

Species richness, taxonomy and peculiarities of the neotropical rust fungi: are they more diverse in the Neotropics?

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Abstract The species richness of rust fungi (*Pucciniales* or *Uredinales*) in the neotropics is reviewed. Species numbers are presented for all neotropical countries and rust-plant-ratios calculated. It is discussed whether the ratio for a given region can be explained by the species richness of vascular plants alone or whether it is caused by additional factors. In the first case, ratios should apply globally and vary only slightly; in the second case, more diverging ratios are expected. Observed ratios ranged between 1:16 and 1:124 in the neotropics. The large differences are certainly influenced by unequal levels of investigation, rendering interpretation difficult. Differences seem also to be influenced by the taxonomic composition of floras regarding the percentage of host families or genera bearing different numbers of rust species. This indicates that rust species richness is not driven solely by plant species richness. Ratios calculated for Switzerland, Austria and Japan are distinctly higher than for the neotropics indicating that certain temperate regions are proportionally richer in rust fungi than the neotropics. Uredinial states and short-cycled rust species prevail in the neotropics. The preponderance of uredinial states may be due to the heterogeneous spatial composition of certain vegetation types in the wet tropics. Short-cycled rusts may be adapted to a pronounced seasonality that can be encountered in many drier neotropical biomes. Future research needs to fill our knowledge gaps on the taxonomy and ecology of neotropical rust fungi are discussed.

Keywords Endemism · Fungal diversity · Neotropics · Rust fungi · Rust-plant-ratio · Species richness · Uredinales

Introduction

The concept of biodiversity is broad and embraces all aspects of biotic diversity and interaction ranging from the molecular to the biome level (e.g. Gaston and Spicer 2004). The term biodiversity is often used to mean organismal diversity, mainly species richness, or the

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number of species occurring in a given region (e.g. Crous et al. 2009; Hawksworth 1991; Hyde and Hawksworth 1997). Species richness is only one facet of biodiversity but probably the most prominent one. Reasons for this may be that species richness is more recognizable and open to direct observation than other facets and that it is intuitively perceived as an important factor for healthy ecosystems and human well-being (Thompson 2010).

Although it was noticed early that species richness was not evenly distributed on earth (e.g. Adams 2009), only in recent decades have biologists obtained reliable species numbers and detailed patterns of global species richness for some popular and well-known organismal groups, notably vascular plants (e.g. Jørgensen et al. 2011; Kier et al. 2005; Mutke and Barthlott 2005) and vertebrates (e.g. mammals: Schipper et al. 2008; birds: Hawkins et al. 2007; amphibians: Wiens 2007). These studies have identified areas of the neotropics as overwhelmingly diverse. Grenyer et al. (2006) and Lamoreux et al. (2006) superimposed maps depicting the species richness of different classes of vertebrates and demonstrated considerable congruence between regions of elevated species numbers. They concluded that data obtained for amphibians, birds and mammals might be used as surrogates to predict regions of outstanding species richness also for other less conspicuous and investigated taxa.

Fungi are a poorly investigated taxon. Only a small part of their global biodiversity is known and almost nothing about spatial patterns of fungal species richness (e.g. Arnold and Lutzoni 2007; Gómez-Hernández et al. 2011). Fungi are intricately linked with plants as mutualistic symbionts, parasites or decomposers. Mycologists have tried to use plant species richness as a surrogate to estimate global or regional species numbers of fungi. Hawksworth (1991) estimated that 1.5 million fungal species may populate the world based on a fungus-vascular plant-ratio of 6:1 in Great Britain. Though modified and criticized (e.g. Fröhlich and Hyde 1999; Hawksworth 2001 and references therein, Shivas and Hyde 1997) the 1.5 million estimate has become widely accepted in the absence of more quantitative data.

Rust fungi (*Basidiomycota*, *Pucciniales* or *Uredinales*) are probably better known than many other microfungi (Crous et al. 2006; Rossman 1994). They comprise ca. 5–7000 species that are distributed around the world wherever terrestrial vegetation is present (Cummins and Hiratsuka 2003). As obligate pathogens of vascular plants rust fungi usually exhibit strong host specificity (genus or species specificity). Because of their specificity it is reasonable to hypothesize that the species richness of rust fungi is mainly a function of the species richness of vascular plants and that the latter may be used to estimate numbers of rust species in regions that are mycologically less investigated. Hennen and McCain (1993) used ratios between species numbers of rust fungi and vascular plants to assess the level of collecting of rusts in Mesoamerican countries and to estimate their species numbers in the respective countries. From the ratios obtained for a well-investigated tropical region, the Mogi-Mirim forest reserve in Brazil (ratio 1:4 to 1:3), and a temperate region, Indiana, USA (ratio 1:16), they extrapolated that rust species may be 5–25% as numerous as plant species. For the Mesoamerican countries they calculated ratios between 1:18 (El Salvador) and 1:138 (Panama) and noted that there was no botanical or geographical reason for these discrepancies.

The present paper revisits the rust fungi of the neotropics in order to investigate the relationships between fungal species richness and vascular plant species richness together with floristic composition. Firstly, it aims to give an overview of the present knowledge of neotropical rust fungi and to compare it to other regions of the world. Secondly, this review examines the hypothesis that rust species richness is congruent with plant species richness. Finally peculiarities of the neotropical rust mycobiota will be discussed with regard to phylogenetic diversity, endemism, life cycle and certain morphological traits.

The neotropical rust mycobiota

State of uredinological inventory and species numbers of rust fungi of neotropical countries

The Neotropics, located in the New World between the tropics of Cancer and Capricorn, comprise the southern half of Mexico, Central America (Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica, Panama), Colombia, Venezuela, the Guianas (Guyana, Suriname, and the French overseas department French Guiana), Ecuador, Peru, most of Bolivia and Brazil, the northern half of Paraguay and the Antilles. Argentina and Chile only reach into the tropics with small parts of their territories. These regions are desert-like or covered by dry ‘Puna’ in Chile, while north-western Argentina has parts of the eastern Andean ‘Yunga’ rain forests and ‘Chaco’ dry forest. Both countries are not considered here. Countries with less than 60% of their territory outside of the tropics are regarded as entirely neotropical (Brazil, Mexico, Paraguay). No attempts were made to calculate species numbers for their tropical and extratropical parts separately since the tropics do not mark a bio-geographic border. The Atlantic rain forests of Brazil, for example, extend to both sides of the tropic of Capricorn and it would be illogical to treat their tropical and extratropical portions separately.

