

Global Geographical Patterns on the Historical Species Description Process of Fig Wasps (Agaonidae)

Xerach Hernández-Aguiar¹, Antonio Rodríguez², Jose-Luis Nieves-Aldrey³, Carlo Polidori⁴, Jose F. Gómez¹, and Diego Gil-Tapetado^{1,4,*}

¹Universidad Complutense de Madrid. Facultad de Ciencias Biológicas, Departamento de Biodiversidad, Ecología y Evolución C/ José Antonio Nováis 12, 28040 Madrid, Spain. E-mail: xeracher@ucm.es (Hernández-Aguiar); jofgomez@ucm.es (Gómez)

²Université Clermont Auvergne, INRAE, VetAgro Sup, UREP, Clermont- Ferrand, France. E-mail: antonio.rodriguez-hernandez@inrae.fr (Rodríguez)

³Museo Nacional de Ciencias Naturales (CSIC), Calle José Gutiérrez Abascal 2, 28006 Madrid, Spain. E-mail: mcenna38@mncn.csic.es (Nieves-Aldrey)

⁴Università Degli Studi di Milano, Dipartimento di Scienze e Politiche Ambientali. Via Celoria 26, 20133, Milan, Italy.

*Correspondence: E-mail: diego.gil@ucm.es (Gil-Tapetado)

E-mail: carlo.polidori@unimi.it (Polidori)

(Received 25 January 2023 / Accepted 10 April 2024 / Published -- 2024)

Communicated by Y. Miles Zhang

ORCID:

Xerach Hernández-Aguiar: <https://orcid.org/0009-0003-6532-7696>

Antonio Rodríguez: <https://orcid.org/0000-0002-0536-9902>

José-Luis Nieves-Aldrey: <https://orcid.org/0000-0002-4711-7455>

Carlo Polidori: <https://orcid.org/0000-0003-4834-0752>

Jose F. Gómez: <https://orcid.org/0000-0001-9553-6614>

Diego Gil-Tapetado: <https://orcid.org/0000-0002-2147-4040>

Fig pollinating wasps (Hymenoptera: Chalcidoidea: Agaonidae) constitute a key ecological role since they are the only known pollinators to *Ficus* (*Moraceae*), founding complex food webs. Taxonomy of Agaonidae is relatively well known due to their ecological importance and their mutualistic closed relationship with *Ficus*. However, the spatial and temporal patterns that have influenced the agaonid distribution as well as the species description record of this family are yet unknown. Here, we aim to study the taxonomical and nomenclatural knowledge status of Agaonidae (following Burks et al. 2022) in each biogeographical region and globally. We analyse taxonomic factors, such as the number of described species or the amount of non-valid binominals, together with their historical description process. By retrieving and analysing all available geographical and nomenclatural data in fig wasps of the Universal Chalcidoidea Database, we have found that the

diversity of Agaonidae is underestimated, existing a high potential dark biodiversity, especially in the tropical areas where highest diversity is observed. The species richness of Agaonidae varies depending on the biogeographical region, being more unknown in the Neotropical region, and higher and better represented other tropical areas as the Afrotropical or Oriental realms. Our results indicate that there is a strong need in increasing sampling efforts and research for a better understanding of Agaonidae' diversity and interspecific relationships, as well as inventory revisions to correct potentially redundant binominal names.

Key words: Agaonidae, *Ficus*, Binominal name, Distribution

Citation: Hernández-Aguilar X, Rodríguez A, Nieves-Aldrey J, Polidori C, Gómez JF, Gil-Tapetado D. 2024. Global geographical patterns on the historical species description process of fig wasps (Agaonidae). *Zool Stud* **63:27**.

BACKGROUND

Species constitute the fundamental elements of biodiversity. It is estimated that 30–40% of total species richness on Earth is currently known (Costello et al. 2013; Mora et al. 2011) and therefore, it exists a great Linnean shortfall (*i.e.*, lack of knowledge on how many species have existed and exist, Hortal et al. 2015) at global scale (Brito 2010). Knowing species diversity is crucial, because it allows us to identify specific or vulnerable areas for conservation purposes or to understand certain processes, such as extinctions and adaptations (Hortal et al. 2015; Margules and Pressey 2000; Rands et al. 2010).

The historical description process of species is key to acknowledge diversity and reduce Linnean shortfall. This process varies in time, being accelerated or slowed due to several factors (*i.e.*, the behavior or the size of species, the location of the sampling site, or the number of researchers which study a specific group (Baselga et al. 2010; Iknayan et al. 2014)). These factors have been studied for various taxa, such as plants (see Kier et al. 2005; Kreft and Jetz 2007), bacteria (see Ribeiro et al. 2018; Tindall et al. 2010) and insects (see Baselga et al. 2007; Baselga et al. 2010; Kaloveloni et al. 2018; Shimizu et al. 2020). Furthermore, problems or imperfections may occur in the description process (*e.g.*, redescription of already described species, grouping of several species into a single biological entity or treating intraspecific variability as interspecific variability), leading to an incomplete knowledge of the real diversity. Two important concepts concerning this topic are 'hidden diversity', *i.e.*, species which are present at the sampling site, but have not been detected; and 'dark diversity', *i.e.*, species which can potentially reach and inhabit the

sampling site, but they are not there and therefore cannot be detected (Pärtel 2014; Pärtel et al. 2011). Thus, knowing a species role is key to understand how it interacts with other of species present within the ecosystem, and also to reduce Eltonian shortfall (*i.e.*, the lack of knowledge on interactions among species and the effects on individual survival and fitness of those interactions) (Hortal et al. 2015). The description process itself (as well as how easy organisms can be sampled and examined) can generate heterogeneity in knowledge about the different taxonomic groups, especially arthropods, since estimations suggest that around 80% of insect species are yet to be described (Stork 2018).

Another issue associated to the Linnean shortfall is the existence of cryptic species complexes (*i.e.*, a biological entity that actually represents a group consisting of two or more species that cannot be morphologically differentiated or at least not easily differentiated, Struck et al. 2018), usually gathered under one binominal name, which leads to an underrepresentation of the actual species diversity (Baselga et al. 2010; Mora et al. 2011).

Fig pollinating wasps (Hymenoptera: Chalcidoidea: Agaonidae) are an example of an insect group whose species diversity remains largely unknown (Cruaud et al. 2010; Rasplus and Soldati 2006). Currently, 362 species of Agaonidae are described (Noyes 2019). Until recently, many fig wasps were included in the Agaonidae, but recently the subfamily Sycophaginae has been transferred to Pteromalidae (Burks et al. 2022). Fig pollinating wasps or fig wasps, here understood as Agaonidae *sensu stricto* after Burks et al. (2022), are only few millimeters long (Gibson, 1993; Kjellberg et al. 2005; Souto-Vilarós et al. 2018), with a highly specialized relationship with the genus *Ficus* L. (*Moraceae*) and are distributed mainly throughout the tropical and subtropical areas around the world (Shi et al. 2018). Fig wasps and *Ficus* are intimately associated: wasps constitute the only pollinators known to *Ficus*' particular inflorescences, called syconium or figs, inhabiting them for most of its life cycle. Furthermore, the specificity within fig wasp-fig mutualism network is generally high, with many cases of monospecific associations (López-Vaamonde et al. 2002; Machado et al. 2005; Souto-Vilarós et al. 2018; Wang et al. 2016). In addition to pollinators, Chalcidoidea and *Ficus* communities include non-pollinating species, including parasitoid species as Sycophaginae (Pteromalidae) (Farache et al. 2018), also highly associated to *Ficus* and host specific.

The taxonomy, phylogeny and biology of fig wasps have been previously and deeply studied in order to understand their mutualism with *Ficus*, their role within specific trophic webs as well as how to optimize the production of edible figs (*Ficus carica* L.) (see Cruaud et al. 2010 2023; Darwell et al. 2014; Erasmus et al. 2007; Khadivi-Khub and Anjam 2016; Kjellberg et al. 2005; Molbo et al. 2003; Munro et al. 2011; Ramírez 1970; Ramírez 1991; Ramírez-Pérez 2020; Rasplus et al. 1998; Zare et al. 2018). These investigations have, for instance, helped to identify the

existence of cryptic species complexes (e.g., Darwell et al., 2014). Thus, considering a usual 1:1 species relationship between fig wasps and figs, if there are 755 *Ficus* species and 362 fig wasps high rates of hidden and dark diversity are very likely. Hence, the current diversity of fig wasps may have a noticeable Linnaean shortfall (van Noort and Rasplus 2021). Furthermore, it is still unknown how biogeographical and historical patterns may have characterized (and influenced) the description process of Agaonidae. These patterns probably have a deep impact on the knowledge of the fig was diversity.

