Article

One hundred and seventy-five new species of Graphidaceae: closing the gap or a drop in the bucket?

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Abstract

Recent studies of the global diversity of the lichenized fungal family Graphidaceae suggest that there are a large number of species remaining to be discovered. No less than 640 species have been described since 2002, including 175 new species introduced in a collaborative global effort in a single issue in this journal. These findings suggest that the largest family of tropical crustose lichens may have an even higher number of species than Parmeliaceae. To estimate whether

the discovery of 175 new species is a significant step forward in cataloguing extant diversity in this family, we employed a parametric method to predict global species richness of Graphidaceae using a GIS-based grid map approach. The model employs linear regression between observed species richness and sample score and vegetation composition per grid to predict individual grid species richness, and interpolation of species grid distributions to predict global species richness. We also applied a non-parametric species-area curve approach and non-parametric species richness estimators (Chao, Jackknife, Bootstrap) to compare the results from the different methods. Our approach resulted in a prediction of 4,330 species of Graphidaceae, including approximately 3,500 (sub-)tropical species in the core subfamilies Fissurinoideae, Graphidoideae, Redonographoideae, plus 125 species restricted to extratropical regions (outside the zone between 30° northern and 30° southern latitude) and 700 species in subfamily Gomphilloideae. Currently, nearly 2,500 species are known in the family, including species not yet formally described. Thus, our model suggests that even after describing 175 species in this issue and with another approximately 140 awaiting publication, the number of species still to be discovered and described is more than 1,800, and much work remains to be done to close this substantial gap. Based on our approach, we predict that most of this undiscovered diversity is to be found in Mexico, the northern Andean region, the eastern Amazon and central and southern Brazil, tropical West Africa, continental Southeast Asia, Indonesia, and Papua New Guinea.

Key words: Gomphillaceae, *Graphis*, *Ocellularia*, Thelotremataceae

Introduction

Graphidaceae is the largest family of tropical crustose lichens, after recent phylogenetic revisions including nearly 1,800 accepted species in subfamilies Fissurinoideae, Graphidoideae, and Redonographoideae, and another 400 in subfamily Gomphilloideae (Staiger 2002; Frisch *et al.* 2006a; Lücking 2008; Rivas Plata *et al.* 2012a, b, 2013; but see Hodkinson 2012). While it is currently exceeded by Parmeliaceae, with more than 2,700 species (Kirk *et al.* 2008; Jaklitsch *et al.*, in prep.), as largest family of lichenized fungi overall, the amount of new species discoveries in tropical and even extratropical areas in recent years suggests that Graphidaceae might contain more species than Parmeliaceae.

Crucial to the recognition of the extraordinary diversity of Graphidaceae was the publication of two seminal monographic revisions that challenged previous classification concepts and provided a new approach to taxonomic inventories in the family (Staiger 2002; Frisch *et al.* 2006a). These works did not only provide revised keys to many of the newly recognized taxa, but stimulated the subsequent publication of further, regional to world-wide keys to large groups (Archer 2009; Lücking *et al.* 2009a; Mangold *et al.* 2009; Rivas Plata *et al.* 2010a; Gaswick & Lücking 2012), including the genera *Chapsa* Massalongo (1860: 257), *Graphis* Adanson (1763: 11), *Ocellularia* Meyer (1825: 327), and *Thelotrema* Acharius (1803: 130), providing tools to identify material that prior to these studies had been considered mostly unidentifiable. The impact of these studies is shown by the dramatic increase in publications on the family including new species discoveries, which between 2003 and 2013 amounted to no less than 140 papers by a diversity of authors, or 13 per year on average, whereas from 1950 to 2002, only 50 papers were published by few authors, or less than one per year on average. Of the nearly 1,800 species currently recognized in the three core subfamilies, more than a quarter were described or reinstated in the past ten years, compared to a more than two century long history of taxonomic contributions to the family, and further 175 are being introduced in the present issue in 18 different contributions, which represents a global effort by 30 authors from 14 countries (Aptroot 2014; Lücking 2014; Sipman 2014; Kalb & Jia 2014; Lendemer & Harris 2014; Cáceres *et al.* 2014; Ferraro *et al.* 2014; Mangold *et al.* 2014; Mercado-Díaz *et al.* 2014; Papong *et al.* 2014a, b; Peláez *et al.* 2014; Poengsungnoen *et al.* 2014a, b; Rivas Plata *et al.* 2014; Sutjaritturakan *et al.* 2014; Van den Broeck *et al.* 2014; Weerakoon *et al.* 2014). At least 140 additional species are awaiting formal description. Adding these to the number of currently accepted species, Graphidaceae now comprises approximately 2,500 known species.

The question, however, arises whether the effort put forward in the past decade, including collaborative initiatives such as the present one, represents a substantial advance to closing the gap in the knowledge of diversity of the family Graphidaceae or whether this is merely the beginning of a trend that will hold for some time to come, adding a substantial amount of further new species not yet discovered. In other words: is the simultaneous description of 175 new species closing the gap or is it merely a drop in the bucket? How many species of Graphidaceae can we expect to exist globally?

In order to address this issue, we used a predictive model based on existing data to extrapolate the diversity of Graphidaceae at a global scale. A large number of approaches have been developed to predict species richness, with different objectives, including both the prediction of species yet unknown to science and the estimation of species richness in a given area without undertaking a complete inventory. These can be divided into roughly three categories: (1) ad-hoc methods that do not use a statistical approximation, (2) statistical methods that use non-biological, accessory data to predict species richness, and (3) statistical methods based on biological traits of the taxa in question.

Ad-hoc methods basically use taxonomic expertise in a given group to come up with predictive estimates (Gastón 1991; Colwell & Coddington 1994), but do not use any quantitative statistical approach. Predictions using non-biological traits include the analysis of publication tendencies over time (Dolphin & Quicke 2001; Costello *et al.* 2011; Joppa *et al.* 2011). These might give useful data, as shown for global lichen diversity by Sipman & Aptroot (2001), but depend on the assumption that there is an underlying correlation between overall species richness of a group in question and the rate of how species were described over time. This is not necessarily the case, since a spike in species descriptions can either indicate an exhaustive approach or the initiation of a large number of new discoveries. Thus, the number of species described over a given period of time is not a reliable predictor of true species richness, unless the pattern displays a more or less predictable behavior over time. The use of patterns of diversity correlated with taxonomic hierarchy (Mora *et al.* 2011) to predict global species richness is another approach that could be classified as non-biological in the sense that hierarchical classification of a species is not a biological trait *per se*, although biological traits do often correlate with lower taxonomic ranks such as genus. Hence, this approach has similar problems as the analysis of publication tendencies, especially since diversification rates can vary greatly between taxa of the same rank and, if using a phylogenetic approach, between sister lineages.

Parametric approaches use statistical analysis of biological traits that correlate with species richness, ranging from habitat preferences to substrate ecology, to phenotype characters. They usually have in common that they use a known data set to formulate a predictive model and then employ the model to extrapolate or interpolate towards unknown species richness in areas where the predictive parameters, such as vegetation diversity, are known. One strategy is the extrapolation from individual samples. An elegant approach to predicting global species richness in insects was put forward by the classic study of Erwin (1982). He analyzed the diversity of beetles collected through fogging from a select number of tropical trees and then categorized them as specialists (associated with a single tree species) or generalists (independent of tree species). Using the estimated number of tree species known from the tropics, he used simple extrapolation to arrive at a global predicted diversity of up to 30 million insect species. This approach was later adapted by Hawksworth (1991, 1997, 2001), using levels of host specificity of fungi, to predict at least 1.5 million fungal species.

Extrapolation from macroecological patterns is another strategy. If for a given area, species richness can be established as a function of habitat diversity and area size, species richness can be predicted for areas in which no complete species inventory has been undertaken but habitat diversity and area size are known. The model is then either direct, by computing values for species richness through correlation with environmental parameters (Radies *et al.* 2009), or indirect, by predicting species distribution ranges (MacDougall & Loo 2002; Edwards *et al.* 2006; Villaseñor *et al.* 2006; Velázquez *et al.* 2009) and subsequently calculating species richness based on these. For lichens, this approach has been proposed at a global scale focusing on tropical taxa by Lücking *et al.* (2009b). Rarefaction through interpolation is also a commonly used approach (Sanders 1968; Heck *et al.* 1975; Coleman 1981; Coleman *et al.* 1982; Foote 1992; Colwell & Coddington 1994; Magurran 2004), although it is sensitive to observed patterns of species abundances (Gotelli & Colwell 2001). In contrast, non-parametric methods uses the frequency of rare species in a dataset to predict overall species richness, calculated by means of estimators such as Chao, Jackknife, and Bootstrap (Burnham & Overton 1978, 1979; Chao 1984, 1987; Smith & Van Belle 1984; Colwell & Coddington 1994; Chazdon *et al.* 1998; Hortal *et al.* 2006). The idea behind such methods is that species not yet sampled will always be rare species and hence their number can be predicted by analyzing the relative frequency of rare species already present in samples.

Related to the previous approach is the use of indicator species, which assumes that particular species or species guilds can replace habitat parameters in predicting overall species richness. This approach is particularly useful at local and regional scale for rapid inventories (Nally & Fleischman 2004) and has been used for lichens in different contexts (Rivas Plata *et al.* 2008; Aragón *et al.* 2013). However, it is not necessarily accurate for

predicting global species richness, since it requires good knowledge of relationships between species and their environment and it also assumes that these relationships do not vary with scale.

A rarely used approach is the analysis of character variation in a given group to identify potentially missing species by predicting likely character combinations that have not yet been observed in known species. For example, if a group of species displays a large number of character state combinations, such as various ascospore types with various chemical compounds in the thallus. Thereby, not all possible combinations will correspond to species but rather, patterns of correlations between character states can be used to predict how many combinations likely represent species. Thus, Messuti & Archer (2009) predicted 1,550 species of *Pertusaria* out of 4,660 possible character state combinations. Lücking (2012) used this approach to predict that in the large group of species centered around *Graphis scripta* (L.) Acharius (1809: 145) species richness might be about twice as high as the known number of species, based on 240 possible character state combinations and 90 combinations likely to exist in nature, 42 of them known in accepted species. This approach can be used for taxa in which the main characters are easily defined and determined and in which a certain level of combinations of presumably independent characters (such as ascospore type and secondary chemistry) is apparent, while it is impractical for groups that display complex morphologies or little overlap in character state combinations. It also depends on a certain level of knowledge already available, being more accurate for groups in which a larger number of species has already been described. Another study that in part used phenotype characters to predict species richness dealt with aquatic beetles (Nilsson-Örtman & Nilsson 2010).

