A GLOBAL ASSESSMENT OF DISTRIBUTION, DIVERSITY, ENDEMISM, AND TAXONOMIC EFFORT IN THE RUBIACEAE[1]

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ABSTRACT

Analyses of distribution, diversity, endemism, and taxonomic effort for Rubiaceae are reported, based on queries from a World Rubiaceae Checklist database. Rubiaceae are widespread and occur in all major regions of the world except the Antarctic Continent, but are predominantly a group in the tropics with greatest diversity in low- to mid-altitude humid forests. A count of Rubiaceae species and genera is given (13,143 spp./611 genera), which confirms that this is the fourth largest angiosperm family. *Psychotria* L. is the largest genus in the Rubiaceae (1834 spp.) and the third largest angiosperm genus. Most genera (72%) have fewer than 10 species and 211 are monotypic. Calculation of relative species diversity and percentage endemism enables areas of high diversity and endemism to be enumerated, and identifies areas where further field collecting and taxonomic research are required. Endemism is generally high in Rubiaceae, which supports data from recent studies showing that many species have restricted distributions. Given the assumed ecologic sensitivity of Rubiaceae, in combination with a range of other factors including restricted distribution, we suggest that species in this family are particularly vulnerable to extinction. The rate at which new species are being described is inadequate; more resources are required before the diversity of Rubiaceae is satisfactorily enumerated.

Key words: Biodiversity, coffee family, conservation, endemics, endemism, Rubiaceae, species diversity, taxonomic databases, Taxonomic Databases Working Group (TDWG), taxonomy.

Target One of the *Global Strategy for Plant Conservation* (Secretariat of the Convention on Biological Diversity, 2002) is the production of "a widely accessible working list of known plant species, as a step towards a complete world flora," which is a fundamental requirement for plant conservation (Nic Lughadha, 2004). For some of the largest flowering plant families and for larger groups (i.e., monocotyledons), several important works have been completed that significantly improve our prospects for achieving Target One. For example, information on Euphorbiaceae (Govaerts et al., 2000; <http://www.kew.org/wcsp/malpigiales/>) is available in print and on the Internet, and for monocotyledons, information is accessible only via the Internet (e.g., Govaerts, 2006; <http://www.kew.org/wcsp/monocots>), as part of the World Checklist Series (<http://www.kew.org/wcsp>). In the Internet-only category, a species checklist for the Rubiaceae has recently become available (Govaerts et al., 2006; <http://www.kew.org/wcsp/rubiaceae>). This work, like others in the series, represents an amalgamation and synthesis of taxonomic work.

These checklists are valuable as widely accessible working lists of accepted plant species, but they also enable broad-scale analysis of distribution and diversity to be undertaken (e.g., Cribb & Govaerts, 2005). As these checklists are taxonomically complete and also include distributions for each accepted species, they provide an interesting counterpoint to more detailed but less complete compilations on plant species diversity that have been recently published (Barthlott et al., 1996, 1999; Kier et al., 2005; Mutke & Barthlott, 2005). These publications have produced impressively precise maps of global plant species diversity, generally modeled from available species lists for different parts of the world (Barthlott et al., 1996, 1999; Kier et al., 2005), but often without having complete species distributions to underpin the estimates of diversity. Herein, we use queries from the World Checklist of Rubiaceae (Govaerts et al., 2006; <http://www.kew.org/wcsp/rubiaceae>) to analyze the distribution, diversity, endemism, and taxonomic effort for Rubiaceae. This represents the first such analysis of the whole family and follows recent work

Volume 96, Number 1
2009

Davis et al.
A Global Assessment of Rubiaceae

69

on a global analysis of plant genus distributions (Brummitt, 2005).

Rubiaceae is a member of the Gentianales and shares many of the features common to other families of the order, particularly basic leaf and floral morphology (Davis & Bridson, 2007; and see below), the presence of colleters, and lack of internal phloem. It is the fourth largest flowering plant family and is estimated to contain around 600 genera and between 6000 and 13,000 species (see below). It is usually easy to identify by the presence of simple, opposite or whorled, entire leaves, interpetiolar stipules, and an inferior ovary. Rubiaceae has a cosmopolitan distribution, but species diversity and biomass are distinctly concentrated in the tropics and the subtropics and especially in lowland humid forest, where it is often the most species-abundant woody plant family. The family is less frequent and less diverse but still very widespread in the temperate regions. It is also found in the subpolar regions of the Arctic and Antarctic (Davis & Bridson, 2007). In the tropical regions, Rubiaceae species are sensitive to disturbance and are rarely found in secondary forest types (A. Davis & D. Bridson, pers. obs.; Davis et al., 2006; Sohmer & Davis, 2007). Most Rubiaceae species are small trees or shrubs, but nearly all life-forms are found, including large trees, annual and perennial herbaceous plants, woody monocaul dwarfs, lianas, epiphytes, geofrutices (more or less herbaceous stems with a woody rootstock), myrmecophiles (hollow stems or special chambered tubers, containing ants or ant colonies), and rarely succulent or aquatic life-forms (Robbrecht, 1988; Davis & Bridson, 2007). Rubiaceae includes coffee (*Coffea* L.), which is by far the most important economic plant within the family and the world's most important commodity after oil (Vega et al., 2003).