The countries are treated in the order listed above. To assess species numbers of rust fungi, uredinological and other mycological publications on the respective countries were consulted. The ‘Fungal Databases’ provided by the U.S. Department of Agriculture, Agricultural Research Service (Farr and Rossman 2011) were queried in addition to obtain data especially for countries not covered by floras, checklists or similar synopses. Lists retrieved from ‘Fungal Databases’ were not checked for possible duplications caused by synonymy or erroneous entries. That may lead to an overestimation of the number of recorded species but this may be regarded as a systematic failure that should apply to all figures obtained from this database. A query for the Cuban rust fungi was analyzed to assess the percentage of duplication due to listing of synonyms, autonyms and anamorph states. At least 51 entries (ca. 17%) of the 295 displayed species names were considered duplicates. This indicates that other species numbers obtained from ‘Fungal Databases’ for the neotropical countries may be similarly reduced in percentage terms. In Table 1, species numbers from ‘Fungal Databases’ were not reduced, other than for Cuba.

It is not feasible to present an exhaustive list of relevant references for each country in a paper reviewing the entire neotropics that cover 17 countries and a French overseas department. In addition to available monographs (dealing with rust taxa: e. g. Beenken et al. 2012; Buriticá 1998, 1999a, b; Buriticá and Hennen 1980; Cummins 1940; Hennen and Pontes Sotão 1996; Hennen et al. 1998; López-Franco and Hennen 1990; Salazar Yepes et al. 2007; dealing with rusts of certain host taxa: e. g. Baxter 1973; Lindquist 1945, 1955, 1958), only those publications are cited that represent the most comprehensive and important works on the rust fungi of a given country. Admittedly, this selection is subjective but it will give the reader access to most of the remaining references.

Country accounts

Mexico

Mains (1935) studied rusts and smuts of the Yucatan peninsula. This work includes also a few reports from Guatemala and Belize. The major reference on Mexican rust fungi is the

Table 1 Rust species richness in relation to vascular plant species richness in neotropical countries

Country	Species number of rust fungi (F&R; data from Farr and Rossman 2011)	Species number of vascular plants (number of native species in brackets where available)	Ratio rust species: vascular plant species	Reference for plant species richness
Mexico	651	23,424	1:36	Villaseñor (2004)
Guatemala	416	8,681	1:21	Earthrends and Environmental Information Portal (2011)
Belize	70 (F&R)	3,408	1:49	Balick et al. (2001)
Honduras	80	5,680	1:71	Earthrends and Environmental Information Portal (2011)
El Salvador	140	2,911	1:21	Earthrends and Environmental Information Portal (2011)
Nicaragua	51	6,347	1:124	Stevens et al. (2001, 2009)
Costa Rica	317 (F&R)	11,467	1:36	INBio (2011)
Panama	113	9,498	1:84	Correa et al. (2004)
Colombia	334	24,405	1:73	Jørgensen et al. (2011)
Venezuela	409 (F&R)	15,820	1:39	Hokche et al. (2008)
Guyana	55	7,112	1:109	Funk et al. (2007)
Surinam	9 (F&R)	4,984	1:554	Funk et al. (2007)
Ecuador	293 (F&R)	16,006 (15,411)	1:55	Jørgensen et al. (2011); Jørgensen and León-Yáñez (1999)
Peru	175 (F&R)	19,232	1:110	Jørgensen et al. (2011)
Bolivia	263 (F&R)	14,387	1:55	Jørgensen et al. (2011)
Brazil	771	32,358	1:42	Forzza et al. (2010)
Paraguay	81	7,851	1:97	Earthrends and Environmental Information Portal (2011)
Cuba	244 (F&R, duplicates eliminated)	6,601 (5,991)	1:27	Acevedo-Rodriguez and Strong (2011)
Hispaniola	180	5,586 (4,612)	1:31	Acevedo-Rodriguez and Strong (2011)

Table 1 continued

Country	Species number of rust fungi (F&R: data from Farr and Rossman 2011)	Species number of vascular plants (number of native species in brackets where available)	Ratio rust species: vascular plant species	Reference for plant species richness
Jamaica	131	3,218 (2,540)	1:25	Acevedo-Rodriguez and Strong (2011)
Puerto Rico (+ Virgin Islands)	201	3,270 (2,221)	1:16	Acevedo-Rodriguez and Strong (2011)
Trinidad	161	2,568 (2,259)	1:16	Adams (2011)
Switzerland	540	3,144	1:6	Bundesamt für Umwelt Schweiz 2009
Austria	500	2,950	1:6	Österreichisches Umweltbundesamt (2011)
Japan	763	5,629	1:7	Flora of Japan Project (2011)

Data for Switzerland, Austria and Japan are added to represent temperate regions for comparison

two volume flora of León Gallegos and Cummins (1981) in which 613 species are listed, among them 42 belonging to the form genera *Uredo* and *Aecidium*. The author has knowledge of 38 additional reports for Mexico (e.g. Carrión and Galván 1984, 1985, 1986; Hennen and McCain 1993) resulting in a total of 651 species.

Guatemala

The majority of Guatemalan rust fungi were described by Arthur (1918b, c, d, e) and Kern (1907, 1911). Cummins (1943) published a check list counting 369 species. Hennen and McCain (1993) raised the number to 416 based on specimens present in the Arthur Herbarium (PUR).

Honduras, Belize, El Salvador, Nicaragua

Rusts of Belize were published by Mains (1939) who reported 58 species. According to Farr and Rossman (2011) Belize is home to 70 species of rust, Honduras to 62, El Salvador to 46 and Nicaragua to 40 species. Hennen and McCain (1993) counted for the same countries 56, 80, 140 and 51 species, respectively. National compendia or checklists are not available but Vol. 7 of 'North American Flora' (Arthur 1906–1940) and Cummins and Stevenson (1956) cover the countries.

Costa Rica

Arthur (1918a) and Sydow (1925a) made fundamental contributions to the rust mycobiota of Costa Rica. A checklist was provided by Berndt (2004) listing 292 species. According to Farr and Rossman (2011) there are 317 species.

