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An annotated checklist of rust fungi (Pucciniales) occurring in Portugal

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In this work we have retrieved and analysed data for 2319 occurrences of rust fungi from 246 Pucciniales taxa in Portugal based on 115 publications and our own surveys, totalizing 683 rust taxon-host taxon unique combinations. This list was updated according to current taxonomic framework and georeferenced using the GBIF's recommended methods. The present checklist includes host names, seasonality, life cycle stage, geographical distribution and comments. A list of rust fungi sorted according to their host plants was also prepared. Altogether, this provides a tool for diagnosis of rust fungi occurring in Portugal (and elsewhere in Europe), enabling to understand their spatio-temporal dynamics and to point out recent introduction of exotic species, along with situations of potential conservation value. Eleven species (*Puccinia addita*, *P. arnoseridis*, *P. avenae-barbatae*, *P. campanulae-herminii*, *P. ficalhoana*, *P. silenicola*, *Uromyces hippomarathricola*, *U. seselis*, *U. vulpiae*, *Aecidium umbilici* and *Uredo pallens*) were recorded only in Portugal and are not reported for decades, raising great concern about their true existence. Five species (*Puccinia jasmini*, *P. saniculae*, *P. tanaceti*, *Chrysomixa rhododendri* and *Naohidemyces vaccinii*) occur on endemic hosts whose populations are physically isolated from other hosts of the same rust species, mostly at the archipelagos of Azores and Madeira, illustrating scenarios where a speciation process may be occurring and thus urging the clarification of their taxonomic and ecological status, following the example of the Madeiran endemic *Dicheirinia maderensis*. The geographical position of Azores and Madeira highlight these territories as entry/detection points for new rusts in Europe, as exemplified by *Coleosporium asterum*, *Puccinia hemerocallidis*, *P. oxalidis*, *P. stenotaphricola* and *P. thaliae*. Additionally, the vast majority of quarantine rusts currently absent from Europe are present in the American continent and several of them (*Austropuccinia psidii*, *Cronartium* spp., *Gymnosporangium* spp., *Puccinia pittieriana* and *Thekopsora minima*) have suitable hosts in the Azores and Madeira. With a rust species:vascular flora ratio of 1:12.2, the Portuguese rust mycobiota can be considered well characterized. The proportion of number of species per genus/family in Portugal is similar to that found in other temperate countries, while tropical areas, and specially the neotropics, present the widest diversity.

Keywords: Basidiomycota, Urediniales, Azores, Madeira, Iberia

Rust fungi (Basidiomycota, Pucciniales) are strict biotrophic pathogens of vascular plants, most frequently with narrow host ranges, occurring on cultivated and non-cultivated plants. Those species infecting cultivated plants can pose phytopathological problems. On the other hand, rust species occurring only on non-cultivated plants may be of conservation concern. There are over 5000 rust species grouped in 13 families and ca. 120 genera (Cummins & Hiratsuka 2003), making this the largest order of phytopathogenic fungi and one of the most speciose orders of fungi (Aime et al. 2017). While ca. 40 % more new species are predicted to occur, particularly in tropical and sub-tropical regions (Cummins & Hiratsuka 2003), many of the species recognized have seldom been reported, raising concerns about their current conservation status.

Portugal is located in the Southwest of Europe, sharing biogeographic and climatic similarities with the Mediterranean basin, but linking with the Temperate Atlantic zone towards the Northwest of the country. The Portuguese archipelagos of Azores and Madeira, located respectively to the West (half way between Europe and America) and the Southwest of the mainland, are of biogeographical rele-

vance, as they may be natural or human-driven entry-points of exotic biological entities into mainland Europe.

In line with the mycological research taking place elsewhere in Europe during the 19th century, and recognising the biogeographic particularities of the Portuguese territory, foreign- and local-driven research initiatives have devoted attention to identify rust fungi occurring in this country. The earliest records of Pucciniales in scientific terms are compiled on the F. Welwitsch's herbarium, collected in Portugal during 1842–1850 (Berkeley 1853, Lagerheim 1889), covering 28 occurrences of 18 species. During the last quarter of the 19th century the series of publications *Contributiones ad floram Mycologicam Lusitaniae*, authored successively by F. Thümen, G. von Niessl and G. Winter, along with parallel initiatives by P. Mesnier, G. Lagerheim, J. Bresadola and P. Saccardo, recorded 120 ocurrences of 60 taxa, representing specimens collected mostly under the initiative of Moller, the director of the Botanical Garden of the University of Coimbra. The first years of the 20th century gave birth to a new series of publications, *Contributiones ad Mycofloram Lusitaniae*, under the initiative of J. Veríssimo de Almeida and E. Sousa da Câmara at Instituto Superior de Agronomia (Lisbon), in parallel with the surveys of C. Torrend mostly focused on the Beira Baixa and Setúbal/Lisbon regions and, for the first time, on the Madeira island. The first survey of rust fungi in the Azores had occurred a few years before, in 1897, by W. Trelease, followed by a report by M. Bensaúde on diseases of cultivated plants in the Azores, but subsequent surveys in both archipelagos only occurred in the late 1930s by G. Viennot–Bourgin and T. Arwidsson, in Madeira and Azores respectively. A total of 361 new records of 101 species were reported in the 1900–1936 period, leading to a compilation by Gonçalves da Cunha (1936b) listing 767 occurrences of 176 species. The prolific work by E. Sousa da Câmara continued with the creation of new series of publications (*Mycetes aliquot Lusitaniae, Fungi Lusitaniae, Species aliquae mycologicae Lusitaniae* and one specifically devoted to the Pucciniales, *Uredales aliquot Lusitaniae*), culminating in a posthumous check list (Câmara 1958) listing 1472 occurences of 235 taxa. The survey efforts in mainland Portugal continued during the 1950–1980s mostly by M.R. Dias, M.R. Lucas and M.C. Lopes, while a new surge occurred in the 1970–90s in the Azores and Madeira with H.B. Gjaerum, R. Dennis and B. Spooner. In the last decades, scientists have preferred to investigate mechanistic processes in detriment of more descriptive studies, leaving a gap in the knowledge on the current ecological status of several rust species. In order to contribute to update such knowledge, in this work we retrieved data from bibliographic references and from our own surveys, which records were updated in their current taxonomy and georeferencing localities.

Data and methods

For this study, a total of 118 bibliographic sources recording the occurrence of Pucciniales in Portugal were analysed and digitally catalogued in MS Excel, with information pertaining to the following Darwin Core terms (Wieczorek et al. 2015) collected: scientificName; higherClassification (and other information related to the taxon); basisOfRecord (including herbarium preserved specimens); identifiedBy; locationAccordingTo; decimalLatitude; decimalLongitude; geographic administrative units including country, municipality, locality; eventDate (year and month of collection); associatedTaxa (i.e., the actual host plant species for each record); lifeStage (spermagonia, aecia, uredinia, telia and/or basidia); associatedReferences (literature).

Georeferencing was performed following Chapman & Wieczorek (2006), using Google Maps to retrieve coordinates based on searches of record localities, complemented, when needed, by the use of the Portuguese gazetteer and online GIS tools provided by Centro de Informação Geoespacial do Exército, Portugal (http://www.igeoe.pt/igeoesig/).

Scientific names, both of the fungi and the host plants, were checked for potential synonyms in Index Fungorum/Species Fungorum (http://www.speciesfungorum.org/Names/Names.asp) and The Plant List (http://www.theplantlist.org/) web sites respectively. Ecological and taxonomic information on the host plants in Portugal were retrieved using the Flora–On web site (Flora-On 2014) and the Check list of Portuguese Flora (Menezes de Sequeira et al. 2011), respectively.

The full list of occurrences catalogued was published through GBIF as an occurrence dataset, available at https://doi.org/10.15468/rsw5cz (Talhinhas 2018). Based on this dataset, the checklist of rust fungi occurring in Portugal was prepared to be published through GBIF, in Darwin Core format, whichisavailableathttps://doi.org/10.15468/2j2nkd, including taxon information (core table) and occurrence and distribution extensions (Talhinhas 2018, Talhinhas et al. 2018). For each fungal species (or infraspecific taxon), the following elements are listed:

Synonyms: this accounts only for synonyms used in the consulted literature;

Life cycle: this information pertains to the species and not to the actual occurrences, but is supplied for a better understanding of the Life cycle stage/host-related information (Macrocyclic, heteroecious; Macrocyclic, autoecious; Microcyclic; Hemicyclic; Demicyclic, heteroecious; Demicyclic, autoecious);

Life stages and hosts: the host species (arranged by botanical families) according to the life cycle stage (aecidial and uredinial/telial); data on the target plant organs was very scarce, and therefore it was not listed;

Monthly distribution of occurrences: depicts the number of occurrences in each calendar month (January through to December), excluding naturally those records that do not have collection date; separated according to the aecidial and uredinial/telial stages for heteroaecious rusts;

Distribution: geographic distribution in mainland Portugal by Districts, and in Azores and Madeira by island;

Districts in mainland Portugal: Aveiro (Ave); Beja (Bej); Braga (Bra); Bragança (Bgç); Castelo Branco (CBr); Coimbra (Coi); Évora (Évo); Faro (Far); Guarda (Gua); Leiria (Lei); Lisbon (Lis); Portalegre (Ptg); Porto (Pto); Santarém (San); Setúbal (Set); Viana do Castelo (Via); Vila Real (VRe); Viseu (Vis);

Islands of the archipelago of the Azores (AZO): Corvo (Cor); Faial (Fai); Flores (Flo); Graciosa (Gra); São Jorge (Jor); Santa Maria (Mar); São Miguel (Mig); Pico (Pic); Terceira (Ter);

Islands of the archipelago of Madeira (MAD): Desertas (Des); Madeira (Mad); Porto Santo (PSa); Selvagens (Sel);

Occurrences URL: Identifier of the link of occurrences of the taxon in Portugal, as available through GBIF. This resource might be updated in the future with new occurrences. The occurrences dataset as of this article is the version 1.7, available at https://ipt.isa.ulisboa.pt/ipt_isa/archive.do?r=puccinialespt&v=1.7;

Notes: Includes comments on the frequency and chronological distribution of occurrences, but also on agronomical and/or ecological aspects of those occurrences when relevant;

References: cited literature pertaining to each taxon.

