












Mapping the status of global taxonomic knowledge of Orthoptera (Arthropoda, Insecta)

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Abstract

The status of taxonomic knowledge varies across the Globe. Quantifying and mapping the geographic patterns of taxonomic status is essential to prioritise regions that require greater attention from the taxonomic community. Here, we compiled all valid orthopteran species names and their synonyms, extracted from the Catalogue of Life (CoL) and allocated them geographically, based on data from the Global Biodiversity Information Facility (GBIF) and the Orthoptera Species File (OSF). This allowed us to create measures of taxonomic effort, based on the date of species descriptions and the number of associated synonyms and combine them across space. Our analyses show that the descriptions of currently valid species increased exponentially since the 19th century, with a temporary decline following World War II, while synonyms outpaced the number of valid species until the 1980s. The number of taxonomists also increased over time, with declines after World Wars, followed by a significant rise from the 1950s onwards, continuing through the 21st century (with > 100 taxonomists currently active). Per-taxonomist description rates transitioned from highly variable before the 20th century to consistent rates of 5–10 species annually with collaborative efforts. Tropical regions and the Southern Hemisphere hold the majority of recently described species names with fewer associated

synonyms, indicating a predominance of alpha taxonomy and highlighting the need for greater taxonomic efforts. In contrast, temperate regions, particularly in Europe and south-western Asia, contain the majority of older names and synonyms, indicating a predominance of beta taxonomy and regions that have been more thoroughly studied. Our findings are discussed in the context of sociopolitical factors, scientific investments and the history of taxonomy. Finally, we propose a framework that makes the links between taxonomy and macroecology accessible for biodiversity in the era of Big Data.

Highlights

- Alpha taxonomy (i.e. the description of new species) and Beta taxonomy (i.e. the revision of the taxonomic status and relationships of already described taxa) vary across space and time.
- We present a framework that connects taxonomy and macroecology, allowing us to assess taxonomic trends to provide information for biodiversity studies in the era of Big Data.
- We mapped alpha taxonomy rates using the date of species descriptions across space and beta taxonomy rates using the number of synonyms associated with each species.

- We combined alpha and beta taxonomy rates to understand the global taxonomic status of Orthoptera (Arthropoda, Insecta), the sixth most species-rich insect order, which includes grasshoppers, crickets, katydids and relatives.
- In tropical regions, orthopteran taxonomy is recent and has few revisions, while in temperate regions, it is older and more consolidated.

Keywords

Alpha taxonomy, beta taxonomy, biodiversity knowledge shortfalls, macroecology, Orthoptera, taxonomic uncertainty

Introduction

Taxonomy is a theoretical and practical science that deals with biodiversity classification (Mayr 1969). It develops hypotheses about species delimitation and classification within the taxonomic hierarchy. Being hypotheses, numerous described and named species become obsolete as taxonomy progresses, as they either are synonyms – different names that have been used for the same species (which has been described at least twice) or refer to two or more distinct entities (Alroy 2002). The state of taxonomic knowledge is uneven amongst taxa and, for many groups, such as Orthoptera, varies widely across different regions (Baselga et al. 2010; Stropp et al. in press). This is due to the uneven geographic distribution of both biodiversity and taxonomists throughout history (Baselga et al. 2010; Rodrigues et al. 2010), which results in varying levels of species detectability in nature, heterogeneous rates of species discovery in the field, diverse taxonomic criteria used in the description of new species and taxonomic uncertainties associated with those already known species (Freeman and Pennell 2021; Stropp et al. 2022; Diniz-Filho et al. 2023; Frateles et al. 2024). These aspects of taxonomic knowledge have generated biases and gaps in different geographic regions, with greater knowledge and accuracy of species in certain locations and profound implications for studies in taxonomy, ecology, evolution and biodiversity conservation.

The discovery and naming of new species represents the first stage of taxonomy, known as alpha taxonomy (see Mayr (1969)). The large-scale spatial distribution of alpha taxonomy can be inferred by combining the date of description of each species name with the locality where the type material was collected and/or is deposited. Although most species inventories still have incomplete spatial coverage, the date of species naming across space is a little-explored indicator that can help guide areas in need of new (or renewed) taxonomic efforts and inventories, as well as provide a historical record of descriptions over time. In this context, regions hosting many recent names indicate ongoing taxonomic efforts, while areas with older

names may reflect past efforts and/or a lack of new ones (see Baselga et al. (2010)).

The second stage of taxonomy, known as beta taxonomy, involves understanding of relationships amongst already described species and higher taxa through their systematic revision (see Mayr (1969)). This stage can result in: (i) taxonomic lumping – identifying species that have been redundantly described several times under different names; and (ii) taxonomic splitting – uncovering ‘new species’ contained within the populations of previously described ones (Baselga et al. 2010; Stropp et al. 2022; Lessa et al. 2024). These processes are inherent to taxonomic advance and their distribution in space can be inferred by the number of synonyms detected for the species occurring in a given region (Baselga et al. 2010). All other things being equal, it can be hypothesised that sites with a higher number of species with synonyms will have been more studied, with comparably more effort devoted to organise, correct and classify species through taxonomic revisions. This implies that the number of synonyms across space provides an indirect indicator of taxonomic revisions (i.e. of beta taxonomy).

Mapping alpha and beta taxonomy across space can help unveil the mechanisms that have driven or limited taxonomic development in different regions, as well as highlight areas with varying levels of taxonomic stability. This, in turn, can enable the prioritisation of locations and territories that need more taxonomic attention in the form of new species descriptions, taxonomic revisions or both. However, to date, very few broad-scale investigations into these issues have been conducted, possibly due to a lack of a strong connection between taxonomic practice and macroecological research (see Stropp et al. (2022)). To create this connection, it is necessary to assess taxonomic uncertainty from the knowledge contained in catalogues, atlases and checklists (Ronquillo et al. 2023; Lessa et al. 2024) and integrate it with the biogeographic knowledge of digitally-accessible massive biodiversity data.

Here, we combine the date of description of both valid species and synonyms and the number of synonyms associated with each valid species name, as proxies for variations in alpha and beta taxonomy across space, in order to map the global trends in the status of taxonomic knowledge. We hypothesise that beta taxonomy is predominant in Europe and temperate regions of the Northern Hemisphere, as the history of taxonomy began with European naturalists in the 18th century. The early description of a large portion of species from these regions should have allowed a subsequent focus on taxonomic revisions. Moreover, the higher research capacity (i.e. advanced technology, specialised expertise, funding and infrastructure) of many countries in the north temperate areas is predicted to be associated with a wider range of contemporary approaches to taxonomy, facilitating higher rates of taxonomic change. In contrast, we expect alpha taxonomy to be predominant in Tropical Regions, reflecting both the megadiversity yet to be documented in these regions, as well as a scarcity of taxonomists and technical capacity. These same factors should also lead to fewer taxonomic revisions.

We test the above hypotheses for the global diversity of Orthoptera (Arthropoda, Insecta), the sixth richest order of insects today, including crickets, grasshoppers, katydids and relatives. Since the publication of “Systema Naturae” (Linnaeus 1758), where only 59 orthopteran species were described for science, the taxonomy of this group has captivated a large community of orthopterists worldwide, resulting in over 29,000 valid species currently described (Bánki et al. 2024). In addition to valid species names for all orthopteran species, Big Data repositories hold description dates and synonymic lists for most of these species, enabling the large-scale mapping of the status of taxonomic knowledge (Cigliano et al. 2024a, b).

Materials and methods

Building a checklist of Orthoptera names

We built a checklist of valid species names (SN) and associated synonyms (SYN) using the taxonomic classification organised from the Orthoptera Species File (OSF). This classification is provided in Darwin Core at the Catalogue of Life (CoL), where it contributes to the higher classification (Suppl. material 1; Cigliano et al. (2024a)). To this end, we considered all taxonomic components of a scientific name, including the binomial names of the species (genus + specific epithet), combined with authorship (author(s) + year) and applied the following filters: (i) Taxonomic status – we disregarded fossil species previously filtered in CoL (Suppl. material 2), subspecies and subspecies synonyms, as well as names lacking the year of description and/or the author and those with potentially dubious taxonomic status (i.e. provisionally accepted and species aggregate); (ii) Taxonomic timeframe – we filtered only names proposed until the year 2023; and (iii) Taxonom-

ic ambiguities – we removed duplicate combinations of genus + epithet from the obtained set of names. This includes disregarding synonymic names resulting from the presence of subgenus syntax (e.g. *Gryllus campestris* = *Gryllus (Gryllus) campestris*) from the synonym(s) associated with each species name (i.e. $SYN \subseteq SN$) (Fig. 1).