METHODS

DATABASE

The production of the World Checklist of Rubiaceae was made from a database encompassing 24 fields, including basic nomenclatural data (genus, species, author, place and data of publication, basionym [if applicable], synonyms [if applicable], and accepted name), distribution data, and life-form. The World Checklist of Rubiaceae (Govaerts et al., 2006) does not include altitude data. Altitude does have a bearing on occurrence and diversity; long-standing knowledge of the family (D. Bridson & A. Davis, pers. obs.) indicates that Rubiaceae species diversity is higher at low to mid-altitudes, with most of the diversity occurring at altitudes of less than

1500 m. The data comply with the data standards proposed by the International Organization for Plant Information (IOPI) (Burnett, 1994), in association with the Taxonomic Databases Working Group (TDWG) (Brummitt et al., 2001). Citation of authors follows Brummitt and Powell (1992); book titles are abbreviated according to Stafleu and Cowan (1976–1988) and Stafleu and Mennega (1992–2000); periodicals are abbreviated according to Bridson and Smith (1991); and the number and three-letter codes used for areas (e.g., 23 CON) follow the TDWG system. Compilation of the database was undertaken using FoxBASE (Microsoft, Redmond, Washington, U.S.A.), a dBASE-class database program for personal computers. The database was founded on the Index Kewensis database, held at the Royal Botanic Gardens, Kew (K). The selection of accepted names and the designation of synonyms were made on the basis of published or otherwise publicly available taxonomic works. Further taxonomic input and accuracy were achieved by: (1) specialist taxonomic review; (2) a complete herbarium survey of the Rubiaceae collections held at K; and (3) a survey of selected parts of the collections housed at L and P (abbreviations from Holmgren et al., 1990). Data collection for procedures (2) and (3) mainly used herbarium specimens cited in taxonomic revisions or identified by specialists; these procedures added a further 2500 geographic records to the World Checklist of Rubiaceae database at TDWG Level 3.

STANDARDIZING RUBIACEAE DIVERSITY FOR DIFFERENT-SIZED AREAS

Counts of taxa for both species and genera for all areas at TDWG Level 3 (369 areas) were extracted from the World Checklist of Rubiaceae (Govaerts et al., 2006). The TDWG World Geographical Scheme for Recording Plant Distributions is based on geopolitical units, which vary widely in size from the Antarctic Continent to tiny oceanic islands. In order to make counts of species and genera comparable between these units, the counts were rescaled to make them independent of area. However, the diversity of a region cannot be simply divided by the size of that region to give a value comparable with other differently sized regions because the relationship between diversity and area is a nonlinear, power-law relationship (Rosenzweig, 1995). Dividing by area overinflates the diversity of small regions and underestimates the diversity of large regions (Brummitt & Nic Lughadha, 2003). Instead, the power-law relationship $S = cA^z$ (where S = number of species, A = area, and c and z represent, respectively, the intercept and the slope of the regression in a log-log

space) can be rewritten as $c = S/A^z$ to give a value for each region that is independent of area (Rosenzweig, 1995). This value is then standardized to a size appropriate for the range of areas being studied, again using the exponent value z.

An important consideration is the exact value of the exponent used to rescale diversity figures. Although small changes in z values do not give very different results (results not shown here), they can nevertheless influence the relative positions of regions close together in size or diversity (i.e., more or less diverse regions might move up or down the list of most diverse areas relative to other regions). The z value is known to vary between different regions, being lower for large, continental regions and higher for small, oceanic regions (Rosenzweig, 1995). For this study, z values appropriate to each region in question could be estimated from the previous study by Kier et al. (2005), which empirically determined z values for each of the 14 biomes of the World Wildlife Fund (WWF) ecoregions (Olson et al., 2001) from smaller-scale studies within each biome. A spatial overlay was used between the TDWG Level 3 areas and the WWF ecoregions, and the mean z value for TDWG regions was calculated with a weighted average by area of the intersection between each TDWG level and the WWF ecoregions.

In this study, the intercept values of relative diversity were standardized to a size of 10,000 km², roughly the median size of TDWG Level 3 areas, similar to and facilitating comparison with the work by Barthlott et al. (1996, 1999) (Brummitt et al., unpublished). The values resulting from the rescaling of species numbers in this way (S/10000) do not reflect actual numbers of taxa, but they do allow relative diversities to be compared for different regions that are independent of the size of that region. In this contribution, only the first 20 records for each database query/analysis are given. Complete results for all 369 TDWG Level 3 areas are available from the authors upon request.