Additionally, a list of all rust species occurring in each host plant species is presented according to the fungal life cycle stage (Cummins & Hiratsuka 2003): spermagonia (0); aecia (I); uredinia (II); telia (III); basidia (IV).

In order to analyse the phytogeographic distribution of genera, their occurrence in 34 countries/regions from all continents was compiled from GBIF and other data sources (Supplementary Data 5). Data were analysed with descriptive statistical tools using Microsoft Excel and by Multivariate Analysis (Cluster Analysis and Principal Component Analysis) using NTSYSpc version 2.02h (Applied Biostatistics Inc.) as previously described (Talhinhas et al. 2006).

Results

A total of 2319 occurrences of Pucciniales fungi were recorded, 79 % of which from the mainland, 11 % from the Azores and 10 % from Madeira archipelagos (Fig. 1). Occurrences were recorded in all 18 Districts in Mainland Portugal and in all islands in the Azores and Madeira archipelagos, although they refer to only 230 of the 308 Portuguese municipalities, illustrating less surveyed areas namely in Trás-os-Montes, Alentejo and some parts of the Centre/North litoral (namely Leiria, Aveiro and Viana do Castelo). Nearly half of these records were collected between 1922 and 1953 (Fig. 2). Most records were obtained in spring (46 %), followed by summer (30 %), winter (13 %) and autumn (11 %).

The 2319 occurrences (Supplementary data 1 and 2) were attributed to 246 taxa in the order Pucciniales, comprising 239 species, three varieties and four formae speciales, representing 27 genera and

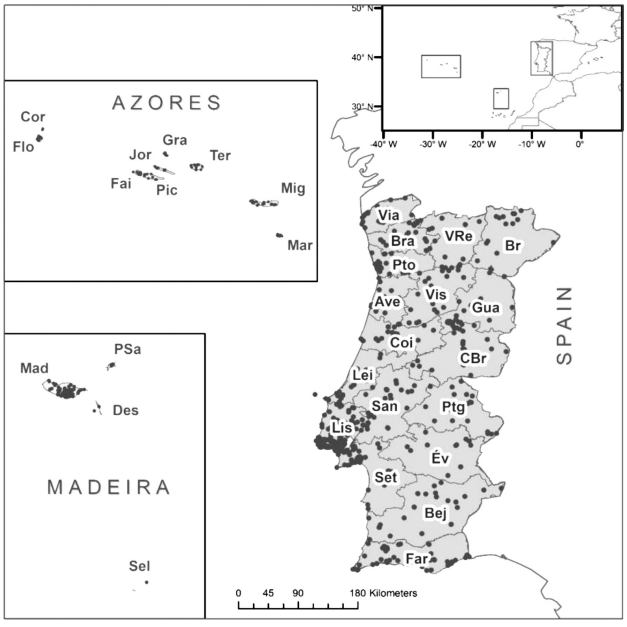

Fig. 1. Geographical distribution of rust occurrence records in Portugal.

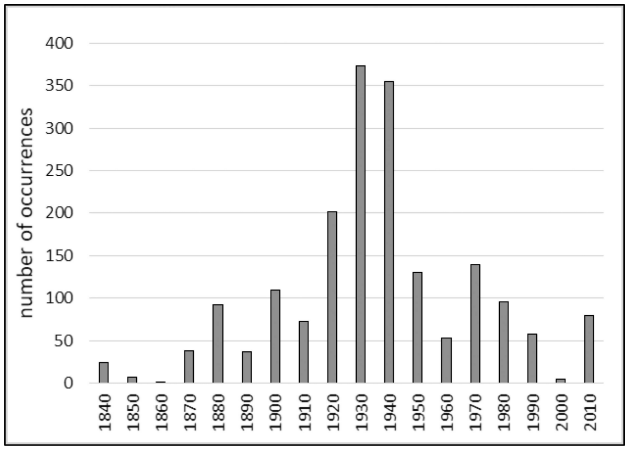

Fig. 2. Number of occurrences of rust fungi recorded in Portugal per decade (beginning in the year shown). Another 449 occurrences are not dated.

11 families, with two genera that could not be placed in a family (incertae sedis). While half of the taxa were recorded only once or twice, the 20 most recorded taxa (Tab. 1) account for 44 % of all occurrences, with an average number of occurrences per species of 9.4. The genus *Puccinia* accounts for approximately half of the occurrences and of the taxa recorded (Tab. 2), followed by *Uromyces*, *Melampsora*, *Phragmidium* and *Coleosporium*. Together, these five genera represent 91 % of the occurrences and 84 % of the taxa recorded. While the average number of occurrences per taxon in the genus *Puccinia* is 9.9, species of *Uromyces* and *Gymnosporangium* occur less frequently (7.7 and 5.2 occurrences per taxon respectively, in average) but those of *Melampsora*, *Tranzschelia*, *Phragmidium* and *Coleosporium* are more frequent in average (15.7, 18.5, 18.6 and 22.6 occurrences per taxon respectively). The vast majority of occurrences were registered in the uredinial/telial stage (35 % uredinia, 34 % uredinia/telia and 20 % telia) (Fig. 3). Nevertheless, 143 taxa recorded are macrocyclic (74 heteroecious and 69 autoecious), 50 are hemicyclic, 30 are microcyclic and 15 are demicyclic, while eight are un-

Tab. 1. List of the 20 most recorded Pucciniales taxa in Portugal.

Taxon	No. of occurrences
Puccinia porri (Sowerby) G. Winter	90
Puccinia recondita Roberge ex Desm.	81
Puccinia graminis Pers.	68
Coleosporium tussilaginis (Pers.) Tul.	67
Puccinia malvacearum Bertero ex Mont.	66
Puccinia striiformis Westend.	66
Melampsora euphorbiae (Ficinus & C. Schub.) Castagne	65
Puccinia hieracii (Röhl.) H. Mart.	65
Phragmidium violaceum (Schultz) G. Winter	46
Puccinia buxi Sowerby	46
Puccinia coronata Corda	44
Uromyces viciae-fabae (Pers.) J. Schröt.	44
Puccinia calcitrapae DC.	42
Puccinia arenariae (Schumach.) J. Schröt.	39
Uromyces rumicis (Schumach.) G. Winter	35
Uromyces pisi-sativi (Pers.) Liro	34
Tranzschelia pruni-spinosae (Pers.) Dietel	33
Uromyces anthyllidis (Grev.) J. Schröt.	33
Uromyces muscari Lév.	33
Puccinia menthae Pers.	30

Tab. 2. Number of occurrences and number of taxa per genus of Pucciniales recorded in Portugal.

Genus	No. of rust occurrences	No. of rust species
Puccinia	1249	126
Uromyces	468	61
Melampsora	141	9
Phragmidium	130	7
Coleosporium	113	5
Tranzschelia	37	2
Gymnosporangium	31	6
Cronartium	24	2
Cerotelium	21	1
Miyagia	21	1
Zaghouania	10	1
Pucciniastrum	8	4
Aecidium	8	5
Pileolaria	7	1
Dicheirinia	6	1
Kuehneola	5	1
Naohidemyces	4	1
Hyalopsora	3	1
Milesina	3	2
Melampsoridium	2	1
Triphragmium	2	1
Chrysomyxa	1	1
Frommeëlla	1	1
Endophyllum	1	1
Melampsorella	1	1
Leucotelium	1	1
Uredo	1	1

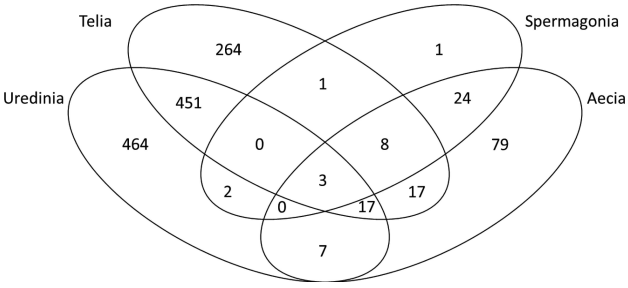

Fig. 3. Venn diagram depicting the number of occurrences of rust fungi in Portugal according to life cycle stage(s) recorded. In percentage, 35 % uredinia, 34 % uredinia/telia and 20 % telia stages.

known. Unlike the uredinial/telial stage, the aecial stage was recorded evenly over the entire year. Over 90 % of the 246 taxa recorded were found in mainland Portugal, while 76 and 83 were recorded in the Azores and Madeira, respectively (Fig. 4). Over 61 % of taxa occur only in mainland Portugal, while 21 % occur on the three geographic areas.