Based on the filtered data, we built temporal species accumulation curves, which describe the accumulation of species names over time and the quantity of new names proposed per year (see Lu and He (2017)). We built these curves for valid species, currently recognised synonyms and taxonomists’ names. For synonyms, we considered both homotypic and heterotypic synonyms (i.e. synonymic names based on, respectively, either the same type specimen or a different one). For taxonomists’ names, we considered each different name associated with the species name. Additionally, we also calculated the number of species names described, divided by the number of taxonomists and the average number of authors per species for each year (see Cunningham et al. (2024)).

Spatial distribution of names: valid species and total names

Using the valid species names filtered in CoL (Fig. 2A), we searched for distributional data (i.e. geographic occurrence records) for these names in the Orthoptera Species File (OSF; Cigliano et al. (2024b)) and the Global Biodiversity Information Facility (GBIF; GBIF 2024) (Suppl. materials 3, 4) (Fig. 2B). We filtered these databases to retain only records identified at species level, with complete information on species authority and those with geographic coordinates with at least one decimal digit of precision. For the data sourced from GBIF, we removed records where the longitude coordinates were equal to the latitude

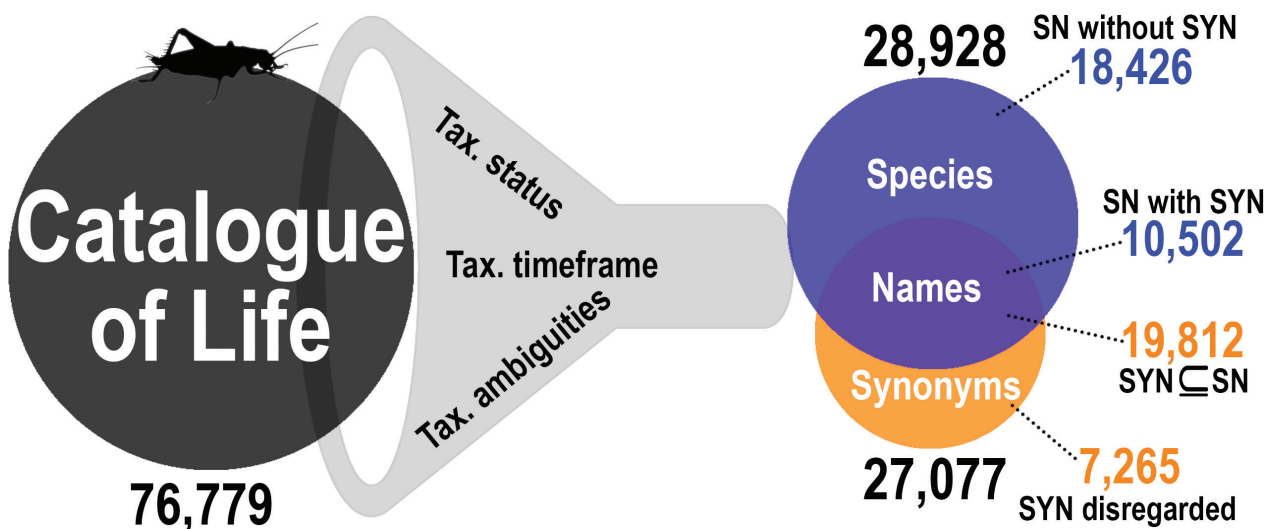


Figure 1. Filtering process and identification of valid species names and synonyms in the Catalogue of Life (CoL) considering all taxonomic components (genus + specific epithet + author(s) + year). The first step consisted in removing fossils, subspecies and synonyms of subspecies (Tax. status). In the second filter, we counted proposed names until 2023 (Tax. timeframe). Finally, the third filter consisted of removing duplicate records in valid species names and synonyms, disregarding synonyms resulting from subgenus syntax (Tax. ambiguities).

coordinates, as well as centroid coordinates of country capitals and provinces, using the CoordinateCleaner package (Zizka et al. 2019). Subsequently, we integrated the information of OSF and GBIF into a single dataset and removed duplicate records, considering the information of the name (binomial name + authorship) and coordinates. We included only the records that were registered in land surface, including islands. For this, we used the Natural Earth platform at 1:10 m resolution (<https://www.naturalearthdata.com/>). Orthoptera occurrence data filtered in OSF and GBIF are available in Suppl. materials 5, 6, respectively.

We calculated the number of valid species names within grid cells (π_i) of 2° resolution (using Projected Coordinate System EPSG-4326). This macroscale approach reduces omission errors in the distribution of many species (see Rondinini et al. (2006); Lemes et al. (2011)), especially due to the scarcity of distributional data for many Orthoptera species, which have only one or a few occurrence records. We also calculated the sum of synonyms associated with all valid species names in each cell, obtaining the total number of names (tn) (Fig. 2B). Note that, with the term synonyms here, we refer to what can be defined as “nomenclatural lumping”, which besides true synonyms may also encompass spelling errors to synonyms, ambiguous synonyms and erroneous combinations attributed to the currently valid species name throughout taxonomic knowledge. However, it disregards synonyms created by the presence of subgeneric syntax (see above). Thus, what we here consider as lumping does not distinguish between species that have been relegated to synonyms after a taxonomic re-evaluation and nomenclatural changes, as discussed by Lessa et al. (2024) (see Suppl. material 7: appendix S1).

Indices of alpha and beta taxonomy

We calculated two different indices as proxies for alpha and beta taxonomy: Alpha Temporal (AT) and Beta Proportion (BP) for all cells of our 2° global grid. Both indices were based on the spatial distribution of currently valid species names obtained from their records, rasterised and mapped at the same 2° grid scale (Fig. 2C, D). Additionally, we also performed a sensitivity analysis of each index (see Suppl. material 7: appendix S2, fig. S1).

Alpha Temporal Index (AT)

The alpha temporal index measures the temporal distribution of species-naming efforts at different cells. AT assumes that cells with recent species names indicate ongoing taxonomic efforts, while cells with older species names do reflect efforts made in the past or the absence of new efforts – in the case that no recent names are present in the cell. To calculate this index, we fitted the year of description of each valid species name to an exponential decay curve, derived from a polynomial function of degree 4, considering the time span of all names. This

curve provides higher weights to older species names; as taxonomy advances with time, the weight for descriptions decreases exponentially. Specifically, we assigned an alpha temporal value for each valid species name AT_{sn} (Eq. 1), based on the time elapsed from the most recent authorship year to the oldest (2023 to 1758 in our data), where species described in 1800 have values of ca. 0.5 and species described in 1900 ca. 0.1 (Fig. 2C, first graph).

$$AT_{sn} = (t_i - t_{max}/h)^4, \quad \text{Eq. 1}$$

where t_i is the year of authorship of the investigated valid species name, t_{max} is the year of the most recent authorship in the checklist of the valid species names and h is the maximum value of the difference between the years when the names were described. Subsequently, taking the values previously assigned to each valid species name (AT_{sn}), we calculate the average value of alpha temporal for each location (π_i), based on the geographical occurrence of each species (Eq. 2).

$$AT_{\pi_i} = \mu AT_{sn}(\pi_i) \quad \text{Eq. 2}$$

AT values range from ~ 0 to 1; we assume that when $AT \sim 0$ or ≤ 0.25 , it indicates that the majority of valid species names in a cell correspond to recent descriptions, meaning alpha taxonomy is predominant. Conversely, values close to ≥ 0.75 or 1 indicate that a large proportion of valid species names in a cell are old, meaning that alpha taxonomy is currently not predominant (Fig. 2D). This general interpretation helps summarising the history of local descriptions.