Panama

Piepenbring (2006) published a checklist of fungi of Panama including 67 species of rusts. Twenty-two species were added by Perdomo-Sánchez and Piepenbring (2008) for a total of 89 species. Presently about 113 species are known (Piepenbring, personal communication).

Colombia

Seminal work on the Colombian rust mycobiota was carried out by Mayor (1914) who reported 158 rust species including 84 new ones. Kern et al. (1933a, b) published an annotated index comprising 215 species. In recent years, the rust fungi of Colombia have been intensively studied mainly by Buriticá, Pardo-Cardona and Salazar Yepes (e.g. Buriticá 1998, 1999a, b; Buriticá and Pardo-Cardona 1996; Pardo-Cardona 1997, 1998, 1999, 2000, 2001; Salazar Yepes and Buriticá Céspedes 2002, 2004). García et al. (2007) listed 326 species. A few additional rust species have since been described (Salazar Yepes and Buriticá Céspedes 2008) resulting in a total of 334 species.

Venezuela

Important contributions to the Venezuelan rust fungi were made by Sydow (1930), Kern et al. (1934), Kern (1938), Kern and Thurston (1943, 1944a, b) and Jørstad (1960). These

works comprise about 319 species. Dennis (1970) compiled the ‘Fungus flora of Venezuela and adjacent countries’ including 593 species of *Uredinales* (*Pucciniales*). Some 300 of those were reported from Venezuela. Iturriaga and Minter (2006) list 295 rust species for Venezuela, Farr and Rossman (2011) list 409.

Guianas

The Guianas may belong to the least investigated neotropical regions for rust fungi. Sydow (1925b) reported 28 rusts from Guyana; Hernández et al. (2005) published a checklist comprising 55 species. Farr and Rossman (2011) list nine species for Suriname; virtually no data are available for French Guiana but a checklist is currently being prepared by the author.

Ecuador

The Swedish mycologist G. Lagerheim collected fungi during a three-year stay in Ecuador and published results together with Patouillard (Patouillard and Lagerheim 1891, 1892, 1895a, b). Their list included 57 rust species. A considerable part of Lagerheim’s rust fungi was determined and published only later by Jørstad (1956, 1959) adding numerous new reports and 14 new species. Another major contribution to the Ecuadorian mycobiota was made by Sydow (1939) who added 21 new species and additional new reports. Presently Farr and Rossman (2011) list ca. 293 species.

Peru

Hennings (1904) reported numerous rust fungi collected by the German botanist and avid collector E. Ule in Peruvian and Brazilian Amazonia; Arthur (1918f) gave an account of Andean, mainly Peruvian rusts collected by Rose & Rose. Arthur (1929) compiled a list of 83 species of rust fungi, almost half of them belonging to form-genera. García-Rada and Stevenson (1942) reported 148 species; presently Farr and Rossman (2011) list ca. 175 species.

Bolivia

Stevenson and Cárdenas (1949) published a list of Bolivian fungi including 197 rusts. This list was supplemented by Farr and Stevenson (1964) adding 20 new reports. Part of the records was based on e.g. Arthur (1925), Jackson (1926, 1927, 1931a, b, c, 1932), Jørstad (1956, 1959) and specimens in the U.S. National Fungus Collection. Further records were added by Lindquist (1982) in his flora of rust fungi of Argentina and adjacent regions. Farr and Rossman (2011) list ca. 263 species.

Brazil

The most important early contributions to the Brazilian rust fungi were based on the collections made by E. Ule (e.g. Dietel 1899; Hennings 1895, 1896, 1899a, b). In the first half of the twentieth century, Jackson (1926, 1927, 1931a, b, c, 1932) published the ‘South American rust fungi’ based on the rich collections made by E. W. D. Holway, a botanist from the U.S., among them many specimens from Brazil. Thurston (1940) published the

rusts of Minas Gerais and Viégas (1945) from many regions of Brazil in a richly illustrated enumeration. Recent research has focused on inventories of representative protected areas in different states of Brazil (e.g. de Carvalho et al. 2006, 2007; Pontes Sotão et al. 2006; Salazar Yepes and Carvalho 2010) and the threatened ‘Cerrado’ biome (e.g. de Carvalho et al. 2008; Dianese et al. 1993, 1997; Rezende and Dianese 2001) or lists of single states (e.g. Almeida de 1988; Lindquist and Da Costa Neto 1963; Pontes Sotão et al. 2001). A most useful annotated checklist of the Brazilian rust fungi that compiles data until 2003 was published by Hennen et al. (2005). It comprises 745 species. Meanwhile at least 26 additional species have been reported, among them 14 new ones, resulting in 771 species for the country.

Paraguay

Spezzazini (1922) published “Fungi paraguayenses” including 47 rust fungi. Lindquist (1982) covered the southern part of Paraguay in his Argentinean rust flora, and Farr and Rossman (2011) enumerate 81 species.

Antilles

Cuban rust fungi were studied by Arthur and Johnston (1918) who reported 136 species. Schmiedeknecht (1983) added 22 new reports and gave a total of 176 species for the country. With 10 additional reports Urban (1990) raised the list to 186 species. Farr and Rossman (2011) list 295 species, 244 if duplications are eliminated.

For Hispaniola data are more or less restricted to the Dominican Republic whose rust fungi were studied by Kern (1928) and Kern et al. (1933a, b). Together, 180 species were reported. The Jamaican rust fungi were surveyed by Dale (1955b) who recorded 102 species. Farr and Rossman (2011) list 131 species. Fungi of Puerto Rico were mainly studied by mycologists from the United States. Arthur (1915, 1916, 1917a) reported 157 species of rusts; in the monograph of Roure (1963), 201 species were treated. Stevenson (1975) counted 211 species for Puerto Rico and the American Virgin Islands together. Arthur (1922) reported 71 rust fungi from Trinidad. Additions were made to this list by Baker and Dale (1951) and Dale (1955a) resulting in 161 species (including a few from Tobago). Barbados and the Windward Islands have 74 rust species according to Baker and Dale (1948).