In this paper, we used a parametric approach to predicting species richness based on a grid map and employing two measures: individual grid richness and average grid distribution per species. This novel approach was first applied by the first author and collaborators to another group of lichenized fungi in the Basidiomycota, the genera *Cora* and *Corella* (Lücking *et al.* 2014). The two measures are related to global diversity (over all grids) by a simple formula: global diversity is the sum of grid diversity divided by average grid distribution per species. Global diversity can thereby be interpreted as gamma diversity over all grids, while individual grid diversity corresponds to alpha diversity and grid distribution is a proxy for beta diversity or species turnover (Whittaker 1960). In the original formula (Whittaker 1960), gamma diversity is the product of average alpha diversity and average beta diversity, and it follows that in our formula, beta diversity corresponds to number of grids / average grid distribution. In other words, a higher number of grids combined with a lower average grid distribution results in higher beta diversity. Similar to Whittaker's (1960) formula, higher grid (alpha) diversity and lower grid distribution (higher beta diversity) will result in higher global (gamma) diversity. The challenge is to estimate individual grid diversity and average grid distribution. The first can be obtained through linear regression factoring in two independent parameters: habitat diversity and sampling effort per grid. The second can be estimated through interpolation of incomplete distribution ranges assumed to be caused by gaps in sampling effort. This approach corresponds to extrapolation from macroecological patterns, since we use biological traits of the taxa in question (correlation with habitat diversity) to predict individual grid richness. To compare this approach with other methods, we also employed two independent, non-parametric estimates: a species-area curve based on randomized subsampling of selected grids, and global species estimators based on frequencies of rare species.

Material and Methods

Since the current knowledge of diversity of Graphidaceae suggests that the majority of species in Graphidaceae are found in tropical areas, we focused in this study on (sub-)tropical regions. We assembled a grid map ranging from 30° northern to 30° southern latitude, with grids 15° wide and high, corresponding to approximately 1,600 km in each direction or approximately 2.5 million km² per grid, about 65% the extension of the United States (Fig. 1). This resulted in 46 grids covering land areas or archipelagos with known data on the three core subfamilies of Graphidaceae (Table 1). "Extratropical" areas (defined as outside the belt delimited by 30° northern to 30° southern latitude) and species exclusively occurring in these areas (Table 2) were excluded from the statistical prediction, since they contribute less than 5% to global species richness in the family and this proportion is within the error margin of the predictive model. However, since these areas do support substantial diversity in absolute numbers, we discuss species occurring exclusively in these areas separately.
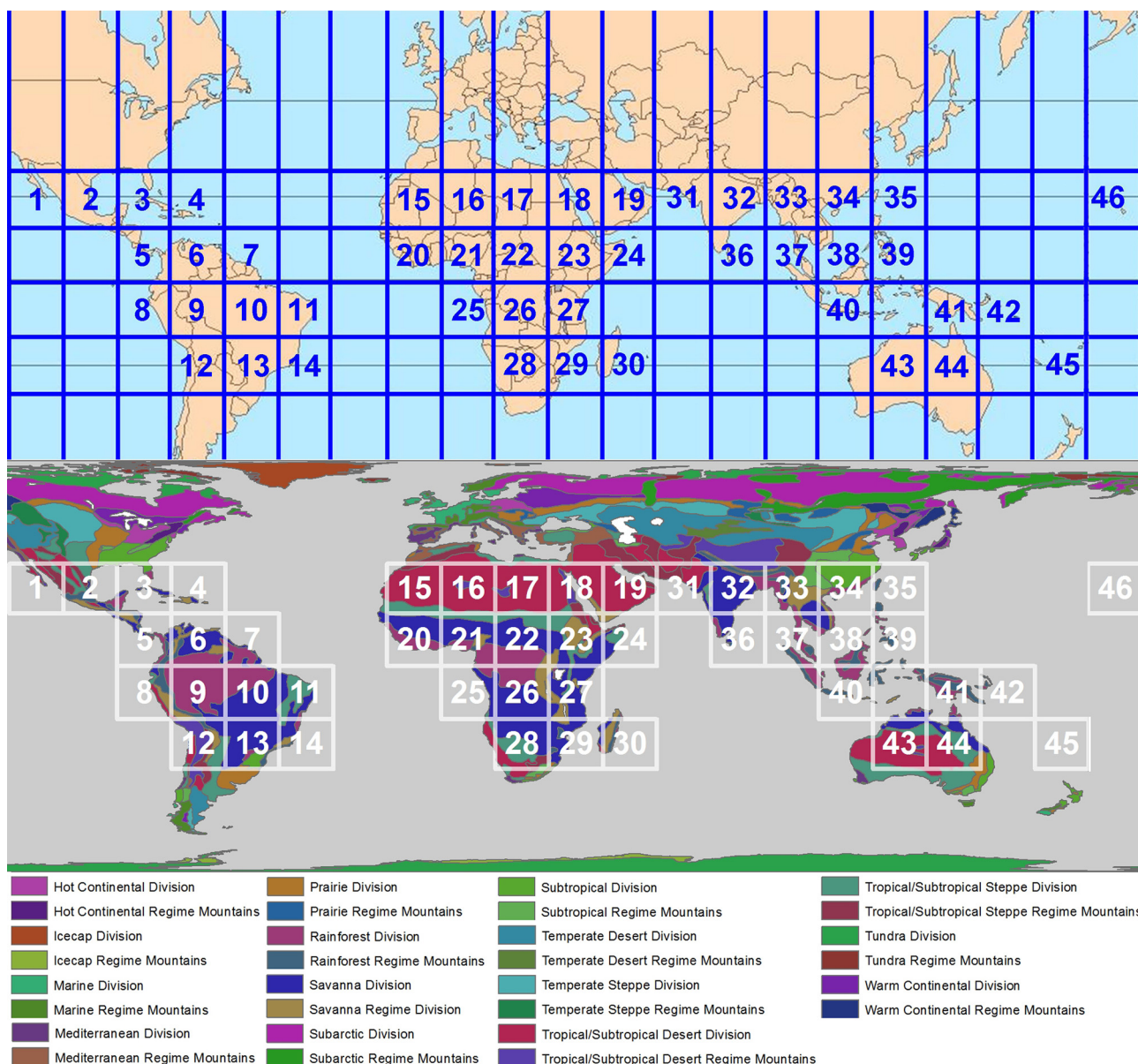
FIGURE 1. Global 15° × 15° gridmap used for the statistical approach to predict global species richness, including vegetation map from Bailey & Hogg (1986) and Bailey (1989) provided in ArcGIS.

TABLE 1. Global 15° × 15° grids, representative areas, and sampling score (from Table 3), GIS score, remote score, (Online Supplement T2) and total score (by multiplication of the three scores).

Grid	Region	Representative area	Sampling	GIS	Remote	Total
1	Neotropics	Sonoran Desert	5	83	1	414
2	Neotropics	Mexico	3	326	1	978
3	Neotropics	Florida, Cuba, Jamaica	8	297	1	2374
4	Neotropics	Hispaniola, Puerto Rico, Lesser Antilles	8	224	1	1792
5	Neotropics	Central America	10	326	1	3260
6	Neotropics	Colombia, Venezuela, Trinidad and Tobago	5	448	1	2238
7	Neotropics	Guayanas	3	288	1	864

TABLE 1. (Continued)

Grid	Region	Representative area	Sampling	GIS	Remote	Total
8	Neotropics	Galapagos Islands, Ecuador, W and central Peru	2	316	1	632
9	Neotropics	W Amazon (Amazonas, Rondonia, Peru)	4	496	1	1984
10	Neotropics	E Amazonia (Pará)	1	363	1	363
11	Neotropics	northE Brasil	6	236	1	1417
12	Neotropics	Bolivia	0	245	1	0
13	Neotropics	central and S Brazil (Pantanal, Cerrado, Chaco)	2	391	1	782
14	Neotropics	SE Brazil (Minas Gerais, Rio de Janeiro)	5	299	1	1496
15	African Paleotropics	Morocco, W Algeria, Mauretania, W Mali	1	59	1	59
16	African Paleotropics	E Algeria and Mali, W Libya, N Nigeria	1	58	1	58
17	African Paleotropics	E Libya, W Egypt, N Chad, W Sudan	1	57	1	57
18	African Paleotropics	E Egypt, E Sudan, W Saudi-Arabia	1	113	1	113
19	African Paleotropics	E Saudi-Arabia, N Jemen, N Oman	1	100	1	100
20	African Paleotropics	Sierra Leone, Guinea, Ghana, Ivory Coast	2	317	1	634
21	African Paleotropics	S Nigeria, Cameroon, São Thomé and Principé	2	429	1	859
22	African Paleotropics	S Chad, southW Sudan, Central African Republic	0	419	1	0
23	African Paleotropics	E Sudan, Ethiopia, W Somalia	0	282	1	0
24	African Paleotropics	E Somalia, S Jemen, S Oman, Socotra	2	152	1	304
25	African Paleotropics	Equatorial Guinea, Gabun, Congo	0	252	1	0
26	African Paleotropics	Democratic Republic of Congo, Angola	0	436	1	0
27	African Paleotropics	Uganda, Kenya, Tanzania	3	317	1	950
28	African Paleotropics	Namibia, Botswana, N South Africa	4	173	1	693
29	African Paleotropics	Zimbabwe, Mozambique	3	217	1	652
30	African Paleotropics	Madagascar, Reunion, Mauritius	3	303	1	908
31	Eastern Paleotropics	Pakistan, northW India	0	120	1	0
32	Eastern Paleotropics	N and central India	5	418	1	2092
33	Eastern Paleotropics	Myanmar, N Thailand	3	475	1	1424
34	Eastern Paleotropics	S China, Hong Kong	4	335	1	1340
35	Eastern Paleotropics	Taiwan, Bonin Islands	2	208	1	417
36	Eastern Paleotropics	S India (Karnataka, Tamil Nadu, Kerala), Sri Lanka	10	278	1	2777
37	Eastern Paleotropics	Andaman Islands, S Thailand, Malaya, Singapore	8	354	1	2835
38	Eastern Paleotropics	Cambodia, Vietnam, Borneo, Labuan	2	347	1	693
39	Eastern Paleotropics	Philippines	8	259	1	2076
40	Eastern Paleotropics	Indonesia	2	337	1	673
41	Eastern Paleotropics	New Guinea	3	377	1	1131
42	Eastern Paleotropics	Solomon Islands	5	182	1	912
43	Eastern Paleotropics	NW Australia (Western Australia, Northern Territory)	3	126	1	378
44	Eastern Paleotropics	northE Australia (Queenslands, N New South Wales)	10	211	1	2108
45	Eastern Paleotropics	New Caledonia, Fiji Islands, Vanuatu, Tonga Islands	6	131	0.7	550
46	Eastern Paleotropics	Hawaii	9	129	0.7	813

TABLE 2. Species of Graphidaceae exclusively reported from regions outside the belt delimited by 30° northern and 30° southern latitude.