Beta Proportion index (BP)

The Beta Proportion index measures the portion of synonymised species names in a given location. We assume that the most studied sites would have more synonyms per species because of the greater effort for thorough taxonomic revisions, although this is not a general rule in taxonomy because of the priority rule in the Zoological Code of Nomenclature (see Braby et al. (2024); <https://www.iczn.org/>). This index can be mapped, based on the known distribution of currently valid species, assuming that their associated synonyms share the same distribution ranges. Although this assumption may not hold valid in many cases, it does indicate the distribution of species that were recently revised, thereby making it appropriate as a proxy for beta taxonomic work. It is important to highlight that some species exhibit greater intraspecific variability, which can result in many synonyms, while others, with less heterogeneity in their phenotypic characteristics, have clearer and more easily distinguishable traits, leading to a lower number of synonyms. However, even less variable species may have been the subject of multiple studies due to different taxonomic circumstances. Additionally, the BP index is sensitive to species with a long history of nomenclatural changes (i.e. many

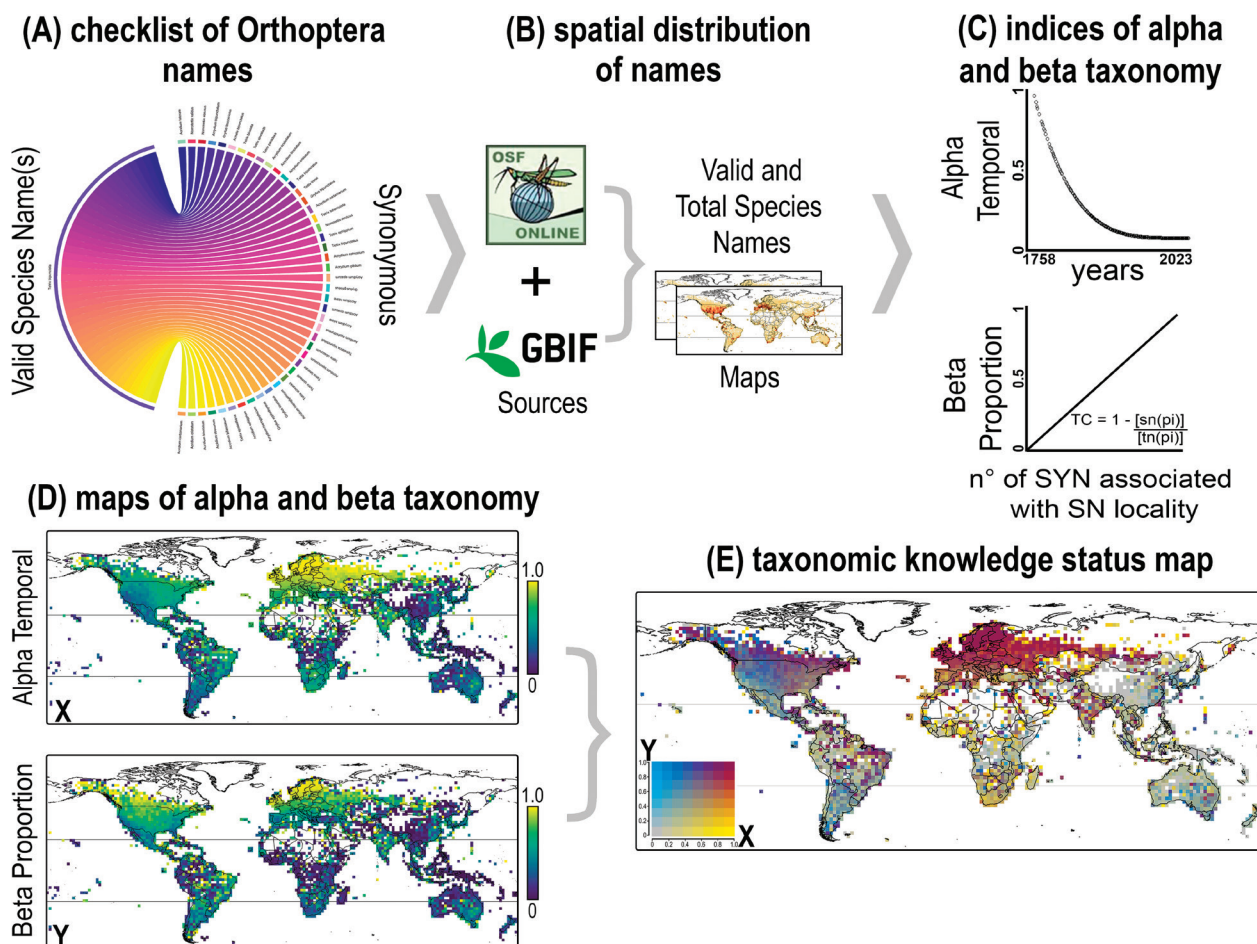


Figure 2. Workflow for building a taxonomic knowledge status map: (A) build a checklist of Orthoptera names (i.e. valid species names and associated synonyms) using data from the Catalogue of Life (CoL); (B) access the geographic distribution of the number of valid and total species names integrating data from the Orthoptera Species File Online (OSF) and the Global Biodiversity Information Facility (GBIF); (C) calculate two indices representing alpha and beta taxonomy: alpha temporal (AT) and beta proportion (BP); (D) build maps of alpha and beta taxonomy, rasterising the indices of AT and BP in each 2° grid cell with data on orthoptera species; and (E) combine the AT (y axis) and BP (x axis) indices into a bivariate taxonomic knowledge status map.

synonyms) and a widespread distribution, which may overlap with species that have few or no synonyms and a more restricted, endemic range. In this context, the BP of a given region may reflect a potentially skewed pattern due to the partial or complete overlap of these species' distributions, potentially distorting the beta taxonomy pattern in areas with few species. Nonetheless, by using this index, we assume that such issues are not widespread and have a minimal impact on our model, as this overlap is ultimately a reflection of the taxonomic history of a specific region or locality.

For each cell (pi), we calculated Beta Proportion using Eq. 3:

$$BP = 1 - [sn(pi)] / [tn(pi)], \quad \text{Eq. 3}$$

where BP_{pi} is the result of 1 minus the ratio of the number of valid species name occurrences (sn) to the total number of name occurrences (tn) for each location (pi) and tn is the result of sn plus all associated synonyms for a given location (pi) (Stropp et al. in press) (Fig. 2C).

BP values range from ~ 0 to 1; BP ~ 0 indicates a low proportion of synonyms relative to the existing species at the location, suggesting that beta taxonomy is not predominant. In contrast, values close to 1 reflect a high proportion of synonyms, indicating that beta taxonomy is predominant. It is important to note that it is not possible to determine whether beta taxonomy is recent or older (Fig. 2D).

Combining alpha and beta taxonomy to map the status of taxonomic knowledge

To identify areas with different levels of alpha and beta taxonomy, we combined the two alpha temporal and beta proportion indices into a bivariate map. For this, we divided the AT and BP values (X and Y axes, respectively) into octiles (eight quantiles) and assigned different colours to different combinations (see Biesecker et al. (2020)). Each colour represents a specific combination of octile shifts (Fig. 2E). All analyses were performed in R (R Core Team 2024).

Results

Species description and taxonomic effort rates

The accumulation of valid species names of Orthoptera has increased exponentially since the mid-19th century, with a brief decline just after World War II (Fig. 3A), although the number of valid species described each year shows large fluctuations over time (Fig. 3B). The temporal accumulation of synonyms exceeded the growth of valid species names until the early 1980s, when it began to decline

(Fig. 3A). The number of synonyms per year also shows large fluctuations, with the highest peaks occurring in the 19th century (Fig. 3B). The accumulation of taxonomists' names increased over time – albeit to a much lesser extent compared to species and associated synonyms, with more than 100 taxonomists currently active and continuing to increase (Fig. 3A). The number of active taxonomists per year shows a slight reduction immediately after World Wars I and II, followed by significant growth, particularly after 1950s, with increasing trend into the 21st century (Fig. 3B).