Rust species richness in relation to species numbers of vascular plants

Preconditions and restrictions of rust-plant-ratios

Rust-plant-ratios are the central figure used to compare or extrapolate the species richness of rust fungi in different countries or regions based on the hypothesis that the species richness of rust fungi is mainly a function of the species richness of vascular plants. If this hypothesis is correct one will expect similar rust-plant-ratios independent from geographical location or biogeographic region. Observing strong differences between rust-plant-ratios of different regions does not necessarily falsify the hypothesis as such an observation could be explained by two other reasons: (1) There are important factors beside plant species richness that drive the diversity of rust fungi, or (2) the available data are insufficient to support the basic hypothesis, i.e. the observed patterns mirror level of investigation rather than reality.

Insufficient data

Ratios can be influenced by the reliability of counts of species numbers of rusts and of the vascular flora, and secondly, underlying taxonomic concepts regarding both parasites and plants.

While most uncertainty in rust-plant-ratios derives from poor knowledge about rust diversity, one should keep in mind that different plant counts may also influence the ratios. For example, Earthtrends and Environmental Information Portal (2011) lists 56,215 vascular plant species for Brazil (data for 2004) whereas most recent data indicate a number reduced by 42%, namely 32,358 species (Forzza et al. 2010). Another complication is created by plant groups comprising similar species that are difficult to distinguish. The northern temperate zone, for example, is rich in large genera of *Asteraceae* and *Rosaceae* like *Hieracium*, *Taraxacum*, *Rubus* and *Alchemilla* that comprise numerous visually similar and often apomictic species (e.g. Fischer et al. 2008; Seybold 2011; Stace 1998). In the relatively small floras of temperate and northern Europe plant species numbers can be considerably influenced by whether or not these visually similar species are distinguished and included in counts.

Nevertheless, knowledge is more restricted about mycobiotas than floras. There is no doubt that rust fungi are still under-collected in many neotropical countries (e.g. Buriticá 2000; Hennen and McCain 1993) so that species numbers are likely to rise and will continue for some time to reflect state of knowledge rather than reality. On the other hand, the inventory of some smaller neotropical regions like Puerto Rico, Trinidad or Cuba (Table 1) may have reached a reasonable level of completeness and species numbers are unlikely to increase dramatically.

Numbers of fungal species do not only depend on mycological exploration but also on taxonomic concepts. More and more rust fungi that formerly have been regarded as single species appear to comprise several species after detailed examination (e.g. Beenken et al. 2012; Berndt 2007, 2010). One may therefore hypothesize initially that rust fungi with a reportedly broad host range could comprise unresolved aggregates of species with narrower host ranges. On the other hand, there are examples that show that rusts originally described as separate species may in fact belong to a few plurivorous species like *Puccinia lagenophorae*, *P. lantanae*, *P. xanthii*, and *P. psidii* (Laundon 1963; Pérez et al. 2010; Scholler et al. 2011; Seier et al. 2009).

Rust-plant-ratios of neotropical countries

Despite these restrictions and difficulties an attempt is made to calculate and interpret rust-plant-ratios for all neotropical countries. Table 1 lists the numbers of rust species and vascular plants for the neotropical countries as well as the ratios calculated from both figures. French Guiana was not included as reasonable rust data are unavailable. The ratios range between 1:16 (Puerto Rico, Trinidad) and 1:124 (Nicaragua). The ratio of 1:554 calculated for Surinam is unrealistically low and denotes our ignorance of the country's rust mycobiota. It is therefore not considered further. Ratios of rather well investigated countries like Brazil, Colombia, Costa Rica, Guatemala, Mexico or Venezuela range between 1:21 and 1:73.

Ratios calculated for northern temperate regions are much higher. In both Switzerland and Austria one rust species occurs on six vascular plant species; in Japan the ratio is very similar with 1:7. It should be noted that Indiana, situated in the temperate U.S., has the same ratio as Puerto Rico and Trinidad, 1:16 (Hennen and McCain 1993).

The strongly different ratios among the neotropical countries and between them and some northern temperate countries contradict the central assumption that the number of rust species in a region is only determined by plant species richness. The question remains whether the observed differences mirror reality or reflect different levels of exploration. The ratios for Honduras (1:71) and Nicaragua (1:124), geographically located between Guatemala (ratio 1:21) and Costa Rica (1:36) hint to the latter. These countries represent adjacent sections of the Central American isthmus and belong to the same floristic province (Takhtajan 1986) so that a different level of exploration is the most likely reason for the strongly diverging ratios. On the other hand, the different ratios for Puerto Rico (1:16) compared to Switzerland and Austria (1:6) do not seem to be explicable in this manner as all these countries are thoroughly studied. This strongly indicates that the number of rust species occurring in a given region does not entirely depend on plant species number but also on additional biological or environmental factors. To estimate the influence of these factors reliably, it would be necessary to find an approach by which ‘level of exploration’ could be eliminated as a possible driving factor.

Rust species richness in relation to taxonomic composition of vascular flora

One parameter that characterizes the flora of a given region is taxonomic composition, i.e. the affiliation of the flora to families and genera. Different families and genera usually have a different share of the flora often resulting in a preponderance of certain taxa. Table 2 lists the ten largest plant families of Mexico together with the number of rust species reported on each. For comparison the ten largest Colombian plant families and their rust numbers are also shown. Mexico is only partly located in the tropics and represents generally drier habitats than Colombia, which is mainly humid but comprises a number of more arid regions in the Andes and in the North (Ruiz et al. 2002).

Asteraceae, *Fabaceae*, *Poaceae*, *Orchidaceae* and *Rubiaceae* rank highly in both countries. Orchids are extremely well represented in Colombia, while in Mexico, the *Asteraceae* and *Fabaceae* occupy the first ranks. Other disparities are cacti, speciose in Mexico but poorly represented in Colombia, and the *Melastomataceae*, which is markedly more species-rich in Colombia than in Mexico.

Analysis shows that different plant families have a different number of rusts. If numbers of rust species were a mere function of numbers of vascular plant species one would expect that large plant families should host a comparatively higher number of rust species, i.e. the ratios calculated should be more or less the same. Whether a country or region has been thoroughly investigated should not matter as the level of exploration will be more or less the same for the whole flora.