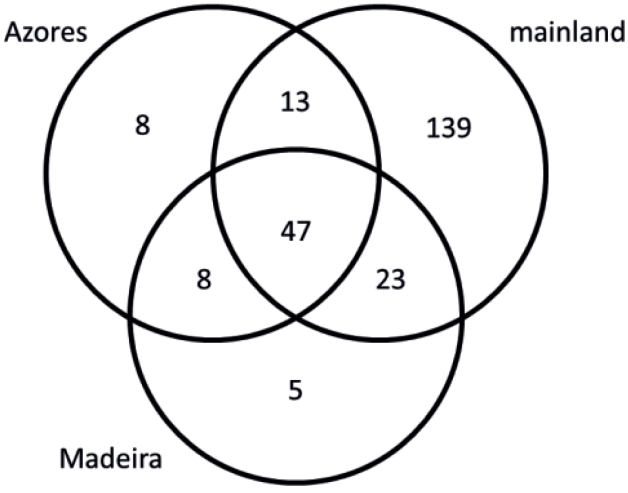

Fig. 4. Venn diagram depicting the number of rust fungi taxa in mainland Portugal, Azores and Madeira.

A total of 598 host plant taxa were recorded, including three ferns, four gymnosperms, 142 monocots and 449 eudicots (Supplementary data 3). The Asteraceae, Poaceae, Fabaceae and Rosaceae were the most frequently recorded families, totalising 51 % of the occurrence records and 33 % of the host taxa (Tab. 3). Only 19 % of all recorded host taxa are referred in five or more occurrences (Tab. 4). The 20 most referred host species include nine cultivated species and there are 476 occurrences in all cultivated hosts (representing 21 % of all occurrences), while the species of cultivated hosts represent only 6 % of all host taxa recorded. Additionally, there are 104 occurrences on 21 exotic host species and 1277 occurrences on 387 authochtonous host taxa, including 22 host taxa endemic to the Iberian Peninsula (four from mainland Portugal), seven host taxa endemic to Madeira and five endemic to the Azores (Tab. 5). The Portuguese flora accounts for 2998 species (Menezes de Sequeira et al. 2011), 410 of which host rust fungi. For some genera, species hosting rust fungi represent an important fraction of all species in such genera in the Portuguese flora (Tab. 6), including *Allium*, *Avena*, *Lolium*, *Bellis*, *Cirsium*, *Euphorbia*, *Lathyrus*, *Lavatera*, *Lotus*, *Lupinus*, *Malva*, *Medicago*, *Potentilla*, *Rumex*, *Salix*, *Scrophularia*, *Senecio*, *Silene*, *Sonchus*, *Stellaria*, *Trifolium*, *Vicia* and *Vinca*. Overall, 53 % of rust taxa were recorded on a single host species. On the other hand, *Puccinia recondita* Roberge ex Desm. was recorded on 36 host taxa (Supplementary data 2). In all, there were recorded 683 rust taxon-host taxon unique combinations.

Tab. 3. Number of occurrences and number of taxa of Pucciniales per host plant family (top 20*) recorded in Portugal.

Host family	No. of rust occurrences	No. of rust species
Asteraceae	395	99
Poaceae	366	79
Fabaceae	205	67
Rosaceae	202	38
Caryophyllaceae	103	26
Amaryllidaceae	92	15
Euphorbiaceae	83	18
Polygonaceae	67	19
Malvaceae	65	13
Apiaceae	54	25
Salicaceae	47	12
Buxaceae	46	1
Lamiaceae	39	17
Cyperaceae	37	15
Asparagaceae	37	12
Xanthorrhoeaceae	31	4
Iridaceae	30	7
Violaceae	26	4
Geraniaceae	25	4
Moraceae	21	2

* Additional families, with 10 or more occurrences or five or more host taxa, are: Amaranthaceae; Apocynaceae; Boraginaceae; Hypericaceae; Juncaceae; Linaceae; Oleaceae; Onagraceae; Paeoniaceae; Plantaginaceae; Plumbaginaceae; Ranunculaceae; Rhamnaceae; Rubiaceae; Scrophulariaceae.

Tab. 4. Number of occurrences of Pucciniales per host plant species (top 20*) recorded in Portugal.

Host species	No. of rust occurrences
Triticum aestivum L.	95
Buxus sempervirens L.	46
Rubus sp.	29
Silene vulgaris (Moench) Garcke	27
Lavatera cretica L.	26
Zea mays L.	25
Allium ampeloprasum L.	24
Delairea odorata Lem.	24
Rosa sp.	23
Senecio vulgaris L.	22
Vicia faba L.	21
Allium sativum L.	20
Dittrichia viscosa (L.) Greuter	18
Rubus ulmifolius Schott	18
Chrysanthemum sp.	17
Carduus tenuiflorus Curt.	16
Ficus carica L.	16
Prunus persica (L.) Batsch	16
Smyrnium olusatrum L.	16
Sorbus aucuparia L.	16

* Additional species, with 10 or more occurrences, are: *Alcea rosea* L.; *Allium sphaerocephalum* L.; *Asphodelus lusitanicus* P. Cout.; *Avena barbata* Pott ex Link; *Bromus madritensis* L.; *Chondrilla juncea* L.; *Crepis capillaris* (L.) Wallr.; *Dianthus caryophyllus* L.; *Duchesnea indica* (Jacks.) Focke; *Euphorbia helioscopia* L.; *E. peplus* L.; *Hordeum vulgare* L.; *Pelargonium zonale* (L.) L'Hér. ex Aiton; *Phaseolus vulgaris* L.; *Polygonum aviculare* L.; *Populus alba* L.; *P. nigra* L.; *Prunus domestica* L.; *Rhamnus alaternus* L.; *Ricinus communis* L.; *Rumex obtusifolius* L.; *R. pulcher* L.; *Sanguisorba minor* Scop.; *Scilla monophyllos* Link; *Sonchus oleraceus* L.; *Urginea maritima* (L.) Baker; *Vigna unguiculata* (L.) Walp.; *Viola* sp.

The number of species per genus was compared with those recorded in other countries/regions using a multivariate analysis approach (Fig. 5 and Supplementary data 5), depicting the most geographically contrasting genera and the geographical patterns of Pucciniales diversity.

Discussion

Puccinia jasmini DC., collected at Serra da Arrábida on *Jasminum fruticans* L. by F. Welwitsch in 1839, is the earliest datable scientific record of a rust fungus in Portugal. Ever since, the 180-years of history of identification of Pucciniales in Portugal has been protagonised by over 200 collectors and researchers, and at certain points reflects the national political history. While in the earliest days the main protagonists were foreign researchers, by the end of the 19th century a generation of Portuguese researchers was emerging based both on religious colleges and on Universities. The 1910 Republican revolution opened the route for a prolific work by University-based researchers, namely at Coimbra and Lisbon. Such work ended up centered on mainland Portugal reflecting the priorities of the 'Estado Novo' regime that ruled the country during the second and third quarters of the 20th century, leaving the Azores and Madeira open to the curiosity of foreign researchers. In this period, arising from breeding programmes for rust resistance on various crops, the colonial nature of the regime led to the creation of the Centro de Investigação das Ferrugens do Cafeeiro, centralising, at international level, research on coffee leaf rust (caused by *Hemileia vastatrix* Berk. & Broome) and playing a fundamental role, until present, on the creation of rust resistant coffee cultivars arroud the world (Talhinhas et al. 2017). However, such studies are not within the geographical scope of this work. Along with the regain of democracy in 1974, in the last quarter of 20th century descriptive work of this nature lost attention, leading to a gradual decrease in the intensity of surveys. Sixty years upon the last compilation of rust fungi in Portugal (Câmara 1958), the present work revises, based on the current taxonomic framework and on contemporary data analysis tools, research published in 118 bibliographic sources (Supplementary data 4), adding another 847 occurrences and 11 taxa to the previous check list, giving rise to the current list of 2319 occurrences and 246 taxa.

The first new rust species described based on a specimen collected in Portugal was *Uredo dorycnopsidis* Thüm. (1877), synonymized to *Uromyces anthyllidis* (Grev.) J. Schröt. Among the most prolific rust taxonomists in Portugal, F. de Thümen stood out as he described another three species in the 1870–1880 decade, followed by G. Lagerheim (three species in 1889–1890) and specially by E. Sousa da Câmara (seven species from 1910–1949). Eminent mycologists such as P. A. Saccardo, P. and H. Sydow and H. Gjaerum have also described new species based on Portuguese specimens, respectively *Uredo pallens* Sacc., *Puccinia galactitis* P. Syd. & Syd. and *Dicheirinia maderensis* Gjaerum (Tab. 7). In all, 22 rust species were described based on Portuguese material. Four of these have been synonymised to broader species, with numerous occurrences in Portugal and elsewhere. However, the status of the remaining 18 species is variable, as described below.