Here, we aim 1) to study the current status of taxonomical and nomenclatural knowledge for Agaonidae, both globally and for each of the biogeographical regions, 2) to assess how the historical description process of the family has influenced our actual knowledge of this group of chalcidoidea and 3) to better understand the interactions occurring between fig wasps and *Ficus*. We hypothesize that there are geographical and historical factors that influence the description of fig wasps and modify their description process differently in different parts of the world (biogeographical regions).

MATERIALS AND METHODS

Data

Taxonomical and nomenclatural information of Agaonidae was obtained from the Universal Chalcidoidea Database (last access in July 2021) (Noyes 2019). This database includes original distribution records for all the valid species and genera within Chalcidoidea, as well as host/associate records and a list of the non-valid names used in literature for each species.

The taxonomy of Chalcidoidea is complex, has undergone many different and profound changes over the years, and seems far from being resolved. Considering this, we rely on the latest work on the phylogeny of this group (Burks et al. 2022), in which Sycophaginae does not belong to Agaonidae, but to Pteromalidae. Based on these Universal Chalcidoidea Database data, we proceeded to compile a dataset containing the number of binominal names for each of the 362 fig wasp species, the author/s of the name and the year it was proposed; countries from which species have been recorded; number of host species; subfamily; and number of parasitized genera and species by fig wasps in case there were any (Table S1). According to the database, we obtained species records for five biogeographical regions: Afrotropical, Nearctic, Neotropical, Oriental, and Palearctic.

Binominal names were considered as “valid” in the case they met the International Commission on Zoological Nomenclature’s (ICZN) (ICZN 1999) criteria, while as “synonyms” if not and are related with a valid fig wasp species. Additionally, when considering the name of the authors who have described a species, if two or more authors participated, they were considered as one entity or group in order to simplify the subsequent analyses.

Each species distribution was extracted considering each country where it had been recorded and was shaped after as rectangular polygon maps. These rectangular polygon maps encompassed the far north (maximum latitude), far south (minimum latitude), far west (maximum longitude) and far east (minimum longitude) of each species’ total extension of its distribution. A total of three different variables was extracted from such maps: (1) centroid of latitude and longitude, (2) distribution ranges and (3) number of biogeographical regions where each species was also considered.

Both latitude and longitude ranges (1) were calculated as the difference between maximum and minimum latitude, as well as the difference between maximum and minimum longitude. Distribution range (2) for each species was calculated by multiplying latitudinal and longitudinal range. Regarding biogeographical regions (3) see Cox 2001; Vigna-Taglianti et al. 1992), fig wasp species were considered as “large-scale distribution” if they are found in two or more regions. Those species present in only one region were categorized according to such region (*e.g.*, if a fig wasp was only present in the Neotropical realm it was categorized as Neotropical). Also, we obtained the number of *Ficus* species (hosts) associated to each fig wasp species, using the data of the Universal Chalcidoidea Database.

Statistical analysis

To understand how diversity of Agaonidae is distributed worldwide, we observed the number of fig wasp species per genus, the number of species per subfamily, the number of species per biogeographical region, the number of binominal names per species, the number of host species per fig wasp species and the number of authors who had described each species (valid names and synonyms). On the other hand, to assess the historical evolution of the description process of Agaonidae species, we plotted accumulation curves for the number of species and binominal names (valid + synonym names) yearly described. These accumulation curves were fitted to exponential and logarithmic trends. R^2 values are included to show which of the two trends has a better fit to the data.

A spatial analysis was carried out using ArcGIS 10.8 software. For each species, we build a rectangular polygon representing its maximum distribution (see Data section) with 1 km² pixel size.

We assigned a value equal to 1 to each polygon and overlapped and summed all of them for visualizing 1) the summatory of species (richness), 2) the number of binominal names, 3) the mean number of authors for each species whether they provided a valid name or a synonym, and 4) the mean values of species' year of description.

We estimate the dark diversity of fig wasp for each country (and in some cases for each region or state in the case of large countries, such as the United States of America) as the number of valid species whose rectangular polygon maps match the country but are not cited instead. To identify statistically significant areas of high and low dark diversity for agaonids at global scale, we used a hotspot analysis based on the Getis-Ord G_i^* statistic considering the 8 nearest neighbours and applying the false discovery rate (FDD) to the p-values obtained in this analysis.

Finally, we used Generalized Linear Models (GLM's) using the R 4.2.2 (R Core Team 2022) program through RStudio Software v 2023.06.1 (Rstudio Team 2023) software to analyse if a significant correlation exists between year of description, number of authors and number of binominal names, as well as the following factors: maximum latitude and longitude, minimum latitude and longitude, latitudinal and longitudinal range, latitude and longitude centroids, range of area and the number of regions a species has been recorded from. These analyses were performed at global and biogeographical region scale.

RESULTS

Diversity analysis of fig wasps

The most diverse subfamilies of Agaonidae are Agaoninae and Kradibiinae, with 191 species (52.76% of the total) and 110 (30.39% of the total) respectively (Fig. 1A). Concerning genera, Agaonidae are currently classified among 20 genera (Fig. 1B), being *Ceratosolen* the most diverse one with 67 species (18.51% of the total). Regarding the geographical distribution of fig wasps, 126 species were recorded in the Oriental region, 73 for both the Afrotropical and Australasian regions, 50 for the Neotropical region, 33 in the Palearctic region and 2 for the Nearctic region (Fig. 1C). Focusing on the total binominal names (valid + synonym names; Fig. 1D), 202 agaonid species had one name (55.80% of the total). Then, a total of 160 species (~44% of the total) have been described and named more than once. Regarding the rate host taxa/number of fig wasp species (Fig. 1E), 133 species that only pollinate one host species (36.74% of the total), 20 fig wasps that pollinate two host species each (5.52% of the total). In the other hand, the host species of *Ficus* remain unknown for 203 agaonids (56.08% of the total). In relation to the rate described species/authors (Fig. 1F),

335 fig wasp species have been described by only one author or group of authors (92.56% of the total).