Considering the ratio of number of species names described by the number of taxonomist over time, the highest fluctuations occurred before the 20th century (with

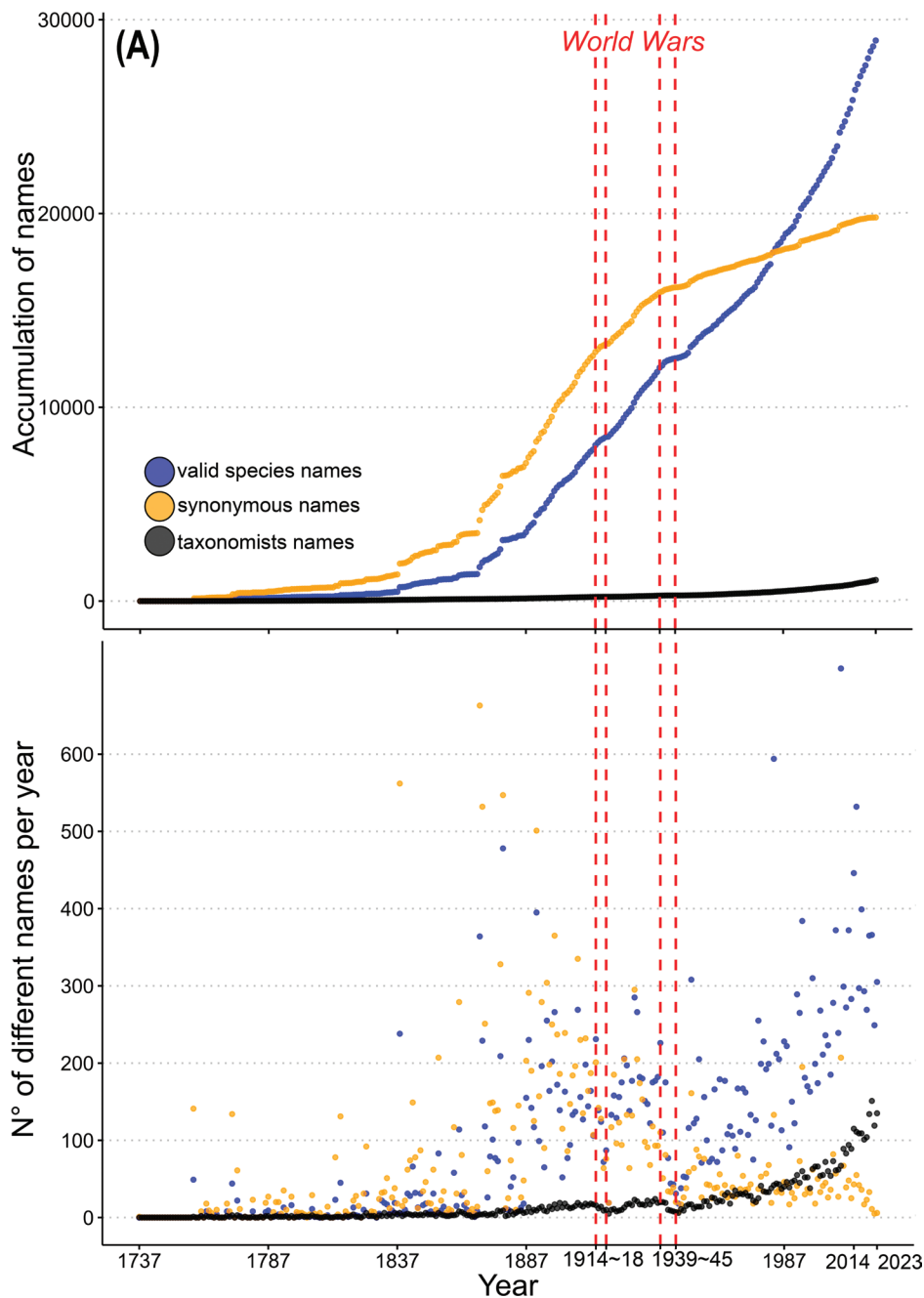


Figure 3. Rates of taxonomic work on Orthoptera names through time. (A) accumulation of valid species names (blue), synonyms (orange) and active taxonomists (black) over time; (B) number of currently valid species (blue), synonyms (orange) and taxonomists' (black) names per year.

cases when a single taxonomist could describe more than 50 species); while more recently, each active taxonomist tends to describe between 5 and 10 species per year (Fig. 4A). The average number of taxonomists per species description has grown over time, reaching more than one at the end of the 19th century and increasing steadily since 1950, exceeding two taxonomists in recent years (Fig. 4B).

Detecting the distribution of orthopteran species names

Our dataset included 76% of currently valid orthopteran species names. Considering only valid species names with synonyms (i.e. $SYN \subseteq SN$), we obtained information for 8,080 out of the 10,502 valid species names in the Catalogue of Life, representing 77% of all currently

recognised species. We obtained spatial information for 21,945 of the 28,928 orthopteran valid species names recorded in CoL. Orthoptera valid species records cover all terrestrial regions of the world, except for northern Africa, western China and the Polar Regions (Fig. 5A). The areas with the highest numbers of valid species recorded are concentrated mostly in temperate latitudes (between 30–50° latitude), mainly in the United States of America and Europe and disjunctly in tropical latitudes (below 30°), such as Central America, north-western South America, some parts of Africa and Indo-Malaysia and Australia (Fig. 5A).

The spatial distribution of the total number of names follows the same pattern (Fig. 5B), though the total number of names is, in some cases, up to five times larger than the number of valid names (see the correlation in Suppl. material 7: fig. S3). The highest number of total names

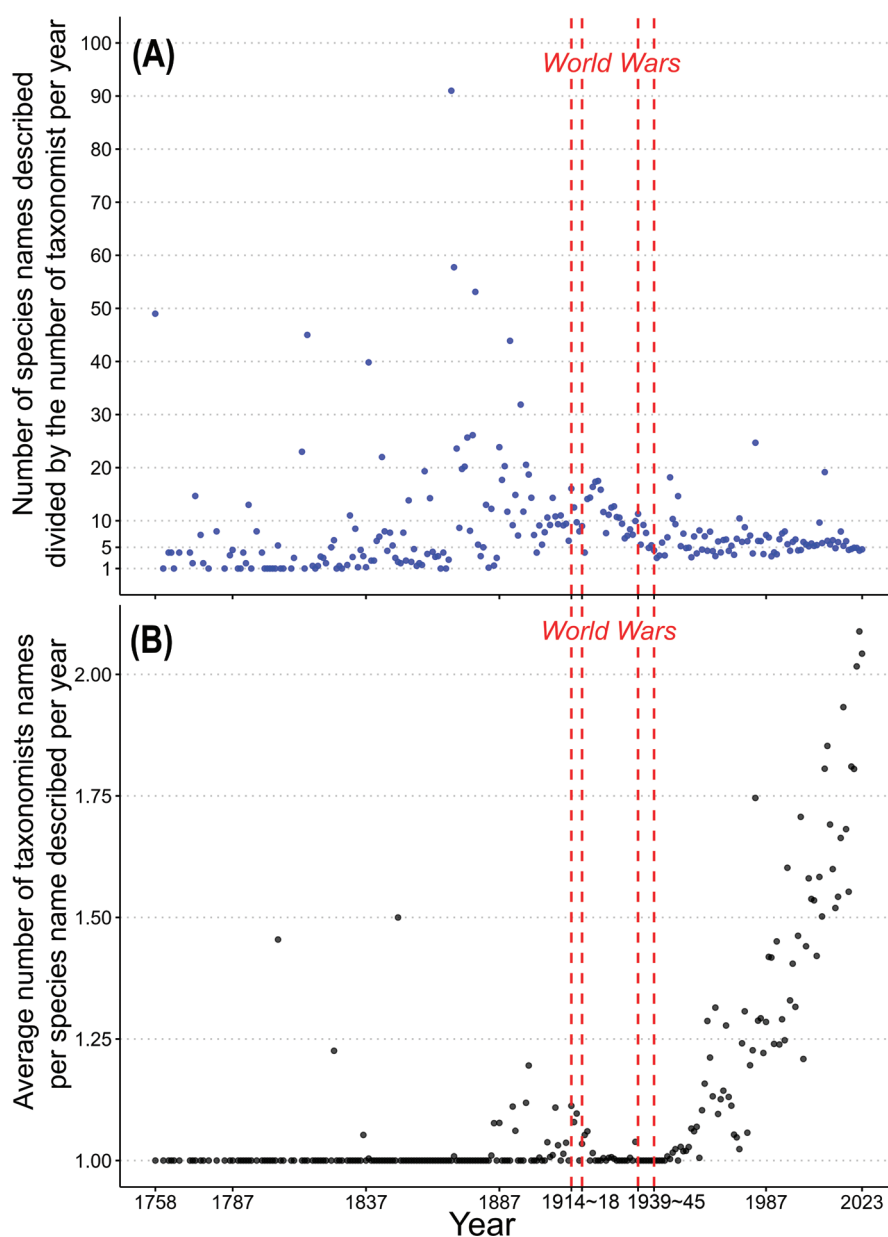


Figure 4. Ratio of species names described by taxonomist per year (A) and average number of taxonomists per species name described (B) over time.

is observed in temperate latitudes of the Northern Hemisphere, covering the United States of America and Europe and scattered in tropical latitudes (Fig. 5B).