Tab. 5. List of endemic plant species hosting rust fungi occurring in Portugal according to their geographical area of endemism and family.

Endemic to	Family	Taxon
Azores	Cyperaceae	*Carex vulcani* Hochst. ex Seub.
	Apiaceae	*Sanicula azorica* Gunthnick ex Seub.
	Asteraceae	*Solidago azorica* Hochst
	Ericaceae	*Vaccinium cylindraceum* Sm.
	Hypericaceae	*Hypericum foliosum* Aiton
Madeira	Asteraceae	*Argyranthemum pinnatifidum* (L.f.) Lowe subsp. *succulentum*
	Ericaceae	*Vaccinium padifolium* Sm.
	Fabaceae	*Teline maderensis* Webb and Berthel.
	Oleaceae	*Jasminum odoratissimum* L.
	Plumbaginaceae	*Armeria maderensis* Lowe
	Rubiaceae	*Galium productum* Lowe.
	Violaceae	*Viola paradoxa* Lowe
mainland Portugal	Asteraceae	*Centaurea sphaerocephala* L. subsp. *lusitanica* (Boiss. & Reut.) Nyman
	Caryophyllaceae	*Silene longicilia* (Brot.) Otth.
	Scrophulariaceae	*Scrophularia grandiflora* DC.
	Scrophulariaceae	*Scrophularia sublyrata* Brot.
Iberia	Iridaceae	*Gladiolus illyricus* W.D.J. Koch subsp. *reuteri* (Boiss.) Cout.
	Juncaceae	*Luzula lactea* (Link) E. Meyer
	Poaceae	*Anthoxanthum amarum* Brot.
	Apiaceae	*Ferula communis* L.
	Asteraceae	*Centaurea nigra* L. subsp. *rivularis* (Brot.) Cout.
	Asteraceae	*Picris hieracioides* L.
	Asteraceae	*Santolina rosmarinifolia* L.
	Boraginaceae	*Anchusa undalata* L.
	Boraginaceae	*Echium lusitanicum* L.
	Campanulaceae	*Campanula herminii* Hoffmanns. & Link
	Ericaceae	*Rhododendron ponticum* L. subsp. *baeticum* (Boiss. & Reut.) Hand.-Mazz.
	Euphorbiaceae	*Euphorbia baetica* Boiss.
	Fabaceae	*Anthyllis vulneraria* L. subsp. *lusitanica* (Cullen & P. Silva) Franco
	Fabaceae	*Lupinus hispanicus* Boiss. & Reut.
	Plumbaginaceae	*Armeria gaditana* Boiss.
	Plumbaginaceae	*Armeria pubigera* (Desf.) Boiss.
	Rosaceae	*Rubus sampaioanus* Sudre ex Samp.
	Rosaceae	*Sanguisorba hybrida* (L.) Font Quer
	Scrophulariaceae	*Antirrhinum graniticum* Rothm.
	Scrophulariaceae	*Antirrhinum linkianum* Boiss. Et Reut.
	Scrophulariaceae	*Antirrhinum meonanthum* Hoffg. et Lk.
	Scrophulariaceae	*Scrophularia hermini* Hoffmanns. & Link

The microcyclic *Puccinia galactitis* P. Syd. & Syd., infecting the Asteraceae *Galactites tomentosa* Moench, is common in Portugal, along with its host plant. While *Galactites*, a monospecific genus, occurs in Iberia and other western and central Mediterranean countries, reports of the fungus are mostly restricted to the western-most area of distribution of the host.

The hemicyclic *Dicheirinia maderensis* Gjaerum inhabits the Madeiran endemic *Teline maderensis* Webb and Berthel. (Fabaceae), and is therefore considered also endemic, as other species of *Teline* host

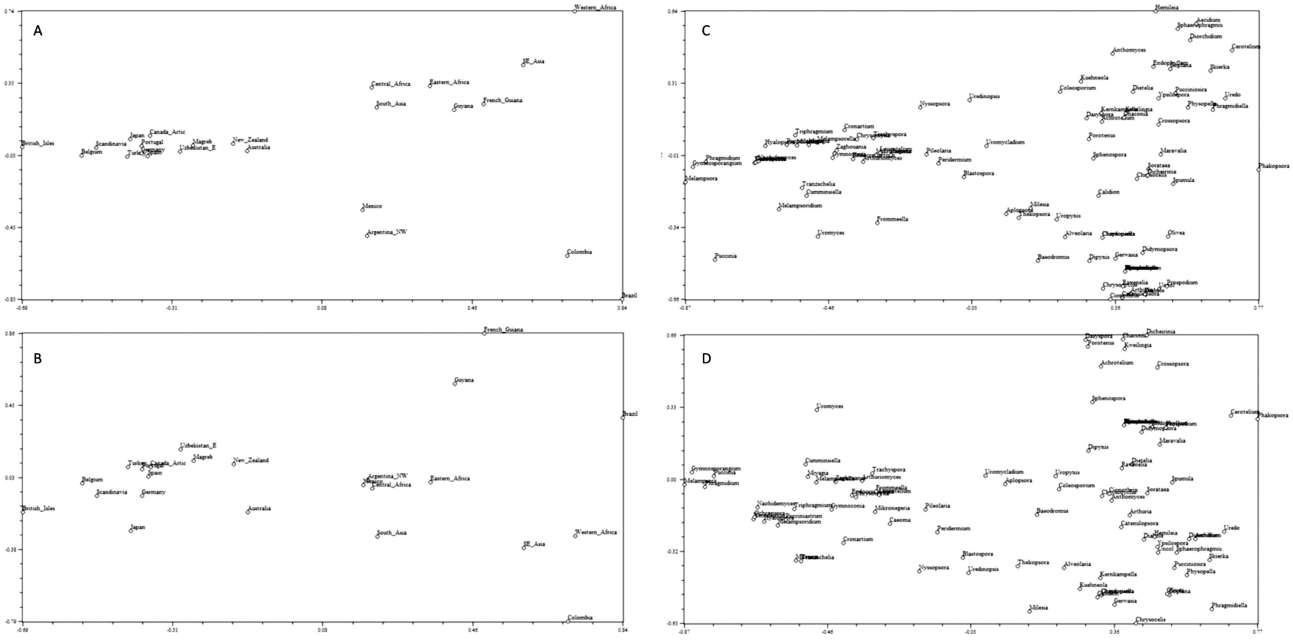

Fig. 5. Principal component analysis depicting the bi-dimensional projection of the number of rust species per genus in % of all species in each country/region (panels A and B) over the Eigen space defined by the Pucciniales genera (panels C and D). Panels A and C refer to the projection of the first (x-axis) and second (y-axis) dimensions and panels B and D refer to the projection of the first (x-axis) and third (y-axis) dimensions.

distinct species of *Dicheirinia*, such as *Dicheirinia canariensis* Urries which infects *T. canariensis* (L.) Webb & Berthel. in the Canary Islands. Although the host plant is categorised of Least Concern in the IUCN Red List of Threatened Species 2017 (da Silva Menezes de Sequeira & Fernandes, 2017) the status of the fungus is unclear and should be under surveillance.

The microcyclic *Puccinia conclusa* Thüm. was recorded only once in Portugal, the species holotype collected at Coimbra in 1878 on *Cyperus longus* L. (Cyperaceae), but it was subsequently reported on various locations in the Australasian region. Similarly, the hemicyclic *Puccinia chrysanthemicola* Sousa da Câmara, Oliveira & Luz was reported in Portugal only concomitantly to its description in 1940 on *Argyranthemum frutescens* (L.) Sch.Bip. and *Chrysanthemum* spp. (Asteraceae), but recently it was reported in multiple occurrences in New Zealand. Also, the hemicyclic *Puccinia biformis* Lagerh., collected on *Rumex bucephalophorus* L. (Polygonaceae) at Trafaria (Setúbal) in 1889, was only recorded thereafter twice, in Morocco. Yet a similar situation occurs for the macrocyclic *Uromyces caraganae* (Thüm.) Magnus: it was first recorded in Portugal (as *Uredo caraganae* Thüm.) in 1879 at Coimbra on *Caragana arborescens* Lam. and never reported again until a single additional report from Austria in 1998. The status of these four species in Portugal is uncertain and of concern, although they seem to be present in other parts of the world.

The hemicyclic *Puccinia silenicola* Sousa da Câmara, Oliveira & Luz was reported on *Silene portensis* L. (Caryophyllaceae) at several locations in the 1940s but it was never reported thereafter. A similar situation occurs for the demicyclic *Uromyces hippomarathricola* Sousa da Câmara, as it was reported three times on *Cachrys sicula* L. (Apiaceae; in turn, the host plant has a limited geographical range - Southern Iberia, Sicily and Morocco) between 1936 and 1952 and not reported ever since. Following an identical pattern, the hemicyclic *Uromyces vulpiae* Sousa da Câmara was reported twice on *Vulpia muralis* (Kunth) Nees (Poaceae) in 1948 and 1960 at Vilarelhos da Vilariça (Bragança) and Serra da Arrábida (Setúbal) with no further reports. Similarly, *Aecidium umbilici* Trotter was only reported from two close locations at Fundão (Castelo Branco) at uncertain dates (likely in the 19th century) on *Umbilicus* spp. (Crassulaceae) and never after. Still following a similar pattern, the presumably macrocyclic heteroecious *Puccinia avenae-barbatae* Gonz. Frag. was recorded only twice at Coimbra and Tabuaço (Viseu) on *Avena barbata* Pott ex Link

Tab. 6. Number of plant species hosting rust fungi in Portugal as compared to the total number of species in each genus (genera for which only one species hosts rusts are not listed).

