



Who is working on ant physiology? There is room to improve international collaborations

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Abstract

Ants are an abundant and diverse group with worldwide distribution. Given their omnipresence, ecosystem services, and potential applications, ants may be excellent models for multiple lines of research such as physiology. However, the focus and worldwide distribution of ant physiology research are unknown. Given the evidence of scientific colonialism in multiple scientific areas – where credit and reward are not given to local scientists from developing nations when scientists from wealthier nations travel for research – we examined the potential for such trends in studies of ant physiology. We investigated the frequency of studies and collaborations across countries during 2015 - 2019, which simultaneously allowed us to estimate the most studied taxa.

We found that the largest proportion of studies was done in Europe and North America. Collaboration trends were mainly among high-income countries. Nearly one third of the countries that served as sampling sites were not represented in authorship (mostly low- and middle-income). Furthermore, low- and middle-income countries show a lower proportion of authorship or co-authorship when these countries served as sampling sites, as compared with high-income countries. This disparity might indicate scientific colonialism in the field. However, collaborations between institutions from the sampling country and their foreign counterparts increased with the per capita Gross Domestic Product, suggesting a link between country's participation in international collaboration and its economic prosperity.

How publications are circulated may further influence trends in scientific colonialism. Both the probability that a study reaches the public sphere (Altmetric) and the number of citations increase with the impact factor (IF) of the journal in which the article was published. Unfortunately, high-IF journals often show the highest Article Processing Charges, which can be a financial impediment for institutions in low- and middle-income countries. Our study highlights factors that influence the process of research in this field. The evidence of scientific colonialism in ant physiology that we highlight in this study calls for urgent measures to promote more equitable collaborative efforts.

Key words: Altmetric, ant physiology, Formicidae, global science, Hymenoptera, impact factor, parachute science, systematic review, scientific colonialism.

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Introduction

Ants are one of the most dominant groups of insects distributed in many distinct habitats, ranging from arctic to tropical ecosystems, as well as desert areas (COLEMAN & WALL 2015). They are estimated to make up to 25% of animal biomass (HÖLLDOBLER & WILSON 1990), highly diverse, with 16,506 species described worldwide (ANTWEB 2021). Given that ant colonies often contain large numbers of workers and occupy many different habitats and niches, ants can provide important ecosystem services such as pollination (GÓMEZ & al. 1996), seed dispersal (HORVITZ & BEATTIE 1980), bioturbation by moving large amounts of soil (TSCHINKEL & SEAL 2016), control of other insect populations (OFFENBERG 2015), and even influence the diversity of other organisms (WILLS & LANDIS 2018). These processes may directly or indirectly affect the flow of energy and matter in the ecosystem (FOLGARAIT 1998). In addition, the ecosystem services provided by ants are relevant for both natural and agricultural landscapes (ELIZALDE & al. 2020). Although the importance of studying ants is clear, information about the distribution of studies per country or region is mostly unknown. According to historic trends in scientific colonialism relating to other biological lines (VARSAVSKY 1967, ASASE & al. 2021), rich countries collect study organisms in poorer countries whilst receiving all the benefits of that research. Moreover, there is a negative correlation pattern between ant diversity and economic growth (SACHS 2001, ECONOMO & al. 2018). Altogether, this led us to examine whether scientific colonialism is taking place in ant research and what mechanisms may be driving it.

All the ecosystem services mentioned above ultimately involve physiological aspects of the ants. In a conservation context, ants' physiological tolerance to temperature can be an important predictive tool for modeling responses to climate change (DIAMOND & CHICK 2018). Moreover, understanding the physiology of ants may provide technological improvements for humans. For instance, REDDY & al. (2011) highlight the potential applications of the unique hollow nanofiber membranes produced by the ant *Oecophylla smaragdina* for tissue engineering and other medical and biotechnology applications. In addition to the current therapeutical applications of some of ants' venoms (KOU & al. 2005), their venoms are another promising area of research for pharmacological applications, providing the possibility of discovering new functional molecules or drug candidates (TORRES & al. 2013, TOUCHARD & al. 2016). Ant venoms are currently being studied as potential sources of novel bioinsecticides, therapeutic agents, antimicrobial substances, among others (TOUCHARD & al. 2016). Therefore, physiological studies, together with the study of behavioral, physical, and the life-history traits of ants are relevant, in order to explore potential new benefits that may address human problems (ELIZALDE & al. 2020).

Despite the evident importance of studying ant physiology, information about the distribution of studies per country, region, or taxon (subfamilies, genus, species) is mostly

unknown. For instance, by analyzing the distribution of studies on urban ants, SANTOS (2016) found a scarcity of studies in tropical regions and Eastern Europe. Likewise, studies on other social insects, like bees, seem to follow similar trends with most studies carried out in USA and Europe (CULLEN & al. 2019). This led us to the hypothesis that ant-physiology studies may follow similar trends. In this light we focused specifically on whether high-income countries tend to collaborate with low- and middle-income countries on publications when these countries are used as sampling sites. If low- and middle-income countries show a lower proportion of co-authorship when being used as sampling sites, then this could be an indicator of scientific colonialism (also known as neo-colonial science, colonial science, parachute science, or helicopter research, among others; DAHDOUH-GUEBAS & al. 2003, MINASNY & al. 2020). Understanding trends in scientific colonialism can help to create the tools to eradicate the practice. For example, reducing scientific colonialism through international collaborations can build scientific capacity in low- and middle-income countries, which benefits them as the generation of knowledge has always been a key component of economic growth and welfare (WAGNER & al. 2001). Moreover, international collaborations can promote the advancement of science by researchers learning from and helping each other, broadening knowledge and the opportunity for multidisciplinary research, among others (DUSDAL & POWELL 2021).

