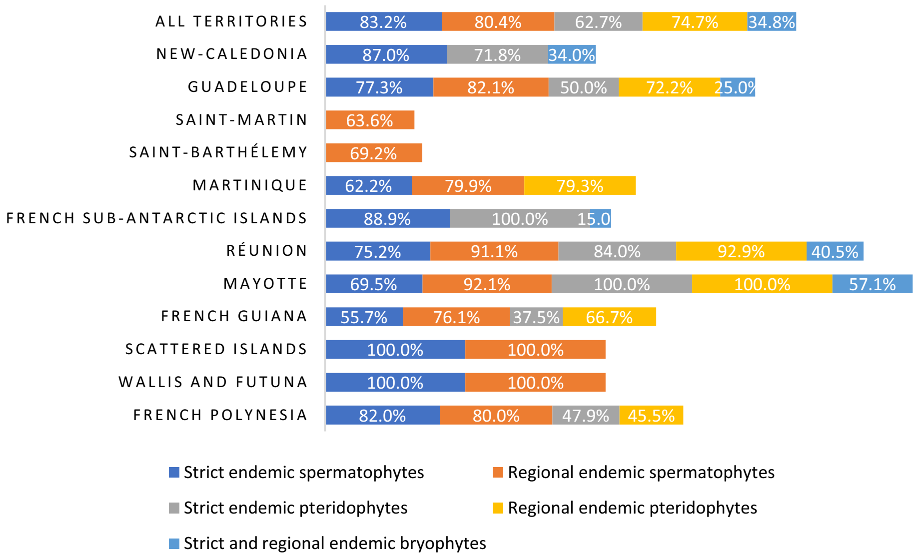


Fig. 10 Proportion of strict endemic and regional endemic taxa having a specimen in P and PC herbaria

pteridophytes, and 448 strict endemic bryophytes have been recorded in the overseas territories. Although some new endemic species of tracheophytes are regularly described, we have questioned the endemic status of many others, because of occurrences discovered in other territories, or because of taxonomic changes. Thus, doubts remain about the endemic status of 566 species. In particular, doubt about endemism or taxonomy has been identified for about half of the bryophyte species and infra-specific taxa. In proportion 94.3%, 98.4% and 99.6% of spermatophytes, pteridophytes and bryophytes endemic to France (including taxa for which a doubt remains) are found overseas. High rates of endemism are observed in these territories because all but two are islands which are systems where evolutionary and ecological processes are at the origin of a high number of endemic species, for example due to past extinctions on the mainland or high speciation rates triggered by isolation (Gillespie and Roderick 2002). Especially, for very remote islands, there are so few colonists to settle that speciation is expected to be the main process for filling the niche space (Emerson and Gillespie 2008). Yet, Clipperton Island and Saint-Pierre-and-Miquelon archipelago do not have endemic species, the first, despite its isolation for edaphic reasons (coral sands and gravel) and submersion by waves (Jost et al. 2019) and the second because of its proximity to the Canadian coast. Saint-Pierre-et-Miquelon however supports the only boreal forest of the FOTs (Gallo 1949). Among spermatophytes, the families Rubiaceae, Orchidaceae and Myrtaceae have the highest proportion of endemic species, mainly due to their high richness in New Caledonia, French Polynesia and Réunion. The territory with by far the highest number and proportion of endemic species is New Caledonia, which is home to 2647 endemic spermatophytes, representing 78.7% of the territory's native taxa. In addition, Kier et al. (2009) also identified New Caledonia as the territory with the highest richness in endemism (an index combining taxon richness and endemism) in vascular plants worldwide. The high rates of endemism in New Caledonia are due to local evolutionary radiations and in particular to the adaptation of species following their colonization of the territory, for example because of metal-rich but nutrient-poor soils, as well as to the geographical, ecological and environmental conditions that allowed species to survive while extinctions were taking place on the continent (Grandcolas et al. 2008). New Caledonia is also the largest island of the FOTs and is isolated from all other land masses, which are well-known factors promoting endemism (MacArthur and Wilson 1967). Other islands with high levels of endemism are French Polynesia and Réunion, which are home to 450 (63.2% of spermatophytes) and 302 (39.8%) endemic spermatophyte species, respectively. A remarkable characteristic of French Polynesia is that it is divided into several archipelagos and a multitude of small islands and that many species are endemic to an archipelago or even a single island (Florence 1997, 2004; Lorence and Wagner 2019, 2020). French Polynesia is also a very remote archipelago as the closest large landmass is located at more than 5400 km. Strict endemic pteridophytes are much less numerous, i.e. 244 in total, and are mostly found in New Caledonia (n = 111), French Polynesia (n = 96) and Réunion (n = 25). This is probably due to the dust-like spores of ferns that have stronger dispersal abilities, through air currents, that facilitate species arrival and successful colonization, and ultimately slow down the speciation process (Smith 1972). Similarly, wind-dispersal is commonly known for bryophytes, for which New Caledonia is the territory with the largest number of endemic taxa, i.e. 347 species and infra-specific taxa as well as 3 genera. New Caledonia is also one of the territories with the highest concentration of bryophytes worldwide (Konrat et al. 2008). However, the bryophyte flora of neighboring Vanuatu Islands has been poorly prospected and it is therefore likely that some of New Caledonian endemic species are actually growing also on these islands. The two other territories with the highest number of endemic species are Réunion (74 species) and the French sub-Antarctic Islands (15 species). Like New Caledonia, Réunion is among the territories with the highest number of bryophyte species per km^2 (von Konrat et al. 2008). The high diversity of bryophytes in Réunion is explained in particular by its position in the subtropical sector, a strong altitudinal gradient, very high rainfall and relative proximity to the main source regions (East Africa, Madagascar), and an important sampling effort (Ah-Peng et al. 2010). In the French sub-Antarctic islands, endemism could be due to long-distance dispersal followed by recent diversification due to the remoteness and young age of these islands but also to poor sampling effort in neighbor territories that could decrease the number of strict endemics but increase the number of regional endemics (Flatberg et al. 2011).