RESULTS AND DISCUSSION

THE NUMBER OF GENERA AND SPECIES IN RUBIACEAE

Recent estimates as to the number of Rubiaceae species and genera are quite constant, apart from the estimates of species numbers by Verdcourt (1976, 1989) and Smith (1988). Estimates are as follows: Verdcourt (1976, 1989), 500 genera and 6000 spp.; Smith (1988), 500 genera and 6500–7000 spp.; Mabberley (1987), 630 genera and 10,400 spp.; Mabberley (1997), 650 genera and 10,200 spp.; Robbrecht (1988), 637 genera and 10,700 spp.; and Brummitt (1992), 606 genera.

According to the World Checklist of Rubiaceae database, the number of accepted Rubiaceae species is 13,143 in 611 genera. Given the rate at which species have been added to Rubiaceae over the past 30 years or so (see below), and assuming that more synonyms have been created than retrieved from synonymy, all previous estimates for species number are much lower than the actual figures would have been at that time, apart from estimates by Bridson and Verdcourt (2003: 650 genera and 13,000 spp.) and Davis and Bridson (2007: 615 genera and 13,150 spp.), which were based on earlier versions of the data used here. This is particularly so for estimates in the 6000–7000 range (which are roughly half of the actual figures for species number presented here). In general, the species diversity for Rubiaceae has been considerably (Verdcourt, 1976, 1989; Smith, 1988) to moderately (e.g., Robbrecht, 1988) underestimated. This is no doubt due to the difficulties in estimating species numbers in large families, particularly where the total number of published names is often considerable. The World Checklist of Rubiaceae database holds a total of 36,385 published names, for example (Govaerts et al., 2006). Estimates as to the number of genera have been quite accurate, mostly because the number of names involved is much lower and presumably also due to the presence of generic indices and similar resources that exist in herbaria and libraries.

At 13,143 species, Rubiaceae is the fourth largest angiosperm family (Robbrecht, 1988) after Orchidaceae (25,158 spp., ca. 830 genera; Cribb & Govaerts, 2005), Asteraceae (23,000–30,000 spp., 1535–1700 genera; Bremer, 1994; Funk et al., 2005), and Leguminosae (19,350 spp.; 727 genera; Lewis et al., 2005); Poaceae is the fifth largest (ca. 11,591 spp., ca. 700 genera; Govaerts, 2006). The numbers for Asteraceae and Leguminosae have been estimated and are not based on definitive counts of accepted species, although Leguminosae has been carefully calculated (Lewis et al., 2005). Parenthetically, of the five largest families, Orchidaceae, Poaceae, and Asteraceae are herbaceous or predominantly so. Leguminosae, like Rubiaceae, includes a mix of woody and herbaceous taxa, although Leguminosae has a greater proportion of herbaceous species. Nic Lughadha et al. (2005) posits that Leguminosae is the most representative family for angiosperm diversity patterns. Rubiaceae is particularly well represented in humid tropical forests and, when coupled with Asteraceae in a global analysis of angiosperm diversity, is shown to comprise one of the most representative pairs of families at species level (N. Brummitt, unpublished).

As with most other flowering plant families, the number of accepted Rubiaceae species is still

Volume 96, Number 1
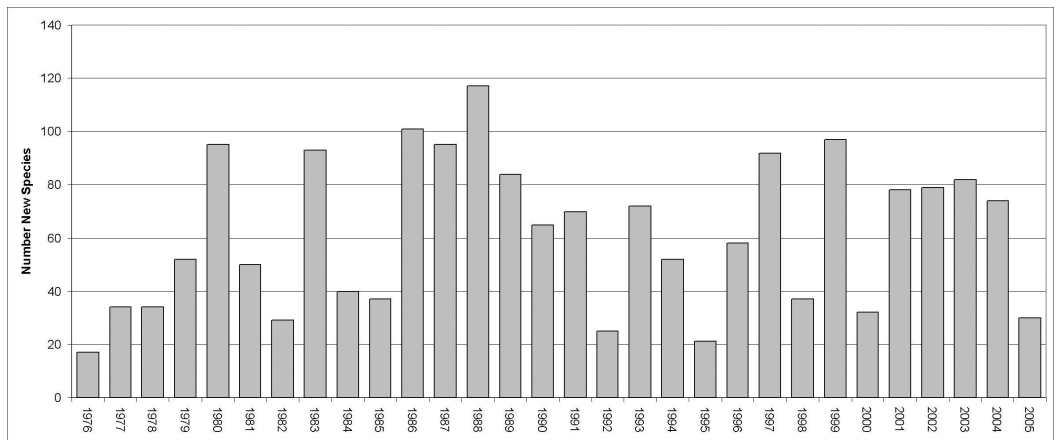2009

Davis et al.
A Global Assessment of Rubiaceae

71

Figure 1.   Number of new Rubiaceae species published each year from 1976–2005.

increasing, year by year, and the final number will be greater than it is today. The total number of Rubiaceae species is estimated at ca. 16,000 (A. Davis, M. Ruhsam & D. Zappi, unpublished), based on a review of herbarium collections (K, P, and L) and an awareness of undescribed species (from databases, literature, fieldwork, and anecdotal evidence). The 2800 or so species required to make a total of 16,000 take into account potential synonymy and may be broken down in the following manner: unplaced names brought into accepted usage (500); undescribed species from tropical South America (500), tropical Africa (400), Madagascar (300; Davis & Bridson, 2003), southern Asia (300), Malesia (500), Australia and the Pacific (100), and other regions (100). There are ca. 1000 unplaced names on the World Checklist of Rubiaceae (Govaerts et al., 2006), and we estimate that nomenclatural and taxonomic work will see at least 500 species added to the current species count from this source alone (Ruhsam et al., 2008).