Historical rates of alpha and beta taxonomy

Based on the Alpha Temporal index, the most recently described valid species (i.e. $AT \leq 0.5$) are primarily found in tropical latitudes, whereas older species (i.e. $AT \geq 0.75$) are mostly located in temperate latitudes, particularly in Europe and western Asia (Fig. 6A). A similar pattern is observed for the Beta Proportion (Fig. 6B), where low proportions of synonyms (i.e. $BP \leq 0.25$) are concentrated in tropical regions, while high proportions of synonyms (i.e. $BP \geq 0.75$) are predominantly found in temperate latitudes, such as northern Europe, Canada and Russia.

Mapping the status of taxonomic knowledge

The bivariate map of alpha and beta taxonomy reveals at least four main types of taxonomic trends around the world (Fig. 6). Regions in process of inventory, characterised by recent species and few synonyms (i.e. low AT and BP; grey in Fig. 6), are predominant across the whole world, especially in the Tropics. In contrast, the regions with

well-established taxonomies based on older valid species and many synonyms (i.e. high AT and BP, purple in Fig. 6), mostly at temperate latitudes, particularly Europe and Asia.

Interestingly, many regions have received intense taxonomic work in the last decades, coupling species descriptions with taxonomic reviews, characterised by recent species and many synonyms (i.e. low AT and high BP, blue in Fig. 7), which is mostly located in temperate latitudes, particularly central and western North America and, to a lesser extent, southern South America and south and east Australia and New Zealand. Finally, places with old species inventories that have not been subject to revision, which have older species and few synonyms (i.e. high AT and low BP), which are relatively rare around the world, except in tropical Africa and at temperate latitudes, in East and Southeast Asia (Fig. 7, yellow).

Discussion

General taxonomic trends over time in Orthopterology

Our analyses show that the number of newly-described Orthoptera species has increased exponentially over time (although this varies depending on the time frame, such as 1-, 5- or 10-year intervals), indicating that we are still far

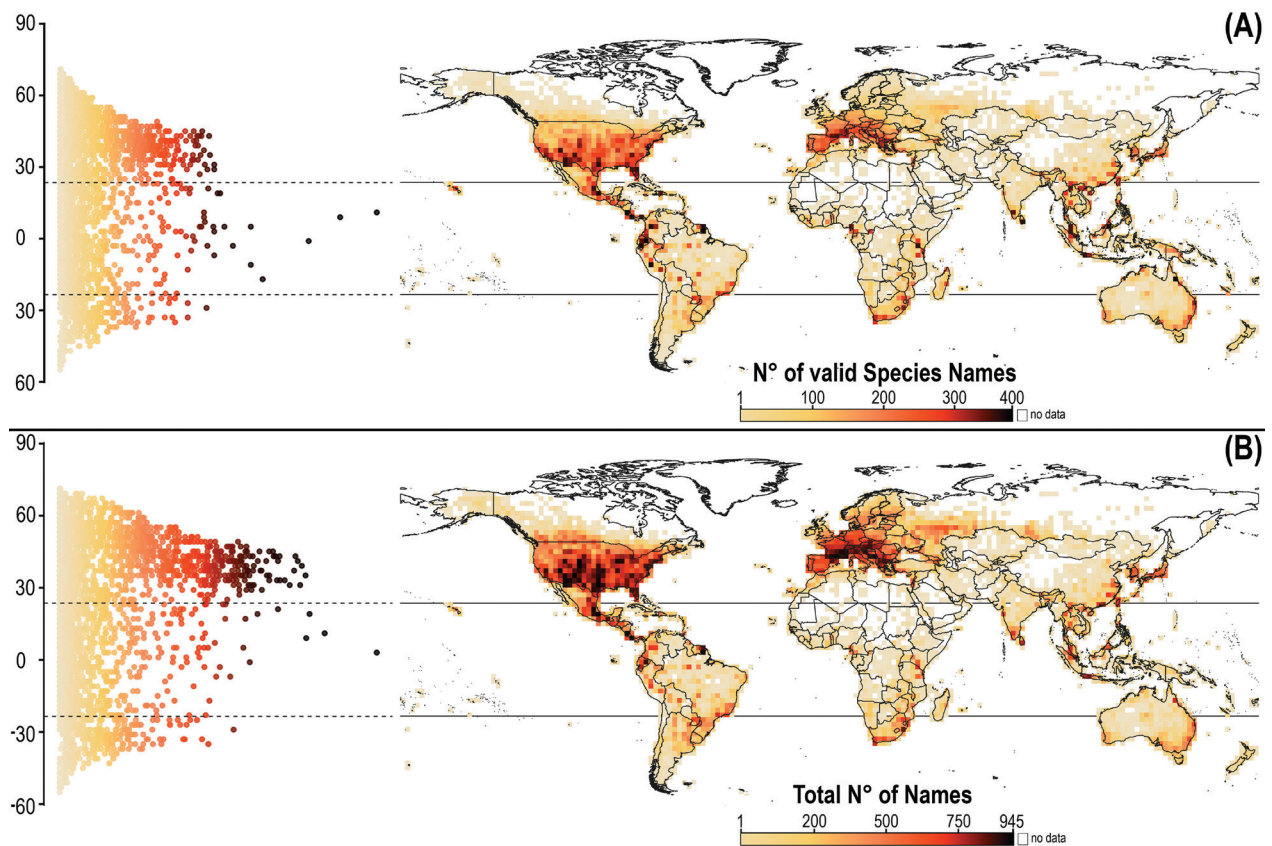


Figure 5. Geographic distribution of the number of valid species names (A) and the total number of Orthoptera names (B). In (A), dark red colours indicate higher richness of valid species names, while light beige regions indicate lower richness. In (B), dark regions present higher total numbers of names (i.e. number of valid species names + number of associated synonymous names), while light colours indicate a lower total number of names.