However, endemism is sometimes more representative of biogeographic patterns and processes when measured at a regional scale (e.g., at the scale of one or more archipelagos) rather than at the scale of a single island. Indeed, for some areas, assessing regional endemism is necessary to explain how the geography, geology, climate or history of the region have shaped its biodiversity (Norder et al. 2018). For example, a territory with high regional endemism for spermatophytes is French Guiana (524 species), due to its inclusion in the Guiana Shield, which has a specific geology, such as widespread large granite-greenstone terrains, and is isolated from other territories by major rivers such as the Amazon (Gibbs and Barron 1983). Martinique, Guadeloupe, Saint-Martin, Saint-Barthélemy also host a greater number of subendemic species compared to strict endemics due to their belonging to the Lesser Antilles and their proximity to other islands. In particular Guadeloupe and Martinique are home to the highest proportion of subendemic pteridophytes in the FOTs. However, the assessment of regional endemism raises several difficulties. In the case of Saint-Martin the island is shared by France and the Netherlands, so that endemics from the Dutch part were not accounted for in our checklist due to the choice to define endemism at the country level. Yet it is likely that species observed on the Dutch side also occur on the French side due to similar habitats, for example *Rondeletia anguillensis* (Dr Franklin Axelrod, pers. com). As for Wallis and Futuna it has only five strict endemic seed plants but probably shares several regional endemic species with the neighboring archipelagoes of Samoa and Tonga which have not yet been published. Regional endemism has been little studied for bryophytes, but it is likely that many species of subendemic bryophytes will be found in the future because of their generally high dispersal capacity which allows them to colonize several territories and the current low sampling efforts in some neighboring territories (see above).