We are aware that variations exist within the expression of scientific colonialism; for instance, settler colonialism in which scientists take over land to develop scientific infrastructures with complete disregard of indigenous populations (PRESCOD-WEINSTEIN & al. 2020); or extractive colonialism which does not entail permanent occupation but extraction of material (MONARREZ & al. 2022). Another form of scientific colonialism is where local scientists do field work and collect data, while foreign collaborators do all the analytical work (DAHDOUH-GUEBAS & al. 2003, BOSHOFF 2009). Our study defines "scientific colonialism" as when foreign authors from high-income countries sample ants in low- and middle-income countries and publish the results without collaboration with any researchers from local institutions and akin to extractive colonialism. Evidence of this in other lines of biology has been observed within North American ecologists working in neotropical countries and European ecologists working in Asia and Africa (STOCKS & al. 2008, RABY 2017, BAKER & al. 2019). In a similar vein, collaborations in biodiversity studies are predominantly between countries located in North America and Europe (TYDECKS & al. 2018). In contrast, some authors have started to promote the use of more inclusive and ethical collaborative practices, decolonializing their research (RADCLIFFE 2017, TRISOS & al. 2021).

Therefore, to evaluate whether some form of scientific colonialism occurs in the study of ant physiology, we used a systematic approach to evaluate the number of studies on ant physiology per geographical region during a five-year period (2015 - 2019). In this approach, we investigated

which countries had published research on ant physiology in that period, which countries were the most prevalent locations for collecting ants, and which ant taxa are the most studied. Moreover, we searched for specific evidence of collaboration by assessing whether the affiliation of authors in the publication included the sampling country where the ants were collected. We evaluated whether the probability of at least one co-author being from the sampling country had a correlation with the per capita Gross Domestic Product (GDP) of the sampling country. Altogether, these results can indicate whether capacity building through scientific collaborations is provided by high-income countries when sampling ants in low- and middle-income countries, the knowledge of which could assist in developing a more equitable and self-sustaining scientific community (BURGESS & CHATAWAY 2021). Finally, we assessed whether the probability that the information from these studies reaches the public (Altmetric value) depends on factors such as the number of citations or impact factor (IF) of the journal. We performed these two comparisons as an indirect measure to estimate whether researchers from high-income countries obtain more citations and more publicity.

Materials and methods

Web of Science's Core Collection was used to search for scientific articles on physiology of ants during the period from 2015 - 2019 (included in the Science Citation Index Expanded), due to its predominance as a tool for performing meta-analysis in many fields (LI & al. 2018, ZHU & LIU 2020) and its perceived reliability as a source of evidence for systematic reviews (GUSENBAUER & HADDAWAY 2020).

The database was accessed on September 1, 2020. First, a basic search by topic was performed using the following terms: "ant", "ants", or "Formicidae". The search topic was then refined by the inclusion of the following terms: "physiology", "tolerance", "thermoregulation", "metabol", "immunity", "cuticular", "hormone", "neuro", "endocrine", "nutrition", or "exocrine". Only research articles were selected, which resulted in 822 articles. Each article was examined individually to verify that it was in fact related to the physiological processes of ants and to exclude the ones that corresponded to other types of studies. The final database included 295 articles. For each article, the following information was extracted: bibliographic reference, countries of publication (according to the authors' affiliations), sampling country (where ants were collected), and species of ants that were studied. It was assumed that the publication reflects the affiliation to where the research was started even if the researchers subsequently changed institutional affiliation. Additionally, the subfamily of the ants studied in each article was added to the database (obtained from AntWiki, BARR 2014). In addition, the number of citations from each study was retrieved from Google Scholar, the IF of the journal from Journal Citation Report 2020 (CLARIVATE ANALYTICS 2020) and the average per capita GDP in US dollars (USD) for 2015 - 2019 of the

sampling country was retrieved from the World Bank's site (WORLD BANK 2020a). Countries were also categorized as low- (LI), middle- (MI), or high-income (HI), following the World Bank's classification (WORLD BANK 2020b). For simplicity, lower-middle and upper-middle income were pooled as MI. Additionally, the Altmetric value of each article was retrieved, which was sourced from the Smithsonian Library Research tools (<https://library.si.edu/research>). The Altmetric score is a weighted count of the attention that a scholarly article has received and is based on an automated algorithm reflecting the relative reach of each type of source (e.g., Twitter, Facebook, Newspaper; <https://www.Altmetric.com>). The higher the value, the more popular the article is, calculated based on the number of mentions it received in different online sources (MELERO 2015).