From 1976–2005, 1842 Rubiaceae species names have been validly published (Fig. 1), which gives an average of 63.5 species per year for this period. The minimum number of species published since 1976 was 17 (in 1976) and the maximum 117 (in 1988). The average for this period does not give us the figure for the increase in accepted names, as the number of synonyms created per year is not included in the above calculations. In fact, it is very difficult to quantify the number of names placed in synonymy per year, as it is not recorded. If we extrapolate by looking at the total number of validly published names produced since the starting date for formal biological nomenclature (1753), over a 252-year period from 1753–2005, the average is 52 species per year, and this gives us some idea of increase of accepted names

per year. The number of new (validly published) genera added over the same 30-year period is 104, making an average of 3.5 genera per year. The maximum number of genera published during this period was 12 (1978) and the minimum was 0 (1976, 1977, 1991, 1992, 2002). If we extrapolate in the same way as we did for species, in order to get some idea of gross increase in new genera per year, the average is 2.4 since 1753. As with the species calculation, the figures for the 30- and 252-year period are not that different. Based on the same evidence as for species (herbarium data, anecdotal evidence, fieldwork, etc.), and taking into account our assumption that estimates for genera are more accurate than those for species, the number of genera is not likely to increase significantly.

Taxonomic effort at the species level for Rubiaceae, as estimated above, is probably much lower than that of most other large plant families (i.e., those with more than 10,000 species), although Orchidaceae is the only other large plant family for which accurate figures are available for comparative purposes. In Orchidaceae, from 1978–2002, the average number of newly described orchid species was over 280 per year, with the number surpassing 500 (per year) twice during this period (Cribb & Govaerts, 2005). Even considering the special interest given to orchids, and the fact that Orchidaceae has approximately twice the number of species of Rubiaceae, taxonomic effort for Rubiaceae is considerably lower. Based on our estimate that there are actually around 16,000 species of Rubiaceae (i.e., 2800 species still requiring scientific names), it will take around 45 years before the species diversity in the family is satisfactorily enumerated, if we continue to describe species at the current rate (see above).

SIZE OF GENERA

The 20 largest genera of the Rubiaceae are listed in Table 1. Despite recent discussions and actions concerning delimitation (Taylor, 1996, 2001; Nepokroeff et al., 1999; Davis et al., 2001; Andersson, 2002), *Psychotria* L. is still the largest genus in Rubiaceae, with 1834 species. Recent publications (Sohmer & Davis, 2007; Davis et al., 2007; Ruhsam et al., 2008) will bring the total number of *Psychotria* species close to 2000, as estimated by Sohmer (1988) and Davis et al. (2001). *Psychotria* is now the world's third largest genus, after *Astragalus* L. (Leguminosae) with ca. 3200 species and *Bulbophyllum* Thouars (Orchidaceae) with ca. 2000 species (Frodin, 2004).

There are 30 Rubiaceae genera with over 100 species, but most contain fewer than 10 species. There are 211 monotypic genera (34.5% of genera; 1.6% of species), 328 genera with three species or fewer (53.7% of genera), and 440 genera with 10 species or fewer (72% of genera). Although all large taxonomic groups have a greater number of small taxa (Clayton, 1972, 1974; Cronk, 1989), the percentage of monotypic genera in Rubiaceae is higher than that in both Orchidaceae, with 211 monotypic genera out of 849 (Cribb & Govaerts, 2005) (24.9% of genera; 0.8% of species) or Leguminosae, with 192 monotypic genera out of 727 genera (Lewis et al., 2005) (26.4% of genera; 1% of species). Similar analyses of other large angiosperm families are needed to understand whether such a large number of monotypic genera in Rubiaceae is unusual, part of a natural phenomenon, or an artifact of our classification systems (Knapp et al., 2005). However, the fact that such strongly skewed frequency distributions are shown not just by taxon size but also by spatial distribution (many narrowly distributed taxa and few very widely distributed taxa) (Colwell & Lees, 2000; Gaston, 2003) and also temporal taxon distribution (many short-lived taxa and few very long-lived taxa) (Rosenzweig, 1995) suggests that this is a natural phenomenon.