Due to the exceptional floristic diversity of the FOTs, and in the current context of the sixth major extinction and France's international commitments (Aichi objectives to stop biodiversity erosion, https://www.cbd.int/sp/targets/), it appears urgent to develop actions concerning these French endemic species. In this sense, knowledge of the flora of the overseas territories appears fundamental to enable the preservation of this natural heritage for which France is responsible. Moreover, the new data acquired during this study contribute to the effort to improve the inventory of plants at a global scale as well as Red Listing. A great deal of knowledge on the endemic flora of the FOTs has recently been acquired (e.g., Carrington et al. 2017,2018; Jost et al. 2019; Barthelat 2019; Boullet et al. 2018; Gradstein and Lavocat Bernard 2020) and this knowledge is continually evolving. In New Caledonia, Gâteblé et al. (2018) estimated that one new endemic plant was discovered per month. In 2019, eight new endemic species were discovered while four species thought to be extinct were rediscovered (Endemia and RLA Flore NC 2019). In order to have an accurate estimate of endemism in the FOTs, it is therefore necessary to continually update the data on endemism. To this aim, the checklist of FOTs compiled during this project is linked to the taxonomic register TAXREF, which is regularly updated and can be accessed through the TAXREF-web back-office: https://taxref.mnhn.fr. Although the endemism of the flora of the FOTs is now better known, this study also made it possible to identify certain gaps, such as the fact that 566 taxa still have a dubious endemic status, as well as solutions to fill them in the short or medium term.

Threats and conservation

Nearly 46% and 38% of the endemic spermatophytes and pteridophytes of the FOTs have been assessed. These rates are much higher than the global vascular plant coverage, i.e. 10.5% (6% for pteridophytes) (Nic Lughadha et al. 2020), possibly due to the higher interest in red listing endemic plants but also to the important regional efforts to assess extinction risks of plants in the FOTs. However, not all FOTs have a regional IUCN Red List, and where one exists, it is sometimes old. In total, 6 territories have been subject to a territory-specific assessment of the threat status of their endemic flora by the IUCN (UICN France et al. 2013a, b, 2014, 2015, 2019; Endemia and RLA Flore NC 2019) but some preliminary lists used by conservationists also exist for bryophytes in Réunion (Ah-Peng et al. 2012) and tracheophytes in Scattered islands (Boullet et al. 2018). These assessments are highly valuable tools as they cover a much higher proportion of endemic species compared to the global IUCN Red List. In addition, territory-specific Red Lists are often more up to date than the global Red List. As an example, 6 endemic species of French Polynesia have a status "Extinct" in the territory-specific Red List but only one of them is considered extinct in the global Red List (UICN France et al. 2015). 51.6% of extant endemic spermatophytes assessed by the IUCN are threatened with extinction, of which 30.1% are CR, 40.7% EN, and 29.2% VU. In comparison, 30.1% of the endemic species present in the metropolitan area are threatened with extinction (UICN et al. 2018) and 43.7% of vascular plant species are threatened globally (Nic Lughadha et al. 2020). Regarding ferns and lycophytes ('pteridophytes'), 36.9% of strict endemics with sufficient data are threatened with extinction, which is lower than the 44% of species threatened at a world scale (Nic Lughadha et al. 2020). Eighteen endemic vascular plant species (17 spermatophytes, 1 pteridophyte) have been reported as extinct, regionally extinct or extinct in the wild. Yet habitat loss and degradation may cause an extinction debt, i.e. delayed extinctions, that could amplify this number (Kuussaari et al. 2009). The territory with the highest proportion of strictly threatened endemic species is Martinique (100%), but only 8 out of 37 endemic species have been assessed and this proportion probably reflects a lack of knowledge rather than the actual rate of threatened endemic species (pers. com. G. Viscardi). Excluding Martinique, Mayotte is the territory with the highest proportion of threatened endemic species, at 73.8%, and existing assessments in this territory cover more than 3/4 all endemic species. All the species described before 1950 in Mayotte were found again during a series of inventories carried out in the 2000s. This despite the fact that only 5% of the natural plant formations remain. This perhaps illustrates the fact that the degradation of natural formations preceded the first inventories (Pascal et al. 2001). Our study also highlights the need to consider not only the threats to strictly endemic species but also to endemic species at the regional level. Indeed, 33.1% of extant subendemic spermatophytes are threatened with extinction, of which 30.2% are Critically Endangered. Despite the fact that strict endemic taxa are the primary responsibility of each country where they occur, subendemic taxa may be considered as another priority. Indeed, if, from a global plant conservation perspective, the emphasis is not placed on protecting regional endemism, a significant proportion of these taxa could disappear and/or their populations could even be reduced. This regional endemism could be the focus of nature conservation collaboration between the countries involved. Among the bryophytes, although they have been included in the IUCN system, a single endemic species of FOTs has been assessed for its extinction status in the global Red List (*Nekeropsis pocsii* that was assessed as critically endangered in Mayotte in the year 2000) and none in territory-specific Red Lists (but see Ah-Peng et al. 2012). This is an important knowledge gap due to the vulnerability of bryophyte species to changes in environmental conditions and the many threats they may face (Désamoré et al. 2012). National Red Lists which have been published show that bryophyte flora is regularly being impoverished (Hallingbäck and Tan 2010). For example, in Europe 22.5% of bryophyte species are considered threatened (Hodgetts 2019). The checklist provided in this study could be used as a basis to evaluate bryophyte threat status and to the publication of a Red List assessment at the scale of overseas territories. Red Lists can be used to provide information on the conservation status of species, identify sites for the implementation of conservation actions, support conservation policies and management, assess the state of biodiversity, and monitor changes in this status over time. For all these reasons, it is important to be able to assess the extinction status of species in the FOTs. However, the remoteness of overseas territories implies that resources for biodiversity conservation are scarce and unequal relative to their exceptional biodiversity and the local and global threats it faces. As showed by Meyer et al. (2018), it is therefore necessary to build research programs dedicated to island terrestrial biodiversity conservation which are more concerted between researchers, managers and island local communities, and between different territories with similar issues. This would make possible the development of common strategies and would demonstrate the relevance of the knowledge issues and the importance for these ultramarine island territories at the national, biogeographic and international levels (Meyer et al. 2018). This paper falls in this context and made it possible to computerize all the herbarium specimens corresponding to species in danger of extinction or for which the status could not be evaluated due to a lack of data. In spite of uncertainties the use of herbarium data to assess extinction risks is “appropriate, necessary and urgent” (Nic Lughadha et al. 2019). In addition to contributing to extinction risk assessments, this type of data is also used to evaluate species distributions, their rarity, and the evolution of the flora of a territory over time. This is central in order to implement effective conservation planning, in particular the establishment of protected areas or of ex-situ conservation actions (Clubbe et al. 2020). Even though, the latter is not sufficient for biodiversity conservation, an adequate system of protected areas is one of its key foundation (Ibanez et al. 2019). For example, in New Caledonia, two studies 20 years apart (Jaffré et al. 1998 then Ibanez et al. 2019), have assessed the effectiveness of the protected areas of the time. Ibanez et al. (2019) concluded that even if some improvements had been made since the study by Jaffré et al. (1998) many shortcomings identified then were still unaddressed and the majority of the threatened species remained outside protected areas. These studies are only possible and relevant when based on the most up-to-date species lists available. This paper tries to accomplish that for the FOTs.