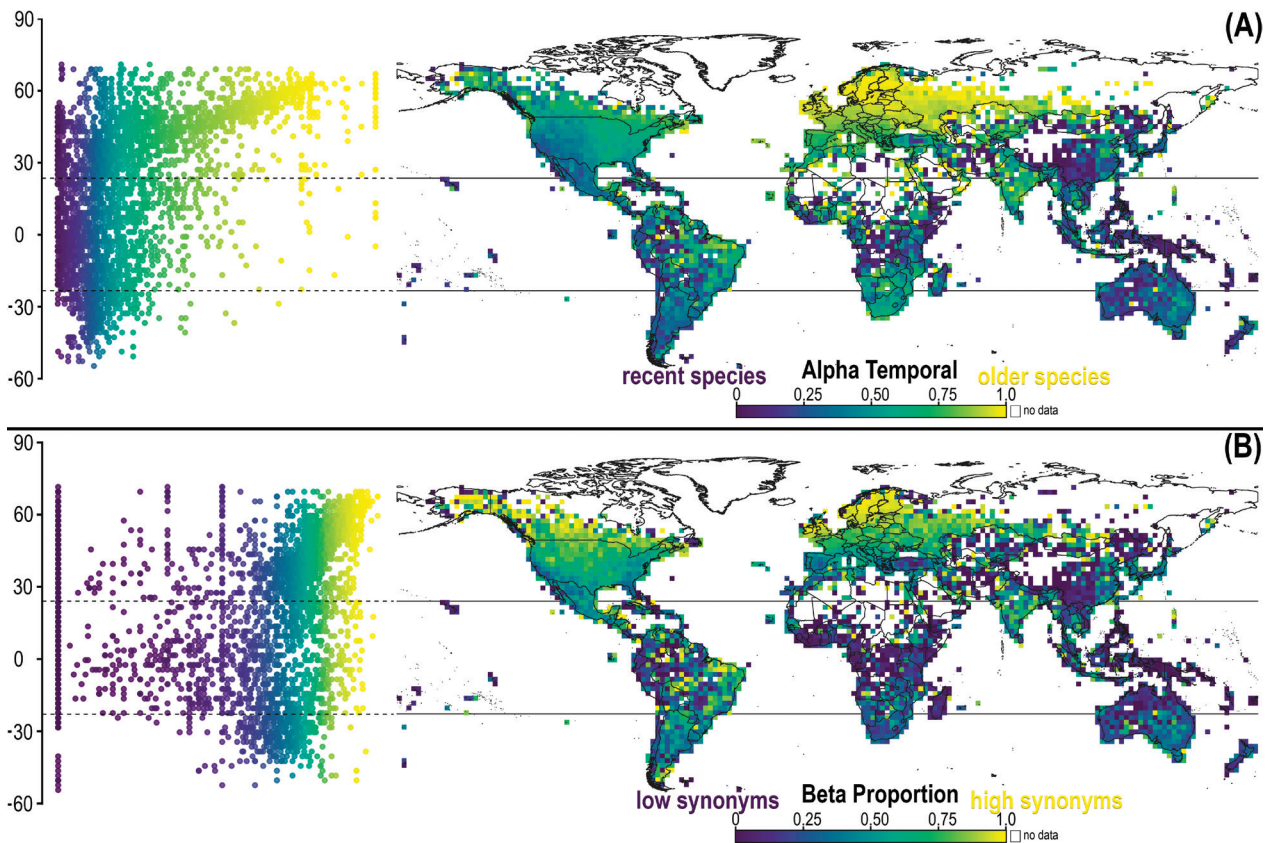


Figure 6. Spatial distribution of Alpha Temporal (A) and Beta Proportion (B) indices for Orthoptera names. In (A), yellow and green indicate older species names, blue represents more recent species names. In (B), yellow and green indicate a higher number of synonyms associated with valid species names, while blue corresponds to regions with lower proportions of synonyms.

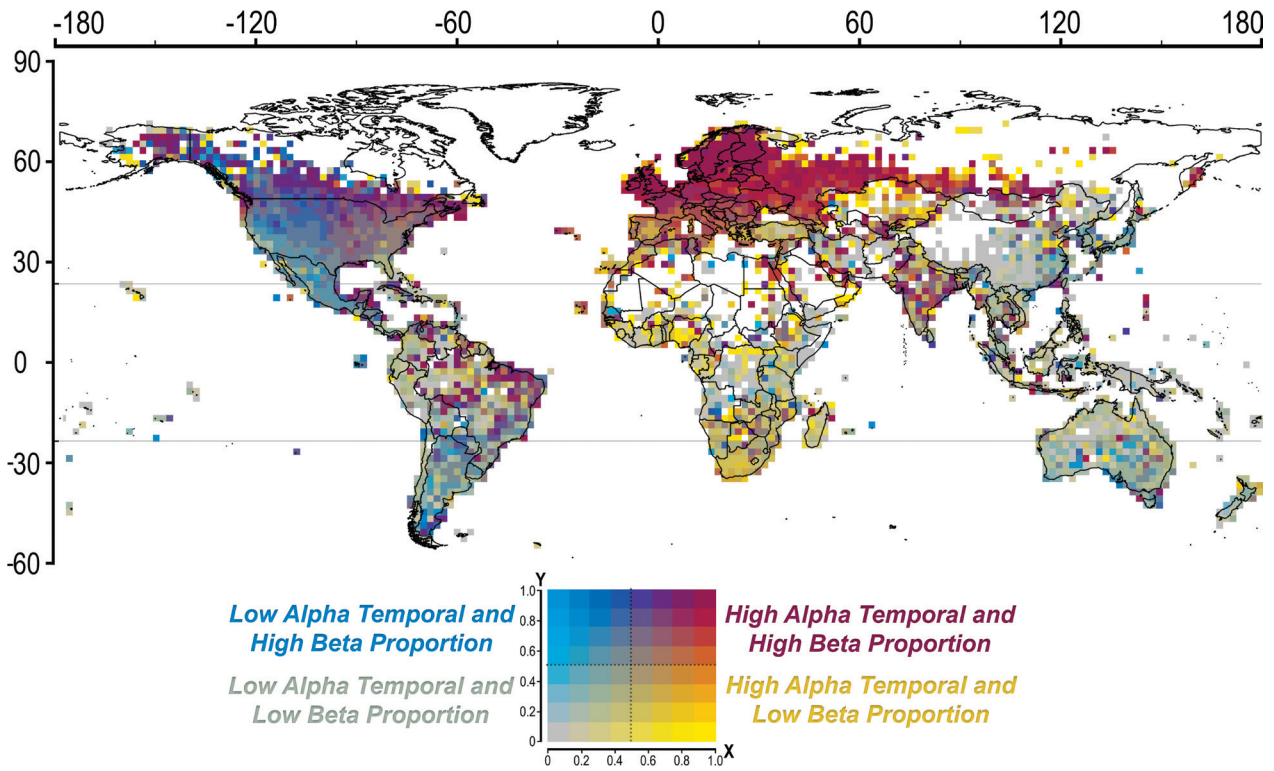


Figure 7. Taxonomic knowledge status map resulting from the combination of alpha temporal (AT, X axis) and beta proportion (BP, Y axis). Regions in blue indicate high numbers of recently described species and synonyms; regions in purple indicate older species names together with many synonyms; regions in grey indicate recent species and few synonyms; and regions in yellow indicate older species and few synonyms.

from reaching a near complete knowledge of the global diversity of this order. However, also importantly, the decline in the number of recorded synonyms over time may reflect a maturation of taxonomy, compared to previous decades. These results reinforce the essential and irreplaceable role of taxonomists, highlighting the need to address new species discoveries, but also that it is crucial that they go hand-in-hand with taxonomic revisions, especially considering the variation across taxonomic groups and the spatial heterogeneity of these patterns, as well as the adoption of new characters for species delimitation (see below).

Since 2014, the number of taxonomists describing new species actively working on Orthoptera has surpassed the mark of 100 (counting all taxonomist authors by valid species name). Currently, each taxonomist describes, on average, between 5 and 10 species per year, often in collaboration with other taxonomists. Although these figures may seem modest, it has driven the description of 200 to 400 new species per year. These findings indicate that Orthopterology is becoming an increasingly collaborative science and that training new taxonomists is essential if we are to catalogue the majority of species before they possibly become extinct in the Anthropocene. Therefore, maintaining this number of active specialists and an active collaboration network amongst them could be strategic goals for 'The Orthopterists' Society', which, in addition to meetings, may be achieved through international specialisation courses that train taxonomists from different parts of the world.

Spatial trends in species description and taxonomic efforts in Orthoptera

The accumulation of valid species names after World War II does not apply uniformly across all groups within this order. For instance, both the number of taxonomists and the rate of species descriptions have declined since the 20th century for Acridomorpha, which comprises approximately 9,000 species (about one-third of all known Orthoptera species) (Amédégnato and Devriese 2008; Song 2010). This decline is also evident at the geographical scale, particularly in regions that were once supposedly well studied (i.e. yellow zones), but are now taxonomically neglected or lack trained taxonomists focused on local biodiversity. However, this may also be a sign of progress and that most species in this group are now described and undescribed species are less frequently discovered. More broadly, progress in taxonomy has been uneven across global regions and taxa (Stropp et al. 2022; Stropp et al. in press; Guedes et al. 2025), as exemplified in the present study on Orthoptera.

The accumulation of synonyms and the proportion of synonyms described per year have declined, particularly since the second half of the 20th century. This trend likely stems from two opposing factors, which can influence the systematics of Orthoptera in different ways. On the one hand, certain regions (e.g. Europe and Southeast Asia) appear to have reached a consolidated knowledge as extensive phylogenetic studies and taxonomic revisions

have been undertaken in recent decades which will have corrected many synonyms. On the other hand, in regions where taxonomy, arguably, remains in its early stages (i.e. grey areas), the decline may indicate a deficiency in synonymy detection, despite the ongoing description of new species. This limitation may introduce an additional source of uncertainty in biodiversity studies (Haila et al. 2014; Guedes et al. 2025), particularly in taxa and regions lacking comprehensive phylogenetic studies and taxonomic revisions (Guedes et al. 2020, 2023, 2025; Stropp et al. 2022). Moreover, it may affect macroecological and biogeographic patterns, as these analyses rely on accurate species lists and well-defined monophyletic groups (Isaac et al. 2004; Jones et al. 2012).