Data analysis

Descriptive statistics were used to quantify the frequency with which different ant taxa were studied (divided by species, genera, and subfamilies), the number of publications per country and the number of samplings per country and geographical region (North America, Central America, South America, Europe, Asia, Africa, Oceania). To quantify the most studied families and genera, only ants identified as belonging to a precise species were taken into consideration (partial identifications were not used; e.g., *Camponotus* sp1.), and the species corresponding to each genus and subfamily were counted. To determine the most studied ant species, the number of publications per species was counted.

The "igraph" package (CSARDI & NEPUSZ 2006) in R (R CORE TEAM 2021) was used to build circular and bipartite social networks as a graphical description of collaboration trends. To define whether collaborative work was undertaken between countries, it was noted if the country where the ants were sampled (sampling country) was the same as the country specified in the authors' affiliations. Therefore, if at least one author had an affiliation from the sampling country together with authors from foreign institutions, then it was counted as a collaboration. If institutions from multiple countries were involved, in addition to a local institution, these were counted as different collaborative efforts. For example, if Argentina was the sampling country and the publication contained one author from Argentina, one author from Brazil, and one author from Uruguay, then this would count as one collaboration for Argentina - Brazil and one collaboration for Argentina - Uruguay.

A chi-square test of independence was used to test whether the proportion of countries in an income category was associated with the probability of publishing at least one study (whether published or not). The same test was also used to examine if the proportion of countries in an income category was associated with the probability that at least one collaboration occurred. Finally, the same test was applied to determine whether the proportion of authorships or co-authorships from a sampling country varied in relation to the income category.

A proportion of 1 (100%) indicates that a sampling country participated in all the publications resulting from those samplings, which would indicate no scientific colonialism in a particular income category. Decreases in that proportion for LI and MI countries would indicate increases in trends of scientific colonialism.

In all cases, a Generalized Linear Model (GLM) with a Quasi-Poisson distribution was used as the use of Poisson distribution alone resulted in over-dispersion. A GLM was applied to investigate whether the number of collaborations in which the sampling country participated with foreign institutions was influenced by the natural logarithm of the per capita GDP of the sampling country. A positive correlation between the number of collaborations (with foreign institutions) and the per capita GDP would be a suggestion of scientific colonialism. Also, a GLM was used to investigate whether the total number of publications on this topic from the sampling country was influenced by the natural logarithm of the per capita GDP. A positive correlation would be another indirect indication of scientific colonialism. Additionally, a GLM was utilized to evaluate whether the Altmetric value was influenced by the number of citations, impact factor, and year of publication. Finally, a GLM was used to explore whether the number of citations depends on the IF of the journal and year of publication. The ggplot2 package was used for the figures associated with the GLMs. Effects were considered statistically significant if $P < 0.05$, and all analyses were done in R (R CORE TEAM 2021).

Results

Taxa, country, and region

We counted 479 species of ants (3% out of 16,506 species worldwide, ANTWEB 2021) that were studied in publications on ant physiology during 2015 - 2019. These species belong to 70 genera that are classified in 13 subfamilies. Most of the species belong to the subfamilies Myrmicinae ($n = 208$) and Formicinae ($n = 158$), followed by Ponerinae ($n = 32$) and Dolichoderinae ($n = 31$, Fig. 1A). When comparing the proportion of species studied in each subfamily (as reported in AntWeb), the subfamilies Pseudomyrmecinae (7%), Formicinae (5%), Dolichoderinae (4%), Ectatomminae (4%), and Myrmicinae (3%) possess the highest percentage of species studied. The genera with the most studied species were *Camponotus* ($n = 54$), *Crematogaster* ($n = 47$), and *Formica* ($n = 34$, Fig. 1B). *Solenopsis invicta*, *Lasius niger*, and *Linepithema humile* were among the most studied species, with 24, 21, and 15 publications, respectively (Fig. 1C).

We found that 50 countries served as sampling sites at least once for studies on ant physiology during 2015 - 2019. Out of this total, sampling was done in 27 HI countries, 18 MI countries, and 5 LI countries. The United States is the country where ants were collected most frequently ($n = 67$, Fig. 2A). Other frequent countries were Brazil, Panama, Australia, France, Japan, and Finland, all of them with at least 13 publications (Fig. 2A). North America and Europe were the continents with the most publications