This expectation is not met in reality. *Asteraceae*, *Poaceae* and legumes are rich in rust fungi (e.g. Schmiedeknecht 1983, 1984) as also found in Mexico and Colombia. In contrast, *Orchidaceae* bear very few rust fungi (Schmiedeknecht 1983). In Colombia, *Orchidaceae* account for almost 15% of the vascular flora but host less than 2% of the country’s rusts. Other species-rich plant families in Colombia that bear only few rust fungi are *Rubiaceae* and *Melastomataceae*. In Mexico, *Orchidaceae* and *Cactaceae* similarly host comparatively few rust fungi. Another diverse group of tropical vascular plants, especially in montane forests, are ferns and fern allies. Vascular cryptogams are not included in Table 2 as they are assigned to a considerable number of families. In Colombia, ferns and allies comprise ca. 1,641 species (Bernal et al. 2007) or ca. 7% of the vascular flora. For Ecuador, the adjacent Andean country, ca. 1,300 species have been catalogued (Jørgensen and León-Yáñez 1999) accounting for ca. 8% of the vascular flora.

Table 2 The ten largest families of Mexican vascular plants and associated rust fungi compared to species numbers from Colombia

Family	Mexico				Colombia			
	Species no.	Rank	No. of associated rust species	Ratio	Species no.	Rank	No. of associated rust species	Ratio
<i>Asteraceae</i>	3021	1	151	1:20	1420	2	91	1:16
<i>Fabaceae</i>	1274	2	57	1:22	568	5	30	1:19
<i>Poaceae</i>	1187	3	95	1:12	813	8	58	1:14
<i>Orchidaceae</i>	1145	4	8	1:143	3588	1	6	1:598
<i>Cactaceae</i>	946	5	1	1:946	38	?	–	–
<i>Euphorbiaceae</i>	782	6	25	1:31	394	11	15	1:26
<i>Rubiaceae</i>	593	7	7	1:85	1214	3	8	1:152
<i>Lamiaceae</i>	530	8	23	1:23	?	?		
<i>Mimosaceae</i>	463	9	59	1:8	?	?		
<i>Scrophulariaceae</i>	437	10	6	1:73	?	?		
<i>Melastomataceae</i>	209	?	–	–	948	4	–	–
<i>Piperaceae</i>	267	?	–	–	605	6	2	1:303
<i>Araceae</i>	125	?	4	1:31	591	7	1	1:591
<i>Bromeliaceae</i>	333	15	4	1:83	493	9	4	1:123
<i>Solanaceae</i>	430	11	8	1:54	441	10	24	1:18

Data for Mexico from Villaseñor (2003), for Colombia from Jørgensen et al. (2011) and Ruiz et al. (2002). Numbers of rust species from Farr and Rossman (2011)

? Data unavailable

Only ca. five species of rusts are known on fern plants in Ecuador, ca. 11 in Colombia and there are only ca. 25 known fern rusts in the entire neotropics.

Disparities between the rust numbers on different plant families can also be noticed in the northern temperate zone. Table 3 lists the 10 most speciose vascular plant families of Switzerland. Again, *Asteraceae*, *Poaceae* and *Fabaceae* are relatively rich in associated rusts while other families like *Brassicaceae* and *Scrophulariaceae* s.l. bear a much lower number of species. Rust fungi of Central Europe are very well known and it is unlikely that the given figures reflect inadequate knowledge.

If different plant families harbor widely different numbers of rusts it is clear that the species-richness of rust fungi in a given region depends both on the species number of vascular plants as well as the taxonomic composition of the flora. In other words, a region that is relatively rich in members of families like *Asteraceae*, *Poaceae* and *Fabaceae* will inherently have a richer rust mycobiota than regions with a high percentage of orchids, cacti, *Melastomataceae* or ferns.

If different plant families and genera support different numbers of rust fungi this will also influence the rust species richness in different biomes whose floras diverge in taxonomic composition. The South African ‘Fynbos’ and ‘Succulent Karoo’ biomes, for example, are very poor in rust fungi in contrast to their rich flora (Berndt 2008). This may be caused by the dominance of a couple of species-rich plant families such as *Mesembryanthemaceae*, *Proteaceae*, *Restionaceae* and the genus *Erica* (Gibbs Russell 1985) that host few or no rust fungi. The savannas and woodlands of the Brazilian ‘Cerrado’ are well-known floristically (e.g. Gottsberger and Silberbauer-Gottsberger 2006; Oliveira and

Table 3 The ten largest vascular plant families of Switzerland (with adjacent regions) and their associated rust fungi

Family	Species no.	Rank	No. of associated rust species	Ratio
<i>Asteraceae</i>	427	1	109	1:4
<i>Rosaceae</i>	272	2	34	1:8
<i>Poaceae</i>	254	3	86	1:3
<i>Fabaceae</i>	214	4	95	1:5
<i>Brassicaceae</i>	199	5	4	1:50
<i>Cyperaceae</i>	156	6	40	1:4
<i>Caryophyllaceae</i>	144	7	13	1:11
<i>Scrophulariaceae</i>	140	8	8	1:17.5
<i>Apiaceae</i>	130	9	42	1:3
<i>Ranunculaceae</i>	119	10	27	1:4.4

Flora data from Hess et al. (2010). Numbers of rust fungi based on provisional checklist of Swiss rust fungi (T. Brodtbeck, unpublished); rust species delimitation after Gäumann (1959)

Marquis 2002; Ratter et al. 2006) and regarding the rust mycobiota (de Carvalho et al. 2008; Dianese et al. 1997; Salazar Yepes and Carvalho 2010). The vascular flora of the Cerrado biome has been estimated to comprise between 6,429 and 10,500 species (Ratter et al. 2006); in the database of the Brazilian flora (Forzza et al. 2010) 11,755 species are listed. The diverging figures may express growing knowledge but also different opinions concerning the expansion and delimitation of the biome. There is consensus that composites, legumes and grasses are the predominant plant families. Based on figures retrieved from Forzza et al. (2010), these families comprise 2,997 species or ca. 25% of the Cerrado flora. The *Orchidaceae*, *Melastomataceae*, *Rubiaceae*, ferns and allies, and *Cactaceae* together account for 1,817 species or ca. 15% of the flora. The prevalence of *Asteraceae*, *Fabaceae* and *Poaceae* would indicate that the Cerrado biome may be comparatively rich in rust fungi. Dianese et al. (1997) stated a number of 250 rust species on native Cerrado plants (=11,556 species according to Forzza et al. 2010). This results in a ratio of 1:46 that is similar to the ratio of 1:42 calculated for the whole country. The number of 250 rust species may be an underestimation, however, as de Carvalho et al. (2008) reported 157 species alone for the remnant Cerrado in the state of São Paulo. More exact species numbers have to be assessed for a detailed analysis and it may be that characteristics of the Cerrado environment, e.g. dryness, xeromorphy of the flora, or effects of fires, may influence the occurrence of rusts.