Family	Genus	No. of plant species	Family	Genus	No. of plant species
Cyperaceae	*Carex*	9/51	Chenopodiaceae	*Beta*	2/4
Iridaceae	*Gladiolus*	2/6	Ericaceae	*Vaccinium*	2/4
Liliaceae	*Allium*	9/21	Euphorbiaceae	*Euphorbia*	10/35
Liliaceae	*Asphodelus*	3/9	Fabaceae	*Lathyrus*	5/21
Liliaceae	*Scilla*	2/8	Fabaceae	*Lotus*	6/18
Poaceae	*Aegilops*	2/3	Fabaceae	*Lupinus*	4/7
Poaceae	*Anthoxanthum*	2/5	Fabaceae	*Medicago*	5/20
Poaceae	*Avena*	4/7	Fabaceae	*Onobrychis*	2/2
Poaceae	*Bromus*	3/16	Fabaceae	*Ornithopus*	2/4
Poaceae	*Holcus*	2/7	Fabaceae	*Trifolium*	6/44
Poaceae	*Lolium*	4/8	Fabaceae	*Vicia*	7/32
Poaceae	*Micropyrum*	2/2	Hypericaceae	*Hypericum*	6/19
Poaceae	*Poa*	3/9	Lamiaceae	*Mentha*	2/7
Poaceae	*Vulpia*	3/9	Linaceae	*Linum*	3/8
Apocynaceae	*Vinca*	3/3	Malvaceae	*Lavatera*	4/7
Asclepiadaceae	*Vincetoxicum*	2/2	Malvaceae	*Malva*	3/6
Asteraceae	*Andryala*	2/7	Oleaceae	*Jasminum*	2/3
Asteraceae	*Asteriscus*	2/2	Oleaceae	*Phillyrea*	2/2
Asteraceae	*Bellis*	3/5	Onagraceae	*Epilobium*	2/7
Asteraceae	*Centaurea*	7/31	Oxalidaceae	*Oxalis*	2/8
Asteraceae	*Cirsium*	4/8	Polygonaceae	*Fallopia*	2/3
Asteraceae	*Crepis*	3/10	Polygonaceae	*Rumex*	7/21
Asteraceae	*Leontodon*	3/10	Ranunculaceae	*Clematis*	2/4
Asteraceae	*Picris*	2/4	Rhamnaceae	*Rhamnus*	2/4
Asteraceae	*Rhagadiolus*	2/2	Rosaceae	*Potentilla*	3/9
Asteraceae	*Senecio*	6/20	Rosaceae	*Sanguisorba*	2/4
Asteraceae	*Sonchus*	3/7	Rubiaceae	*Crucianella*	2/3
Betulaceae	*Betula*	2/2	Rubiaceae	*Galium*	4/23
Boraginaceae	*Anchusa*	2/4	Salicaceae	*Populus*	3/3
Campanulaceae	*Campanula*	2/6	Salicaceae	*Salix*	4/13
Caryophyllaceae	*Corrigiola*	2/2	Scrophulariaceae	*Antirrhinum*	4/8
Caryophyllaceae	*Silene*	6/43	Scrophulariaceae	*Scrophularia*	5/16
Caryophyllaceae	*Stellaria*	3/4	Violaceae	*Viola*	3/14

(Poaceae) in 1878 and 1922 but not ever after. These five rust species are presumably endemic, but the prolonged absence of new records poses great concern on their ecological status.

Yet of greater concern are the six species for which there is a single report, corresponding to the species holotype, and that were never reported again in the world: the hemicyclic *Puccinia addita* Syd. collected on *Phalaris brachystachys* Link (Poaceae) at Funchal (Madeira) in 1939; the hemicyclic *Puccinia arnoseridis* Sousa da Câmara collected on *Arnoseris minima* (L.) Schwgg. & Körte (Asteraceae) at Serra de Montemuro (Viseu) in 1948; the microcyclic *Puccinia campanulae-herminii* Gonz. Frag. collected on the Iberian endemic *Campanula herminii* Hoffmanns. & Link (Campanulaceae) at Serra da Estrela in 1916; the mysterious *Puccinia ficalhoana* Lagerh. (unknown life cycle and location) described in 1890 from *Hyacinthoides hispanica* (Mill.) Rothm. (Asparagaceae) herbarium material; the microcyclic *Uromyces seselis* Sousa da Câmara collected on *Seseli tortuosum* L. (Apiaceae)

Tab. 7. List of Pucciniales species described based on Portuguese specimens, with reference to the date of publication, the number of occurrences in Portugal and in the world and their ecological status*.

Taxon	Date of taxon	Occurrences		Status
		Portugal	World	
Gymnosporangium oxycedri Bres. (syn. *Gymnosporangium confusum* Plowr.)	1903	6	351	common
Puccinia addita Syd.	1939	1	1	Endemic (Madeira), reported only once (1936)
Puccinia arnoseridis Sousa da Câmara	1949	1	1	Endemic (Portugal), reported only once (1948)
Puccinia avenae-barbatae Gonz. Frag.	1924	2	2	Endemic (Portugal), not reported since 1922
Puccinia biformis Lagerh.	1890	1	3	rare in Portugal
Puccinia campanulae-herminii Gonz. Frag.	1914	1	1	Endemic (Portugal), reported only once (1916)
Puccinia chrysanthemicola Sousa da Câmara, Oliveira & Luz	1940	8	23	rare in Portugal
Puccinia conclusa Thüm.	1879	1	34	rare in Portugal
Puccinia ficalhoana Lagerh.	1890	1	1	Endemic (Portugal), reported only once (1890)
Puccinia galactitis P. Syd. & Syd.	1902	7	37	common
Puccinia mesnieriana Thüm.	1878	12	113	common
Puccinia piptatheri Lagerh. (syn. *Puccinia recondita* Roberge ex Desm.)	1889	81	5027	common
Puccinia silenicola Sousa da Câmara, Oliveira & Luz	1940	5	5	Endemic (Portugal), not reported since the 1940s
Uromyces hippomarathricola Sousa da Câmara	1936	3	3	Endemic (Portugal), not reported since 1951
Uromyces seselis Sousa da Câmara	1949	1	1	Endemic (Portugal), reported only once (1948)
Uromyces vulpiae Sousa da Câmara	1949	2	2	Endemic (Portugal), not reported since 1960
Dicheirinia maderensis Gjaerum	1982	6	6	Endemic (Madeira)
Aecidium umbilici Trotter	1901	3	3	Endemic (Portugal), not reported since 1936
Caeoma androsaemi J.V. Almeida & Sousa da Câmara (syn. *Melampsora hypericorum* (DC.) J. Schröt.)	1910	14	639	Common
Uredo caraganae Thüm. (syn. *Uromyces caraganae* (Thüm.) Magnus)	1879	1	2	very rare
Uredo dorycnopsidis Thüm. (syn. *Uromyces anthyllidis* (Grev.) J. Schröt.)	1877	33	623	common
Uredo pallens Sacc.	1893	1	1	Endemic (Portugal), reported only once (1890)

* For species with an accepted synonym, the number of occurrences given refers to the currently accepted name; occurrences in the world were retrieved using GBIF

at Ílhavo (Aveiro) in 1948; *Uredo pallens* Sacc. collected on the exotic *Vasconcellea quercifolia* A. St.–Hil. (Caricaceae) at Coimbra in 1890. While none of these host plant species currently incurs on conservation concerns, the six rust species can be considered endemic to Portugal, although their true existence is much questionable, as they have not been reported since their first occurrence.

From the 18 valid rust taxa described based on Portuguese specimens, 12 are endemic (10 from the

mainland and two from Madeira; Tab. 7), although only one (*Dicheirinia maderensis* Gjaerum) is currently known from nature. None of the other 11 endemics has been reported from nature for decades, or in some cases for over one century, raising great concern on their conservation status. Besides these, another four species described based on Portuguese material are rare in the world and could also incur on conservation problems.

Another five rust species occur on endemic hosts whose populations are physically isolated from other hosts of the same rust species.

The microcyclic *Puccinia jasmini* DC. occurs at the mainland on *Jasminum fruticans* L. (Oleceae) and at Madeira on the endemic *Jasminum odoratissimum* L. On the latter, the fungus presents a sori distribution pattern differing from the classic description for the species (Gjaerum 1982).

The macrocyclic autoecious *Puccinia saniculae* Grev. occurs on *Sanicula* spp. (Apiaceae) throughout the world, and notably on *S. europaea* L. across Europe. At the Azores, the fungus occurs on the endemic *S. azorica* Gunthnick ex Seub. (an iconic and protected plant species), thus isolated from other fungal populations occurring elsewhere and inhabiting a host plant that has undergone a speciation process.