Species	Region
Acanthothecis gyridia (Stirt.) A.W. Archer	Australia
Acanthothecis leucoxanthoides Lendemer & R.C. Harris	North America
Acanthothecis paucispora Lendemer & R.C. Harris	North America
Acanthothecis subaggregans (Müll. Arg.) A.W. Archer	Australia
Acanthothecis virguicola Kantvilas	Australia
Anomalographis madeirensis (Tav.) Kalb	Europe
Anomomorpha roseola A. W. Archer & Elix	Australia
Carbacanthographis iriomotensis (M. Nakan.) M. Nakan. & Kashiw.	Japan
Chapsa asteliae (Kantvilas & Vĕzda) Mangold	Australia
Chapsa lamellifera (Kantvilas & Vĕzda) Mangold	Australia
Chapsa lordhowensis Mangold	Australia
Chapsa minor (Kantvilas & Vĕzda) Mangold & Lumbsch	Australia
Clandestinotrema aff. *antoninii*	Europe
Crutarndina petractoides (P. M. Jørg. & Brodo) Parnmen, Lücking & Lumbsch	Europe
Fissurina alboscripta (Coppins & P. James) Staiger	Europe
Fissurina alligatorensis Lendemer & R.C. Harris	North America
Fissurina elixii (A. W. Archer) A.W. Archer	Australia
Fissurina flavicans (Kashiw.) M. Nakan. & Kashiw.	Japan
Fissurina fujisanensis (Kashiw. & M. Nakan.) M. Nakan. & Kashiw.	Japan
Fissurina howeana (A. W. Archer) A.W. Archer	Australia
Fissurina novae-zelandiae C. Knight	New Zealand
Fissurina psoromica (A. W. Archer) A.W. Archer	Australia
Fissurina subtropica (M. Nakan.) M. Nakan. & Kashiw.	Japan
Fissurina undulata (Müll. Arg.) M. Nakan. & Kashiw.	Japan
Graphis betulina (Pers.) Ach.	Europe
Graphis centrifuga Räsänen	Australia
Graphis flavopalmicola Y. Joshi, Lücking & Hur	South Korea
Graphis jejuensis K. H. Moon, M. Nakan. & Kashiw.	South Korea
Graphis koreana S. Joshi & Hur	South Korea
Graphis kousyuensis (Horik. & M. Nakan.) Lücking	Japan
Graphis macrocarpa (Pers.) Röhl.	Europe
Graphis parallela Müll. Arg.	Japan
Graphis pulverulenta (Pers.) Ach.	Europe
Graphis sophisticascens Nyl.	North America
Graphis sterlingiana E.A. Tripp & Lendemer	North America
Graphis uruguayensis ined.	Uruguay
Gymnographopsis chilena C.W. Dodge	Chile
Hemithecium argopholis (C. Knight ex Müll. Arg.) A.W. Archer	Australia
Hemithecium endofuscum (M. Nakan.) M. Nakan. & Kashiw.	Japan
Hemithecium polymorphum (M. Nakan.) M. Nakan. & Kashiw.	Japan
Leiorreuma yakushimensis (M. Nakan.) M. Nakan. & Kashiw.	Japan
Leucodecton desquamescens (Vain.) Rivas Plata & Lücking	Japan

TABLE 2. (Continued)

Species	Region
Leucodecton isidioides (Borrer) Lücking & Breuss	Europe
Mangoldia atronitens (A. W. Archer) Lücking, Parnmen & Lumbsch	Australia
Mangoldia australiana Lücking, Parnmen & Lumbsch	Australia
Melanotopelia blepharostoma Lumbsch & Divakar	South America
Melanotopelia toensbergii (Vězda & Kantvilas) Lumbsch & Mangold	North America
Ocellularia pauciseptata (Purvis & P. James) Aptroot	Europe
Phaeographis oricola Lendemer & R.C. Harris	North America
Phaeographis patagonica Zahlbr.	Chile
Platygramme buxi (Etayo) Etayo	Europe
Platygramme pseudomontagnei (M. Nakan.) M. Nakan. & Kashiw.	Japan
Pseudoramonia richeae Kantvilas & Vězda	Australia
Pseudoramonia stipitata (Vězda & Hertel) Kantvilas & Vězda	Tasmania
Redonographa chilensis (Zahlbr.) Lücking & Tehler	Chile
Redonographa saxiseda (Zahlbr.) Lücking & Tehler	Chile
Schizotrema aff. *schizoloma*	Australia
Schizotrema subguadalupense ined.	Australia
Schizotrema subzebrinum Mangold	Australia
Thelotrema aemulans Kremp.	New Zealand
Thelotrema canescens Tat. Matsumoto	Japan
Thelotrema infundibularis Tat. Matsumoto	Japan
Thelotrema laurisilvae Lücking & Breuss	Europe
Thelotrema macrosporum P.M. Jørg. & P. James	Europe
Thelotrema nipponicum Tat. Matsumoto	Japan
Topeliopsis athallina Lumbsch & Mangold	New Zealand
Topeliopsis azorica (P. James & Purvis) Coppins & Aptroot	Australia
Topeliopsis aff. *azorica* (P. James & Purvis) Coppins & Aptroot	Europe
Topeliopsis decorticans (Müll. Arg.) Frisch & Kalb	Australia
Topeliopsis kantvilasii Mangold & Lumbsch	Australia
Topeliopsis lomatiae (Messuti, Lumbsch & Vězda) Messuti & Mangold	Argentina
Topeliopsis macrocarpa (C. W. Dodge) Mangold & Lumbsch	Subantarctic
Topeliopsis patagonica Mangold & Lumbsch	Chile
Topeliopsis tasmanica (Kantvilas & Vězda) Mangold	Australia

We assembled a global working checklist of species in Graphidaceae (Online Supplement T1; http://www.fieldmuseum.org/sites/default/files/online_supplement_T1.txt), focusing on the three core subfamilies Fissurinoideae, Graphidoideae, and Redonographoideae, from published literature and unpublished data (Wirth & Hale 1963, 1978; Hale 1973, 1974a, b, 1975, 1978, 1980, 1981; Lumbsch 1989, 1993; Harris 1989, 1990, 1995; Nagarkar & Hale 1989; Mies & Lumbsch 1990; Mies 1994a, b; Lumbsch & Aptroot 1993; Guderley & Lumbsch 1996; Marcano *et al.* 1996; Aptroot *et al.* 1997, 2007; Boonpragob *et al.* 1998; Staiger & Kalb 1999; Komposch & Hafellner 1999, 2000, 2003; Kalb & Staiger 2000; Breuss 2000, 2001, 2002, 2004, 2008, 2011; Sipman 2001; Nakanishi *et al.* 2001, 2003, 2010; Staiger 2002; Wolseley *et al.* 2002; Nash *et al.* 2002, 2004, 2007; López de Silanes & Alvarez 2003; Messuti *et al.* 2003; Archer 2004, 2006, 2007, 2009; Kalb 2004, 2008, 2009; Adawadkar & Makhija 2004, 2005, 2006, 2007; Kalb *et al.* 2004, 2009a, b; Nayaka *et al.* 2004; Makhija & Adwadkar 2005a, b; Makhija *et al.* 2005, 2006, 2009; Frisch 2006; Frisch & Kalb 2006a, b; Frisch *et al.* 2006a, b; Cáceres 2007;

Galloway 2007; Aptroot & Sipman 2007; Jia & Wei 2007, 2008, 2009a, b; Lumbsch & Mangold 2007; Lücking 2007, 2008; Breuss & Neuwirth 2007; Tewari & Upreti 2007a, b; Jagadeesh Ram *et al.* 2007; Miao *et al.* 2007; Lücking *et al.* 2007, 2008, 2009a, b, 2010, 2011a, b, 2012a, b, c, 2013; van den Boom *et al.* 2007, 2013; Moon *et al.* 2008, 2011, 2012; Dal-Forno 2009; Archer & Elix 2009, 2013; Neuwirth & Lücking 2009; Sharma & Makhija 2009a, b; Chitale *et al.* 2009, 2011; Joshi *et al.* 2009, 2010a, b, 2012a, b, c, 2013a, b, c; Papong *et al.* 2009, 2010; Sérusiaux *et al.* 2009; Tripp *et al.* 2009; Lendemer 2010; Dal-Forno & Eliasaro 2010; Singh & Sinha 2010; Dubey *et al.* 2010; Kocourková *et al.* 2010; Nelsen *et al.* 2010, 2012; Rivas Plata *et al.* 2010a, b, 2012a, 2012b; Lumbsch *et al.* 2010, 2011a, b; Sharma *et al.* 2010a, b, 2012; Jia 2011; Mercado-Díaz 2009; Rincón-Espitia & Lücking 2011; Seavey & Seavey 2011; Sharma & Khadilkar 2011, 2012; Mongkolsuk *et al.* 2011; Rincón *et al.* 2011; Upreti *et al.* 2011; Lücking & Breuss 2012; Lücking & McCune 2012; Schumm & Aptroot 2012a, b; Cáceres *et al.* 2012a, b, 2013; Jia *et al.* 2012; Perlmutter *et al.* 2012; Rosabal *et al.* 2012; Sipman *et al.* 2012; Soto Medina *et al.* 2012; Weerakoon *et al.* 2012a, b; Wijeyaratne *et al.* 2012; Parnmen *et al.* 2012a, b, 2013; Jia & Kalb 2013; Rivas Plata & Lücking 2013; Bárcenas-Peña *et al.* 2014; Lendemer *et al.* 2013). For unpublished data, we included revision of herbarium material housed in the following herbaria: ABL, B, BM, F, FH, H, M, MSC, PC, S, TUR, US, W, hb. Henssen, hb. Kalb. All reported names were updated where possible using current genus and species concepts (Staiger 2002; Frisch *et al.* 2006a; Lücking *et al.* 2009a; Rivas Plata *et al.* 2010a). Subfamily Gomphilloideae, comprising an additional 400 known species, was excluded from the predictive model, as we currently do not have an extensive set of molecular data for this lineage to assess species concepts. We used a combination of morphological and molecular data (Parnmen *et al.* 2012a; Rivas Plata *et al.* 2012a, b, 2013), including revision of type material, to verify the status of each species included in the list. Molecular data are currently available for nearly 500 species within the core Graphidaceae (Staiger 2002; Frisch *et al.* 2006a; Staiger *et al.* 2006; Tehler *et al.* 2009; Lücking *et al.* 2013; Rivas Plata *et al.* 2013; Kraichak *et al.* 2014a; Lumbsch *et al.* 2014), allowing to evaluate the usefulness of phenotype characters for species delimitation in taxa where no molecular data are yet available (Berger *et al.* 2011; Parnmen *et al.* 2012a; Rivas Plata *et al.* 2012b). For example, since molecular data suggest that hymenium inspersion and secondary chemistry are uniform within a phylogenetically defined species in the family (Rivas Plata *et al.* 2012b, 2013), we generally separated species based on these characters. We then used the same source references to assess occurrences of each species within each grid. Specifically, where possible we critically revised data and material on taxa reportedly pantropical, and those kept in the dataset as pantropical or widely distributed were either supported by molecular data or else have a high likeliness of being correct, based on indirect evidence.

We employed detrended correspondence analysis (DCA) ordination to visualize the arrangement of grids in species space and patterns apparent from observed species distributions. DCA was performed by down-weighting rare species and rescaling the axes into 25 segments. In addition, we performed indicator species analysis using the three main tropical regions (Neotropics: grids 1–14; African Paleotropics: grids 15–30; Eastern Paleotropics: grids 31–46) as grouping variable. This approach uses Monte-Carlo randomization to shuffle the original data and tests species distributions among regions comparing them to a random distribution. Both approaches were done in PC-ORD 5.0 (McCune & Mefford 1999; McCune *et al.* 2002).