One can deduce that rust-plant-ratios are determined by absolute numbers of the vascular flora of a region as well as the composition of the flora, and potentially other environmental factors. Consequently, rust-plant-ratios calculated for a well-investigated area are not applicable globally, though they may be extrapolated for nearby regions with similar environmental conditions and biological context. In addition, the available data indicate that at least some temperate regions may be proportionally richer in rust fungi than the neotropics. This contrasts with many other groups of organisms including vascular plants.

Endemism and phylogenetic diversity of neotropical rust fungi

Although species richness is a central parameter of biodiversity, it describes only a part of the taxonomic diversity and uniqueness of a given biota. For a more comprehensive view,

endemism and taxonomic distinctiveness need to be considered. Endemism stands for uniqueness and irreplaceability of a biota, while taxonomic distinctiveness reflects the evolutionary history of organisms.

The label ‘endemic’ confers to any kind of organism an aura of rarity, a sign of vulnerability and need of protection. The term ‘rate of endemism’ is therefore almost inevitably combined with species richness when the biological value of a region or when priority areas for conservation have to be identified (e.g. Jørgensen et al. 2011; Kier et al. 2009; Lamoreux et al. 2006; Myers et al. 2000). Endemism, understood in a broad sense, means that a species or other taxon is confined to a restricted area such as an island, a mountain range, a biome or even a country. How one defines ‘restricted area’ is arbitrary, and endemism is an imprecise term.

What does endemism mean in relation to rust fungi in general and what do we know about endemism in neotropical rusts? Aspects of endemism were discussed for southern African rust fungi by Berndt (2008). It was noted that at the species level, endemism of rust fungi is primarily a matter of host specificity as the distribution of a given rust species cannot be wider than the distribution area of its host(s). Thus, each rust fungus that is specific to an endemic plant will necessarily be itself an endemic (host-dependent endemism). A less trivial facet of endemism is exhibited by rusts that do not occur in the whole geographic range of their host(s) (rust-innate endemism). The latter is difficult to prove, especially in regions of the world where collections of rusts are too sparse to give a clear and reliable picture of the distribution. The last aspect to be considered is ‘endemism by ignorance’. Newly described species or species that have been collected only rarely and rusts whose host range is insufficiently known may be incorrectly considered endemics. Conversely, some rust species with an allegedly wide geographic distribution and broad host range may be endemics in reality as more detailed examination may reveal that they represent groups of species, each with a restricted geographic range and narrow host specificity (e.g. Beenken et al. 2012; Berndt 2007, 2010; Chatasiri and Ono 2008). Taking these aspects into account, the particularities of rust fungi and our present knowledge do not seem to allow a meaningful analysis of endemism of rust fungi at the species level. It may be more useful to analyze the composition and endemism of a given rust mycobiota at genus and family level. One has to keep in mind that a number of rust genera and families are not well circumscribed (e.g. Aime 2006).

The neotropics boast ca. 75 teleomorph genera of rusts and represent ca. 61% of the 120 teleomorph genera recognized by Cummins and Hiratsuka (2003) plus three described since 2003 (Kirk et al. 2008). Of these 75 genera the following 28 are currently considered restricted to the neotropics (families added in brackets: Cha = *Chaenaceae*, Pha = *Phakopsoraceae*, Puc = *Pucciniaceae*, “Psi” = “*Puccinosiraceae*”, Rav = *Raveneliaceae*, Uro = *Uropyxidaceae*, inc. sed. = of unknown affiliation. Underlined genera may be synonymous with earlier described ones):

Allotelium (Rav), *Alveolaria* (“Psi”), *Anthomyces* (Rav), *Apra* (Rav), *Batistopsora* (Pha), *Botryorhiza* (Cha), *Cerradoa* (inc. sed.), *Chardoniella* (“Psi”), *Chrysella* (Puc), *Chrysocyclus* (Puc), *Chrysopsora* (Puc), *Cionothrix* (“Psi”), *Cleptomycetes* (Puc), *Cystomyces* (Rav), *Dasyspora* (Uro), *Desmosorus* (inc. sed.), *Diabole* (Rav), *Diabolidium* (Rav), [*Diorchidiella* (Rav), also subtrop.], *Dipyxis* (Uro), *Edythea* (inc. sed.), *Esalque* (Rav), *Hennenia* (Rav), *Kimuromycetes* (Uro), *Lipocystis* (Rav), *Mimema* (Uro), *Porotenus* (Uro), [*Prosopidium* (Uro), also subtrop.]; three species described from Africa and India].

These genera represent ca. 23% of the 123 teleomorphic rust genera. At least five of them may be synonymous with earlier described ones: *Diabolidium* is hardly distinguishable from *Allotelium*, *Batistopsora* from *Phakopsora*, *Cerradoa* from *Edythea*, *Hennenia* from

Esalque and *Porotenus* from *Prospodium/Sorataea*. But even the remaining 23 genera represent ca. 19% of the world's rust genera. A look at their familial affiliation shows a prevalence of members of *Raveneliaceae* (eight genera) over *Uropyxidaceae* (four), *Pucciniaceae* (four) and “*Puccinosiraceae*” (three). The eight raveneliaceous genera account for more than a third of the 22 genera accepted in *Raveneliaceae* by Cummins and Hiratsuka (2003). Altogether *Raveneliaceae* comprise 17 genera in the neotropics.

These figures warrant comparison with the number of rust genera of tropical Asia, Africa, and USA plus Canada. Tropical Asia (Indian subcontinent, Indochina, Indonesia, Philippines) is home to ca. 60 teleomorph genera of which seven appear restricted to the region (*Anthomycetella*, *Ceropsora* [= *Chrysomyxa*?], *Diaphanopellis*, *Hiratsukamyces*, *Corbulopsora*, *Kernella* [also subtrop.], *Pucciniostele* [also subtrop.]). Eight of the 60 genera belong to the *Raveneliaceae*, with one of them, *Anthomycetella*, probably restricted to the Philippines. Only 59 teleomorphic rust genera have been recorded for the entire African continent of which only three (*Cumminsina*, *Joerstadia*, *Stomatisora*) appear to be restricted to it. Nine of those genera belong to *Raveneliaceae*. The US and Canada comprise ca. 36 rust genera, four of them *Raveneliaceae*. None of the genera are restricted to the region.