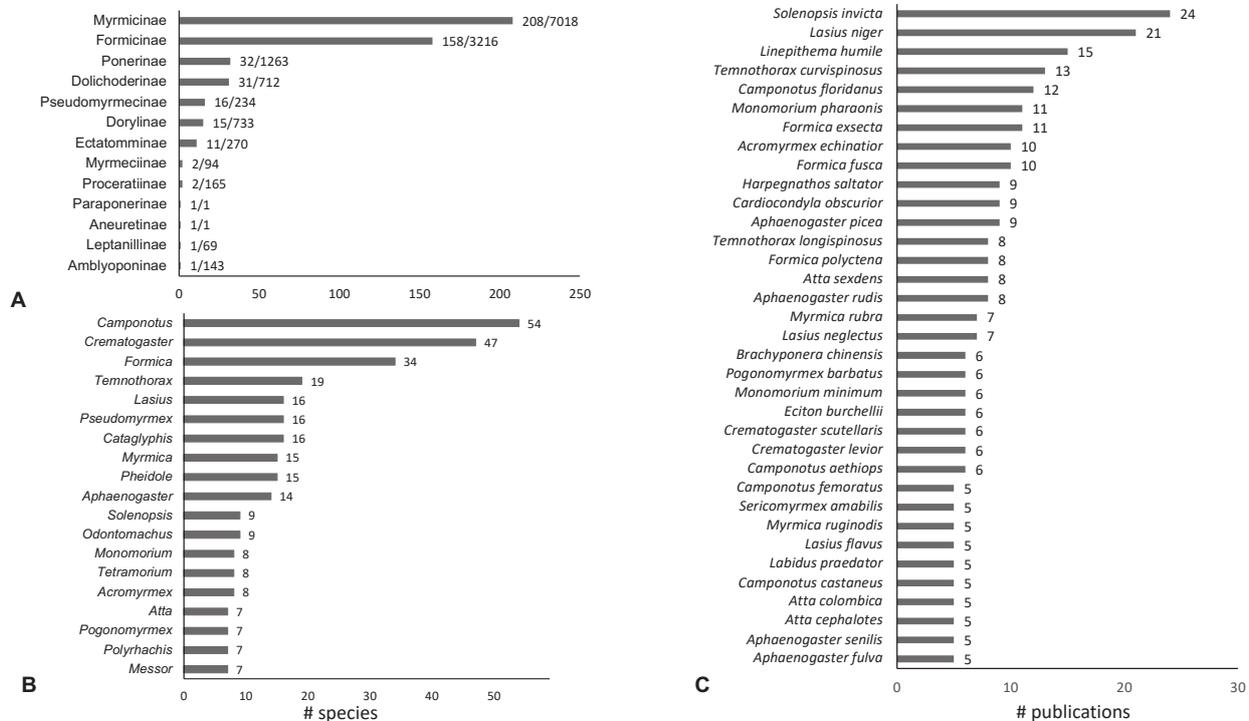


Fig. 1: Number of ant species per subfamily (A) and per genera (B) that were investigated in studies on physiology during the 2015 - 2019 period. In (A), the fraction indicates the number of species found in this review over the total number of species per subfamily, as reported in ANTWEB (2021). In (B), genera with fewer than seven species are not shown. (C) depicts the number of publications on ant physiology per ant species. Species with less than five publications are not shown.

(Fig. 2B), covering 22% and 16% of the species in those regions, respectively (Tab.S1, as digital supplementary material to this article, at the journal's web pages; ANTWEB 2021). Studies on species in the rest of the regions covered between 2 - 6% of the species described in the region (Tab.S1).

Per capita GDP, collaborations, and total publications

Publications on ant physiology, during the period 2015 - 2019, came from 41 countries around the world. In the global context, 2 out of 27 LI countries (7%), 10 out of 110 MI countries (9%), and 24 out of 80 HI countries (30%) published at least one study. This indicates that the income category is associated with the probability that a country publishes a study ($X^2 = 16.5$, d.f. = 2, $p = 0.0003$). For instance, the United States (HI), Germany (HI), Brazil (MI), France (HI), and Belgium (HI) were among the countries with the highest number of publications (Fig. 2C). Additionally, institutions from some countries seem to sample ants more frequently in certain countries than in others, irrespective of whether collaborations occurred (e.g., United States institutions sampling in Panama, Fig. 3).

A number of collaborations between countries can be identified (Fig. 4). When a country serves as a sampling site, the probability that it participates in the publication (authorship or co-authorship) is associated with the income category of the country ($X^2 = 41.9$, d.f. = 2, $p < 0.0001$). When serving as a sampling site, HI countries

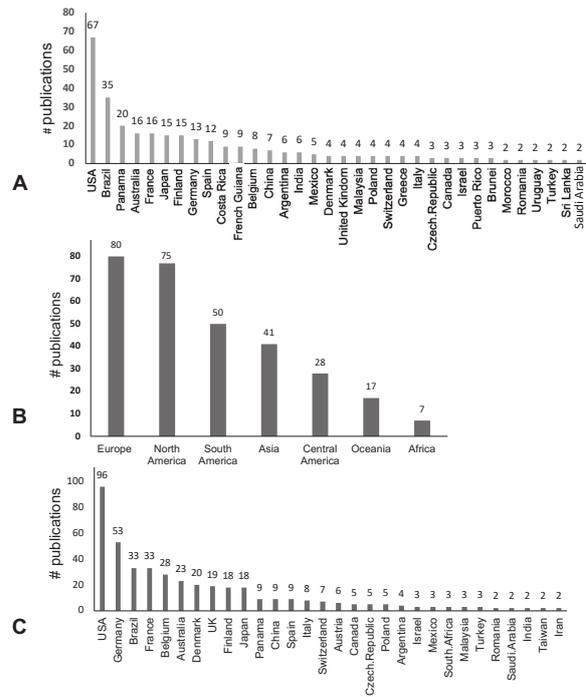


Fig. 2: Number of publications in which different countries served as sampling sites for research on ant physiology during the period 2015 - 2019. In (A), countries with one study are not shown. (B) depicts data from (A) grouped per geographical region. (C) Total number of publications on ants' physiology by country, during the period 2015 - 2019. Countries with one publication are not shown.