The hemicyclic *Puccinia tanaceti* DC. occurs on several species of *Chrysanthemum* and *Tanacetum* (Asteraceae) at the Azores and mainland, while at Madeira, this species occurs on *Argyranthemum pinnatifidum* (L. f.) Lowe, one of the several *Argyranthemum* endemics.

The macrocyclic heteroaecious *Chrysomyxa rhododendri* de Bary is recorded in Portugal in the uredinial stage only, as the aecial hosts (*Picea* spp.) are quite infrequent. The uredinial host taxon recorded is endemic to Iberia with two isolated and rarefied populations, at Serra do Caramulo and Serra de Monchique. Several *Chrysomyxa* spp. occur on *Rhododendron* (Ericaceae), either in telial or aecial forms, along with *Puccinia rhododendri* Fuckel. Several species were identified from within *Chrysomyxa rhododendri* de Bary, and new species are likely to be identified in areas where host plants are part of the native flora, as could be the case for the Portuguese populations of *R. ponticum* subsp. *baeticum* (Crane 2001).

The macrocyclic heteroecious *Naohidemyces vaccinii* (Jørst.) S. Sato, Katsuya & Y. Hirats. ex Vanderweyen & Fraiture occurs in Portugal only in the uredinial stage, as the aecial hosts (*Tsuga* spp.) are quite infrequent. The fungus occurs both at Azores and Madeira, respectively on the local endemics *Vaccinium cylindraceum* Sm. and *V. padifolium* Sm. (Ericaceae). While this may suggest a scenario favouring speciation, additional confusion arises from the fact that blueberry rust is a disease of economic relevance subjected to quarantine measures and that the taxonomy of pathogens causing rust on *Vaccinium* spp. has undergone recent changes.

These situations, three of them occurring at Madeira, two in the Azores and one in the mainland, illustrate scenarios where a speciation process may be occurring, in parallel to the speciation processes of their hosts. Most of these fungi are seldom reported, suggesting that research should be conducted in order to clarify their taxonomic and ecological status.

From the 246 taxa reported in Portugal, 98 are not reported since the 1940s/50s, in spite of recent surveys. Most of these were reported only once (64 taxa) or twice (eight taxa), raising concern on their current status in Portugal (Supplementary data 2). Eleven of such species are also rarely reported elsewhere in the world, as shown below.

The microcyclic *Puccinia chamaecyparidis* Trott. was recorded only once in 1945, on the Iberian endemic *Santolina rosmarinifolia* L. (Asteraceae) at Tróia (Setúbal) and seldom elsewhere in Spain.

The demicyclic *Puccinia claytoniata* (Schwein.) P. Syd. & Syd. was reported once in 1950 on *Portulaca oleracea* L. (Portulacaceae) at Alenquer (Lisbon) and sporadically in the USA in the 19th century and once recently.

The hemicyclic *Puccinia lithospermi* Ellis & Kellerm. was reported once in 1952 on *Glandora diffusa* (Lag.) D.C.Thomas (Boraginaceae) at Pégões (Setúbal), with sporadic and ancient occurrences in different American countries.

The hemicyclic *Puccinia magydaridis* Pat. & Trab. was reported once in 1961 on *Magydaris panacifolia* (Vahl) Lange (Apiaceae) at São Marcos da Serra (Faro), while reports from elsewhere (Spain, Morocco, Algeria and Tunisia) are also scarce and old. The host genus encompasses only two species, both restricted to the Western Mediterranean basin.

The microcyclic *Puccinia melanopsis* P. Syd. & Syd. was reported once in 1936 on *Moraea sisyrinchium* (L.) Ker Gawl. (Iridaceae) at Parede (Lisbon), while other reports from Morocco, Tunisia, Israel, Turkey and Greece are scarce and older.

The microcyclic *Puccinia montagnei* De Toni was reported once in 1892 on *Herniaria glabra* L. (Caryophyllaceae) at Lisbon and twice elsewhere only (in Spain and France). The host species, how-

ever, is very common in Europe, while the genus contains several Portuguese endemics.

The macrocyclic heteroecious *Puccinia panici* Diet. was reported once in 1935 at Colares (Lisbon) on *Panicum repens* L. (Poaceae), while reports from elsewhere in the world (USA) are also scarce and ancient.

The hemicyclic *Puccinia scolymi* P. Syd. & Syd. was reported once in 1940 on *Scolymus hispanicus* L. (Asteraceae) at Póvoa de Lanhoso (Braga), while other reports (Europe and North Africa) are also scarce and older.

The microcyclic *Puccinia sedi* Körn. was reported once in 1939 on *Sedum sediforme* (Jacq.) Pau (Crassulaceae) at Trafaria (Setúbal), while other reports from Western Europe (Spain, Italy and Germany) are scarce and older.

Aecidium punicum Juel was reported in 1939 on *Thapsia villosa* L. var. *minor* Hoffgg. et Lk. (Apiaceae) at Miranda do Douro (Bragança), while other occurrences in Spain, Algeria and Tunisia are even older.

Although the host taxa for these 11 rusts are common and widespread (either in the Mediterranean region or elsewhere), the occurrences of these rusts are seldom and mostly ancient, raising concern on their conservation status.

While most rusts occur on the native spontaneous flora, some infect agricultural crops and can be of economic relevance. On cereals, such diseases include oat and barley crown rust (*Puccinia coronata* Corda), barley brown rust (*Puccinia hordei* G.H. Otth), wheat stem rust (*Puccinia graminis* Pers.), wheat brown rust (*Puccinia recondita* Roberge ex Desm.), wheat stripe rust (*Puccinia striiformis* Westend), sorghum rust (*Puccinia purpurea* Cooke) and maize rust (*Puccinia sorghi* Schwein.). On horticultural and other field crops, noteworthy rusts are *Puccinia cymbopogonis* Massee on lemon grass, *Puccinia hieracii* (Röhl.) H. Mart. on endive, *Puccinia menthae* Pers. on mints and oregano, *Puccinia porri* (Sowerby) G. Winter on garlic and leek, *Uromyces anthyllidis* (Grev.) J. Schröt. on lupins, *Uromyces appendiculatus* (Pers.) Link on common bean, *Uromyces beticola* (Bellynck) Boerema, Loer. & Hamers on beet, *Uromyces ciceris-arietini* (Grognot) Jacz. & G. Boyer on chickpea, *Uromyces pisisativi* (Pers.) Liro on grass pea, *Uromyces viciae-fabae* (Pers.) J. Schröt. on faba bean and *Uromyces vignae* Barclay on cowpea. Relevant rusts on fruit trees include fig tree rust (*Cerotelium fici* (Castagne) Arthur) and apricot, peach and plum trees rust (*Tranzschelia discolor* (Fuckel) Tranzschel & M.A. Litv. and *Tranzschelia pruni-spinosae* (Pers.) Dietel). Notorious rusts on ornamental plants include *Gymnosporangium confusum* Plowr. on common hawthorn, *Phragmidium mexicanum* (Mains) H.Y. Yun, Minnis & Aime on mock strawberry, *Puccinia arenariae* (Schumach.) J. Schröt. on annual baby's-breath, *Puccinia buxi* Sowerby on boxwood, *Puccinia chrysanthemi* Roze on chrysanthemum, *Puccinia hemerocallidis* Thüm. on daylily, *Puccinia oxalidis* Dietel & Ellis on oxalis, *Puccinia pelargonii-zonalis* Doidge on pelargonium, *Puccinia thaliae* Dietel on Indian shot, *Uromyces dianthi* (Pers.) Niessl on carnation and *Uromyces transversalis* (Thüm.) G. Winter on gladiolus. On forest species, rust diseases can be found on birch (*Melampsoridium betulinum* (Pers.) Kleb. and on poplars (*Melampsora* spp.), although several rusts have relative discret life stages on gymnosperms, namely the telial stage of several *Gymnosporangium* spp. on junipers and the aecial stage of *Coleosporium* spp. on pine trees.

Rust records in Portugal illustrate the arrival of new pathogens to Europe.

The hemicyclic *Puccinia antirrhini* Dietel & Holw., originary from North American native *Antirrhinus* spp., is known in Europe since the 1930s, where it was first reported in the United Kingdom on *Antirrhinus majus* L. (Preece 2003) and soon it was reported from mainland Portugal (Lisbon area) on snapdragon but also on endemic species (*Antirrhinum graniticum* Rothm., *A. linkianum* Boiss. & Reut., and *A. meonanthum* Hoffg. & Lk.). It is unsure whether it occurs on other Iberian or Portuguese endemics, such as *A. cirrhigerum* (Welw. ex Ficalho) Rothm., *A. lopesianum* Rothm., *A. onubense* (Fern. Casas) Fern. Casas, *A. rothmaleri* (Pinto da Silva) Amich, Bernardos & García–Barrius. The disease subsequently spread to the Azores and Madeira, as well as throughout Europe.

The hemicyclic *Puccinia pelargonii-zonalis* Doidge was first discovered on pelargonium in South Africa in 1926 (Doidge 1926) and soon after was reported in Australia and New Zealand. In Europe it was first established in the early 1960s on the shores of the Ligurian Sea, spreading to several countries, reaching Madeira in 1969 and the Azores and mainland Portugal in 1975 (Dennis 1993).