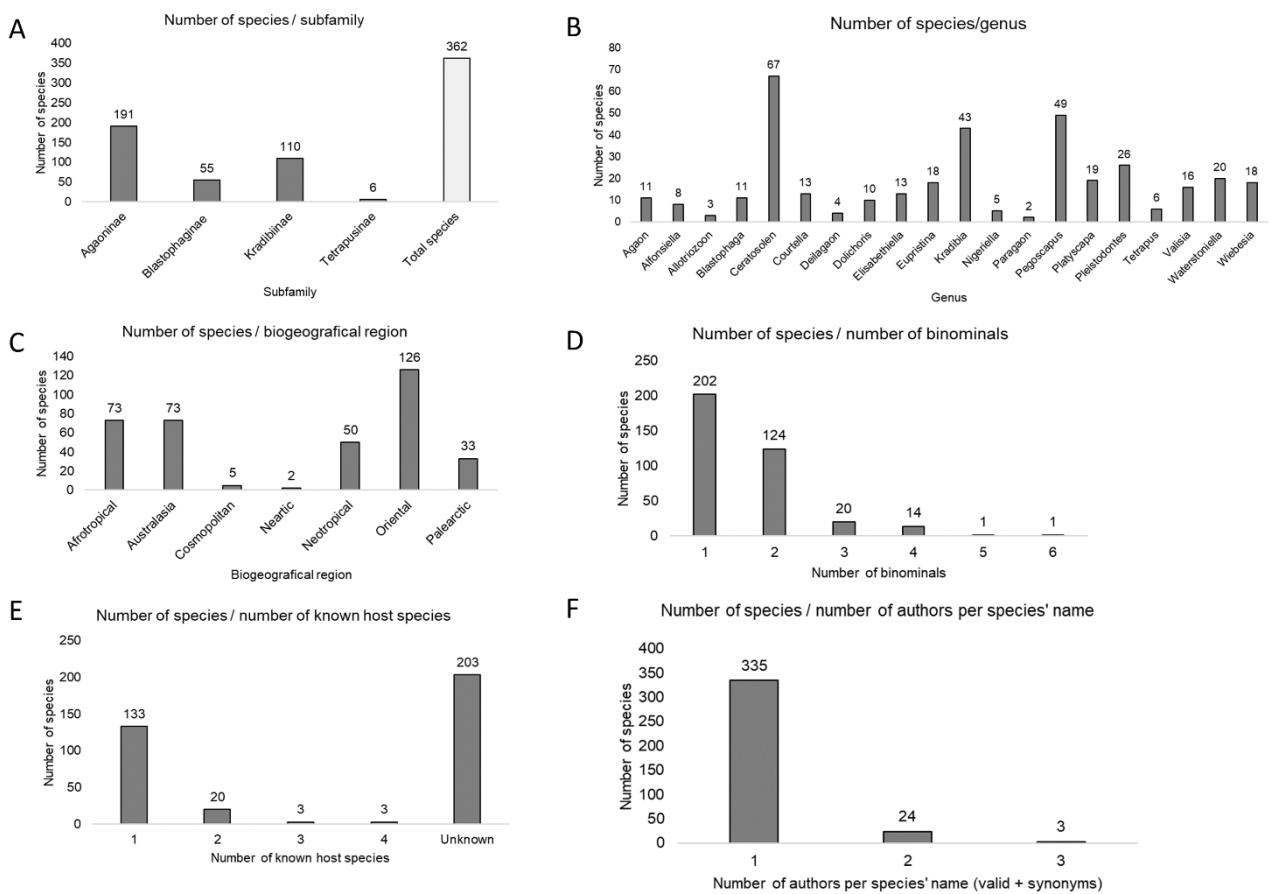


Fig. 1. Column charts portraying different features of Agaonidae described diversity to date. Each one represents the number of species according to subfamily (A) and genus (B) level; biogeographical region (C), including cosmopolitan species (found in 3 or more regions); number of binominal names for each species (D), *i.e.*, valid names + synonyms; number of authors of groups of authors who have described any species (E), whether this description were valid or resulted in a synonym; and number of host plant species per fig wasp species (F).

Accumulation curves

The accumulation curves of valid species and binominal names increase proportionally at global scale (Fig. 2A). Different regions follow either a logarithmic trend (it approaches an asymptote, and the species richness can be properly described) or an exponential trend (it does not approach an asymptote and the Agaonidae richness of this area has an important Linnean knowledge deficit). Afrotropical and Oriental regions clearly show an exponential trend in the knowledge deficit, while the Palaearctic or the Neotropical show that the number of species is approaching an asymptote of total species richness. Australasian region shows no better fit to one trend or the other, and the Nearctic could not be calculated due to the few species exclusive to the

region. as is the case for globally distributed species. More precisely, the trends of description processes of Agaonidae in each biogeographical region have been influenced by scientific contributions and can be described as follows: In the Afrotropical region (Fig. 2B), abrupt increases can be observed in both curves for the years 1916, 1974 and 1989, when authors, Grandi (1916) and specially Wiebes (1974a b 1989a b c) contributed with the description of several species. In the Australasian region (Fig. 2C), abrupt increases happened between the years 1960 and 1980 due to numerous descriptions provided by Wiebes (Bouček 1988; Wiebes 1963 1980). In the Neotropical region (Fig. 2E), the species accumulation has grown steadily and without sharp increases since the 1940s.). In the Oriental region (Fig. 2E), abrupt increases occurred during 1926, and 1990s can be explained by the contributions of Grandi (1926), Wiebes (1963 1992a b 1993a b c), Hill (1969), Chen and Chou (1997), and Priyadarsanan and Abdurahiman (1997a b). Finally, the Palearctic region (Fig. 2F) shows a grown steadily similar to that of the Neotropical region, although there are slight perceptible increases in the accumulation curve during 1885 and 1926, due to the synonymization of several redundant names from species found in this region, which were originally described by Mayr (1885) and Grandi (1926), slowing down the increase, during those years.

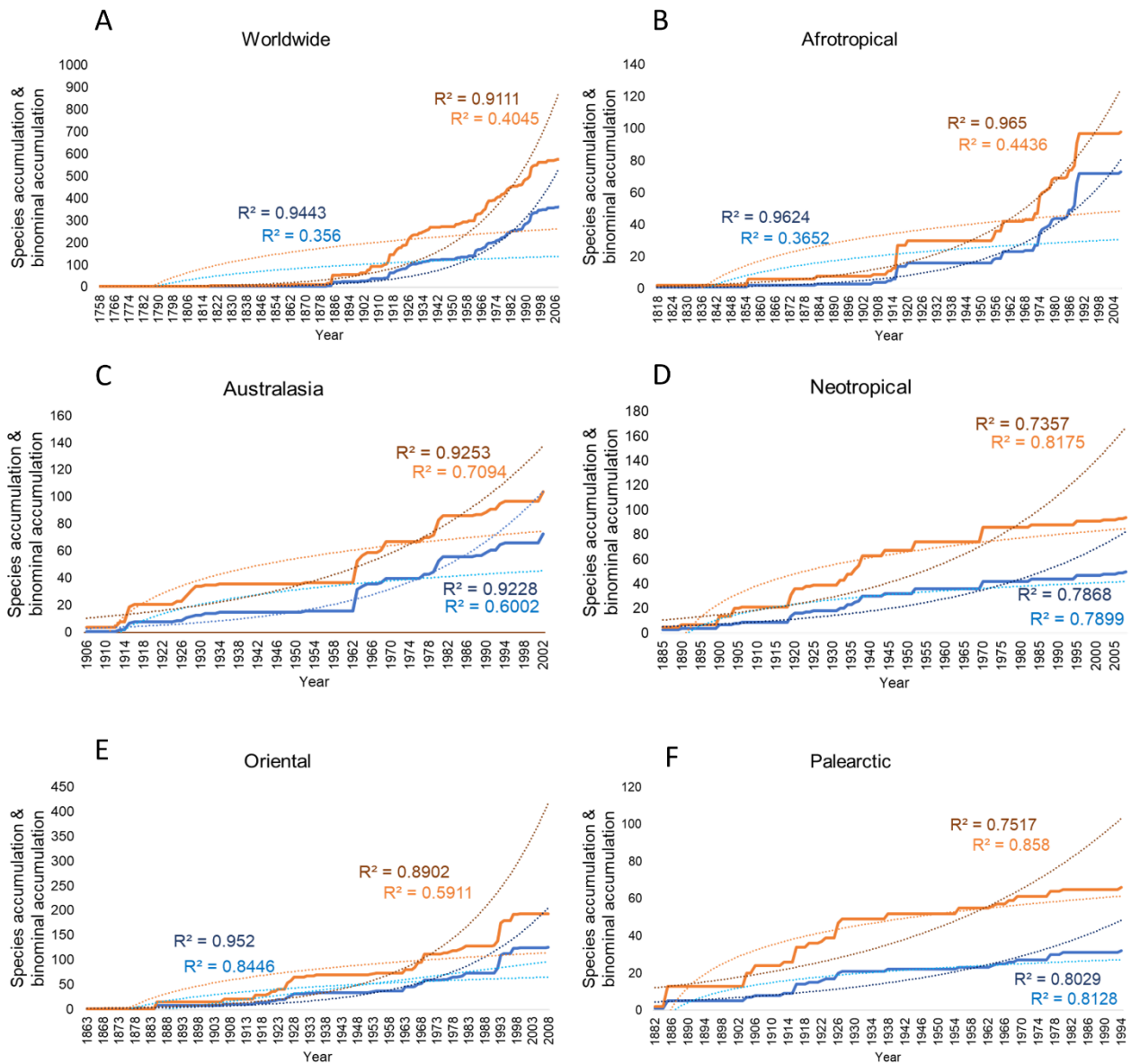


Fig. 2. Curves portraying both processes of species accumulation (blue line) and binominal name accumulation (valid names + synonyms; orange line) throughout time, and at a global and regional scale. At a global scale (A), the value of species accumulation (N) adds up to 441 and to 722 in the case of binominal name accumulations (NNom); for the Afrotropical (B), N = 102 and NNom = 162; for Australasia (C), N = 102 and NNom = 161; and NNom = 38; for Neotropical (D), N = 89 and NNom = 166; for Oriental (E) N = 165 and NNom = 284; and for the Palearctic (F) N = 25 and NNom = 59. Linear and logarithmic trends also provided and the R² value to show if the species accumulation curve fits to growth towards an asymptote or without an asymptote.

Spatial analysis distribution

Concerning the map of the number of species (Fig. 3A), the highest values for species accumulation are found throughout Afrotropical, Oriental and Australasian regions, and a small highly diverse patch in the Neotropical realm, in Costa Rica and Panama, while the rest of this region showed medium diversity rates. In general, the farther we get from these mainly tropical and

subtropical territories, the more the diversity rates decrease. The accumulation of synonym names (Fig. 3B) and the mean of year of description (Fig. 3C) maps show a similar pattern: high rates observed for the Afrotropical, Oriental, Australasian and Neotropical regions which gradually decrease to non-tropical territories. On the other hand, the trend of the mean of authors (Fig. 3D), show the opposite trend with higher values in the Palearctic and Nearctic areas.