In light of ongoing Rubiaceae research (De Block et al., 2006), it is evident that even over the next five years or so the size of many of the large genera will change quite considerably (in particular *Ixora* L., *Spermacoce* L., *Oldenlandia* L., *Tarenna* Gaertn., and *Canthium* Lam.), as their circumscriptions are altered in the light of new systematic data. Some genera will increase in size, owing to the necessary inclusion of other genera, most notably *Ixora*, whereas others will decrease in size, such as *Canthium* (Lantz & Bremer, 2004; Razafimandimbison et al., unpublished). Of the largest 20 Rubiaceae genera, only *Pavetta* L. (Bremekamp, 1934) has been monographed, and for

Table 1. The 20 largest (by species number) genera in Rubiaceae.

No.	Genus	No. of species
1	*Psychotria* L.	1834
2	*Galium* L.	621
3	*Ixora* L.	530
4	*Pavetta* L.	357
5	*Ophiorrhiza* L.	317
6	*Palicourea* Aubl.	313
7	*Rondeletia* L.	260
8	*Spermacoce* L.	257
9	*Oldenlandia* L.	249
10	*Lasianthus* Jack	228
11	*Faramea* Aubl.	208
12	*Tarenna* Gaertn.	203
13	*Mussaenda* L.	200
14	*Asperula* L.	182
15	*Timonius* DC.	169
16	*Argostemma* Wall.	162
17	*Guettarda* L.	159
18	*Gardenia* Ellis	143
19	*Coussarea* Aubl.	133
20	*Canthium* Lam.	130

the largest 50 genera, there are only a few with complete taxonomic treatments, e.g., *Sabicea* Aubl. (Wernham, 1914), *Manettia* Mutis ex L. (Wernham, 1918–1919), *Coffea* (Chevalier, 1947), and *Leptodermis* Wall. (Winkler, 1922), although contemporary monographs are now needed for these four genera.

DISTRIBUTION OF RUBIACEAE

Rubiaceae occur in every region of the world (at TDWG Level 3), except for the Antarctic Continent, which only has two native vascular plant species (*Deschampsia antarctica* E. Desv. and *Colobanthus quitensis* (Kunth) Bartl.). Rubiaceae is a predominantly tropical family, with species diversity decreasing rapidly from the subtropics through the temperate regions to the poles. There are usually hundreds of species in each of the tropical TDWG Level 3 areas, tens in the temperate areas, and usually fewer than 10 in subarctic regions; the entire Subarctic America region (TDWG 70) has only eight *Galium* L. species, for example. There are, however, specific areas in the tropical belt that do not have high numbers of species or high species diversity for Rubiaceae (see below).

DISTRIBUTION OF SPECIES DIVERSITY

Table 2 gives the 20 most species-rich regions for Rubiaceae based on gross number of indigenous species for each TDWG Level 3 area. This makes a useful comparison between TDWG Level 3 areas but

Volume 96, Number 1
2009

Davis et al.
A Global Assessment of Rubiaceae

73

Table 2. The 20 most diverse regions (TDWG Level 3) for Rubiaceae, based on total species numbers and irrespective of area.

Rank	TDWG Level 3 code	Area (narrative)	No. of species	Area (km²)
1	CLM	Colombia	1026	1,140,598
2	VEN	Venezuela	785	914,096
3	NWG	New Guinea	725	819,979
4	BZN	Brazil North	645	3,849,262
5	ZAI	Democratic Republic of Congo	644	2,336,991
6	BZL	Brazil Southeast	619	926,896
7	PER	Peru	594	1,296,128
8	ECU	Ecuador	583	249,014
9	BOR	Borneo	578	743,470
10	MDG	Madagascar	569	594,765
11	TAN	Tanzania	559	945,437
12	CMN	Cameroon	553	466,814
13	PHI	Philippines	535	295,856
14	MLY	Malaya	485	132,735
15	CUB	Cuba	438	110,269
16	THA	Thailand	400	514,630
17	PAN	Panama	391	74,845
18	GAB	Gabon	353	261,859
19	CHC	South-Central China	342	1,309,801
20	SUM	Sumatera	342	473,039

does not give us a realistic idea of species richness because of the considerable differences in unit area (square kilometers). In simple terms, TDWG Level 3 areas in the tropics with large unit areas will tend to hold higher numbers of Rubiaceae species than smaller ones, given that other factors (such as forest type and altitude) are comparable. It is expected that areas with a large percentage of low- to mid-altitude humid forest (e.g., Colombia [83 CLM], Venezuela [82 VEN], New Guinea [43 NWG]) will have large numbers of Rubiaceae species per unit areas, for example. Table 3 shows the 20 most diverse areas for Rubiaceae based on relative species richness (species number/area log-transformed [S/1000; Brummitt & Nic Lughadha, 2003; see Methods), at TDWG Level 3 (Fig. 2). In Table 3, Venezuela (82 VEN) and Colombia (83 CLM) are in comparable positions with those of Table 2 (gross species number), and many other areas remain in Table 3, but the order of areas changes considerably between tables. In Table 3, Brazil North (84 BZN), South-Central China (36 CHC), and Sumatera (42 SUM) are not among the 20 most species-rich areas (cf. Table 2), but instead Costa Rica (80 COS), Gulf of Guinea islands (23 GGI), and New Caledonia (60 NWC) are present. The Gulf of Guinea islands are equatorial continental islands with appreciable amounts of primary lowland forest (Figueiredo, 2005; Davis & Figueiredo, 2007). All major tropical regions (South America, Africa, Indian Ocean, South Asia, Southeast Asia, and the Pacific) are represented in the 20 most species-rich areas,