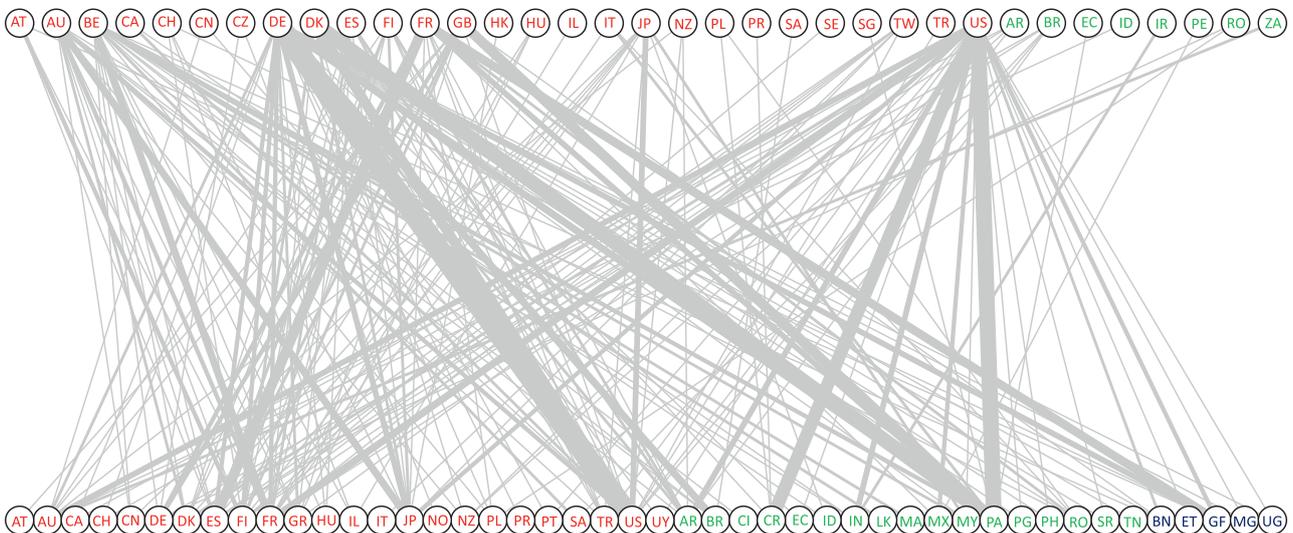


Fig. 3: Bipartite network showing country of author affiliation in a publication (top row) and country where ants were sampled ("sampling country", bottom row), during 2015 - 2019, alphabetically ordered and grouped in high- (red), middle- (green), and low-income countries (blue). The thickness of the line that joins two countries corresponds to the number of times that the country of author affiliation obtained ants from the sampling country. Country codes: AR: Argentina, AU: Australia, AT: Austria, BE: Belgium, BN: Brunei, BR: Brazil, CA: Canada, CH: Switzerland, CI: Ivory Coast, CN: China, CR: Costa Rica, CZ: Czech Republic, DE: Germany, DK: Denmark, EC: Ecuador, ES: Spain, ET: Ethiopia, FI: Finland, FR: France, GB: Great Britain, GF: French Guiana, GR: Greece, HU: Hungary, HK: Hong Kong, ID: Indonesia, IN: India, IR: Iran, IL: Israel, IT: Italy, JP: Japan, LK: Sri Lanka, MA: Morocco, MG: Madagascar, MX: Mexico, MY: Malaysia, NO: Norway, NZ: New Zealand, PA: Panama, PG: Papua New Guinea, PH: Philippines, PE: Peru, PL: Poland, PR: Puerto Rico, PT: Portugal, RO: Romania, SA: Saudi Arabia, SG: Singapore, SE: Sweden, SR: Suriname, TN: Tunisia, TR: Turkey, TW: Taiwan, UG: Uganda, US: United States, UY: Uruguay, and ZA: South Africa.

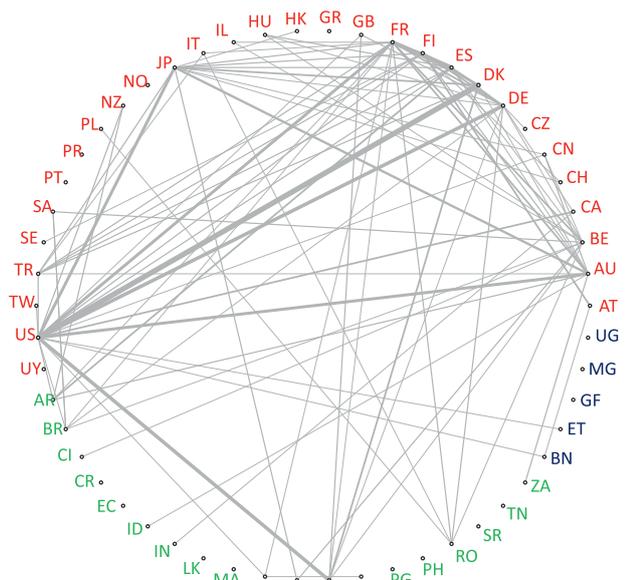


Fig. 4: Circular social network showing collaboration trends between institutions from different countries when at least one institution from the sampling country participated in the publication. Countries with no connections represent sampling countries in which no local institution collaborated with foreign institutions in publications, during 2015 - 2019. See legend in Figure 4 for description of country codes. Country codes in red represent high-income countries, green are for medium-income, and blue are for low-income countries.