For each grid, we established three sets of scores: (1) scores representing the sampling effort per grid in graphidoid and thelotremoid Graphidaceae, ranging from 0 to 5 for each group (combined 0 to 10); (2) scores representing the presence of global vegetation types in each grid; and (3) scores indicating small, remote oceanic islands (more than 1,000 km from the next continent or large island). For the latter, we scored each grid as 1 except grids 45 and 46 (New Caledonia, Hawaii), which were scored as 0.7 (Table 1). Sampling scores were derived from data obtained from published literature and unpublished revisions of herbarium collections and recent field work (Table 3). We employed separate sampling scores for graphidoid and thelotremoid taxa since until recently, these were treated as separate families and hence available literature often results in a bias towards one or the other group in a given region. Three grids were defined as well-sampled, receiving the maximum score of 10: grids 5, 36, and 44. Although these grids have not been completely sampled, we applied the maximum score as conservative calibration for the model.

TABLE 3. Scoring system for the parameter sampling effort per grid.

Sampling score	
Score 0	Less than 10 species reported per group for grids with predominantly humid vegetation or less than five species for grids with semi-arid vegetation
Score 1	Less than 50 species reported per group for grids with predominantly humid vegetation or less than 10 species for grids with semi-arid vegetation
Score 2	Limited treatments available for one to several localities across grid, with 50 or more species reported per group for grids with predominantly humid vegetation or 10 ore more species reported for grids with semi-arid vegetation
Score 3	Modern taxonomic treatments available for one locality within grid or limited treatments available for additional localities across grid
Score 4	Modern taxonomic treatments available for a one to three locality within grid and limited treatments available for additional localities across grid
Score 5	Modern taxonomic treatments available for more than three localities across grid

Vegetation types were defined the global vegetation map provided by Bailey & Hogg (1986), and Bailey (1989), using their intermediate division classification level (Online Supplement T2; http://www.fieldmuseum.org/sites/default/files/online_supplement_T2.txt). The land area of each division was calculated for each 15° latitude by 15° longitude grid cells (Fig. 1) using the "tabulate area" tool in ArcGIS version ArcGIS 10.1 with the Spatial Analyst extension. We used a cylindrical equal area projection for area calculations, which equally spaces longitudinal lines to form similarly sized rectangular grids (sub-tropical cells were 7% smaller than tropical cells). When comparing the land area of divisions, we used the relative area within grid cells rather than the absolute area between grid cells. We also accounted for ocean surface present within grid cells (Online Supplement T2). Since species richness is logarithmically correlated with area size, we transformed all area values using the exponent 0.25 (Online Supplement T2). This exponent was derived as best fitting model ($R_{Pearson}$ = 0.99) from the following average species richness values of Graphidaceae observed in areas of a given size: ≈ 100 species (1 ha or 0.01 km^2; Florida, Venezuela, Peru, Philippines: Lücking *et al.* 2011a, 2012c; Parnmen *et al.* 2012b; Rivas Plata & Lücking 2013); ≈ 300 species (50,000 km^2; Costa Rica: Lücking *et al.* 2008; Sipman *et al.* 2012); ≈ 500 species (700,000 km^2; Central America: combined from Wirth & Hale 1963, 1978; Hale 1978; Sipman 2001; Breuss 2000, 2001, 2002, 2004, 2008, 2011; Breuss & Neuwirth 2007; van den Boom *et al.* 2007, 2013; Lücking *et al.* 2008; Sipman *et al.* 2012); ≈ 1000 species (1.8 million km^2; Neotropics). The exponent depends only on relative species richness increasing with scale, independent of absolute species richness, and hence is not sensitive to sampling bias as long as reasonably similar sampling effort is assumed for each scale. We assigned each vegetation type (Bailey division) a score corresponding to the diversity of Graphidaceae expected within that vegetation type (Table 4), using data from quantitative studies to rank vegetation types according to expected diversity (Lücking 2003; Cáceres *et al.* 2008; Rivas Plata *et al.* 2008). These data also suggest that the vegetation types that contribute uniquely and substantially to overall species richness are the rainforest and rainforest mountains divisions, whereas the savanna and savanna mountains divisions mostly harbor species also found in the rainforest canopy. Therefore, to avoid overestimation of species richness when computing a cumulative score for grids in which both rainforest and savanna divisions were present, the diversity score for the savanna divisions was scaled back as follows: if the rainforest division area was larger than the savanna division area, it was set to 0 (then assuming that the savanna division would not contribute unique species); if the savanna division was larger but less than twice as large, it was set to 1; if the savanna division was between two and ten times as large, it was set to 2; and if the savanna division was more than ten times as large, it was set to the full score of 3 (Online Supplement T2). Sampling and vegetation scores were combined into a total prediction score for each grid by multiplication (Table 1). Since the Bailey vegetation map does not contain data for small islands, we assembled the data for grids 45 and 46 (New Caledonia, Hawaii) manually using the above criteria; also, the data for grid 4 (Hispaniola, Puerto Rico, Lesser Antilles) were manually corrected since they suggested absence of rainforest areas.

TABLE 4. Scoring system for the parameter Graphidaceae diversity versus vegetation type (Bailey divisions).

Sampling score	
Score 1	Prairie division
	Subtropical division
	Subtropical Mountains division
	Tropical/Subtropical Desert division
	Tropical/Subtropical Steppe division
	Tropical/Subtropical Desert Mountains division
	Tropical/Subtropical Steppe Mountains division
Score 3	Savanna division
	Savanna Mountains division
Score 5	Rainforest Mountains division
Score 10	Rainforest division

We compared the variation of observed species richness per grid with the variation in total prediction scores and established a linear regression as best fit for the correlation between the two variables, using the distribution fitting module in STATISTICA 6.0 and observed correlation coefficient R as evaluation parameter. We then computed predicted species richness per grid based on the linear model by using the maximum sampling score for each grid (10). From the predicted grid data, predicted global species richness was calculated by dividing the sum total of individual grid species richness by the average grid distribution per species, i.e. the average number of grids in which a species is present. Since the observed grid distribution is underestimated by biased sampling effort, we applied interpolation to estimate expected grid distribution per species, by assuming presence of each species in grids that connect grids with observed occurrences and share the same vegetation types in which the species occur. We thereby used a conservative approach, assuming no dispersal limitations for except between continental areas and hence occurrences of species in grids in which such occurrences cannot necessarily be expected for geographic reasons. For example, if a species was found in tropical rainforest in Mexico, Colombia, and southeastern Brazil, we assumed occurrence in all neotropical grids, including the Caribbean, whereas the species might actually be absent from that region due to dispersal limitations. This approach results in a higher estimate for average grid distribution and hence in a lower estimate for global species richness, thus balancing possible errors made in assuming that species do not occur outside the area determined by the grids in which a species was observed. The predicted global species richness was then calculated by dividing the sum total of predicted grid species richness by the interpolated average for species grid distributions.

To compare this approach with other methods, we also employed two separate, non-parametric extrapolation techniques. First, we computed a species-area curve based on eight well-sampled grids (3, 4, 5, 9, 36, 37, 39, 44), with sampling scores between 8 and 10, for an average of 8.9 (SD = 0.99). The species-area curve was computed using a randomized subsampling approach in PC-ORD 5.0 with 500 repetitions and the Sørensen distance measure (McCune & Mefford 1999; McCune *et al.* 2002). Since we included grids with incomplete sampling scores, for an average of 8.9 out of 10, this approach underestimates global diversity, as ideally each grid would have a maximum sampling score of 10 if completely sampled. Hence, we corrected each cumulative grid estimate resulting from the subsampling approach with the factor 1.12 (= 10 / 8.9). The corrected cumulative grid values were used to establish a non-linear model of species richness versus grid number via non-linear estimation in STATISTICA 6.0, employing the best-fitting formula $y = a + b \times \log_2(x)^c$, under least squares regression with a Levenberg-Marquart estimation, a maximum of 50 iterations, and 0.000001 as convergence criterion. The obtained model was used to predict global species richness by extrapolating from eight grids to the total of 46. Since this method is based on well-sampled grids only, it is biased towards sampling effort in ecogeographical terms, since no well-sampled grid represented tropical Africa and also no well-sampled grid represented one of the grids dominated by (semi-)desert vegetation. However, these two shortcomings have opposing effects on the extrapolated value and hence partially balance each other. Since the method assumes a continuous area rather than geographically separate regions, it will underestimate global species richness since it does not take into account that absences of species in particular grids are real, rather than sampling artifact; hence, the estimated species-area curve will appear flatter than it should be. On the other hand, since about 15% of the grids represent areas dominated by (semi-)desert vegetation, with low species richness to be expected, whereas the grids sampled for the species-area curve do not include such grids, the extrapolated model will overestimate global species richness. A way to correct for this uncertainty would be to

compute the model separately for each of the three major tropical regions and include low-diversity (semi-)desert dominated grids; however, the data did not allow this since too few grids had sufficiently high sampling scores.

In addition, we used the *specpool* function as part of the VEGAN package in R (Oksanen *et al.* 2013) to estimate global species richness based on rare species occurrences (singletons and doubletons) within all grids (Palmer 1990; Colwell & Coddington 1994). The method computes four different estimators for global species richness, plus their standard errors: Chao 2, first and second order Jackknife, and Bootstrap, with Chao 2 being the most progressive (likely overestimating) and Bootstrap the most conservative (likely underestimating) measure. We also employed the *betadiver* function in VEGAN to compute patterns of beta diversity between grids.

Results

We assembled a list of 2,079 taxa of Graphidaceae in subfamilies Fissurinoideae, Graphidoideae, and Redonographoideae (Online Supplement T1). Among these are 1,766 previously accepted species, plus 175 new species described in this issue, plus an additional at least 138 taxa that still await formal description. Among the 175 newly described species in this issue (Aptroot 2014; Lücking 2014; Sipman 2014; Kalb & Jia 2014; Lendemer & Harris 2014; Cáceres *et al.* 2014; Ferraro *et al.* 2014; Kraichak *et al.* 2014a; Lumbsch *et al.* 2014; Mangold *et al.* 2014; Mercado-Díaz *et al.* 2014; Papong *et al.* 2014a, b; Peláez *et al.* 2014; Poengsungnoen *et al.* 2014a, b; Rivas Plata *et al.* 2014; Sutjaritturakan *et al.* 2014; Van den Broeck *et al.* 2014), there are four novel generic lineages. By far most of the new species are in the genus *Ocellularia* (46 species), followed by *Fissurina* Fée (1825: xxxv; 24 species), *Graphis* (15), *Diorygma* Eschweiler (1824: 13, 25; 12 species), *Rhabdodiscus* Vainio (1921: 84; 10 species), and *Thelotrema* (nine species). Among the larger genera now containing 50 or more species, the genera with the highest proportion of newly described species are *Diorygma*, with 16.9%, *Ocellularia*, with 16.3%, and *Fissurina*, with 15.3% (Table 5). The highest proportion of new species was found in two small genera: *Myriochapsa* M. Cáceres, Lücking & Lumbsch in Parnmen *et al.* (2013: 128), with 66.7%, and *Compositrema* Rivas Plata, Lücking & Lumbsch (2012b: 1172), with 50%.

TABLE 5. Species per genus recognized in the core Graphidaceae and number and proportion of new species described in contributions in this volume.