The macrocyclic heteroaecious *Puccinia oxalidis* Dietel & Ellis, originary from the American continent, is known in the United Kingdom since the late 1940s. Additional reports in Europe were not referred until the late 1970s, when it was reported from the Azores and soon after from Madeira.

Spreading throughout the British Isles in the 1980s and 1990s, it was not until the late 2000s that the disease became reported in mainland Europe. In Portugal, the disease is reported in the Lisbon area since 2014 on ornamental *Oxalis* spp. but it was not reported on autochthonous species nor on *Oxalis pes-caprae* L, a widespread invasive weed.

The macrocyclic heteroecious *Coleosporium asterum* (Dietel) Syd. & P. Syd. is originary from North America and reports from Europe are confused by taxonomical ambiguities (Sansford 2015). Unambiguous records in Europe were first recorded in the Azores in 1996 on *Solidago canadensis* L. and *S. sempervirens* Michx. (Asteraceae), while the present study is the first report of this fungus on the Azorean endemic *Solidago azorica* Hochst. This pathogen is of concern because it is the causal agent of Western pine-aster rust of *Pinus* spp.

The hemicyclic *Puccinia stenotaphricola* J. Walker (synonym *Puccinia stenotaphri* Cumm.) is presumably originary from South America (the origin of its host, *Stenotaphrum secundatum* (Walter) Kuntze) and is potentially a biological control of St. Augustine grass, an aggressive invasive weed. The fungus is reported only sporadically, although from various continents, but in Europe it has only been recorded in Madeira (1982) and Azores (1996).

The hemicyclic *Puccinia thaliae* Dietel, of South American origin (along with its host, *Canna indica* L.), was first reported in Europe in 2015, simultaneously in Azores and Madeira. It has not been reported in mainland Europe, although the host is a common garden plant.

The macrocyclic heteroecious *Puccinia hemerocallidis* Thüm. originated in East Asia along with its hosts (*Hemerocallis* spp.), disseminating to all continents in the beginning of the 21st century, reaching Europe in 2015 where it was detected simultaneously in Madeira and mainland Portugal (Carvalho et al. 2018).

These seven examples illustrate the forefront position of Portugal in relation to the entry or dissemination of new rusts in Europe, with Azores and Madeira frequently anticipanting the detection on the mainland. The Southwesterly position of Portugal in relation to the rest of Europe and the West-Southwesterly position of Azores and Madeira in relation to mainland Portugal highlight these territories as entry points, and simultaneously as early detection points, for the arrival of new rust fungi in Europe. The examples referred, situated in different chronological points and at diverse dissemination stages, further reinforce this.

Tab. 8. Number of rust species identified in Portugal and other regions according to the ecological status.

Region	No. of species	Exotic (%)	Native (%)
Portugal	246	14,2	85,8
mainland Portugal	224	13,8	86,2
Azores	78	21,8	75,6
Madeira	85	17,6	80,0
Belgium[1]	235	9,8	90,2
British Isles[2]	265	6,0	94,0
New Zealand[3]	234	46,2	53,8

[1] Vanderweyen & Fraiture (2007, 2008, 2011); [2] Henderson (2000); [3] McKenzie (1998)

From the 246 taxa occurring in Portugal 35 are exotic (Supplementary data 2), as they infect only exotic hosts or their entry was recent, while 12 taxa are endemic and the remaining are considered native, since they occur on native hosts. In the Azores, 22 % of rusts are exotic, while these represent 18 % and 14 % of Pucciniales from Madeira and mainland respectively (Tab. 8). Similarly, exotic vascular plant species are more numerous in the Azores and less in the mainland (70 % in the Azores, 35 % in Madeira and 23 % in the mainland; Menezes de Sequeira et al. 2011). In Belgium and the British Isles exotic rusts represent 10 % and 6 % of all rust species (Henderson 2000; Vanderweyen & Fraiture 2007, 2008, 2011), while in New Zealand they account for 46 % of the rust mycobiota (McKenzie 1998), although the total number of rust species is quite similar, ranging between 234 in New Zealand and 265 in the British Isles.

The European Plant Protection Organisation currently lists 14 Pucciniales species (in a total of 35 fungal species) in the A1 List of pests recommended for regulation as quarantine pests (EPPO

Tab. 9. Pucciniales species that may cause phytosanitary problems in Europe, with notes on their hosts, current distribution and likelihood of entering Europe through Portugal based on host occurrence.

Species/disease	Uredinial/telial host	Aecial host	Distribution	Notes
Austropuccinia psidii (G. Winter) Beenken (rust of eucalyptus)	Myrtaceae	(autoecious)	global, except Europe	several hosts are common (*Eucalyptus* spp.) or native (*Myrtus communis*)
Chrysomyxa arctostaphyli Dietel (broom rust of spruce)	*Arctostaphylos uva-ursi*	*Picea* spp.	North America	hosts infrequent in Portugal
Cronartium coleosporioides Arthur (stalactiform blister rust of pine)	*Castilleja* spp., *Melampyrum lineare*	*Pinus banksiana*, *P. contorta*, *P. jeffreyi*, *P. ponderosa*	North America	hosts infrequent in Portugal
Cronartium comandrae Peck (comandra blister rust of pine)	*Comandra livida*, *C. umbellata*	*Pinus banksiana*, *P. contorta* (major), *P. nigra*, *P. pinaster*, *P. sylvestris* and other *Pinus* spp. (minor)	North America	uredinial host infrequent in Portugal
Cronartium comptoniae Arthur (sweet fern blister rust)	*Comptonia peregrina, Myrica gale*	*Pinus banksiana*, *P. contorta, P. rigida* (major), *P. nigra*, *P. pinaster*, *P. sylvestris* and other *Pinus* spp. (minor/incidental)	North America	uredinial host native from Portugal; *Myrica faya* is common in Azores and Madeira
Cronartium fusiforme Hedgc. & N.R. Hunt ex Cummins (southern fusiform rust of pine)	*Castanea dentata, Quercus nigra, Q. phellos*	*Pinus elliottii*, *P. taeda* (major), *P. canariensis, P. halepensis, P. nigra, P. pinea* (indicators)	North America	uredinial host infrequent in Portugal
Cronartium harknessii (J.P. Moore) E. Meinecke (western gall rust of pine)	none; endocyclic	*Pinus banksiana*, *P. contorta*, *P. ponderosa* (major), *P. halepensis, P. nigra, P. radiata, P. sylvestris* and other *Pinus* spp. (minor/incidental)	North and Central America	major hosts infrequent in Portugal
Cronartium himalayense Bagchee (blister rust of chir pine)	*Swertia angustifolia*	*Pinus roxburghii*	Asia (Himalayas)	hosts very infrequent in Portugal
Cronartium kamtschaticum Jørst. (Japanese rust of white pine)	*Castilleja* spp., *Pedicularis* spp., *Ribes* spp.	*Pinus cembra*, *P. pumila*, *P. strobus*	Northeast Asia	aecial hosts not cultivated in Portugal
Cronartium quercuum (Berk.) Miyabe ex Shirai (eastern gall rust of pine)	*Castanea* spp., *Quercus* spp.	*Pinus banksiana*, *P. densiflora, P. echinata, P. thumbergii, P. virginiana* (major), *P. nigra, P. sylvestris* and other *Pinus* spp. (minor/incidental)	Americas and Asia	reported in Portugal, but not found for over 60 years
Gymnosporangium asiaticum Miyabe ex G.Yamada (leaf rust of Japanese pear)	*Juniperus chinensis, J. rigida*	*Pyrus pyrifolia* (major) and other Rosaceae (incidental)	Central and East Asia and North America	aecial host not cultivated in Portugal

Species/disease	Uredinial/telial host	Aecial host	Distribution	Notes
Gymnosporangium clavipes Cooke & Peck (rust of quince)	*Juniperus communis, J. virginiana*	*Cydonia oblonga* (major), *Malus domestica* (minor) and other Rosaceae (incidental)	North and Central America	reported once, over 80 years ago; aecial and telial hosts common (cultivated and native)
Gymnosporangium globosum Farl. (American rust of hawthorn)	*Juniperus virginiana*	*Crataegus* spp. (major), *Malus domestica* (minor) and other Rosaeceae (incidental)	North and Central America	aecial and telial hosts common (cultivated and native)
Gymnosporangium juniperi-virginianae Schwein. (American rust of apple)	*Juniperus virginiana*	*Malus domestica* (major)	North America	aecial and telial hosts common (cultivated and native)
Gymnosporangium yamadae Miyabe (Japanese rust of apple)	*Juniperus chinensis*	*Malus domestica* (major) and other *Malus* spp. (minor)	North America and Asia	uredinial host infrequent in Portugal
Melampsora farlowii (Arthur) Davis (rust of hemlock)	*Tsuga canadensis*, *T. caroliniana*	None (microcyclic)	North America	hosts infrequent in Portugal
Melampsora medusae Thüm. (conifer/poplar rust)	*Populusbalsamifera, P. deltoides, P. nigra, P. tremuloides*	Pinaceae	global, with sporadic reports in Europe	possibility of confusion with other rusts on poplar
Puccinia hemerocallidis Thüm. (daylily rust)	*Hemerocallis* spp.	*Patrinia* spp.	global; in Europe only in Portugal (mainland and Madeira)	identified in Portugal in 2015
Puccinia pittieriana Henn. (common rust of potato)	*Solanum tuberosum* (major), *S. lycopersicum* and *S. demissum* (incidental)	none (microcyclic)	Central and South America	hosts common (cultivated)
Thekopsora minima (Arthur) Syd. & P. Syd. (leaf rust of blueberry)	*Vaccinium* spp. and other Ericaceae	*Tsuga canadensis*, *T. diversifolia*, *T. sieboldii*	global, with sporadic reports in Europe	possible confusion with other rusts on *Vaccinium* spp.; *Naohidemyces vaccinii* was identified on endemic *Vaccinium* spp. in Azores and Madeira