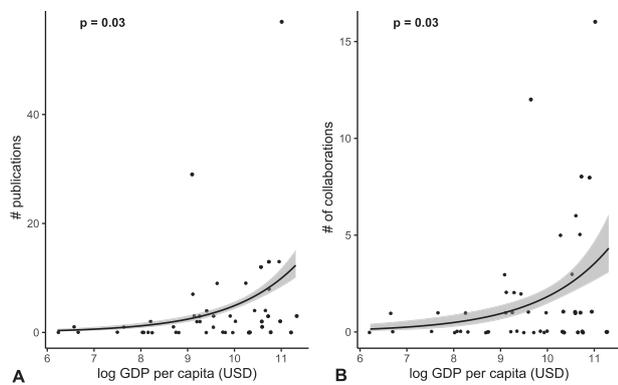


Fig. 5: Relationship between the number of publications in ant physiology and the per capita Gross Domestic Product of the country (log transformed). (A) Number of publications by at least one local institution. (B) Number of collaborations (publications) in which at least one local institution from the sampling country (where ants were sampled) participated with foreign institutions in the publication.

participated in 80%, MI countries in 54%, and LI countries in 13% of the publications that resulted from those samplings. Globally, 2 out of 27 LI countries (7%), 11 out of 110 MI countries (10%), and 26 out of 80 HI countries (33%) collaborated at least once, which indicates a significant association between the income category and the probability of international collaboration ($X^2 = 18.2$,

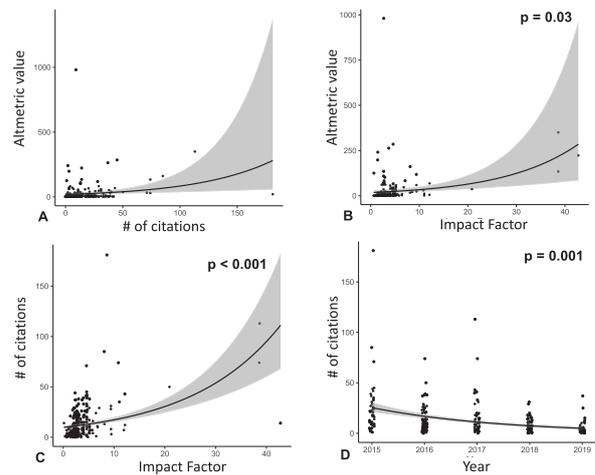


Fig. 6: Relationship between the value of exposure to the public (Altmetric score) of publications on ants' physiology and (A) the number of citations and (B) the impact factor of the journal. Relationship between the number of citations and the IF of the journal (C) and the year of publication (D).

d.f. = 2, $p = 0.0001$). Specifically, there were 16 countries (of 50 countries) that only served as a sampling site (Africa: 4, America: 6, Asia: 2, Europe: 3, Oceania: 1; corresponding to LI: 3, MI: 9, HI: 4) and did not participate in the publication of the study (unconnected nodes in Fig. 4).

The number of publications in which local institutions of the sampling country participated increased with the per capita GDP (GLM, $z = 2.2$, $p = 0.03$, Fig. 5A). The number of collaborations between local and foreign institutions increased with the per capita GDP of the sampling country (GLM, $z = 2.26$, $p = 0.03$, Fig. 5B).

Altmetric, citations, and impact factor

By using the Altmetric value as a proxy, the probability that an article reached the public was not influenced by the number of citations it received (GLM, $t = 1.3$, $p = 0.19$, Fig. 6A) or the year of publication (GLM, $t = 0.55$, $p = 0.58$). However, the probability that an article gained public interest increased with the IF of the journal (GLM, $t = 2.2$, $p = 0.03$; Fig. 6B). The number of citations increased with the IF of the journal (GLM, $z = 11.53$, $p < 0.001$; Fig. 6C) and decreased with the year of publication (GLM, $t = -10.1$, $p = 0.001$, Fig. 6D).

Discussion

Our study highlights trends relating to inequality between low-, middle-, and high-income countries in terms of publications and collaborations. Moreover, our findings also suggest that authors that publish in high IF journals are more likely to obtain publicity, and likely benefit academically from such exposure. At the same time, our results highlight the fact that only a handful of ant species is studied widely at present. Additionally, researchers from most countries in the world seemed underrepresented in the list of authors that publish studies on ant physiology, at least during our study period.

The relatively large proportion of studies with species of Myrmicinae, Formicinae, Ponerinae, and Dolichoderinae is likely related to their higher diversity (BOROWIEC & al. 2020). Additionally, a large number of studies on ants from these subfamilies have been undertaken in temperate zones, indicating that these trends are driven by the high proportion of HI countries in those regions. However, these subfamilies are also common in other parts of the world and their higher diversity makes them prime research targets for the study of physiological responses at the community and ecosystem level. However, less than 2% of the species in Amblyoponinae, Leptanillinae, and Proceratiinae were studied. Species in these subfamilies are rarely found because they have underground or leaf-litter habitats, so that they require special sampling methods (BROWN 1960, MASUKO 1990, LÓPEZ & al. 1994), making them less likely to be used in physiological studies. Additionally, in some cases, their distribution is predominantly in low-income regions (e.g., GUÉNARD & al. 2013), making them even more unlikely to be studied.