Different methods have been proposed to measure taxonomic heterogeneity of a given set of species or taxa (e.g. Faith 1992: phylogenetic diversity, Rosauer et al. 2009: phylogenetic endemism, Vane-Wright et al. 1991: taxic diversity). None of these methods could be applied to the sets of genera compiled for different regions of the world as they require stable and comprehensive phylogenies. Unfortunately, available phylograms of the entire *Uredinales* (*Puccinales*) or their families are still incomplete; tropical genera and their members are underrepresented and type species of genera are often not included so that results remain preliminary (e.g. Aime 2006; Wingfield et al. 2004; Zuluaga et al. 2011). Though taxonomic diversity of rust fungi cannot be quantified at the moment it is evident that the neotropics harbour an above-average diversity of genera with a high number of probably endemic genera that represent ca. one-fifth of all teleomorphic genera. The neotropical rust mycobiota comprises all families as circumscribed by Cummins and Hiratsuka (2003) with *Raveneliaceae* especially well represented by 17 of 22 recognized genera.

Life cycles, prevalence of uredinial states, morphological peculiarities

In a paper on the rusts of the West Indies, Arthur (1917b) observed a “heavy preponderance of collections showing only urediniospores” and the occurrence of a “large proportion of short cycle species.” He noted that these trends were observable in tropical and temperate representatives and stated further that certain rust species that pass through an expanded life cycle in temperate regions are only found in their uredinial state in the tropics. Arthur concluded that both propagation by repeating spores and short-cycling “are the expression of two ways the rusts have found to meet one and the same set of conditions that menace their existence.” Arthur's ideas were elaborated by Schmiedeknecht (1983, 1984, 1986) in a series of papers on the Cuban rust fungi. Schmiedeknecht showed that rusts were more commonly heteroecious in temperate regions, exemplified by data from the former German Democratic Republic, while in Cuba autoecious species prevailed. Like Arthur, he observed that in Cuba even rusts with a proven heteroecious life cycle generally appeared to remain uredinial. Buriticá (2000) made similar observations in Colombia and adjacent Andean countries.

Among the short-cycled rusts a number of genera have been described with a modified life cycle designated ‘endophylloid’ after the genus *Endophyllum*. In endophylloid genera, teliospores are produced in basipetal succession and separated by intercalary cells (Jackson

1931d). Most of these genera have been lumped together to form the heterogeneous family “Puccinosiraceae”. The neotropics are richer in genera assigned to “Puccinosiraceae” than other tropical regions. Of the nine genera recognized by Cummins and Hiratsuka (2003) plus *Gambleola*—often regarded as a synonym of *Puccinosira*—only *Ceratocoma* and *Gambleola* are lacking in the Neotropics. Africa has *Ceratocoma*, *Didymopsora*, *Dietelia*, and *Puccinosira*. In Asia, *Dietelia*, *Gambleola* and *Puccinosira* are known.

Which are the particular conditions of the tropics that Arthur (1917b) supposed to menace the rusts’ existence and which apparently cause the prevalence of certain life strategies among tropical rust fungi? Based on observations in alpine environments and high latitudes, shortened life cycles have generally been considered an adaptation of the rusts to short growing seasons and a strategy to infect and colonize hosts and form teliospores in limited time. Both Arthur (1917b) and Schmiedeknecht (1986) emphasized that this hypothesis does not explain the preponderance of short-cycle species in the tropics where “the evergreen tropical vegetation always provides enough host tissue in an optimal state for infection and the existence of obligate biotrophs ...” (Schmiedeknecht 1986, p. 199, translated by the author). The absence of seasonality and the availability of vigorous vegetation over the entire year does not hold true for considerable parts of the neotropics. There are regions in the lowlands that experience pronounced dry seasons and are covered by dry deciduous forest, open woodland or savanna. The climatic situation may be exacerbated by edaphic conditions, for example in the Brazilian ‘Caatinga’, a vegetation type that once covered large areas of NE Brazil with a stunted, xerophytic scrub (Furley 2007). Buritica (2000) emphasized the role of tropical mountain ranges that cause a diversity of climatic regimes and different types of vegetation, which may influence both the composition of the rust mycobiota and the evolution of morphological traits and life cycles. In the Andes, leeward slopes and especially deep intermontane valleys are sheltered from moisture-loaded air masses and bear in the natural state a dry vegetation of semi-deciduous forest, dry forest or shrub (Young et al. 2007). That means that the neotropics have many environments with a restricted growing season in which a shortened life cycle may be advantageous for rust fungi.

It is difficult to generalize ecological conditions in an area as vast as the neotropics and to relate the conditions to traits observed in rust fungi. Neotropical lowland moist forests are renowned for their species richness of vascular plants, especially woody plants, and the scattered, non-dominant occurrence of the individuals of the different species (e.g. Gentry 1988; ter Steege et al. 2000). The scattered occurrence of a particular host species in such moist forests may be disadvantageous for specific rust species, as susceptible host individuals may not be present in the vicinity of an infected one. One may hypothesize that the dominance of uredinial states observed in the neotropics is adaptive to this condition and aids to colonize even distant host plants through increased inoculum levels. Despite enormous dilution in space urediniospores can colonize appropriate hosts over wide distances (Nagarajan and Singh 1990). Basidiospores of *Gymnosporangium cornutum* Arth. were found capable of infecting the alternate *Sorbus* host effectively more than 50 m from the source of inoculum (Wennström and Eriksson 1997). Wind and atmospheric currents are crucial for long distance dispersal. Wind seems also to play a major role for transport over shorter distances. It is questionable, however, whether wind is really an effective disperser of rust spores in the understory or subcanopy of a closed lowland rain forest. Two microclimatic conditions of this environment appear unfavorable for spore dispersal: the generally low wind speed and the high and persistent humidity that keeps plant surfaces wet (e.g. Dietz et al. 2007; Pohlman et al. 2007). In such a microclimate, rust spores might be transported more effectively and specifically to the hosts by plant-specific insects,

especially herbivores and pollinators (comp. Kluth et al. 2002; Kok and Abad 1994; Shaw 1990). The author is unaware, however, of any publications providing evidence of this in tropical rusts.