Genus	Total	New	Percentage	Genus	Total	New	Percentage
Graphis	441	15	3.4%	*Halegrapha*	7	1	14.2%
Ocellularia	282	46	16.3%	*Wirthiotrema*	7	0	0.0%
Fissurina	157	24	15.3%	*Gyrotrema*	6	1	16.7%
Phaeographis	156	7	4.5%	*Acanthotrema*	5	1	20.0%
Thelotrema	106	9	8.5%	*Asteristion*	5	0	0.0%
Diorygma	71	12	16.9%	*Cruentotrema*	5	1	20.0%
Myriotrema	66	5	7.6%	*Glaucotrema*	5	1	20.0%
Chapsa	61	4	6.6%	*Kalbographa*	5	0	0.0%
Acanthothecis	56	5	8.9%	*Nitidochapsa*	5	1	20.0%
Hemithecium	51	0	0.0%	*Redonographa*	5	0	0.0%
Rhabdodiscus	42	10	23.8%	*Compositrema*	4	2	50.0%
Sarcographa	37	0	0.0%	*Dyplolabia*	4	0	0.0%
Diploschistes	31	0	0.0%	*Melanotopelia*	4	0	0.0%
Platygramme	30	3	10.0%	*Pseudotopeliopsis*	4	1	25.0%
Astrochapsa	28	4	14.2%	*Thecaria*	4	0	0.0%
Carbacanthographis	28	0	0.0%	*Leptotrema*	3	0	0.0%
Leucodecton	28	5	17.9%	*Myriochapsa*	3	2	66.7%

TABLE 5. (Continued)

Genus	Total	New	Percentage	Genus	Total	New	Percentage
Platythecium	26	2	7.7%	*Phaeographopsis*	3	0	0.0%
Topeliopsis	20	0	0.0%	*Pseudoramonia*	3	1	33.3%
Thalloloma	19	2	10.5%	*Schistophoron*	3	0	0.0%
Ampliotrema	18	0	0.0%	*Thecographa*	3	0	0.0%
Melanotrema	18	1	5.6%	*Anomalographis*	2	0	0.0%
Clandestinotrema	17	1	5.9%	*Diaphorographis*	2	0	0.0%
Pseudochapsa	17	1	5.9%	*Gymnographopsis*	2	0	0.0%
Fibrillithecis	16	0	0.0%	*Heiomasia*	2	0	0.0%
Leiorreuma	15	1	6.7%	*Mangoldia*	2	0	0.0%
Stegobolus	15	1	6.7%	*Nadvornikia*	2	0	0.0%
Chroodiscus	14	0	0.0%	*Reimnitzia*	2	0	0.0%
Schizotrema	13	0	0.0%	*Sarcographina*	2	0	0.0%
Pallidogramme	12	0	0.0%	*Crutarndina*	1	0	0.0%
Redingeria	12	1	8.3%	*Enigmotrema*	1	0	0.0%
Glyphis	10	0	0.0%	*Malmographina*	1	0	0.0%
Anomomorpha	8	0	0.0%	*Phlegographa*	1	0	0.0%
				Pycnotrema	1	0	0.0%

Seventy-four taxa (3.5% of the total) are known exclusively from "extratropical" regions in the Northern and Southern Hemisphere north and south of 30° northern and southern latitude. These are mostly from North America, Europe, and eastern Asia (South Korea, Japan). Since the tropics are usually defined as the zone between 23° northern and southern latitude, we labeled these species "extratropical"; however, most of these are actually subtropical in nature, considering that the subtropics are defined as the zone between 23° and 35° northern and southern latitude. These were not included in the predictive computations but are listed separately (Table 2), leaving 2,005 (sub-)tropical or widely distributed species occurring within the grid area, with a total of 5,571 occurrences. "Subtropical" species included within the grid area are mostly those occurring in subtropical, (semi-)arid zones, such as in the genus *Diploschistes*.

Observed species richness per grid ranged from zero to 499 species (Table 6). The highest numbers were observed in grid 36 (southern India, Sri Lanka), with 499 species, grid 5 (Central America: Guatemala through Panama), with 443 species, grid 6 (Colombia, Venezuela, Trinidad), with 334 species, grid 37 (Andaman Islands, southern Thailand, Singapore, peninsular Malaysia), with 332 species, and grid 44 (Australia: Queensland and northern New South Wales), with 317 species. Other grids with high observed diversity were grid 3 (Louisiana, Florida, Cuba, Jamaica), grid 4 (Hispaniola, Puerto Rico, Lesser Antilles), grid 9 (western Amazon in Brazil and Peru), grid 32 (northern and central India), and grid 39 (Philippines). Comparatively low values were observed for all grids in tropical Africa and several grids in tropical Asia, as well as grids 10 and 12 (western Amazon, Bolivia) in tropical America.

Using DCA ordination, the grids separated well into four main groups (Fig. 2). On the vertical axis, grids were grouped into those dominated by subtropical, (semi-)arid desert areas and those with a substantial portion of tropical rainforest. Notably, the (semi-)arid grids are dominated by species of *Diploschistes* Norman (1852: 232) growing on inorganic substrata (soil, rock), whereas the tropical rainforest grids are dominated by all other genera (with mostly epiphytic species). On the horizontal axis, the grids separated well into neotropical, African paleotropical, and eastern paleotropical regions. Indicator species analysis showed that a large number of species (183) was significantly indicative for one of the three regions at $p < 0.05$ (Table 7), and another 107 marginally significant at $p < 0.1$. Considering that only species with presence in a certain number of grids will result in significant values and only 313 out of 2,005 species were found in five or more grids, this implies that almost all species have a biogeographical distribution bias with regard to one or two of the three main tropical regions and only very few species are truly pantropical. Indeed, only 155 species had occurrence data in two or more of the three main tropical regions; notably, one third of these were species of Graphis, and other well-represented genera included *Diploschistes*, *Dyplolabia* Massalongo (1854: 6), *Glyphis* Acharius (1814: 106), *Thecaria* Fée (1825: xlii,97), and *Thelotrema* (Online Supplement T1).
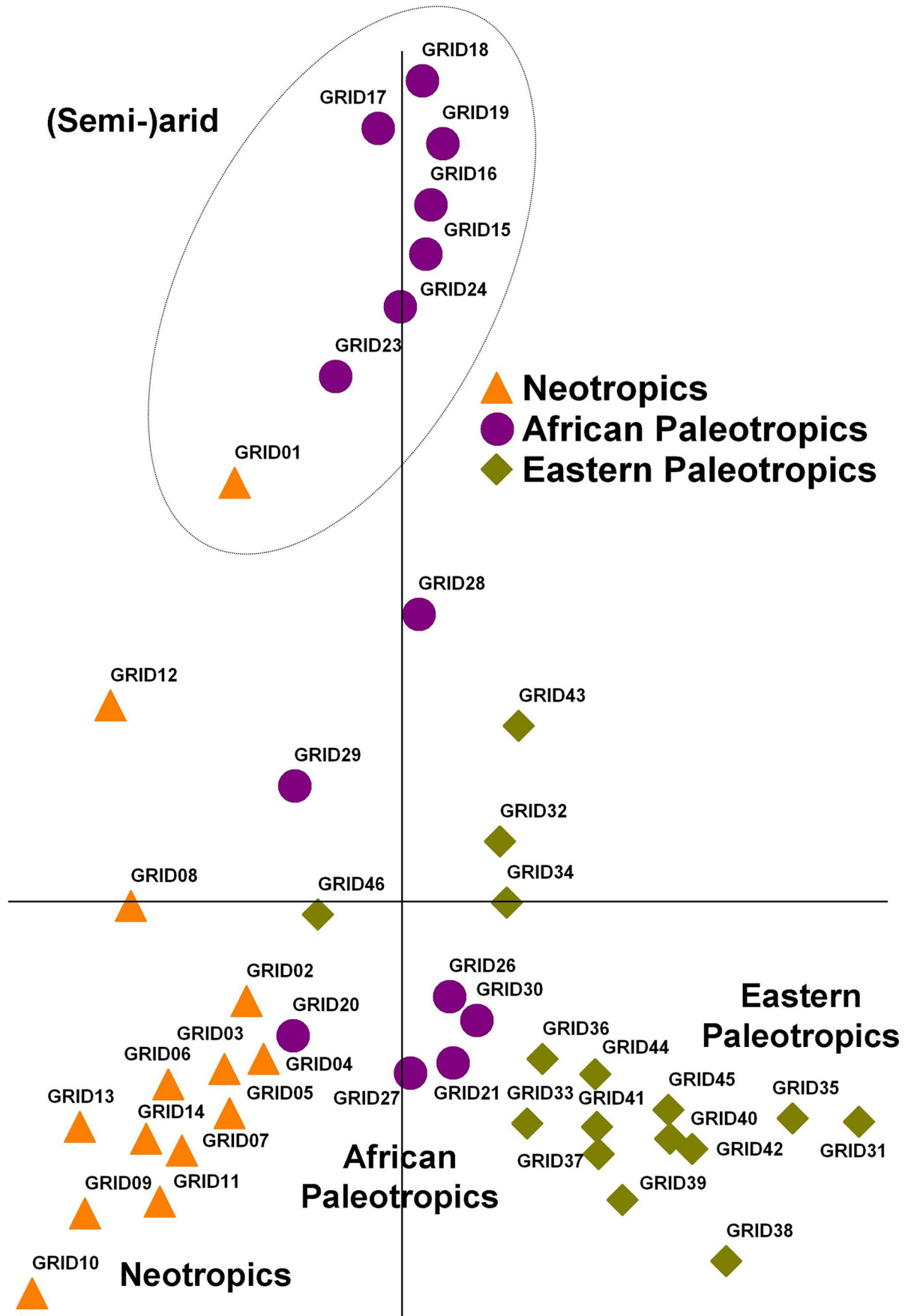
FIGURE 2. DCA ordination of the 46 grids based on observed species composition..

TABLE 6. Observed and predicted species richness per grid, difference, and indication of grids as "discovery hotspots" of undiscovered species based on difference between predicted and observed species richness; (+) difference 150–250 species, (++) difference 250–400 species, (+++) difference more than 400 species.