Commonality and diversity are often used as criteria for studying a particular genus (Bos & al. 2019). Some of the species richest genera worldwide were among the most studied: *Camponotus*, *Crematogaster*, and *Formica* (ANTWEB 2021). Although identification of genera per country is outside of the main scope of this study, it should be noted that *Camponotus* and *Formica* were studied mostly by HI countries (Fig. 1). The dominance of HI countries in publishing ant physiology studies that we have found, therefore, helps to explain the higher frequency of studies on *Camponotus* and *Formica*. Moreover, their frequent occurrence worldwide in a range of different habitats, spanning natural and agricultural lands (YOUNG & al. 1996, WATT & al. 2002, GRAHAM & al. 2004, FLOREN & al. 2014, TRIYOGO & al. 2020) allows for comparative physiological studies across species – which should favor international collaborations – to reveal evolutionary trends under a variety of environmental conditions (MENZEL & al. 2017, DIAMOND & CHICK 2018).

Overall, the most studied species tend to be invasive species or species that have become model organisms because of their abundance and easiness to keep in laboratory conditions (e.g., *Linepithema humile*, *Camponotus floridanus*, *Lasius niger*, *Monomorium pharaonis*, *Solenopsis invicta*, *Harpegnathos saltator*; SMITH & al. 2009). There is ample opportunity for research in ant physiology with around only 3% of the total species investigated during our study period. Two of the most studied species are worldwide invasive pests: fire ants (*Solenopsis invicta*) and Argentine ants (*Linepithema humile*), which would justify the higher frequency of studies. *Lasius niger* is a preferred species by European researchers because one can easily collect hundreds of queens after their nuptial flights, that produce new colonies under laboratory conditions (PARKER & PARKER 2006).

Only 25% of the countries of the world were sampled at least once during our review period. The top 15 countries publishing work on ant physiology are mostly HI countries

(except for Brazil and Panama), a trend also seen in other lines of research (DAHDOUH-GUEBAS & al. 2003, NATURE INDEX 2020). Despite the higher ant diversity in the tropics (ECONOMO & al. 2018), most tropical regions in the world are the poorest and least studied, as is also the case with studies on ecology and biodiversity (STOCKS & al. 2008, TITLEY & al. 2017). In African countries, for example, we found that only 2% of the species were studied at least once during this period. With such a small proportion of species studied in most LI regions, we can but speculate how much we do not know about ant physiology. How many more discoveries are waiting to happen in barely known species in poorly studied regions? For instance, the desert ant *Cataglyphis bombycina* shows increased protein stability when exposed to acute heat stress (WILLOT & al. 2017). We extrapolate that there may be a myriad of potential applications that might emerge from a better understanding of ant physiology, such as creating protein stability against heat stress in crops or insects of economic importance. Future work may one day allow ideas like these to come true.

Current trends suggest that innovations based on published knowledge on ants will come from HI countries. In our analysis of collaborations, 16 countries (3 LI, 8 MI, and 5 HI) out of 50 countries served purely as sampling sites during our study period. Moreover, we found that there is an increase in number of publications and collaborations in studying ant physiology with per capita GDP of the sampling country. This is similar to what ASASE & al. (2021) found in ecological and conservation studies. However, these correlational trends could be a function of the country's economy. For example, a country's investment in research and development might increase as GDP increases (ANDERSSON & FREDRIKSSON 2018). Nevertheless, our strongest result suggesting scientific colonialism is the lower proportion of times that LI and MI countries participated in publications (13 and 54%, respectively) when the country served as a sampling site, as compared with HI countries (80%). High-income countries tend to dominate publication on ant physiology (52% of studies published by European and North American authors). In a similar vein, the largest proportion of collaborations were in Europe and North America and between them (50%). LI-MI collaborations did not occur, and collaborations between MI countries were scarce (e.g., $n = 1$ for MX-PE). For other regions, only a handful of countries contributed the majority of the overall count of publications: Japan (HI) and China (HI) in Asia, Panama (MI) in Central America, Brazil (MI) and Argentina (MI) in South America, South Africa (MI) in Africa, and Australia (HI) in Oceania. Therefore, our results indicate that this adverse historic trend of dominance by industrialized countries in multiple scientific disciplines (DAHDOUH-GUEBAS & al. 2003) is not improving with time, at least in the study of ant physiology.

Fortunately, researchers and journals in several fields are becoming aware of the importance of reducing global inequalities in science, supporting colleagues and academics from middle- and low-income countries (PETTORELLI

& al. 2021). Best practices in the reduction of such post-colonial dynamics in global scientific research methodology refute such “parachute science” (scientific colonialism) in the field of biodiversity studies (ASASE & al. 2021, HAELEWATERS & al. 2021) which we find equally applicable to physiological studies of insects. It remains unclear whether “scientific colonizers” in ant physiology are implementing any level of capacity building, financial aid, or investment in local infrastructures as a compensation. However, data from other fields suggest that lack of co-authorship often comes with the absence of the aforementioned compensatory capacity building initiatives. The latter would, in some way, serve to establish equitable partnerships, to some extent mitigating the post-colonial dynamic (MINASNY & al. 2020). Future studies should evaluate whether compensatory measures are being implemented in any line of research to decolonialize global academia (e.g., LEPORÉ & al. 2021).