with no obvious bias to any one of these regions. Of the 20 most species-rich areas, 13 are continental, five are large islands, one is a large island archipelago (Philippines [42 PHI]), and one is a small island group (Gulf of Guinea islands [23 GGI]).

Figure 2 shows the areas within the tropical regions where low relative species richness is anticipated given the paucity of preferred macrohabitat for Rubiaceae (i.e., low- to medium-altitude, humid forest), for example, Rwanda (23 RWA) and perhaps Burundi (23 BUR), where high altitude excludes many species present in surrounding countries, and central and eastern Brazil (84 BZC, BZE), which is largely composed of savanna vegetation (cerrado). Figure 2 also clearly shows several TDWG Level 3 areas where significant relative species richness is expected (proximity to the equator and a prevalence of low-altitude, humid forest) but is not present in our analyses. These areas include Equatorial Guinea (23 EQG), the Democratic Republic of Congo (23 CON), Cambodia (41 CBD), Laos (41 LAO), Sulawesi (42 SUL), and Suriname (82 SUR). For these areas, we assume that low relative species richness is due to low specimen-collecting density per unit area (A. Davis and D. Bridson, pers. obs.) and low levels of taxonomic effort including determination of specimens to species, although these activities are closely associated. We assume that the relatively low collecting densities for the Democratic Republic of Congo (23 CON), Cambodia (41 CBD), and Laos (41 LAO) are due to previous military conflicts and resulting limited

Table 3. Twenty most diverse regions for Rubiaceae based on relative diversity (species number/area log-transformed at TDWG Level 3).

Rank*	TDWG Level 3 code	Area (narrative)	No. of species	Area (km²)	Mean of z	$c = S/A^z$	S/10,000
1 (2)	VEN	Venezuela	785	914,096	0.2331	32.0157	274.0075
2 (1)	CLM	Colombia	1026	1,140,598	0.2862	18.9494	264.4819
3 (15)	CUB	Cuba	438	110,269	0.2116	37.5397	263.5670
4 (10)	MDG	Madagascar	569	594,765	0.2029	38.3264	248.3691
5 (14)	MLY	Malaya	485	132,735	0.2593	22.7694	248.0571
6 (12)	CMN	Cameroon	553	466,814	0.2108	35.2915	245.9629
7 (3)	NWG	New Guinea	725	819,979	0.2486	24.5565	242.4190
8 (11)	TAN	Tanzania	559	945,437	0.1840	44.4524	242.0446
9 (8)	ECU	Ecuador	583	249,014	0.2931	15.2769	227.2141
10 (13)	PHI	Philippines	535	295,856	0.2583	20.6621	223.0354
11 (17)	PAN	Panama	391	74,845	0.3058	12.6374	211.2797
12 (5)	ZAI	Democratic Republic of Congo	644	2,336,991	0.2093	29.9175	205.6487
13 (6)	BZL	Brazil Southeast	619	926,896	0.2513	19.5964	198.3242
14 (9)	BOR	Borneo	578	743,470	0.2526	19.0041	194.6465
15 (25)	COS	Costa Rica	300	51,273	0.3070	10.7445	181.6291
16 (274)	GGI	Gulf of Guinea islands	133	3,208	0.2400	19.1582	174.7251
17 (41)	NWC	New Caledonia	203	19,283	0.2483	17.5181	172.4595
18 (18)	GAB	Gabon	353	261,859	0.2254	21.2101	169.0995
19 (7)	PER	Peru	594	1,296,128	0.2675	13.7611	161.6788
20 16)	THA	Thailand	400	514,630	0.2324	18.8239	160.0695

A = area, c and z = intercept and slope, respectively, of the regression in a log-log space, S = number of species.