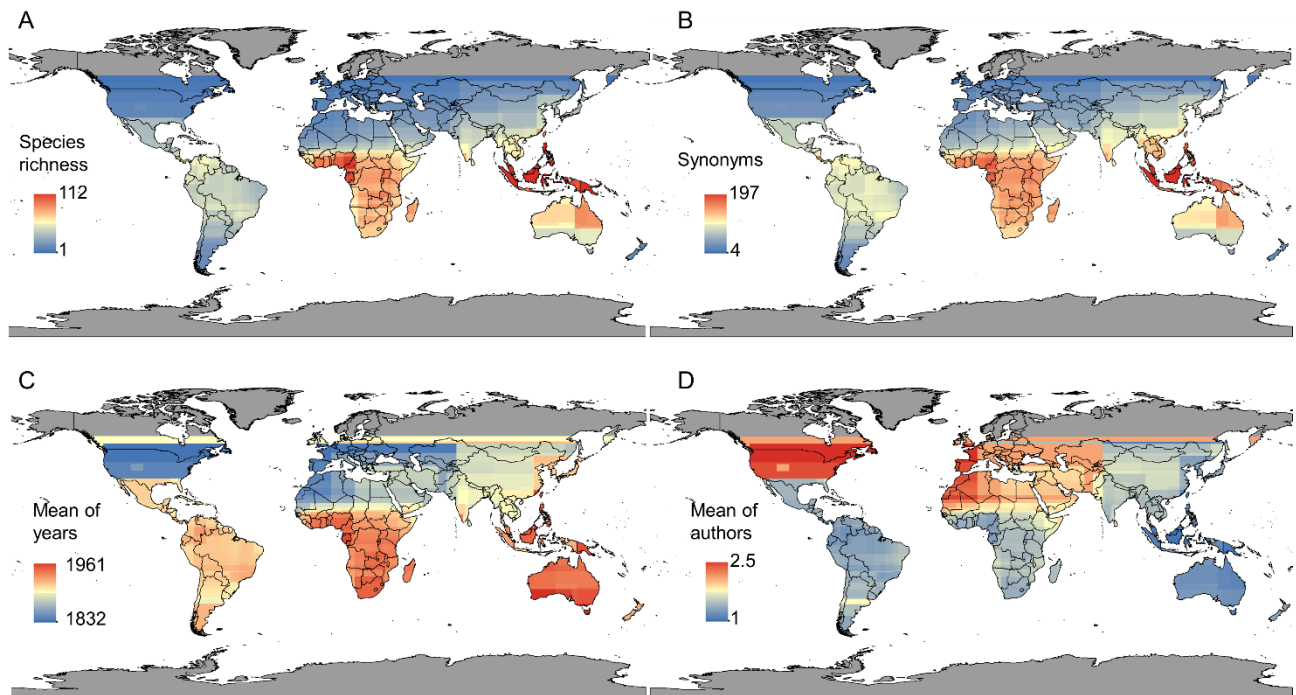


Fig. 3. (A) Species accumulation (*i.e.*, species richness) obtained by overlapping rectangular polygon maps. The higher the levels of overlapping, the higher the values of species accumulation in such area and the darker the tone of red; and the darker the tone of blue, the lower the values of species accumulation, which translates into less diversity of fig wasps. (B) Accumulations of synonyms obtained by overlapping polygons. The higher the levels of overlapping, the higher the accumulation values in such area and the deeper red; whereas the lower the values of accumulation, the darker blue. (C) Mean of number of authors obtained by overlapping polygons according to where fig wasps species have been described from. The darker the red, the higher the accumulation; while the darker the blue, the lower the accumulation values. (D) Mean of years when a species was first described by overlapping polygons. The higher the overlapping the darker the red, meaning that in this area species have been described more recently; whereas the darker the blue, more years have passed since the last species description in the area.

Dark diversity of fig wasps for each country or territory ranged from 0 to 64 species (Fig. 4A), with a median and mean values of 8 and ~10 species respectively. Values over the median (3rd and 4th quartiles; Fig. 4A) were concentrated mostly between the tropics. Getis-Ord G_i^* statistic showed how low fig wasp dark diversity areas were concentrated at high latitudes, whereas Caribbean, Central and South African countries, and the island countries between the Indian and the Pacific Ocean were hotspots of dark diversity (Fig. 4B).

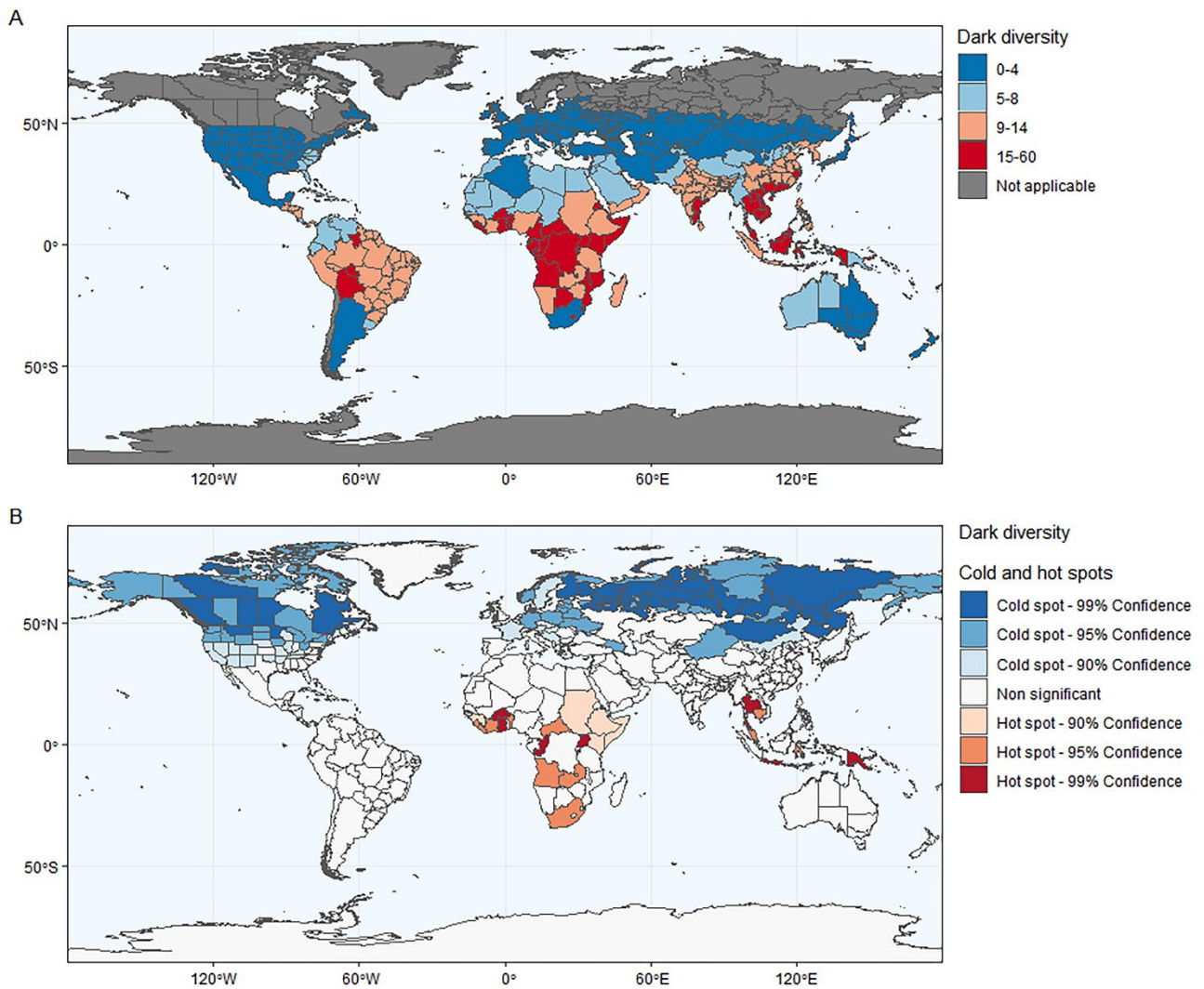


Fig. 4. (A) Worldwide distribution of Agaonidae dark diversity. Results were represented in quartiles. (B) Hot spot analysis of Agaonidae dark diversity. Blue: cold spots (clusters of countries where dark diversity values were significantly lower than in the rest of the world). Red: hot spots (clusters of countries where the dark diversity values were significantly higher than in the rest of the world).