One significant factor influencing global taxonomy in recent decades is the availability and accessibility of online databases. Their benefits include maximising access to species descriptions, taxa distributions, data infrastructures and community discussions (Hobern et al. 2019). For Orthoptera, the most valuable database is the Orthoptera Species File (OSF), which had its initial version available online in 1997. To date, the OSF catalogues 30,206 valid species (including 29,294 extant species) and contains approximately 115,000 species images and 97,000 specimen records. In addition to online databases, an increasingly detailed species description, including high-quality images and DNA barcoding (Bisby et al. 2002), has contributed to a reduction in errors or gaps within alpha taxonomy in recent years. Consequently, fewer synonymies are being detected by beta taxonomy.

The increasing number of Orthoptera taxonomists over time results from various social and traditional factors. In some cases, it reflects the continuity of established taxonomic schools, where senior taxonomists often train networks of new taxonomists in specific taxa. Collaborative practice in taxonomy is also relevant (see Costello et al. (2012)), when it often involves field collectors sampling new species and senior taxonomists describing them in the lab. Ideally, in these cases, all of them are recognised as authors. Historical events have also influenced taxonomic activity. For instance, the First and Second World Wars led to a decline in both the number of taxonomists and the average number of species described per researcher (see Costello et al. (2012)). Similar impacts have been documented in the study of Chinese flora, global monocotyledons, European spiders and butterflies (Lu and He 2021) and fungi (Cunningham et al. 2024), consequently affecting the rate of documented synonymies.

Mapping the status of Orthoptera taxonomy

The taxonomic status varies significantly across the world, depending on the taxa (Stropp et al. 2022; Guedes et al. 2025). Nonetheless, some general patterns can be inferred. In terrestrial vertebrates, for instance, tropical regions (e.g. the Tropical Andes, the Atlantic Forest in Brazil, Mesoamerica, the West Indies, eastern Africa, Madagascar, southern

India and Sri Lanka and Southeast Asia) stand out due to the high number of taxa yet to be discovered and described. In contrast, most temperate regions, such as North America, Europe and northern Asia (e.g. Russia), have already documented the majority of their taxa (see Moura and Jetz (2021)). For invertebrates, the global scenario is more complex, given the vast number of undescribed species, particularly amongst arthropods, including millipedes, arachnids and insects (Mora et al. 2011).

For Orthoptera, the tropical regions contain the majority of recently described valid species, with fewer associated synonyms. This supports the previous hypothesis that these regions still require extensive taxonomic revisionary efforts (i.e. beta taxonomy), given the continued under-representation of their estimated species richness. On the other hand, temperate regions are dominated by older valid species names and a higher proportion of synonyms, reinforcing the idea that beta taxonomy is more prevalent in these areas.

The widespread distribution of areas with recent names and few synonyms reflects an emerging orthopteran alpha taxonomy, but little beta taxonomy, characterised by species discoveries which are not yet accompanied by comparing taxa across regions and refining their classifications through taxonomic revisions. This can be attributed to a historical shortage of taxonomists in megadiverse regions – the taxonomic impediment *sensu* Engel et al. (2021), which results in that, in particular for the richest taxa, species diversity has so far outpaced the available taxonomic expertise. Due to this, many tropical areas, such as South America, South-East Asia and Australasia, are currently undergoing extensive activity in alpha taxonomy. However, besides the lack of taxonomic research, this task is also hampered by the location of most of the reference natural history collections in countries from mainly temperate regions, which still store much of the material collected in tropical regions by early naturalists (Hawksworth 1995; Bakker et al. 2020; Raja et al. 2021; Weber 2021) (see Suppl. material 7: appendix S3, fig. S4A). This scenario can be understood as a taxonomic impediment, creating a logistic obstacle for researchers from tropical regions, who often need access to type material deposited in Old World collections to advance their taxonomic revisions (e.g. Raja et al. (2021); Nakamura et al. (2024); Suppl. material 7: fig. S4B). In the case of Orthoptera, the impact of this effect of scientific colonialism is partially minimised due to the availability of extensive type data (i.e. photos and drawings) within the Orthoptera Species File (OSF), compared to other taxonomic groups that lack these resources.

This contrasts with the situation in the historical centres of taxonomic research, as in Europe or North America, for instance, which are currently more active on beta taxonomy. These areas already hold a long history of taxonomic efforts, with a large number of taxonomic changes that result in a combination of older valid names and many synonyms. It is most likely that these regions are taxonomically saturated to some extent, with a significant proportion of their actual species richness already known, described and included in taxonomic reviews or catalogues

(see Green (1998); Heller et al. (1998); <https://www.grasshoppersofeurope.com/>). Indeed, most temperate regions are taxonomically well-studied and thoroughly documented for the majority of the Orthoptera fauna (see Waloff and Popov (1990); Song (2010)). Thus, there the current focus is on either refining existing knowledge by describing species from remote areas and inaccessible habitats, such as caves and mesovoid soil substrate or conducting broader analyses on systematics and evolutionary relationships, using state-of-the-art techniques such as “omics” (e.g. phylogenomics, museomics or transcriptomics; Song et al. (2020); Kociński et al. (2021); Kim et al. (2024a)).

A large number of areas hold, on average, recent names and numerous synonyms. In these regions, the active research in both alpha and beta taxonomy couples the discovery of new species with taxonomic reviews and the publication of synonym lists. In some regions, such as in North America, these areas are adjacent to territories with older names and a large proportions of synonyms. This may indicate that, although regional checklists were previously thought to be complete (e.g. Song (2010)), the fine-scale exploration of these territories may still uncover previously unknown taxonomic gaps that end up in the discovery of new species (see Castro-Souza et al. (2024)). Such discoveries have likely been facilitated in the USA by the high presence of reference biological collections and the quantity of Orthoptera types deposited in their natural history collections (see Suppl. material 7: appendix S3, fig. S4A, B). In certain countries and regions, these taxonomic contributions stem from the enduring legacy of local senior taxonomists, who play a crucial role in training new taxonomists. This, in turn, helps sustain the tradition of Orthoptera taxonomy and ensures its relevance in these regions. In other parts of the Globe, some regions possibly reflect legacies of European colonialism in megadiverse locations (Weber 2021) or higher levels of international scientific collaboration. In any case, this level of taxonomic development is less concerning than that of areas where only alpha taxonomy has been conducted. Behind the large number of synonyms and recent valid names in these areas may lie studies utilising an integrative and more modern taxonomic approach, such as bioacoustics and/or molecular techniques (e.g. Braswell et al. (2006); Nattier et al. (2011); Husemann et al. (2013); Heller et al. (2017); Riede (2018); Uluar et al. (2021); Kim et al. (2024b)), which are based on novel criteria and species concepts that end up generating numerous taxonomic adjustments even in well-known species.

Very few areas hold a combination of older names and few synonyms, which indicates only past inventory effort, but little or no revisionary work. This may be due to two distinct, yet non-complementary, phenomena. In the best-case scenario, in these areas, current taxonomic knowledge comes from studies that produced classifications well-structured in terms of nomenclature and taxonomic relationships in the past, which have persisted until the present day, even with evidence coming from new taxonomic approaches. Alternatively, the current regional checklists

in these regions come from taxonomic work conducted in the past that has not been revisited or revised later on. Importantly, a significant part of these areas is distributed in countries where socio-political impediments have occurred in the past or are occurring nowadays (Institute for Economics and Peace 2024). This not only hinders inventorying their biodiversity (Hanson et al. 2009), but also impacts taxonomy due to lack of trained taxonomists, low and discontinued investment and the discouragement of research and collaboration from international taxonomists due to high personal security risks and logistical issues (see Hilario-Husain et al. (2024)). This type of taxonomic status is the most critical, compared to the other types identified here and the areas holding it require strong attention from the taxonomic community. In areas lacking capacity or investment, these efforts could be facilitated by creating partnerships with local scholars and institutions (see Hanson et al. (2009)), even in the absence of regional Orthoptera taxonomists. Other areas holding such a status in impediment-free countries, such as Canada, Australia, New Zealand and some small parts of Europe (Institute for Economics and Peace 2024) correspond to spatial gaps within well-known regions and could be easily revisited by regional taxonomists.