* For rank, numbers in parentheses represent rank based on gross species number per TDWG Level 3 area (Table 2). Areas listed in Table 2 but not appearing in Table 3, with ranking based on relative diversity in parentheses: Brazil North (44), South-Central China (29), and Sumatera (27).
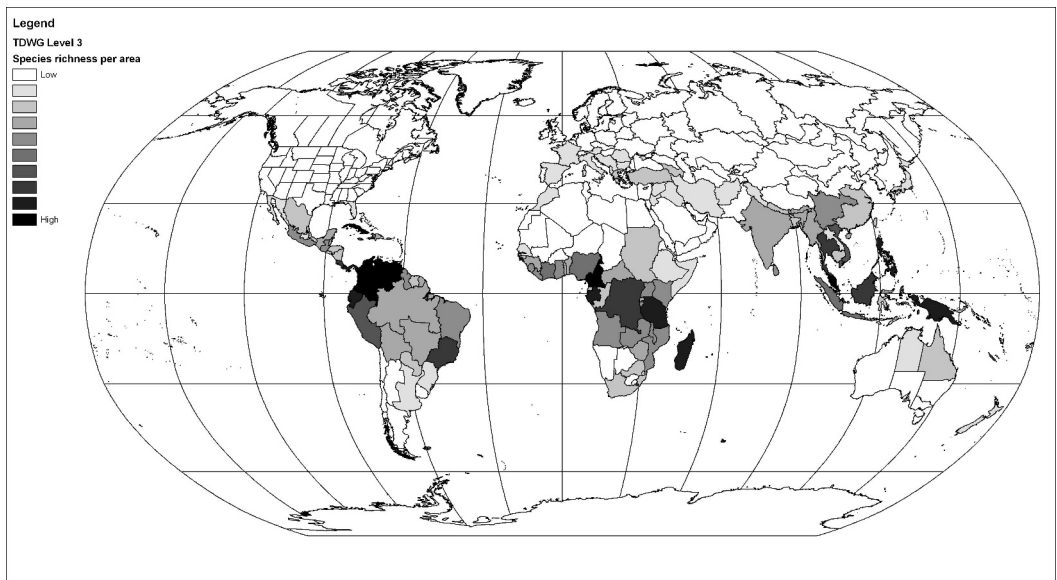

Figure 2. Relative species richness of Rubiaceae at TDWG Level 3 regions rescaled by the size of that region using a power-law species area relationship and standardized to 10,000 km².

Volume 96, Number 1
2009

Davis et al.
A Global Assessment of Rubiaceae

75

Table 4.   The 20 highest areas for gross number of endemic Rubiaceae species.

Rank	TDWG Level 3 code	Area (narrative)	No. of species	Endemic species, No. (%)
1	NWG	New Guinea	725	620 (86)
2	MDG	Madagascar	569	520 (91)
3	PHI	Philippines	535	443 (83)
4	BOR	Borneo	578	428 (74)
5	CUB	Cuba	438	344 (76)
6	BZL	Brazil Southeast	619	311 (50)
7	CLM	Colombia	1026	265 (26)
8	VEN	Venezuela	785	252 (32)
9	MLY	Malaya	485	213 (44)
10	NWC	New Caledonia	203	200 (99)
11	TAN	Tanzania	559	190 (34)
12	THA	Thailand	400	179 (45)
13	IND	India	326	169 (52)
14	BZN	Brazil Northeast	702	165 (24)
15	SUM	Sumatera	342	161 (47)
16	CHC	South-Central China	342	149 (44)
17	PER	Peru	594	147 (25)
18	PAN	Panama	391	136 (35)
19	FIJ	Fiji	166	134 (81)
20	VIE	Vietnam	443	129 (29)

access, although priorities set in the colonial era may have also played a role.

ENDEMISM

We provide two crude measures for investigating endemism in Rubiaceae: total number of endemics (Table 4) and percentage of endemism (Table 5) for each TDWG Level 3 area. A few areas of known high endemism cannot be shown by analyses of our data because they are split between different TDWG Level 3 areas. This is particularly marked where mountain ranges coincide with country boundaries (e.g., Rwenzori Mountains, split between the Democratic Republic of Congo [23 ZAI], Rwanda [23 RWA], and Uganda [25 UGA]). For the gross number of endemic species at TDWG Level 3, eight of the 20 highest areas are large islands or island groups, with the first five falling into the island category. The other 12 are continental areas. In terms of percentage of endemism, the first 27 TDWG Level 3 areas are islands, both small and large; Table 5 shows the highest 20 areas for percentage of endemicity. High numbers of endemics and percentage of endemics are expected for islands owing to the specific evolutionary scenarios associated with island floras, and, in the case of Rubiaceae, recent and rapid radiations following dispersal (Malcomber, 2002; Maurin et al., 2007) have been particularly important. Continental areas with a high percentage of endemism (44%–50%, e.g., Brazil Southeast [84 BZL], India [40 IND], Thailand [41 THA], South-Central China [36 CHC], Malaya [42

MLY]; Table 4) require further explanation on a case-by-case basis corresponding to their historical and present-day physiography, climate, and biology. Apart from the smaller islands, which have a 100% endemicity based on very few species, New Caledonia (60 MWC), Hawaii (63 HAW), and Madagascar (29 MDG) are outstanding in terms of percentage endemicity (Table 5). Low percentage endemicity is biased toward areas within continental regions, including areas with relatively high number of species but negligible levels of percentage of endemicity, such as Liberia (22 LBR), with 210 spp./0% endemicity; Ghana (23 GHA), with 248 spp./2% endemicity; Malawi (26 MLW), with 213 spp./2% endemicity; Uganda (25 UGA), with 212 spp./2% endemicity; Central African Republic (23 CAF), with 242 spp./2% endemicity; Ivory Coast (22 IVO), with 311 spp./3% endemicity; and Nigeria (22 NGA), with 360 spp./4% endemicity.