Generalized linear models

Regarding the number of binominal names (Table 1), these are related positively with the range area in the Afrotropical region (*i.e.*, the larger the range of the species, the greater the number of binomial names), and with the number of regions in the Palearctic region (*i.e.*, the more widely distributed the species is in other regions, the more binominal names it has). In the Neotropical area, the number of binominal names increases with the maximum and minimum latitude (*i.e.*, the further north the distribution of the species reaches, the more binominal names it has) and decreases with the centroid of the latitude (*i.e.*, the further south the center of its range is, the more binominals the species will have). The number of authors, is positively related at a global scale with maximum

latitude and longitude, minimum latitude and longitude (*i.e.*, the wider the distribution of the species, the more authors have been involved in the description process), and negative related with longitude and latitude centroids (*i.e.*, The further north and east, the fewer authors have been involved, and the further south and west, the more authors have been involved). At regional scale, the number of authors in the Afrotropical and Oriental regions is positively related with the range area of the species (*i.e.*, the more widespread the species is in these regions, the more authors have been involved in the process of describing the species.). On other hand, the year of description, is negatively related at a global scale with number of regions (*i.e.*, the more different biogeographical regions the species is found in, the earlier in time it has been described and *vice versa*). At a regional scale, the year of description in the Australasian region is positively related with the range area and negatively with the number of regions (*i.e.*, the larger the distribution of the species and it is found only in this region, the earlier it has been described), whereas in the Neotropical region increases positively with the centroid of the latitude but negatively with the maximum and minimum latitude (*i.e.*, the further north the center of the species distribution is, but it is not widely distributed in this region, it has been previously described), and in the Palearctic region is negatively related number of regions (the same as the global scale).

Table 1. Non-significant correlations were noted with “-”. *area*: total area where a species is present. *Nregions*: number of regions where a species is present. *maxlat*: maximum latitude where a species is found. *maxlong*: maximum longitude where a species is found. *minlat*: minimum latitude where a species is found. *minlong*: minimum longitude where a species is found. *x_centroid*: mean value between *maxlat* and *minlat*. *y_centroid*: mean value between *maxlong* and *minlong*

	Biogeographical region	Variable	Estimate	SE	t-value	p
Number of binominal names	Worldwide (N = 362)	-	-	-	-	-
	Afrotropical (N = 73)	area	0.0008	0.0003	3.157	0.002
	Australasia (N = 73)	-	-	-	-	-
	Nearctic (N = 2)	-	-	-	-	-
	Neotropical (N = 50)	maxlat	4.31E+07	1.72E+07	2.5010	0.016
		minlat	4.31E+07	1.72E+07	2.5010	0.016
		y_centroid	-8.62E+07	3.45E+07	-2.5010	0.016
	Oriental (N = 126)	-	-	-	-	-
	Palearctic (N = 33)	Nregions	1.614	0.7753	2.082	0.048
Number of authors	Worldwide (N = 362)	maxlat	0.0300	0.0106	2.831	0.005
		maxlong	0.0254	0.0103	2.465	0.014
		minlat	0.0209	0.0103	2.025	0.044
		minlong	0.0236	0.0102	2.305	0.022
		x_centroid	-0.0490	0.0205	-2.391	0.017
		y_centroid	-0.0499	0.0205	-2.434	0.015
	Afrotropical (N = 73)	area	0.0005	0.0001	3.852	< 0.001
	Australasia (N = 73)	-	-	-	-	-
	Nearctic (N = 2)	-	-	-	-	-

	Neotropical (N = 50)	-	-	-	-	-
	Oriental (N = 126)	area	0.0005	0.0001	4.060	< 0.001
	Palaearctic (N = 33)	-	-	-	-	-
Year of description	Worldwide (N = 362)	Nregions	-12.741	5.249	-2.427	0.016
	Afrotropical (N = 73)	-	-	-	-	-
	Australasia (N = 73)	area	0.002	0.001	2.0124	0.036
		Nregions	-15.325	4.978	-3.079	0.003
	Nearctic (N = 2)	-	-	-	-	-
	Neotropical (N = 50)	maxlat	-1.87E+09	6.90E+08	-2.706	0.010
		minlat	-1.87E+09	6.90E+08	-2.706	0.010
		y_centroid	3.73E+09	1.38E+09	2.706	0.010
	Oriental (N = 126)	-	-	-	-	-
	Palaearctic (N = 33)	Nregions	-64.49	28.44	-2.267	0.033

DISCUSSION

Diversity analysis of Agaonidae

Our results, derived from what is currently known, show that 36.74% of Agaonidae specifically interact with only one known host plant species and 7.18% with two or more host species. *A priori*, those results of currently known associations do not concur with the 1:1 ratio previously described for this fig wasp-fig mutualism (Lopez-Vaamonde et al. 2002; Machado et al. 2005; Souto-Vilarós et al. 2018; Wang et al. 2016). Nevertheless, more than 56% of *Ficus* and fig wasps' relationships are currently unknown and considering only the currently known data, the most common ratio is 1:1 between *Ficus* host and Agaonidae pollinator (*i.e.*, 84% of the known Agaonidae-*Ficus* interactions are 1:1 and 16% are not). Therefore, it exists a gap of knowledge when it comes to this group of wasps and a remarkable Eltonian shortfall as well, with the current data not showing a 1:1 ratio between fig wasps and *Ficus*. However, there are known examples where the mutualism is not strictly 1:1; there are also several species of *Ficus* that are pollinated by several geographically isolated wasp species. Furthermore, there are reports of pollinators and non-pollinators within the same genus, breaking the 1:1 mutualism (van Noort and Rasplus 2021). Also, a considerable part of diversity of fig wasps remains unknown, which leads to high dark diversity within the family. Moreover, our results suggest that dark diversity of Agaonidae could be concentrated in certain areas at tropical latitudes, as in the Neotropical or Australasian regions, which are richness hotspots of *Ficus* (dos Anjos Cruz et al. 2022). In fact, these richness patterns of Agaonidae and *Ficus* coincide, with both groups having diversified more in the same areas. Some approaches that may help us tackle this high dark diversity rates are, on one hand, sampling methods such as passive trap methods as the malaise traps (installed on the canopy by ropes) and

the fogging technique, which provides a quick easy way to capture individuals. However, this sampling methods helping to reduce Linnean but not Eltonian shortfall, since it is inefficient to get to know given relationships between *Ficus* and fig wasp species. On the other hand, more specific techniques, such as syconium picking, allow us to establish interrelationships, reducing Eltonian and Linnean shortfalls, although this method is quite laborious, because it requires plant identification, reaching syconia to pick them, etc. Along with this and most importantly, there is also a problem of taxonomic impediment, as not enough people are able to identify the groups to speed up the description process. Training and preparing taxonomists of Agaonidae is undoubtedly the greatest solution to address the Linnaean knowledge shortfall of this group of insects.

The high percentage for species that have been described by only one author or groups of authors (92.5%), contrasting with the number of synonyms that exist in the group (160 synonyms or non-valid binominal), indicates that only a few authors have done the work of describing the Agaonidae, but that they have made a large number of modifications.

Analysis of the species description of Agaonidae

The trend of fig wasp species described worldwide is increasing, and it has not yet stabilized in an asymptote, showing that a considerable and high potential number of species of Agaonidae remains unknown. Furthermore, it is impossible at this point in time to state a reliable estimate of how many fig wasp species remain to be described. Causes of this lack of knowledge are diverse, for example, it is difficult to directly sample fig wasp individuals due to that barely few species are larger than a couple millimeters and most of their life cycles occurs as larvae inside syconia (*i.e.*, adults only live long enough to reproduce and usually only females are able to leave the syconia) (Gibson, 1993; Kjellberg et al. 2005; Souto-Vilarós et al. 2018). Besides, this family includes some cryptic species (Moe and Weiblen, 2010; Molbo et al. 2003), which may have influenced the species description process by disguising several taxa as only one or few species. Consequently, molecular studies are much needed to ensure the real diversity of existing fig wasp species will be known in the future. The two types of curve fitting, and the best fit to a logarithmic or exponential curve, highlight the effort that exists and needs to be made in each biogeographical region. For example, in the Palearctic region, the trend fits an asymptote, a defined potential richness, in contrast to the Afrotropical region, where the asymptote is far from being defined. In general, the regions of the Southern Hemisphere that are more closely associated with the tropics show this pattern, except for the Neotropics. However, looking at the species richness maps (see Fig. 3A), most of the Neotropical Agaonidae species are located in Costa Rica and Panama, so this trend

curve is biased by the nature of the data and responds more to an asymptote of species accumulated in these countries than to the biogeographic region.