Biases and historical patterns in the global taxonomic knowledge

It is worth noting that the global distribution of taxonomic knowledge depicted by our work is not only the result of taxonomic work, but also of sampling effort. Regions with frequent field surveys tend to have more species recorded in their checklists, leading to more opportunities for taxonomic effort, such as the identification of new species or the revision of already described ones. Conversely, areas with historically low levels of sampling effort can appear under-represented in terms of the occurrence of newer species simply because fewer surveys have been conducted there, not because they have fewer species. The regions with continuous taxonomic effort often have a history of consistent sampling and research investment, leading to more refined taxonomic studies (Wege et al. 2015; Wilkinson et al. 2021). Thus, while we recognise the key role of sampling effort in determining the accumulation of both valid species names and synonyms, we believe that the observed patterns provide a meaningful indication of the history and intensity of the taxonomic research across the world.

This relationship between sampling effort and taxonomic progress is further reflected in how species names are distributed globally. The indices of alpha and beta taxonomy rely on the spatial distribution of valid species names around the world. However, most species distribution data are limited to fieldwork observations and digitised records from natural history museums. In general, these limitations tend to bias species occurrences toward roads, navigable rivers and major cities, leading to spatially skewed sampling efforts (Kadmon et al. 2004; Moerman

and Estabrook 2006; Boakes et al. 2010; Vale and Jenkins 2012; Sousa-Baena et al. 2014; Tessarolo et al. 2014; Oliveira et al. 2016). Additionally, other social and geographic factors can further constrain the accuracy and availability of these data, such as uneven financial and institutional resources across different regions of the world and a lack of international scientific collaboration (Moerman and Estabrook 2006; Boakes et al. 2010; Vollmar et al. 2010; Ahrends et al. 2011; Amano et al. 2013; Yang et al. 2014).

In this context, it is not surprising that regions with a higher concentration of natural history museums tend to have a lower proportion of undescribed species (Linnean shortfall) and better-documented occurrences of already described species (Wallacean shortfall). Supporting this inference, the largest natural history museums are located in North America and Europe. Indeed, most museums that house more than 1 billion objects (e.g. natural and cultural collections) are found in either the USA or central and northern Europe (Johnson et al. 2023).

Most of America was the target of expeditions by European naturalists focused on inventorying natural resources and, amongst them, species (Egerton 2006, 2007). The patterns unveiled by our analyses corroborate that the global taxonomic status has been directly or indirectly shaped by the history of biodiversity explorations. In general, there is a latitudinal gradient of decreasing survey completeness from temperate to tropical regions, as observed in other animal and plant groups (Mora et al. 2007; Meyer et al. 2015, 2016; García-Roselló et al. 2023; Chanachai et al. 2024). In Orthoptera, data on species distributions show low survey effort, taxonomic refinement and temporal coverage in tropical regions, whereas temperate regions present areas of relatively high data quality, albeit with significant deficiencies in most of temperate Asia, South America and Africa (Castro-Souza et al. 2024).

Based on our results, this latitudinal gradient also reflects in well-known regions holding revisions (old AT and high BP), indicating the influence of, for instance, European expeditions in America over time on the representation of fauna. These expeditions typically landed on the eastern coast of the Americas and moved inland, documenting the biodiversity of the New World (Vanzolini 1993, 1996). This is somehow mimicked by the latitudinal gradient shown by poorly-developed old taxonomies (old AT and low BP) reflecting the efforts of naturalists from that era to document the biodiversity of the Old World, although these efforts have not continued into the present day. In contrast, the areas with recent AT and high BP evidence the existence of a new wave of biodiversity researchers that revise the classification at the same time as they describe species, many of them academic descendants of local taxonomists. Nonetheless, although we only analysed Orthoptera taxonomy, the situation is likely to be quite similar for other arthropod groups with historical taxonomic studies in tropical regions primarily conducted by European and North American researchers, such as spiders, mites, millipedes, centipedes and many others (Jacinavicius et al. 2018; Iniesta et al. 2023a, b; World Spider Catalog 2024).

Conclusions

Even though taxonomy has played a pivotal role in biological science since the 18th century proposal of Linnaeus' *Systema Naturae*, assessing the current status of taxonomic knowledge for any taxon remains crucial. It helps identifying understudied and undersampled areas requiring further attention and anticipates future trends in systematics, especially in relation to related fields such as molecular phylogenetics, biogeography and ecology. In general, spatial biases in both alpha and beta taxonomy can be influenced by various factors, including a lack of funding for monitoring and biodiversity studies and the shortage of trained taxonomists. Importantly, taxonomic advancements have largely been driven by increased knowledge from regions with consolidated and emerging research groups, for Orthoptera and other arthropod taxa. This is evident in regions with high alpha temporal and beta proportion, which are known for having historical zoological collections, curatorial assistance and scientific funding. In this sense, species richness revealed through taxonomic studies is not only linked to biodiversity patterns, but also driven by social, cultural and political factors, such as governmental funding, logistical challenges, the exodus of type material from its original locality and the shifting priorities of different historical periods.

We show that mapping the status of taxonomic knowledge allows the identification of regional trends in species description and revision. For the order Orthoptera, our model highlights that, in South America, Africa, Southeast Asia and Australasia, taxonomic efforts are needed not only for species description, but also for reviewing and integrating phylogenetic and biogeographic studies. Bearing this in mind, in the short term, tropical zones in grey and yellow in our map should prioritise alpha taxonomy, as these areas have a large species debt. In the long term, however, these same regions will need to advance towards the development of beta taxonomy, allowing for the revision and refinement of existing taxonomic knowledge. Additionally, we suggest that, in the short term, tropical zones in purple should be revisited by contemporary taxonomists, as these areas have great potential for the discovery of new species, especially through integrative approaches.

With this work, we aim to provide a foundation for exploring future challenges in Orthopterology, for both established taxonomists and new trainees, as well as for ecologists and biogeographers. However, more importantly, the framework presented here brings together taxonomy and macroecology in an accessible way for biodiversity studies in the era of Big Data.

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Author contributions

R.A.C.S., J.S., T.S.S. and J.H. conceived the study with input from all authors; investigation, all authors; data curation, R.A.C.S., T.S.S. and J.H.; formal analysis, R.A.C.S., T.S.S. and J.H.; visualisation, R.A.C.S. and J.H.; funding acquisition, J.A.D.F., T.S.S. and J.H.; writing – original draft, R.A.C.S., T.S.S., L.I. and J.H.; writing – review and editing, J.S., L.I., R.J.L., G.T., N.S. and J.A.D.F.; All authors have read, discussed the results and approved the final manuscript.

Data accessibility statement

The datasets used in this study are available in the supplementary material. The most updated versions of the original data can also be downloaded from Catalogue of Life (CoL), Orthoptera Species File (OSF) and Global Biodiversity and Information (GBIF). The underlying code for this study is not publicly available, but may be made available to qualified researchers on reasonable request from the corresponding author.

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Supplementary materials

Supplementary material 1

Orthoptera data available in Catalogue of Life (table S1) (.tsv)

Link: <https://doi.org/10.21425/fob.18.145455.suppl1>

Supplementary material 2

Fossil Orthoptera data available in Catalogue of Life (table S2) (.xlsx)

Link: <https://doi.org/10.21425/fob.18.145455.suppl2>

Supplementary material 3

Orthoptera occurrence available in Orthoptera Species File (table S3) (.csv)

Link: <https://doi.org/10.21425/fob.18.145455.suppl3>

Supplementary material 4

Orthoptera occurrence available in Global Biodiversity Information Facility (table S4) (.7z)

Link: <https://doi.org/10.21425/fob.18.145455.suppl4>

Supplementary material 5

Orthoptera occurrence filtered in Orthoptera Species File (table S5) (.zip)

Link: <https://doi.org/10.21425/fob.18.145455.suppl5>

Supplementary material 6

Orthoptera occurrence filtered in Global Biodiversity Information Facility (table S6) (.zip)

Link: <https://doi.org/10.21425/fob.18.145455.suppl6>

Supplementary material 7

figure S1: Sensitivity analysis between synonyms and valid species names; figure S2: Density curves of alpha temporal and beta proportion indices; figure S3: Correlation between the number of valid species names and the total number of names; figure S4: Distribution of global scientific collections and types of Orthoptera; appendix S1: The ‘nomenclatural’ lumping; appendix S2: Assessing the sensitivity of alpha temporal and beta proportion indices; appendix S3: Distribution of global scientific collections and types of orthoptera (.docx)

Link: <https://doi.org/10.21425/fob.18.145455.suppl7>