Grid	Region	Representative area	Observed	Predicted	Difference	Hotspot
1	Neotropics	Sonoran Desert	24	109	85	
2	Neotropics	Mexico	112	429	317	++
3	Neotropics	Florida, Cuba, Jamaica	282	391	109	
4	Neotropics	Hispaniola, Puerto Rico, Lesser Antilles	260	295	35	
5	Neotropics	Central America, Chocó	443	430	[–13]	
6	Neotropics	Colombia, Venezuela, Trinidad and Tobago	334	590	256	++
7	Neotropics	Guayanas	136	379	243	+
8	Neotropics	Galapagos Islands, Ecuador, W and central Peru	62	416	354	++
9	Neotropics	W Amazon (Amazonas, Rondonia, Peru)	260	653	393	++
10	Neotropics	E Amazonia (Pará)	24	478	454	+++
11	Neotropics	NE Brasil	134	311	177	+
12	Neotropics	Bolivia	14	322	308	++
13	Neotropics	Central and S Brazil (Pantanal, Cerrado, Chaco)	105	515	410	+++
14	Neotropics	SE Brazil (Minas Gerais, Rio de Janeiro)	162	394	232	+
15	African Paleotropics	Morocco, W Algeria, Mauretania, W Mali	8	77	69	
16	African Paleotropics	E Algeria and Mali, W Libya, N Nigeria	8	76	68	
17	African Paleotropics	E Libya, W Egypt, N Chad, W Sudan	4	75	71	
18	African Paleotropics	E Egypt, E Sudan, W Saudi-Arabia	4	148	144	
19	African Paleotropics	E Saudi-Arabia, N Jemen, N Oman	6	132	126	
20	African Paleotropics	Sierra Leone, Guinea, Ghana, Ivory Coast	49	418	369	++
21	African Paleotropics	S Nigeria, Cameroon	87	566	479	+++
22	African Paleotropics	S Chad, southW Sudan, Central African Republic	0	552	552	+++
23	African Paleotropics	E Sudan, Ethiopia, W Somalia	3	371	368	++
24	African Paleotropics	E Somalia, S Jemen, S Oman, Socotra	11	200	189	+
25	African Paleotropics	São Thomé and Principé, Equ. Guinea, Gabun, Congo	0	332	332	++
26	African Paleotropics	Democratic Republic of Congo, Angola	14	575	561	+++
27	African Paleotropics	Uganda, Kenya, Tanzania	79	417	338	++
28	African Paleotropics	Namibia, Botswana, N South Africa	61	228	167	+
29	African Paleotropics	Zimbabwe, Mozambique	55	286	231	+
30	African Paleotropics	Madagascar, Reunion, Mauritius	109	399	290	++
31	Eastern Paleotropics	Pakistan, northW India	1	158	157	+
32	Eastern Paleotropics	N and central India	248	551	303	+
33	Eastern Paleotropics	Myanmar, N Thailand	159	625	466	+++
34	Eastern Paleotropics	S China, Hong Kong	160	441	281	++
35	Eastern Paleotropics	Taiwan, Bonin Islands	24	275	251	++
36	Eastern Paleotropics	S India (Karnataka, Tamil Nadu, Kerala), Sri Lanka	499	366	[–133]	
37	Eastern Paleotropics	Andaman Islands, S Thailand, Malaya, Singapore	332	467	135	
38	Eastern Paleotropics	Cambodia, Vietnam, Borneo, Labuan	96	457	361	++
39	Eastern Paleotropics	Philippines	277	342	65	
40	Eastern Paleotropics	Indonesia	82	444	362	++
41	Eastern Paleotropics	New Guinea	129	497	368	++
42	Eastern Paleotropics	Solomon Islands	109	240	131	

TABLE 6. (Continued)

Grid	Region	Representative area	Observed	Predicted	Difference	Hotspot
43	Eastern Paleotropics	NW Australia (Western Australia, Northern Territory)	56	166	110	
44	Eastern Paleotropics	northE Australia (Queenslands, N New South Wales)	317	278	[–39]	
45	Eastern Paleotropics	New Caledonia, Fiji Islands, Vanuatu, Tonga Islands	110	173	63	
46	Eastern Paleotropics	Hawaii	122	170	48	

TABLE 7. Results of indicator species test comparing observed species distribution with main tropical regions.

Region	Significant (p < 0.05)	Marginally significant (p < 0.10	Total
Neotropics	94	63	157
African Paleotropics	3	3	6
Eastern Paleotropics	86	41	127
Total	183	107	290

Correlation between observed species richness per grid and total prediction score per grid resulted in a linear model, $y = 0.13 \times$ (Fig. 3), with a strong and highly significant correlation R = 0.97 and $p < 0.001$ and R^2 (variance explained) = 94%. Using the model by assuming a maximum sampling score (10) per grid, we predicted the highest species richness values for grid 9 (653 species) and grid 6 (590 species) in the Neotropics, grid 26 (575 species) and grid 21 (566 species) in tropical east Africa, and grid 33 (625 species) and grid 32 (551 species) in tropical Asia and Australia, respectively (Table 6). The predicted grid sum total was 16,217. Note that the prediction for three grids (5, 36, 44), including the two grids with the highest observed richness, was lower than the observed value in both cases, owing to the smoothing function of the linear model but also indicating that the model is conservative.
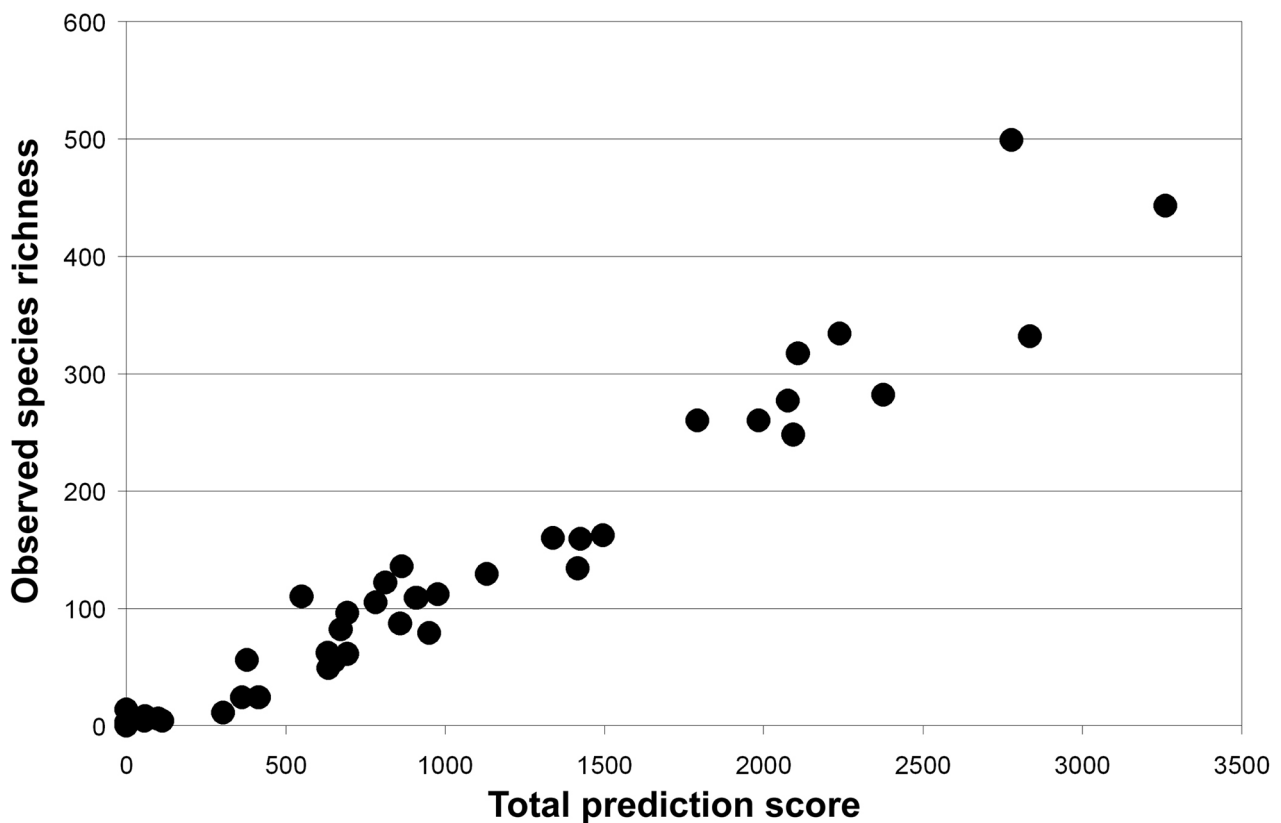
FIGURE 3. Observed species richness per grid plotted against total prediction score derived from sampling, vegetation diversity and landmass, and remote scores.

Observed grid distribution per species was 5,571 / 2,005 = 2.78 grids, corresponding to 7 million km² on average per species. More than half of the species (1,110) were observed in a single grid only and another 313 species in two grids, together accounting for 70% of all (sub-)tropical species. The highest number of grids in which a species was observed was 28 (*Dyplolabia afzelii*), followed by 27 (*Glyphis cicatricosa*), 25 (*Glyphis scyphulifera*), 24 (*Graphis glaucescens*), and 22 (*Graphis tenella*). Notably, of the 25 species with the highest grid distribution, 20 represented graphidoid taxa formerly placed in Graphidaceae, and only five thelotremoid taxa of the former family Thelotremataceae. The low average grid distribution resulted in comparatively high measures of beta diversity between grids, ranging mostly between 0.8 and 1.0 and with an average of 0.91 (Fig. 4). After interpolating species distributions, the estimated grid distribution per species was 4.63 grids, or approximately 11.5 million km², which is about three times the size of the United States. Beta diversity then decreased to an average of 0.79 (Fig. 4). Using this value, global predicted species richness for (sub-)tropical core Graphidaceae was 16,217 / 4.63 = 3,503 species. This corresponds to a 74% increase compared to the observed number of 2,005 species, or nearly 1,500 additional species.
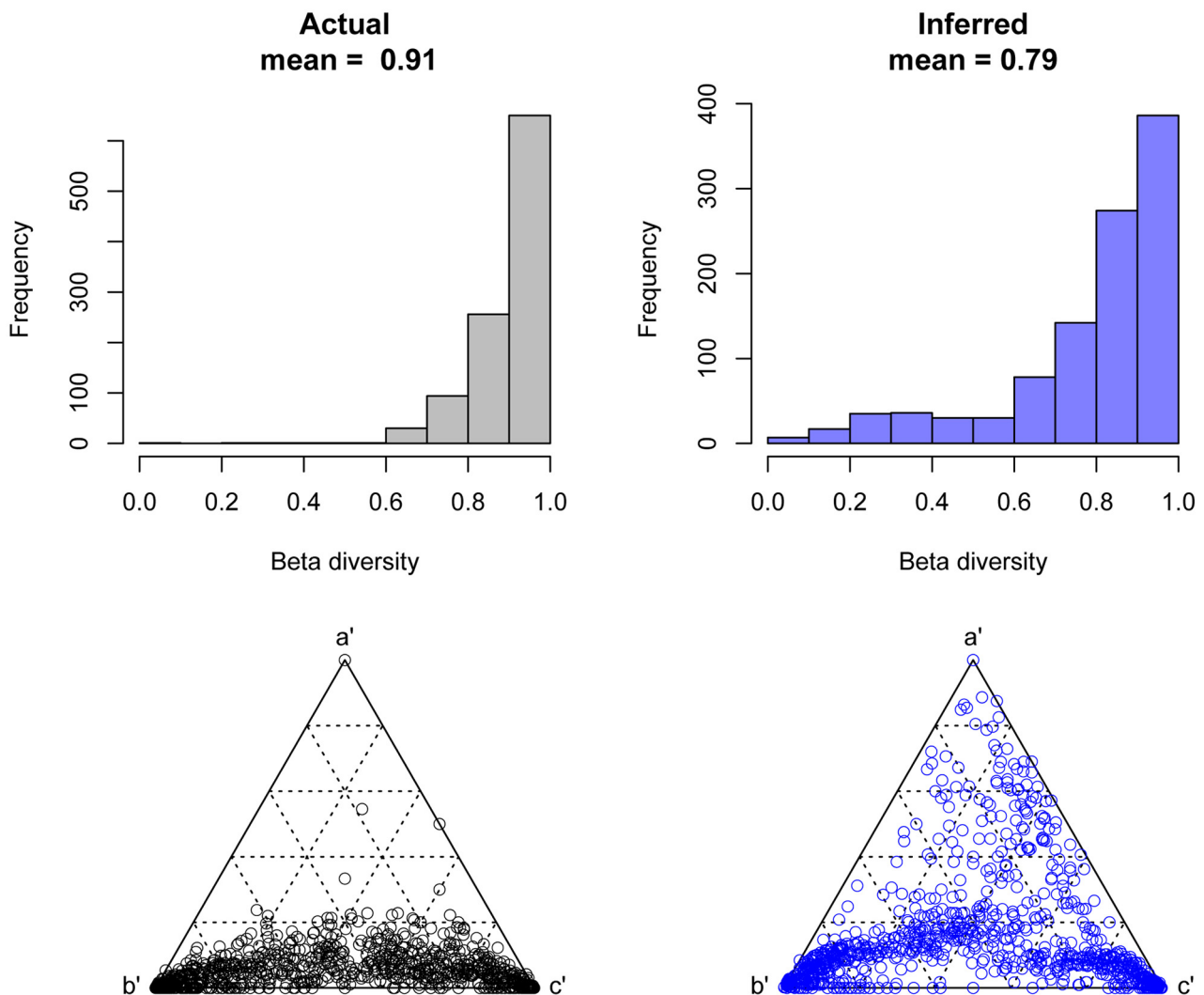
FIGURE 4. Beta diversity based on observed and interpolated grid occurrences.

