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

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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, exhibiting a high potential dark biodiversity, especially in the tropical areas where the 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 such as the Afrotropical or Oriental realms. Our results indicate that there is a strong need for 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

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, a great Linnean shortfall (*i.e.*, lack of knowledge on how many species

have existed and exist, Hortal et al. 2015) exists at a 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 extinction and adaptation (Hortal et al. 2015; Margules and Pressey 2000; Rands et al. 2010).

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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 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 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 are not present 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 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 easily 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 with Linnean shortfall is the existence of cryptic species complexes (*i.e.*, a biological entity that represents a group consisting of two or more species that cannot be easily morphologically 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 a few millimeters long (Gibson 1993; Kjellberg et al. 2005; Souto-Vilarós et al. 2018), have 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 their life cycle. Furthermore, the specificity within the 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 and parasitoid species such as Sycophaginae (Pteromalidae) (Farache et al. 2018), also highly associated with Ficus and host specific.

The taxonomy, phylogeny and biology of fig wasps have been previously 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 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 fig wasp 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 chalcidoids 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 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 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 (Table S1). According to the database, we obtained species records for five biogeographical regions: Afrotropical, Nearctic, Neotropical, Oriental, and Palearctic.

Binominal names were considered "valid" if they met the International Commission on Zoological Nomenclature's (ICZN) (ICZN 1999) criteria, while if they did not, they were considered "synonyms" of a valid fig wasp species. Additionally, if two or more authors participated in describing a species, they were considered as one entity to simplify the subsequent analysis.

Species distributions were extracted from countries where they have been recorded and were subsequently modeled as rectangular polygon maps. These maps encompassed the far north (maximum latitude), far south (minimum latitude), far west (maximum longitude) and far east (minimum longitude) of each species' total distribution range. Three different variables were extracted from these 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) and VignaTaglianti et al. (1992), fig wasp species were considered as "large-scale distribution" if they were found in two or more regions. Those species present in only one region were categorized according to that 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 with 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). 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) described each year. These accumulation curves were fitted to exponential and logarithmic trends. R² 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 built 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 them to visualize 1) the sum 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 estimated the dark diversity of fig wasps for each country (and in the cases of large countries, such as the United States of America, for each region or state) as the number of valid species whose rectangular polygon maps match the country but are not cited. 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 Gi* 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) to analyse if a significant correlation exists between year of description, number of authors and number of binominal names, and 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 (52.76% of the total) and 110 (30.39% of the total) species respectively (Fig. 1A). Concerning genera, Agaonidae are currently classified among 20 genera (Fig. 1B), with *Ceratosolen* being 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 in both the Afrotropical and Australasian regions, 50 in the Neotropical region, 33 in the Palearctic region and 2 in 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). 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 only pollinate one host species (36.74% of the total) and 20 fig wasps pollinate two host species each (5.52% of the total). On 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).

Accumulation curves

The accumulation curves of valid species and



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) leves; 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 these descriptions were valid or resulted in a synonym; and number of host plant species per fig wasp species (F).

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 Palearctic 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. More precisely, the trends of description processes of Agaonidae in each biogeographical region have been influenced by scientific contributions and can



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 and the R^2 value are provided to show if the species accumulation curve fits to growth towards an asymptote or without an asymptote.

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 the 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 since the 1940s.) In the Oriental region (Fig. 2E), abrupt increases occurred during 1926, and the 1990s can be explained by the contributions of Grandi (1926), Wiebes (1963 1992a b 1993a b c), Hill (1969), Chen and Chou (1997), and Privadarsanan and Abdurahiman (1997a b). Finally, the Palearctic region (Fig. 2F) shows steady growth 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).

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 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 mean of authors (Fig. 3D), shows the opposite trend with higher values in the Palearctic and Nearctic areas.

Dark diversity of fig wasps for each country or territory ranged from 0 to 64 species (Fig. 4A), with median and mean values of 8 and ~10 species respectively. Values over the median (3rd and 4th quartiles; Fig. 4A) were concentrated mostly between



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 an 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 an 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.

the tropics. Getis-Ord Gi* 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).

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 negatively 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



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).

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 the other hand, the year of description is negatively related at a global scale with the 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 related to the number of regions (*i.e.*, the larger the distribution of the species in this region, the earlier it has been described), whereas in the Neotropical region, year of description 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, it has been previously described), and in the Palearctic region is negatively related number of regions (the same as the global scale).

DISCUSSION

Diversity analysis of Agaonidae

Our results, derived from what is currently known, show that 36.74% of Agaonidae specifically interact

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. *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 | <i>t</i> -value | р |
|---------------------------|--------------------------|------------|-----------|----------|-----------------|---------|
| 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 |
| | Palearctic ($N = 33$) | - | - | - | - | - |
| 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) | - | - | - | - | - |
| | Palearctic $(N = 33)$ | Nregions | -64.49 | 28.44 | -2.267 | 0.033 |

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 (López-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, a gap of knowledge and a remarkable Eltonian shortfall exists when it comes to this group of wasps, 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 potential number of species of Agaonidae remain 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 their small size, and most of their life cycles occur 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 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 coevolution of fig wasps and *Ficus* has produced, and the common 1:1 relationship (López-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 vet to be completed. On the other hand, there are only two native species of *Ficus* in the Nearctic which are exclusive from this region (Pegoscapus 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 were 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, in 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 also underscores the relevance of taxonomic biases from an ecological perspective and shows 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.

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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)