Species endemism is generally high in Rubiaceae. Of the 13,143 species of Rubiaceae, there are 8456 endemics at TDWG Level 3, which means that 64% of Rubiaceae species are endemics at this area level. This level is similar to those of many other large tropical families (e.g., Orchidaceae [Cribb & Govaerts, 2005]) but is much greater than other big families (e.g., Poaceae) that do not have species diversity concentrated in the tropical regions of the world (Govaerts et al., 2006). This may be partly due to the evolutionary history and dynamics of tropical forests but also because dispersal and diversification in Rubiaceae at the species level seem to have

Table 5. The 20 highest areas for gross percentage of endemic Rubiaceae species.

Rank	TDWG Level 3 code	Area (narrative)	Total no. of species	No. of nonendemic species	Endemic species	Endemism, %
1	ASC	Ascension	1	0	1	100
2	STH	St. Helena	1	0	1	100
3	NFK	Norfolk Islands	9	0	9	100
4	KER	Kermadec Islands	2	0	2	100
5	MXI	Mexican Pacific islands	2	0	2	100
6	CPI	Central America Pacific islands	1	0	1	100
7	NWC	New Caledonia	203	3	200	99
8	HAW	Hawaii	47	2	45	96
9	MDG	Madagascar	569	49	520	91
10	NWG	New Guinea	725	105	620	86
11	PHI	Philippines	535	92	443	83
12	FIJ	Fiji	166	32	134	81
13	CUB	Cuba	438	94	344	76
14	MRQ	Marquesas Islands	17	4	13	76
15	BOR	Borneo	578	150	428	74
16	MAU	Mauritius	54	16	38	70
17	SCI	Society Islands	46	14	32	70
18	SOC	Socotra	21	7	14	67
19	ROD	Rodrigues	9	3	6	67
20	JNF	Juan Fernández Islands	6	2	4	67

occurred very recently in many groups (e.g., Malcomber, 2002; Maurin et al., 2007). At the present time, we simply do not have enough data to make supportable assumptions regarding the causes of rapid diversification in Rubiaceae. Considerable levels of endemism occur on both large and small islands and also in continental areas. In studies where area of occurrence and extent of occurrence (IUCN, 2001) have been calculated for Rubiaceae, it appears that many species are highly localized and an alarming number are restricted to area polygons (extent of occurrence) of less than 100 km² (e.g., ca. 14% in *Coffea* [Davis et al., 2006]). Restricted distributions increase the likelihood of extinction, and for groups where extinction threat has been calculated (IUCN, 2001), the number of Threatened taxa is very high, e.g., ca. 70% in *Coffea* (Davis et al., 2006) and 74% in Philippine *Psychotria* (including nearly 10% extinction; Sohmer & Davis, 2007).

CONCLUSION

With 13,183 species in 611 genera, the importance of Rubiaceae in terms of species number is supported by our study, and its position as the fourth largest angiosperm family is confirmed (Robbrecht, 1988) after Orchidaceae, Asteraceae, and Leguminosae. Based on estimates of total species number in

Rubiaceae (i.e., 16,000), we estimate that with current resources it will take us 45 years to fully enumerate species diversity in Rubiaceae. This calculation is oversimplified, as it does not take into account other variables such as names added to or removed from synonymy, and extinction (we have no way of knowing how many species will become extinct before they are discovered), but it does give us some idea of what needs to be done and an indication of where to focus taxonomic resources.

Our assessment of Rubiaceae species diversity for each of the 369 areas of TDWG Level 3 using a measure of relative species diversity (Table 3, Fig. 2) has provided a useful tool for identifying the major areas of relative species diversity for the family. Our analyses confirm that species richness in Rubiaceae is greatest in the tropical regions, particularly in continental areas and larger islands (Table 3, Fig. 2). Practical applications of our species-level diversity analysis include the identification of areas that require further field collections and/or taxonomic study, and the targeting of areas for efficient sample collection (e.g., DNA sampling). Future analyses requiring more precise measures of diversity will need finer division of area and measurement of suitable Rubiaceae habitat, particularly areas of remaining primary vegetation. In addition, reanalysis of Rubiaceae data would be required as our knowledge of the family improves and progresses.

Volume 96, Number 1
2009

Davis et al.
A Global Assessment of Rubiaceae

77

Basic analyses of endemism show that species endemism in Rubiaceae is considerable, with 64% of species endemic at the level of TDWG Level 3, and that percentage endemism is distinctly higher for islands, large and small.

Given the ecologic sensitivity of Rubiaceae (e.g., in the tropical regions mostly requiring primary forest), coupled with the restricted distribution of species, it is evident that many species are vulnerable to extinction, particularly in an era of global environmental change and huge anthropogenic influence at the local level.

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