The none-dominance and scattered appearance of woody plant species in the moist forests of Amazonia is not a rule. More recent studies indicate that large expanses of forest can be dominated by limited sets ('oligarchies') of relatively common species and that this dominance is most pronounced at the family level (e.g. Macía and Svenning 2005). One would assume that rusts can colonize populations of dominant plant species more easily than widely scattered hosts and it would be interesting to compare the rust load of dominants and non-dominants.

The prevalence of uredinial rusts in the neotropics has triggered interest and research in their morphology, and in recent years numerous new form genera have been proposed to accommodate morphologically distinct uredinia and aecia (e.g. Buriticá and Hennen 1994; Hennen and Figueiredo 1979; de Carvalho and Hennen 2010; Salazar Yepes et al. 2007). As a consequence, many named *Uredo* spp. and unnamed uredinial or aecial states of known telial species were given new names that today enrich the dictionary of the *Uredinales* (*Pucciniales*). Though comparative data are lacking, one cannot assume that uredinial anamorphs are more diverse in the neotropics than in other warm regions. In temperate regions, where some tropical rust families are lacking or scarce, e.g. *Chaenaceae*, *Phakopsoraceae* and *Raveneliaceae*, uredinia may be more uniform. It may be that in temperate regions unnecessary creation of new form genera has not been exhausted.

A trait that seems to be restricted to tropical rusts is the formation of superstomatal sori that apparently evolved convergently in a number of rust genera (Buriticá 2000). In superstomatal sori, only one or a few sporogenous cells, rarely probasidia, penetrate a stoma without rupturing it and form a tiny uredinium or telium. Eight genera in which superstomatal sori are known occur in the Neotropics, viz. *Calidion* (gen. anam.), *Desmella*, *Desmosorus*, *Edythea* (incl. *Cerradoa*), *Hemileia*, *Hennenia*, *Prospodium* and *Puccinia* (*P. lygodii*) (Cummins and Hiratsuka 2003; Ritschel et al. 2005). In Africa, by comparison, *Hemileia*, *Prospodium* (*P. baphicola*), *Puccinia* (*Desmellopsis aframomicola*), and *Stomatisora* have species with superstomatal sori. Tropical Asia is home to five genera with superstomatal sori, viz. *Blastospora*, *Crossospora* (*C. kemangae*), *Gerwasia*, *Hemileia*, and *Prospodium* (*P. erebiae*, *P. tirumalensis*). It is likely that superstomatal rust species will also be discovered in genera whose members have hymenial sori. The adaptive value of superstomatal sori is unknown.

Conclusions

This review aims to summarize the present knowledge about species richness in neotropical rust fungi, and it tries to reveal factors that influence species diversity. Three main questions considered are: (1) Is the neotropical rust mycobiota particularly diverse? (2) Does the species richness of neotropical rust fungi reflect vascular plant species richness? (3) Have the neotropical rust fungi evolved features of morphology and life cycle adapted to the neotropical environment?

The species richness of rust fungi is incompletely known in the neotropics and the level of knowledge about them is unequal in different countries. Current rust-plant-ratios may not be accurate and observed differences may reflect our incomplete knowledge. There are several neotropical countries where rust-plant-ratios allow a cautious analysis. None of the ratios calculated in the neotropics matches the high ratios found in some temperate regions.

This indicates that temperate regions may be proportionally more species rich in rust fungi than the tropics. It was further shown that differences among ratios are influenced by the taxonomic composition of the vascular flora of a given region. Certain plant families like *Asteraceae*, *Poaceae* and *Fabaceae* are especially rich in rust fungi while others, like *Orchidaceae*, *Melastomataceae*, *Cactaceae* and ferns and their allies are host to relatively few rusts. Depending on the contribution of such families to a given flora, the latter may be inherently richer or poorer in rust fungi. This contradicts the assumption that the numbers of rust species are a function of the number of plant species.

The present data indicate that the taxonomic diversity of rust fungi is above average in the neotropics. Of the 75 teleomorph genera reported from the neotropics, 28 may be restricted to that region, accounting for almost a fourth of teleomorphic genera worldwide. Members of *Raveneliaceae* are especially well represented.

Lastly, there are traits of life cycle and morphology that seem to be overrepresented or characteristic in the tropics. These traits are possibly adaptations to environmental factors.

Promising lines of further research

This review indicates gaps in our knowledge of the neotropical rust fungi. These gaps include the taxonomy of rusts, patterns of their biodiversity, and their response to ecological factors. Most of the following suggestions on how to fill these knowledge gaps are also applicable to temperate regions (comp. Helfer et al. 2011).

There is a strong need for more monographs and revisions that deal with entire rust genera or the rust fungi of certain host families or genera. Carefully prepared monographs are the most efficient way to discover new species, to tidy up synonymy and to provide keys, detailed descriptions and illustrations which are indispensable for any ongoing research.

Additionally, critical checklists are needed for every country so that reliable species numbers become available. The Brazilian checklist (Hennen et al. 2005) is an excellent example. Preferably, data for the entire neotropics might be collected in a single database. This would offer unprecedented possibilities to detect distribution patterns and to make comparisons among countries.

It was emphasized that parts of the neotropics are severely under-collected. An effort to collect rust fungi in regions that have been poorly investigated should be made. Priority regions to be covered need to be identified by national specialists.

Phylogenetic analysis of DNA sequences has become an essential tool in taxonomic research. As Zuluaga et al. (2011) noted, few of the tropical genera have been included in these studies. Analyses often suffer from the failure to include authentic material of types of rust genera or families, so that phylogenetic hypotheses remain ambiguous. It is important that relevant types and carefully selected genera should be included in analyses.

The ecology of rust fungi is not well understood. We may know their host specificity relatively well but can only speculate on the mechanisms and factors that underlie their distribution patterns and influence life cycles and morphological traits. Comprehensive data on the distribution of rusts and their affiliation with certain vegetation types might test hypotheses about a possible interdependency between observed traits and ecological factors.

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