Global spatial distribution patterns of Agaonidae

The most diverse biogeographical regions are the Oriental, the Afrotropical, the Australasian and Neotropical, this last one stands out due to the great number of described species in Costa Rica and Panama. In general, this diversity of fig wasps is specially concentrated along tropical and/or subtropical areas, where *Ficus* species are also diverse (Shi et al. 2018). Given the mutualism and intimate relationship that co-evolution of fig wasps and *Ficus* has produced, and the common 1:1 relationship (Lopez-Vaamonde et al. 2002; Machado et al. 2005; Souto-Vilarós et al. 2018; Wang et al. 2016), we can expect that whenever one of the components of this relationship is present (*Ficus* or Agaonidae), the other component will be as well. Therefore, uneven values between fig wasps and *Ficus* species may be attributed to dark diversity. We found contrasting proportions between *Ficus* and fig wasps depending on the biogeographical region, expecting that there will be at least as many pollinating wasps as *Ficus* richness. For example, in the Oriental and Australasian regions both sum up 511 *Ficus* species (van Noort and Rasplus 2021) and 199 fig wasps, so it is likely that agaonid species inventories in these regions are yet to be completed. On the other hand, there are only two native species of *Ficus* in the Nearctic which are exclusive from this region (*Pegoscopus franki* Wiebes, 1983 and *Tetrapus mayri* Brues, 1910). In relation to the Neotropical region, there are 132 *Ficus* species (van Noort and Rasplus 2021) and 50 fig wasps, most of them from Costa Rica and Panama, which are due to the intense sampling efforts that have been carried out in this country (Bouček 1993; De Santis 1981; Ramírez 1970). The fact that so many species have only been described in Costa Rica and Panama suggests that the Neotropical region remains both poorly and heterogeneously sampled, also leading to a Wallacean deficit (*i.e.*, lack of knowledge of the geographical distribution of a species; Hortal et al. 2015) and dark diversity. This lack of sampling could be attributed to how far sampling areas are from any institution and that many are hard to access or simply inaccessible. Interestingly, high Agaonidae dark diversity values were concentrated in these areas where the gap between fig wasps and *Ficus* species was more conspicuous: the tropical and subtropical areas of America, Africa and Oceania. The apparent lack of knowledge when it comes to which agaonids pollinate each fig turns into Eltonian shortfall, meaning we do not fully understand the interactions that occur in these ecosystems and how they affect each species of *Ficus*.

The significant variables related to the number of valid names reinforce the biodiversity bias result found for the Neotropical region, as well as the spatial heterogeneity of its richness in this

region. Costa Rica and Panama are relatively small countries in comparison with all the Neotropical region, where sampling efforts have helped to describe a great number of species in contrast with the rest of this biogeographical region. This explains why the range area variable turned out negative in the Neotropical region.

At a global scale, the negative relationship between the centroid of longitude and the *number of authors* indicates that there are more authors in areas of the New World, while a positive value of the centroid of latitude indicates an increase of number of authors in the Northern Hemisphere. This can be explained because the high number of institutions and researchers which study fig wasps in the Europe (high latitude and low longitude values) in comparison with the Australasian and Oriental regions (low latitude and high longitude values). Significant *number of regions* values related with number of binominal names and year of description Palearctic region could be due to the higher facility for finding, and therefore describing redundantly, those species present in more than one region (Baselga et al. 2007, 2010; Jiménez-Valverde and Ortuño 2007) and because it was in Europe that researchers and naturalists historically began to describe organisms.

Some of these shortfalls in description patterns of Agaonidae are similar or common to other groups. For instance, a previous study about Eupelmidae in Afrotropical and Palearctic regions (Baselga et al. 2010), the authors also suggested the sampling effort is still incomplete. For Eupelmidae, there are different geographical factors influencing species discovery, such as taxonomist distribution and biome location, with widespread species being described earlier, the work underscores as well the relevance of taxonomic biases from an ecological perspective and showing that species with wide-host range are more likely to be discovered and redundantly described than specialists (Baselga et al. 2010). Furthermore, as we posit for Agaonidae, there is a clear taxonomic bias and Linnean deficit in this group due to the presence of cryptic species complexes, underestimating the real species richness of Eupelmidae (Al Khatib et al. 2014).

CONCLUSIONS

Our study shows that despite Agaonidae having been studied for quite long time, several traits and aspects about this family remain unknown, such as the real number of species, their mutualism with *Ficus* and their distribution. Thus, current data underestimate fig wasp diversity and their relationship with *Ficus*. Currently, there are areas such as South America and Oceania, where a high diversity of fig wasps is expected, yet relatively few species have been described. This indicates that more sampling efforts and inventory revisions are required to classify this still unknown diversity and to locate cryptic species and/or invalid names. Studies such as this one

review and analyse the history of group description and provide clues as to where remaining descriptive efforts might be directed to fill the gaps in knowledge that remain to be unraveled in nature.

Acknowledgments: The authors are very grateful to John S. Noyes and the Natural History Museum of London, for the development and maintenance of the Universal Chalcidoidea Database <https://www.nhm.ac.uk/our-science/data/chalcidoids/database/>, since without their important work in making available the total knowledge on Chalcidoidea, this study would not have been possible. The Universal Chalcidoidea Database has been duplicated to the taxon works framework and is now reachable under <https://ucd.chalcid.org>, where it will be further developed and updated. We would also like to thank the current curators of this website (Roger Burks, Lucian Fusu, D. Christopher Darling, John Heraty, Petr Janšta, Mircea-Dan Mitroiu, Pâmella Machado Saguiah, Natalie Dale-Skey and James B. Woolley) as well the TaxonWorks Development and Outreach Team for maintaining this important Chalcidoidea data collection project and make it possible to consult them now and in the future. We thank the reviewers for their hard work in improving the article.

Authors' contributions: Conceived and designed the work: JFG, DGT Performed the experiments and analysed the data: XHA, DGT, AR, CP

Contributed materials/analysis tools: AR, DGT, XHA Wrote the paper: XHA, DGT, AR, JLNA, CP

Competing interests: Authors declare no competing interest.

Availability of data and materials: All the data analyzed in this article are available at the Universal Chalcidoidea Database <https://www.nhm.ac.uk/our-science/data/chalcidoids/database/> (Noyes, 2019), hosted in the website of the Natural History Museum of London <https://www.nhm.ac.uk/>

Consent for publication: Not applicable

Ethics approval consent to participate: Not applicable.

REFERENCES

- Al Khatib F, Fusu L, Cruaud A, Gibson G, Borowiec N, Rasplus JY, ... Delvare G. 2014. An integrative approach to species discrimination in the *Eupelmus urozonus* complex (Hymenoptera, Eupelmidae), with the description of 11 new species from the Western Palaearctic. *Syst Entomol* **39(4)**:806–862. doi:10.1111/syen.12089.
- Baselga A, Hortal J, Jiménez-Valverde A, Gómez J, Lobo J. 2007. Which leaf beetles have not yet been described? Determinants of the description of Western Palaearctic *Aphthona* species (Coleoptera: Chrysomelidae). *Biodivers Conserv* **16(5)**:1409–1421. doi:10.1007/s10531-006-6738-9.
- Baselga A, Lobo J, Hortal J, Jiménez-Valverde A, Gómez J. 2010. Assessing alpha and beta taxonomy in eupelmid wasps: determinants of the probability of describing good species and synonyms. *J Zool Syst Evol Res* **48(1)**:40–49. doi:10.1111/j.1439-0469.2009.00523.x.
- Bouček Z. 1988. Australasian Chalcidoidea (Hymenoptera). A biosystematic revision of genera of fourteen families, with a reclassification of species. Cab International. Wallingford, Oxon, U.K.
- Bouček Z. 1993. The genera of chalcidoid wasps from *Ficus* fruit in the New World. *J Nat Hist* **27(1)**:173–217. doi:10.1080/00222939300770071.
- Brito D. 2010. Overcoming the Linnean shortfall: data deficiency and biological survey priorities. *Basic Appl Ecol* **11(8)**:709–713. doi:10.1016/j.baae.2010.09.007.
- Burks R, Mitroiu MD, Fusu L, Heraty JM, Janšta P, Heydon S, et al. 2022. From hell's heart I stab at thee! A determined approach towards a monophyletic Pteromalidae and reclassification of Chalcidoidea (Hymenoptera). *J Hymenopt Res* **94**:13–88. doi:10.3897/jhr.94.94263.
- Chen C, Chou L. 1997. The Blastophagini of Taiwan (Hymenoptera: Agaonidae: Agaoninae). *Journal of Taiwan Museum* **50(2)**:113–154. doi:10.6532/JTM.199712_50(2).0005.
- Costello M, May R, Stork N. 2013. Can we name Earth's species before they go extinct? *Science* **339(6118)**:413–416. doi:10.1126/science.1230318.
- Cox B. 2001. The biogeographic regions reconsidered. *J Biogeogr* **28(4)**:511–523. doi:10.1046/j.1365-2699.2001.00566.x.
- Cruaud A, Jabbour-Zahab R, Genson G, Cruaud C, Couloux A, Kjellberg F. et al. 2010. Laying the foundations for a new classification of Agaonidae (Hymenoptera: Chalcidoidea), a multilocus phylogenetic approach. *Cladistics* **26(4)**:359387. doi:10.1111/j.1096-0031.2009.00291.x.
- Cruaud A, Rasplus J-Y, Zhang J, Burks R, Delvare G, Fusu L, Gumovsky A, Huber JT, Janšta P, Mitroiu M-D, Noyes JS, van Noort S, Baker A, Böhmová J, Baur H, Blaimer BB, Brady SG, Bubeníková K, Chartois M, Copeland RS, Dale-Skey Papilloud N, Dal Molin A, Dominguez C, Gebiola M, Guerrieri E, Kresslein RL, Krogmann L, Lemmon E, Murray EA, Nidelet S, Nieves-Aldrey JL, Perry RK, Peters RS, Polaszek A, Sauné L, Torréns J, Triapitsyn S, Tselikh EV, Yoder M, Lemmon AR, Woolley JB, Heraty JM. 2023. The Chalcidoidea bush of life:

- evolutionary history of a massive radiation of minute wasps. *Cladistics* **40**:34–63.
doi:10.1111/cla.12561.
- Darwell CT, Al-Beidh S, Cook JM. 2014. Molecular species delimitation of a symbiotic fig-pollinating wasp species complex reveals extreme deviation from reciprocal partner specificity. *BMC Evolutionary Biology* **14**:1–10. doi:10.1186/s12862-014-0189-9.
- De Santis L. 1981. Catálogo de los Himenópteros Calcidoideos de América al Sur de los Estados Unidos - Primer Suplemento. *Revista Peruana De Entomología* **24**(1):1–38.
- dos Anjos Cruz JM, Corrêa RF, Lamarão CV, Sanches EA, Campelo PH, de Araújo Bezerra J. 2022. *Ficus* spp.: Phytochemical composition and medicinal potential. *Research, Society and Development* **11**(12):e265111234135. doi:10.33448/rsd-v11i12.34135.
- Erasmus J, van Noort S, Jousselein E, Greeff J. 2007. Molecular phylogeny of fig wasp pollinators (Agaonidae, Hymenoptera) of *Ficus* section *Galoglychia*. *Zool Scr* **36**(1):61–78.
doi:10.1111/j.1463-6409.2007.00259.x.
- Farache F, Cruaud A, Rasplus JY, Cerezini MT, Rattis L, Kjellberg F, Pereira RAS. 2018. Insights into the structure of plant-insect communities: specialism and generalism in a regional set of non-pollinating fig wasp communities. *Acta Oecol* **90**:49-59. doi:10.1016/j.actao.2018.02.006
- Gibson G. 1993. Superfamilies Mymarommatoidea and Chalcidoidea. *In*: Goulet H, Tuber J (eds). *Hymenoptera of the world: an identification guide to families*. 3^a ed. Centre for Land and Biological Resources Research Ottawa, Ontario. pp. 570–614.
- Grandi G. 1916. Gli agaonini (Hymenoptera Chalcidicae) raccolti nell'Africa occidentale dal prof. F. Silvestri. *ill. Bollettino del Laboratorio di zoologia generale e agraria della R. Scuola superiore d'agricoltura in Portici* **10**:121–286.
- Grandi G. 1926. Hyménoptères sycophiles récoltés à Sumatra et à Java par E. Jacobson. *Treubia* **8**(3-4):352–364.
- Hill D 1969. Revision of the genus *Liporrhopalum* Waterston, 1920 (Hymenoptera Chalcidoidea, Agaonidae). *Zoologische Verhandelingen* **100**(1):1–36.
- Hortal J, de Bello F, Diniz-Filho J, Lewinsohn T, Lobo J, Ladle R. 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu Rev Ecol Evol S* **46**(1):523-549.
doi:10.1146/annurev-ecolsys-112414-054400.
- ICZN (International Commission of Zoological Nomenclature). 1999. *International code of zoological nomenclature [the Code]*. Fourth edition. The International Trust for Zoological Nomenclature. Natural History Museum of London. 306 pp.
- Iknayan K, Tingley M, Furnas B, Beissinger S. 2014. Detecting diversity: emerging methods to estimate species diversity. *Trends Ecol Evol* **29**(2):97–106. doi:10.1016/j.tree.2013.10.012.

- Jiménez-Valverde A, Ortuño V. 2007. The history of endemic Iberian ground beetle description (Insecta, Coleoptera, Carabidae): which species were described first? *Acta Oecol* **31(1)**:1331. doi:10.1016/j.actao.2006.02.010
- Kaloveloni A, Tscheulin T, Petanidou T. 2018. Geography, climate, ecology: What is more important in determining bee diversity in the Aegean Archipelago?. *J Biogeogr* **45(12)**:2690–2700. doi:10.1111/jbi.13436
- Khadivi-Khub A, Anjam K. 2016. The relationship of fruit size and light condition with number, activity and price of *Blastophaga psenes* wasp in caprifigs. *Trees* **30(5)**:1855–1862. doi:10.1007/s00468-016-1418-1
- Kier G, Mutke J, Dinerstein E, Ricketts T, Küper W, Kreft H, Barthlott W. 2005. Global patterns of plant diversity and floristic knowledge. *J Biogeogr* **32(7)**:1107–1116. doi:10.1111/j.1365-2699.2005.01272.x.
- Kjellberg F, Jouselin E, Hossaert-Mckey M, Rasplus J. 2005. Biology, ecology and evolution of fig-pollinating wasps (Chalcidoidea: Agaonidae). In Raman A, Schaefer C, Withers T. *Biology, ecology and evolution of gall-inducing arthropods*. Science Publishers. pp. 539–572.
- Kreft H, Jetz, W. 2007. Global patterns and determinants of vascular plant diversity. *P Natl Acad Sci Usa* **104(14)**:5925–5930. doi:10.1073/pnas.0608361104.
- Lopez-Vaamonde C, Dixon D, Cook J, Rasplus J. 2002. Revision of the Australian species of *Pleistodontes* (Hymenoptera: Agaonidae) fig-pollinating wasps and their host-plant associations. *Zool J Linn Soc-Lond* **136(4)**:637–683. doi:10.1046/j.1096-3642.2002.00040.x.
- Machado C, Robbins N, Gilbert M, Herre E. 2005. Critical review of host specificity and its coevolutionary implications in the fig/fig-wasp mutualism. *P Natl Acad Sci Usa* **102(1)**:6558–6565. doi:10.1073/pnas.0501840102.
- Margules C, Pressey R. 2000. Systematic conservation planning. *Nature* **405(6783)**:243253. doi:10.1038/35012251
- Mayr G. 1885. *Verhandlungen der Zoologisch-Botanischen gesellschaft in Wien. Feigeninsecten* **35**:147–250.
- Moe A, Weiblen G. 2010. Molecular divergence in allopatric *Ceratosolen* (Agaonidae) pollinators of geographically widespread *Ficus* (*Moraceae*) species. *Ann Entomol Soc Am* **103(6)**:1025–1037. doi:10.1603/AN10083
- Molbo D, Machado C, Sevenster J, Keller L, Herre E. 2003. Cryptic species of figpollinating wasps: implications for the evolution of the fig-wasp mutualism, sex allocation, and precision of adaptation. *P Natl Acad Sci Usa* **100(10)**:5867–5872. doi:10.1073/pnas.0930903100.