Contribution of herbaria to the knowledge of the flora of the French Overseas Territories

Herbaria have an undeniable contribution to knowledge on biodiversity (e.g., Bebber et al. 2010; Lavoie 2013; Le Bras et al. 2017; Heberling et al. 2019). According to Lavoie (2013) "*herbarium specimens could provide in the near future exciting new spatio-temporal perspectives that are currently unimaginable*". During the FEnTOM project the herbarium data used were mainly those of the Paris herbarium (P and PC). A large proportion of the endemic species of the FOTs have a specimen in P, around 75%, but including data from other herbaria (e.g. BISH http://nsdb.bishopmuseum.org/, PTBG https://ntbg.org/database/herbarium, US https://collections.nmnh.si.edu/search/botany/) and in particular herbaria in the overseas territories [e.g. French Polynesia (PAP) http://nadeaud.ilm.pf, Martinique (MAR), Guadeloupe (GUA), New Caledonia (NOU), French Guiana (CAY), Réunion (REU)], would in the future allow specimens to be obtained for an even larger proportion of the endemic species of the FOTs. These data have proved to be essential to confirm the presence of a taxa in a territory but also to review the status of endemism. Indeed, the existence of a specimen corresponding to a locality outside the accepted range of an endemic taxon is an indication of the possible questioning of its endemic status. In some cases, this may have been due to misidentification of the taxon or to errors in labelling or digitization of data. In other cases, the endemic status of the taxon has been directly questioned and, with the help of project collaborators, sometimes modified. However, some of the FOTs herbaria only contain specimens too ancient to represent the current state of plant diversity. It is necessary to make new collections to monitor the flora’s evolution (e.g., population size, distribution, new species description, threat status), understand the species’ response to environmental changes (e.g. phenological response to climate change), and help define conservation priorities. Especially, collect of recent and fertile specimens, as well as DNA extraction, would be of great help to taxonomists to better describe plant species, possibly discovering new ones, and revise their endemic status.