2018). Additionally, other rusts species absent from Europe could cause economic losses in crops if they enter the continent (Tab. 9). The vast majority of these fungi are present in the American continent, thus suggesting that Portugal and particularly Azores and Madeira could be early detection points for the natural dispersal of such rusts, particularly in the cases where host plants occur there. This is the case of macrocyclic autoecious *Austropuccinia psidii* (G. Winter) Beenken, the causal agent of rusts on Myrtaceae, that could pose problems to eucalyptus plantations in Southwest Europe, or of the microcyclic *Puccinia pittieriana* Henn., the causal agent of common rust of potato. Most *Cronartium* spp. listed in Tab. 9 have uredinial hosts infrequent in Portugal and are therefore unlikely to enter Europe throught this territory. Exceptions to this, leading to additional risks, are: *Cronartium comptoniae* Arthur, infecting *Myrica* spp. in the uredinial/telial stage, being *Myrica gale* L. native of mainland Portugal and *Myrica faya* Aiton common in Azores and Madeira; *Cronartium kamtschaticum* Jørst., infecting *Pedicularis* spp., in the uredinial/telial stage, being *Pedicularis sylvatica* L. native from mainland Portugal; and *Cronartium quercuum* (Berk.) Miyabe ex Shirai, infecting *Quercus* spp. and *Castanea* spp. widespread in Portugal (in fact, this rust was recorded both in the aecial and uredinial/telial stages on *Pinus pinaster* Aiton and on *Quercus* spp. in several locations in Portugal, although it is not recorded for over 60 years). On the contrary, the risk of introduction of the several *Gymnosporangium* spp. listed in Tab. 9 is higher in general, as the uredinial/telial hosts (*Juniperus* spp.) are part of the Portuguese flora, including three endemics (*Juniperus cedrus* Webb & Berthel. subsp. *maderensis* (Menezes) Rivas Mart., Capelo, J.C. Costa, Lousã, Fontinha, R.Jardim & M.Seq. in Madeira, *Juniperus brevifolia* (Seub.) Antoine in the Azores and *Juniperus navicularis* Gand. in Iberia). Some aecial hosts are important fruit tree crops, including quince (preferentially infected by *Gymnosporangium clavipes* Cooke & Peck) and apple (preferentially infected by *Gymnosporangium juniperi-virginianae* Schwein.), while *Crataegus monogyna* Jacq. (the preferential host of *Gymnosporangium globosum* Farl.) is native and widespread in mainland Portugal and also found in Madeira.

The database Species Fungorum (http://www.speciesfungorum.org) records 8093 nonsynonymous Pucciniales species. The present study lists 239 species occurring in Portugal, representing 2.95 % of all rust species. Some genera are over-represented in Portugal, namely *Gymnosporangium* (8.5 % of all species), *Melampsora* (8.0 %), *Pucciniastrum* (7.4 %), *Phragmidium* (6.8 %) and *Uromyces* (6.1 %), while *Coleosporium* and *Puccinia* (3.9 % each) present intermediate values. On the contrary, underrepresented taxa are the families Uropyxidaceae (1.8 % of all species in the family), Pileolariaceae (1.6 %), Raveneliaceae (0.5 %), Phakopsoraceae (0.4 %), Chaconiaceae (0 %), Pucciniosiraceae (0 %) and Mikronegeriaceae (0 %). While members of the Uropyxidaceae and Phakopsoraceae (i.e., *Tranzschelia* spp. and *Cerotelium fici* (Castagne) Arthur, respectively) occur on exotic (cultivated) hosts, and are presumably exotic, *Pileolaria terebinthi* (DC.) Castagne (Pileolariaceae) occurs on an autochtonous host and is presumably native, and *Dicheirinia maderensis* Gjaerum (Raveneliaceae), inhabiting a Madeiran endemic, is in fact one of the few endemic rust species.

In Portugal, species of *Puccinia* and *Uromyces* together account for 77 % of all rust species, a proportion similar to that found in non-tropical areas (e.g., 86 % in Central Asia, 79 % in Turkey, 76 % in the Middle East, 75 % in Belgium, 74 % in Spain and North Africa and 66 % in the British Isles, Germany and New Zealand), while such species represent a lesser fraction of rusts in tropical areas (50 % in Brazil, 41 % in French Guiana, 41 % in Sub-Saharian Africa and 39 % in South and Southeast Asia). The Table presented in Supplementary data 5 compares countries or regions in all continents according to the relative proportion of number of species per family (or per genus, for the most populated genera) in relation to the total number of rust species in each country/region. The relative proportion of species in each genus/family in Portugal follows those found in other temperate climate countries, differing notably from those found in Southern Asia, Sub-Saharian Africa and South America, with the latter exhibiting the wider variability in the relative proportion of species per genera/family. Multivariate analysis performed on the proportion of number of species per genus referred to the total number of rust species per country/region depicts three main geographical clusters, one (the one with least diversity) composed by temperate/sub-tropical countries/regions in both hemispheres, another composed by tropical areas of Africa and Asia, and a third one (the most diverse) composed by the neotropics (Fig. 5, panels A and C). *Melampsora*, *Gymnosporangium* and *Phragmidium* are the genera that better correlate with the temperate clade. *Phakopsora* best represents the tropical and neotropical clades, with genera such as *Hemileia* (along with

a complex combination of other genera) best defining the African/Asian clade and *Prospodium* (along with several others) defining the diverse neotropical clade (Fig. 5, panels B and D).

The ratio between the number of rust species and that of vascular plant species has been used to infer the level of mycological knowledge of a region (Hennen & McCain 1993, Berndt 2012a). In the present study, the overall ratio calculated for Portugal is 1:12.2, while it is 1:13.2 and 1:14.5 for the Azores and Madeira respectively, presenting higher values than those calculated for Southern Africa (1:38; Berndt 2008) and for the Neotropics (ranging between 1:16 in Puerto Rico and in Trinidad and 1:124 in Nicaragua, with intermediate values of 1:26 in Cuba, 1:36 in Mexico and Costa Rica, 1:73 in Colombia and 1:42 in Brazil; Berndt 2012a), but lower than those calculated for Japan (1:7) and for Switzerland and Austria (1:6 in each country). While climatic, ecological and botanical differences among regions are expected to cause the real rust species:host species ratio to be uneven across the globe, as discussed by Berndt (2012a), the higher saturation of such ratios in temperate climate countries contrasts with the narrower diversity depicted by the multivariate analysis results. This reinforces the view that, in spite of an uneven depth of research on rust mycobiota in tropical and neotropical countries, rust fungi are more diverse in these areas and particularly in the neotropics. In this context, Portugal is positioned in close proximity to other temperate countries, particularly with other Mediterranean climate countries.

Conclusions

This study has updated the knowledge on the Portuguese rust mycobiota. With a rust species:host species ratio of 1:12.2, the Portuguese rust mycobiota is relatively well known, although the overall diversity, either in absolute or relative values depicted respectively by the total number of taxa (246) or by the percentage of rust species per genera, is moderate and within the range of diversity of other temperate climate countries. In contrast, this study showed tropical regions, and particularly the neotropics, as the areas harbouring the highest diversity.

The Southwesterly position of Portugal in relation to the rest of Europe, and the West-Southwesterly position of Azores and Madeira in relation to mainland Portugal, highlight these territories as entry points, and simultaneously as early detection points, for the arrival of new rust fungi in Europe, as illustrated by the detection of *Coleosporium asterum* (Dietel) Syd. & P. Syd., *Puccinia hemerocallidis* Thüm., *P. stenotaphricola* J. Walker and *P. thaliae* Dietel in the Azores and/or Madeira, while other rusts may enter Europe through these territories as suitable hosts are present, including *Austropuccinia psidii* (G. Winter) Beenken, *Puccinia pittieriana* Henn., some *Cronartium* spp. and several *Gymnosporangium* spp.

The Pucciniales is recognized as one of the most speciose orders of fungi. Many species, although valid in formal terms, have seldom been reported after their first description. Species described from or recorded in Portugal in such circumstances are listed, including six species recorded in Portugal only once and never elsewhere in the world and five species seldom recorded either in Portugal or in the rest of the world, raising concern on their conservation status. On the other hand, five rust species that occur on endemic hosts whose populations are physically isolated from other hosts of the same rust species are listed as potentially being under speciation processes.

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