- Mora C, Tittensor D, Adl S, Simpson A, Worm B. 2011. How many species are there on Earth and in the ocean? *Plos Biol* **9**(8):e1001127. doi:10.1371/journal.pbio.1001127
- Munro J, Heraty J, Burks R, Hawks D, Mottern J, Cruaud A et al. 2011. A molecular phylogeny of the Chalcidoidea (Hymenoptera). *PLoS ONE* **6**(11):e27023. doi:10.1371/journal.pone.0027023.
- Noyes JS. 2019. Universal Chalcidoidea Database. *In*: Natural History Museum of London. <http://www.nhm.ac.uk/chalcidoids>. Accessed 20 Jul. 2021.
- Pärtel M. 2014. Community ecology of absent species: hidden and dark diversity. *J Veg Sci* **25**(5):1154–1159. doi:10.1111/jvs.12169
- Pärtel M, Szava-Kovats R, Zobel M. 2011. Dark diversity: shedding light on absent species. *Trends Ecol Evol* **26**(3):124–128. doi:10.1016/j.tree.2010.12.004.
- Priyadarsanan DR, Abdurahiman UC. 1997. Descriptions of three new species of *Platyscapa* Motschoulsky (Hymenoptera: Chalcidoidea, Agaonidae) from India. *Proceedings. Koninklijke Nederlandse Akademie van Wetenschappen, Amsterdam* **100**(1-2):171–180.
- Priyadarsanan D, Abdurahiman U. 1997b. Two new species of Agaonidae (Chalcidoidea: Hymenoptera) from *Ficus mollis* Vahl. (*Moraceae*). *Entomon-Trivandrum* **22**:213216.
- R Core Team 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ramírez W. 1970. Taxonomic and biological studies of neotropical fig wasps (Hymenoptera: Agaonidae). *Estudios taxonómicos y biológicos de las avispas de los higos neotropicales* (Hymenoptera: Agaonidae). *Univ Kansas Sci Bull* **49**(1):1–44.
- Ramírez W. 1991. Evolution of the mandibular appendage in fig wasps (Hymenoptera: Agaonidae). *Revista de Biología Tropical* **39**(1):87–95.
- Ramírez-Pérez C. 2020. Composición y diversidad de avispas Agaonidae (Hymenoptera: Chalcidoidea) en tres especies de *Ficus* L. (*Moraceae*) del Parque Mirador Sur en Santo Domingo, República Dominicana. *Novitates Caribaea* **15**:9–17. doi:10.33800/nc.vi15.211.
- Rands M, Adams W, Bennun L, Butchart S, Clements A, Coomes D et al. 2010. Biodiversity conservation: challenges beyond 2010. *Science* **329**(5997):1298–1303. doi:10.1126/science.1189138.
- Rasplus J, Kerdelhué C, Le Clainche I, Mondor G. 1998. Molecular phylogeny of fig wasps Agaonidae are not monophyletic. *Comptes Rendus De L'académie Des Sciences - Series III - Sciences De La Vie* **321**(6):517–527. doi:10.1016/S0764-4469(98)80784-1.
- Rasplus J, Soldati L. 2006. Familia Agaonidae. *In* Fernández F, Sharkey MJ (eds) *Introducción a los Hymenoptera de la región Neotropical* Sociedad Colombiana de Entomología y Universidad Nacional de Colombia. Bogotá, Colombia. pp. 683–698.

- Ribeiro KF, Duarte L, Crossetti LO. 2018. Everything is not everywhere: a tale on the biogeography of cyanobacteria. *Hydrobiologia* **820(1)**:23–48. doi:10.1007/s10750-018-3669-x.
- RStudio Team 2023. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL <http://www.rstudio.com/>.
- Shi Y, Mon A, Fu Y, Zhang Y, Wang C, Yang X, Wang Y. 2018. The genus *Ficus* (*Moraceae*) used in diet: its plant diversity, distribution, traditional uses and ethnopharmacological importance. *J Ethnopharmacol* **226**:185–196. doi:10.1016/j.jep.2018.07.027
- Shimizu S, Broad GR, Maeto K. 2020. Integrative taxonomy and analysis of species richness patterns of nocturnal Darwin wasps of the genus *Enicospilus* Stephens (Hymenoptera, Ichneumonidae, Ophioninae) in Japan. *ZooKeys* **990**:1. doi:10.3897/zookeys.990.55542.
- Souto-Vilarós D, Proffit M, Buatois B, Rindos M, Sisol M, Kuyaiva T et al. 2018. Pollination along an elevational gradient mediated both by floral scent and pollinator compatibility in the fig and fig-wasp mutualism. *J Ecol* **106(6)**:2256–2273. doi:10.1111/1365-2745.12995.
- Stork N. 2018. How many species of insects and other terrestrial arthropods are there on Earth? *Annu Rev Entomol* **63(1)**:31-45. doi:10.1146/annurev-ento-020117-043348.
- Struck T, Feder J, Bendiksbj M, Birkeland S, Cerca J, Gusarov V et al. 2018. Finding evolutionary processes hidden in cryptic species. *Trends Ecol Evol* **33(3)**:153–163. doi:10.1016/j.tree.2017.11.007.
- Tindall B, Rosselló-Móra R, Busse H, Ludwig W, Kämpfer P. 2010. Notes on the characterization of prokaryote strains for taxonomic purposes. *Int J Syst Evol Micr* **60(1)**:249–266. doi:10.1099/ijs.0.016949-0.
- van Noort S, Rasplus JY. 2021. Figweb: figs and fig wasps of the world. www.figweb.org Accessed 18 Aug. 2021.
- Vigna-Taglianti A, Audisio PA, Belfiore C, Biondi M, Bologna MA, Carpaneto GM, Zoia S et al. 1992. Riflessioni di gruppo sui corotipi fondamentali della fauna Wpaleartica ed in particolare italiana. *Biogeographia* **16(1)**:159–179. doi:10.21426/B616110375.
- Wang G, Cannon C, Chen J. 2016. Pollinator sharing and gene flow among closely related sympatric dioecious fig taxa. *P Roy Entomol Soc B: Biol Sci* **283(1828)**:20152963. doi:10.1098/rspb.2015.2963.
- Wiebes J. 1963. Taxonomy and host preference of Indo-Australian fig wasps of the genus *Ceratosolen* (Agaonidae). *Tijdschrift voor Entomologie* **106**:1–112.
- Wiebes J. 1974a. *Nigeriella*, a new genus of West African fig wasps allied to *Elisabethiella* Grandi (Hymenoptera Chalcidoidea, Agaonidae). *Zoologische Mededelingen* **48(5)**:29–42.
- Wiebes J. 1974b. Species of *Agaon* Dalman and *Allotriozone* Grandi from Africa and Malagasy (Hymenoptera Chalcidoidea, Agaonidae). *Zoologische Mededelingen* **48(13)**:123–143.

- Wiebes J. 1980. Records and descriptions of Agaonidae from New Guinea and the Solomon Islands. Proc Kon Ned Akad v Wetensch **83(1)**:89–107.
- Wiebes J. 1989a. Agaonidae (Hymenoptera: Chalcidoidea) and *Ficus* (*Moraceae*) fig wasps and their figs. III. *Elizabethiella*. Proc Kon Ned Akad v Wetensch **92(1)**:117136.
- Wiebes J. 1989b. Agaonidae (Hymenoptera: Chalcidoidea) and *Ficus* (*Moraceae*) fig wasps and their figs. IV. African *Ceratosolen*. Proc Kon Ned Akad v Wetensch **92(2)**:251–266.
- Wiebes J. 1989c. Agaonidae (Hymenoptera Chalcidoidea) and *Ficus* (*Moraceae*): fig wasps and their figs, V (*Agaon*). Proc Kon Ned Akad v Wetensch **92(3)**:395–407.
- Wiebes J. 1992a. Agaonidae (Hymenoptera: Chalcidoidea) and *Ficus* (*Moraceae*): fig wasps and their figs, IX (*Waterstoniella*). Proc Kon Ned Akad v Wetensch **95(4)**:499–514.
- Wiebes J. 1992b. Agaonidae (Hymenoptera: Chalcidoidea) and *Ficus* (*Moraceae*): fig wasps and their figs. VIII. *Eupristina* s.l. Proc Kon Ned Akad v Wetensch **95(1)**:109125.
- Wiebes J. 1993a. Agaonidae (Hymenoptera Chalcidoidea) and *Ficus* (*Moraceae*): fig wasps and their figs, XII (Indo-Australian *Kradibia*). Proc Kon Ned Akad v Wetensch **96(4)**:481–501.
- Wiebes J. 1993b. Agaonidae (Hymenoptera Chalcidoidea) and *Ficus* (*Moraceae*): fig wasps and their figs, XI (*Blastophaga* s.l.). Proc Kon Ned Akad v Wetensch **96(3)**:347–367.
- Wiebes J. 1993c. Agaonidae (Hymenoptera Chalcidoidea) and *Ficus* (*Moraceae*): fig wasps and their figs, X (*Wiebesia*). Proc Kon Ned Akad v Wetensch **96(1)**:91–114.
- Zare H, Darvishzadeh H, Rastegari N. 2018. Effect of cold storage on *Blastophaga psenes* (Hymenoptera: Agaonidae) wasp inside different caprifig cultivars syconium. Plant Protection J **9(1)**:1–32.

Supplementary materials

Table S1. Dataset of species of Agaonidae used for the analyses in this article (see details in the Material and Methods Section). (download)

Table S2. Detailed summary of the models presented in table 1. (download)

Fig. S1. Colour-blind versions of Figures 3 and 4. (download)