The species-area curve reconstructed from eight well-sampled grids via subsampling showed absence of a plateau (Fig. 5). Based on this curve and corrected for sampling effort, the non-linear model was estimated as $y = 362 + 222 \times \log_2(x)^{1.50}$, with R = 0.9996, $p < 0.001$, explaining 99.9% of the variance in the data. Using this model, the global predicted species richness of (sub-)tropical core Graphidaceae projected to 46 grids was 3,244 species (Fig. 6). The *specpool* approach as part of the VEGAN package yielded the following estimates: Chao 2 = 3,962 ±

168 species; first order Jackknife = 3,084 ± 253; second order Jackknife = 3,850; Bootstrap = 2,454 ± 139. The average and the median over all predictors are 3,350 and 3,374 species, respectively; excluding the Bootstrap, which is generally considered a poor estimator (Chazdon *et al.* 1998), the average and median amount to 3,529 and 3,503 species, respectively. Thus, among all measures, the grid method provided the estimate closest to the central tendency of all estimators, rounding to approximately 3,500 species (Fig. 7).
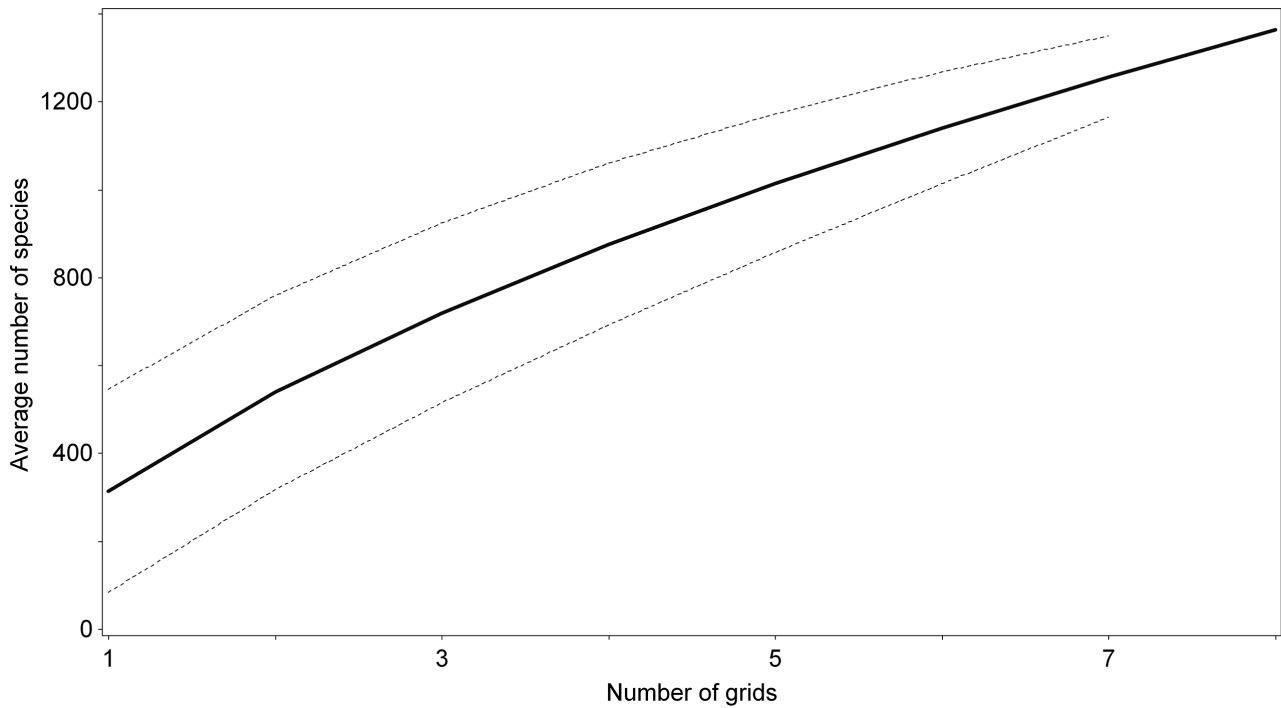
FIGURE 5. Species-area curve derived through randomized subsampling of eight selected grids with high sampling scores.
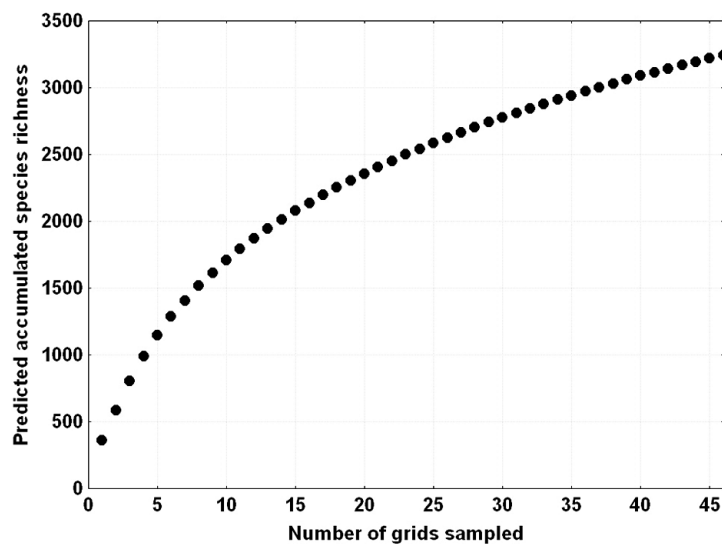
FIGURE 6. Non-linear estimation of global species richness derived from species-area curve and extrapolated to 46 grids.

Assuming the same proportional increase as found in species found within the grid area, the total species richness in extratropical regions could be estimated at $1.74 \times 74 \approx 130$ species. Likewise, global species richness in

subfamily Gomphilloideae, with currently 400 accepted species, could be estimated at $1.74 \times 400 \approx 700$ species. This is likely an underestimation, since many species in this subfamily are currently assumed to be pantropical, and no molecular data are available to test this assumption; in the core Graphidaceae, many supposedly subtropical species turned out to represent more than one species, usually with restricted distribution. This would result in a total of approximately $3,500 + 130 + 700 = 4,330$ species predicted for the entire family. Considering that approximately 2,326 have been formally described and accepted at this point (including subfamily Gomphilloideae), with further 140 awaiting description, an additional approximately 1,850 are awaiting discovery (Table 8), nearly 1,500 of which are (sub-)tropical taxa in the core Graphidaceae (subfamilies Fissurinoideae and Graphidoideae).
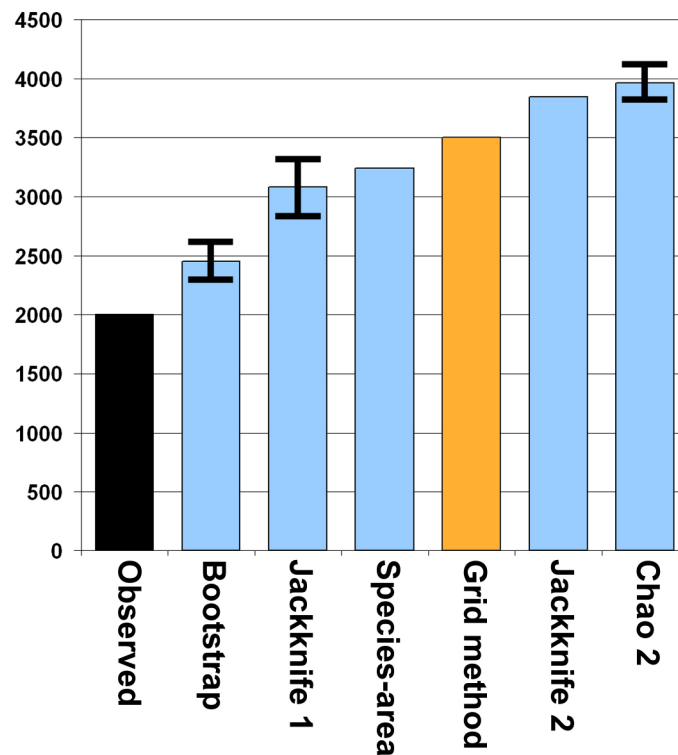
FIGURE 7. Comparison of prediction of global species richness of (sub-)tropical core Graphidaceae using different approaches.

TABLE 8. Observed (known) and predicted global species richness for Graphidaceae.

Group	Observed	Predicted	To be discovered
(Sub-)tropical core Graphidaceae (subfamilies Fissurinoideae, Graphidoideae, Redonographoideae)	2,005	≈ 3,500	≈ 1,500
Extratropical core Graphidaceae	74	≈ 130	≈ 55
Subfamily Gomphilloideae	400	≈ 700	≈ 300
Total	2,479	≈ 4,330	≈ 1,850

Our method allowed us to identify regions in which this predicted diversity is likely to be discovered, so-called "discovery hotspots" (Table 6, Fig. 8). These are in particular grid 2 (Mexico), grid 6 (Colombia, Venezuela), grid 8 (continental Ecuador, western and central Peru), grid 10 (eastern Amazon), grid 12 (Bolivia), grids 20–22 and 26 (tropical West Africa), grid 27 (tropical East Africa), grid 30 (Madagascar, Reunion, Mauritius), grid 33 (Myanmar, northern Thailand), grid 34 (China), grids 40 and 41 (Indonesia, Papua New Guinea), and grid 43 (Australia: Northern Territory).
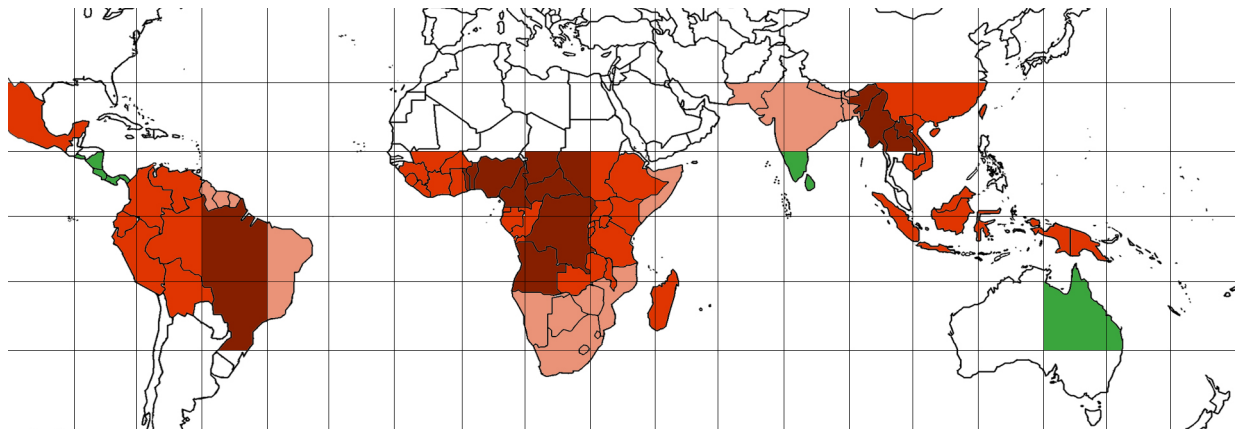
FIGURE 8. Predicted hotspots of undiscovered species richness in Graphidaceae (see Table 5; dark red +++, red ++, light red +) and areas of high observed species richness used to calibrate the predictive model (see Table 5; green; colors online only; the green regions are southern Central America, southern India, Sri Lanka and northwest Australia).