The databasing of herbarium data is particularly valuable for conducting new research. Lavoie (2013) was thus able to show that studies using collections available in digital format had access to 70 times more data than studies using collections that were not digitalized. Our study made it possible to computerize a significant proportion of the specimens of endemic species from the overseas territories (42%), many of them according to their

IUCN threat status. These new data allow a revision of the endemic status, as explained above, and sometimes a taxonomic revision. Moreover, these data become accessible to the whole scientific community, conservation professionals and amateur naturalists alike. However, there are still many specimens for which all the information contained on herbarium sheets has not been databased. In particular many bryophyte species, including some endemic ones, are not yet available in digital format. Consequently, although this study is a step forward in the assessment of endemism in French Overseas territories, there is still knowledge to be gained from herbarium data, which could help to update the FEnTOM dataset and support further conservation actions as well as the increase of inventory efforts and the implementation of new plant collections.

Appendix 1

Main data sources

FOT	Spermatophytes	Pteridophytes	Bryophytes
New-Caledonia	Munzinger et al. (2020)	Munzinger et al. (2020)	Thouvenot and Bardat (2010); Thouvenot et al. (2011)
French Polynesia	Chevillotte et al. (2019)	Chevillotte et al. (2019)	Söderström pers comm. (2020)
Wallis and Futuna	Meyer (2017)	Meyer (2017)	No data/unknown
La Réunion island	Boullet and Picot (2020)	Boullet and Picot (2020)	Gargominy et al. (2019)
Mayotte	Boullet and Dimassi (2020)	Boullet and Dimassi (2020)	Ah-Peng and Guérot (2019)
Eparses islands	Hivert and Cuidet (2020)	Hivert and Cuidet (2020)	No data/unknown
French sub-antarctic islands	Reichardt (1871); Hemsley (1885); Schenck and Schimper (1905); Wagstaff and Hennion (2007); Putten et al. (2010); Lehnebach et al. (2017); Timaná (2018); Timaná et al. (2019)	Sundue et al. (2010)	Flatberg et al. (2011); Ochyra et al. (2014); Váňa et al. (2014)
La Martinique	Stehlé (1939); Howard (1973); Howard (1979); Howard (1988); Howard (1989a; 1989 b); Fournet (2002a; 2002b); Acevedos and Strong (2012); Bernard et al. (2014); Baksh-Comeau et al. (2016); Judd et al. (2018); UICN Comité français et al. (2019); Ulloa et al. (2017); Viscardi (2020)	Bernard (2015); Viscardi (2020)	Lavocat-Bernard (2018)
Guadeloupe		Mickel (1997); Sundue (2010); Bernard (2010); Prado (2015); Ulloa et al. (2017)	Gradstein and Lavocat (2020)

FOT	Spermatophytes	Pteridophytes	Bryophytes
Saint-Barthélémy	ATE Saint Barthélemy (2020)	ATE Saint Barthélemy (2020)	No data/unknow?
Saint-Martin	Fournet (2002a; 2002b); Franklin S. Axelrod pers. comm. (2020)	Fournet (2002a; 2002b)	No data/unknown
French Guiana	Gargominy et al. (2019); Poncy pers comm., 2020	Gargominy et al. (2019); Poncy pers comm, 2020	Gradstein et al. (2001)
Clipperton	Jost and Meyer (2019)	Jost and Meyer (2019)	No data/unknown
Saint-Pierre and Miquelon	Etchebery et al. (2010)	Etchebery et al. (2010)	Etcheberry et al. (1987)

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Data availability Data are available in a dryad repository (https://doi.org/10.5061/dryad.xpnvx0kfd).

Code availability Not applicable.

Declarations

Conflict of interest Not applicable.

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