Public exposure to peer-reviewed articles (approximated using Altmetric value) increased with the IF of the journal, following similar trends in medical (CHANG & al. 2019, NOCERA & al. 2019), ecological, and conservation studies (LAMB & al. 2018). Unfortunately, it is common for journals with high IF to have the highest article processing charges (APC, SOLOMON & BJÖRK 2012, YUEN & al. 2019). This consequently places MI and LI academic institutions at a disadvantage as APCs are unaffordable (BURCHARDT 2014, TANG & al. 2017), resulting in their work being less likely to gain a broad audience or recognition. Moreover, our results reveal that the number of citations also tend to increase with IF, as seen in other fields (WEALE & al. 2004, MAMMOLA & al. 2021). This combination of factors perpetuates the cycle in which authors and institutions in HI countries can promote their research to the public, obtaining more citations and prestige, as well as attracting more scientists and funding, generating a type of Matthew effect (BOL & al. 2018). Our study highlights the urgent need to develop capacity building and strengthen research in LI and MI countries.

Conclusion

Ant physiology is a fertile area for research and discoveries. However, reviews, or meta-analysis on aspects of ant physiology that could highlight gaps and guide researchers towards new lines of research are surprisingly scarce (e.g., GRZEŚ 2010, FELDHAAR & OTTI 2020, FERGUSON & al. 2021). Work on poorly known species must be made a priority, given the alarming rates of biodiversity loss worldwide (CEBALLOS & al. 2017) and high threat of habitat destruction of hotspots for discovery of ant species (GUÉNARD & al. 2012). The field's focus on studying only a handful of species for understanding ant physiology is alarming because the poorest countries show the largest proportion of threatened species (TYDECKS & al. 2018) as well as the largest research deficits. This geographic imbalance in research must be addressed by the targeted promotion and support of local institutions and researchers, especially in the LI and MI countries. Complex empirical

methods require sophisticated equipment with significant associated costs. Although the factor of equipment costs was not directly studied, it is a relevant sub-factor within the economic categorization and GDP of the countries involved. The relationship between equipment cost, APCs, and academic grants seems to be exacerbating the gap between researchers in LI, MI, and HI countries. Therefore, research networks should promote and sponsor the use of new technologies by researchers, such as laboratory equipment, in less affluent regions, together with promoting their academic freedom, to reduce the Matthew effect (MERTON 1968). For this, we must develop strategies to ensure that researchers from HI countries try to collaborate with researchers in MI and LI sampling countries. One way would be that publishers ask authors to provide a justification statement in scenarios where ants were sampled from a country without any local co-authors listed.

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Positionality statements

Brenda Sofia Virola obtained her degree in Biology at the University of Panama, and she is currently a master's student in the Entomology program at the University of Panama. She comes from a rural area in Panama where it is very difficult to follow a scientific career as there are not enough institutions dedicated to research, making it difficult to gain experience. To continue her dream of doing research, she moved to the capital, thanks to financial support from several scholarships. She is interested in contributing to the promotion of research collaborations between high- and low-income countries.

Jean Carlos Abrego L. obtained a degree in Biology from the University of Panama, and he is currently completing a master's degree in Entomology at the University of Panama. Jean Carlos can testify that participating in scientific research in Panama is complicated due to the lack of available research centers. In addition, obtaining funding to do basic research, such as systematics and taxonomy, is even more challenging, although he hopes that this will change in the future.

Dilma Castillo obtained her undergraduate degree in Biology at the University of Panama, and she is currently a master's student studying in the Entomology Program at the University of Panama. As a student, she was hampered in applying for funding or job opportunities in scientific research, due to the strict thresholds in English proficiency, level of experience, and quantity of scientific publications. The English language barrier represents a ubiquitous limitation for many students from public institutions when collaborating with foreign academic institutions. Often, available funding is focused more on applied science than on pure science, which limits the freedom to develop research ideas. She truly aspires to become a researcher

and to generate new knowledge, in the fields of molecular biology and medical entomology.

Eleodoro Bonilla is a biology undergraduate student at the University of Panama. He comes from a densely populated, economically disadvantaged area of Panama City. Despite numerous challenges, he has made great progress in promoting the study and conservation of wildlife in Panama, especially by participating in science fairs and related events in academic institutions. One of the main problems that he has come across is the limited support scientists receive in Panama and the lack of attention afforded to nature conservation research there. He believes that the popularization of science is the main bridge between the scientific world and society.

Dumas Gálvez obtained his undergraduate degree at the University of Panama and later obtained a master's and PhD from the University of Groningen (NL) and Lausanne (CH), respectively. He has witnessed both sides of the coin in terms of resource availability for research and he would like to contribute to the promotion of science in Panama; as well as promoting concepts related to global science and the deconstruction of scientific colonialism through international collaborations.

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