Discussion

Our statistical approach predicted approximately 1,850 species awaiting discovery in the lichen family Graphidaceae, most of them (about 1,500) representing (sub-)tropical taxa in subfamilies Fissurinoideae, Graphidoideae, and Redonographoideae. The approach we used is rather robust, since it relies on two simple measures: sum total of predicted grid richness, and average grid distribution. The predictive model assumes a simplified linear relationship between grid species richness and a score derived from sampling effort and vegetation diversity, as well as landmass. This model shows a high correlation, explaining nearly 95% of the variance in the data, but is not necessarily accurate for individual grid predictions. There are other parameters explaining grid species richness, such as evolutionary history of the area in question and dispersal limitations of individual species, often correlated with their ecological preferences. Not including these parameters in the model might lead to over- or underestimation of species richness in particular grids. However, since only the sum total of predicted grid richness is required for the prediction of global species richness, the global prediction is not especially sensitive against inaccurate individual grid predictions, since overestimates for certain grids are balanced by underestimates in other grids. For example, we observed the highest grid species richness in grid 36 (southern India, Sri Lanka), with 499 species, but the simplified model predicts only 366 species for this grid, which is a substantial underestimation. In this case, the particular evolutionary history of the Indian subcontinent as 'biotic ferry' between Gondwana and Laurasia (McKenna 1973; Scotese 2001; Conti *et al.* 2002; Hedges 2003) might have generated a unique lichen biota later mixed with southeast Asian elements, leading to an unusual high species richness that cannot be explained by vegetation diversity alone. Our predictive model takes a conservative approach in this respect by downweighting this unusual high grid species richness when used for calibration. Thus, our prediction might still be an underestimation of the real global species richness.

The highest values predicted for individual grids, ranging between 625 and 653 species, are not far off from the highest observed numbers found in grids 5 (Central America) and 36 (southern India, Sri Lanka), with 443 and 499 species, respectively. Partially ongoing surveys including or focusing on Graphidaceae in these two grids (Wirth & Hale 1963, 1978; Hale 1978; Breuss 2000, 2001, 2002, 2004, 2008, 2011; Adawadkar & Makhija 2004, 2005, 2006, 2007; Makhija & Adawadkar 2005a, b, 2007; Makhija *et al.* 2005, 2006, 2009; Breuss & Neuwirth 2007; van den Boom *et al.* 2007, 2013; Chitale *et al.* 2009, 2011; Lücking *et al.* 2008; Sharma & Makhija 2009a, b; Sharma *et al.* 2010a, b, 2012; Sharma & Khadilkar 2011, 2012; Sipman *et al.* 2012; Weerakoon *et al.* 2012a, b; Wijeyaratne *et al.* 2012; Bárcenas-Peña *et al.* 2013) have been rather thorough but are by no means complete, so that it is a rather safe to predict that individual grids may harbour more than 600 species.

Our results are further supported by the results from two separate, non-parametric methods. The approach of assembling a non-linear model based on a species-area curve derived from eight well-sampled grids yielded a very

similar prediction for global species richness of (sub-tropical) core Graphidaceae (3,244 versus 3,503 species). The species estimators yielded variable results, between 2,454 (Bootstrap) and 3,962 (Chao 2). The bootstrap estimator provided much lower estimates than the other estimators, only slightly higher than the observed number of species in the dataset. This estimator is generally considered a poor measure (Chazdon *et al.* 1998). The second order Jackknife is considered one of the best estimators for extrapolated species richness, supposed to be least susceptible to sampling bias (Chazdon *et al.* 1998; Hortal *et al.* 2006). The estimate of 3,850 species was about 10% above the estimate from the grid method and slightly lower than the Chao 2 estimate. Both Chao 2 and first order Jackknife are considered the most effective estimators if the number of samples is small relative to the sampling universe (Colwell & Coddington 1994; Brose *et al.* 2003; Walther & Moore 2005). Notably, many studies suggest that even progressive estimators such as Chao 2 and first order Jackknife underestimate true species richness. However, richness estimators are optimized to extrapolate from a small number of samples representing a fraction of the sampling universe and hence might not work effectively on grid data which cover the maximum number of samples but vary greatly in sampling effort. Hence, we consider the estimate from the grid method, which is close to the central tendency of all methods compared, as most realistic, also because it uses a broad set of underlying data, rather than focusing on the frequency of rare species.

An uncertainty level has to be attached to the interpolated estimation of grid distribution per species, since it can be assumed that increasing sampling will increase known species distributions not only by adding grids between disjunctions, but also by adding grids beyond the known range of a species. Interpolation techniques only consider the former, in our case increasing estimated average grid distribution from 2.78 to 4.63 grids, which corresponds to an area of approximately 11.5 million km^2 or almost three times the size of the United States. While this is a large area, lichen species are known to occupy much larger areas and pantropical or even cosmopolitan taxa have been confirmed through molecular data in Graphidaceae, such as *Dyplolabia afzelii* and *Thelotrema lepadinum* (Rivas Plata *et al.* 2013). On the other hand, molecular studies also suggest that the bulk of species in lichenized fungi have a much more restricted distribution than previously assumed, corresponding to areas smaller than the average estimated here and often to areas smaller than a single grid (Lücking *et al.* 2013; Moncada *et al.* 2013a, b; Rivas Plata *et al.* 2013). Notably, the confirmed widespread species are mostly graphidoid taxa found in more exposed microsites and often in disturbed habitats, which appears to facilitate dispersal even under changing climatic conditions through time. Thus far, none of the species that are more characteristic of tropical rainforest understories, such as in the genera *Fissurina*, *Ocellularia*, *Rhabdodiscus*, and *Stegobolus*, has been confirmed as being pantropical by means of molecular data (Rivas Plata *et al.* 2013). Using grid ordination and randomization of grid occurrences by means of an indicator species test, we could show that indeed most species in the family are confined to one of the three large tropical regions, and many are known from a single grid only. Hence, we can assume than the interpolated average calculated here is a rather realistic value. This is also supported when looking at the observed maximum grid distributions per species and the maximum expected values these can obtain. The maximum value of 28 grids in *Dyplolabia afzelii* corresponds to 61% of all grids, meaning that a proportional increase of grid distribution per species assuming the possible maximum of 46 for the species with the widest range would yield an increase in average grid distribution by the factor 46 / 28 = 1.64. If we multiply the observed average grid distribution of 2.78 by 1.64, we obtain a predicted value of 4.56, very similar to the value of 4.63 obtained through interpolation of grid distribution ranges.

The predicted number of 1,850 undiscovered species, including 1,500 species in the core Graphidaceae, amounts to more than 75% of the currently known species. This proportion is rather close to the prediction made by Lücking *et al.* (2009b) for all lichenized species globally, with 28,000 predicted species compared to 17,500 currently known (Feuerer & Hawksworth 2007), or a 63% increase. Not all lichen groups have a similar proportion of unknown species; hence, with over 75% of the currently known species, the estimate for Graphidaceae, one of the larger and less well-studied families, seems in line with the global prediction for all lichenized species. Yes, 1,850 species is a huge number, which raises two important questions: (1) Where are these species to be found taxonomically and geographically and (2) how fast can they be discovered and described and what effort is necessary for this? In terms of taxonomic affinities, our data suggest that the bulk of undiscovered species richness is to be found in genera that already have a larger number of species and which are not well-studied, either because of lack of proper identification tools or because they largely occur in hard-to-reach virgin rain forest areas. Among the new species introduced in this issue, genera with a high number of new species (*Ocellularia*, *Fissurina*) combine the following atributes: (1) already containing a large number of species; (2) largely confined to well-

conserved tropical rain forest; (3) not well-studied but with increasing amount of molecular data becoming available; and (4) global identification tools becoming available, such as the interactive key to thelotremoid taxa including tribe Ocellularieae assembled by Gaswick & Lücking (2012) and a global key for species in the genus *Fissurina* (Lücking, in prep.). This contrasts with the comparatively low proportion of new species in the large genera *Graphis*, *Phaeographis*, and *Thelotrema*. Both *Graphis* and *Thelotrema* are mostly found in (semi-)exposed situations in montane regions, and for both genera, global identification tools have been available for a few years already. This could suggest that the rate of species discoveries in these genera is decreasing and the bulk of new species have been discovered in the past few years. The low number of new species in *Phaeographis*, on the other hand, is apparently due to the lack of reliable nomenclatural and taxonomic resources in this group, which makes formal new species descriptions difficult. We therefore predict that the majority of undiscovered species belong to the genera *Fissurina*, *Ocellularia*, and *Phaeographis* and their relatives, in particular *Myriotrema*, *Rhabdodiscus*, *Sacrographa*, and *Stegobolus*. Some of these species might not be genuinely new but correspond to names in historical publications that had been subsumed into synonymy or never revised after their original descriptions.

Geographically, our findings suggests that most of this unknown diversity is to be discovered in Mexico, the Andean countries from Venezuela down to Bolivia, the eastern Amazon, most of tropical West Africa, parts of continental southeast Asia (in particular China and adjacent areas to the southwest, such as Myanmar), and Indonesia and Papua New Guinea. Considering that substantial efforts in the past decade to catalogue the diversity of Graphidaceae have concentrated on a few regions only (southeastern North America, Costa Rica, the western Amazon, small parts of tropical Africa, India, Sri Lanka, Thailand, Australia, New Caledonia), and these efforts have unearthed over 600 new species, finding an additional 1,850 new species in the vast area covered by the aforementioned "discovery hotspot" regions seems not out of the ordinary. If we assume a similar-sized global task force and a continued collaborative effort as currently available, 600 species described in ten years translates to about 30 years required to describe an additional 1,850 species. However, this is only possible if there is continued substantial support for fieldwork, taxonomic work, and molecular work at a global scale, which will require increased efforts of taxonomists to explain the importance of this fundamental research for our understanding of the diversity of the globe to the public and funding agencies.

Acknowledgements

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