# Colonial history and global economics distort our understanding of deep-time biodiversity

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# Colonial history and global economics distort our understanding of deep-time biodiversity

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**Sampling variations in the fossil record distort estimates of past biodiversity. However, compilations of global fossil occurrences used in these analyses not only reflect the geological and spatial aspects of the fossil record, but also the historical collation of these data. Here, we demonstrate how the legacy of colonialism as well as socio-economic factors such as wealth, education and political stability impact research output in paleontology. Researchers in high or upper middle income countries contribute to 97% of fossil occurrence data, not only leading to spatial sampling biases but also generating a global power imbalance within the discipline. This work illustrates that our efforts to mitigate the effects of sampling biases to obtain a truly representative view of past biodiversity are not disconnected from the aim of diversifying our field.**

**paleontology | biodiversity | sampling biases | scientific colonialism | research ethics | scientometrics**

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## Introduction

The fossil record is our only direct evidence of how life on Earth has evolved over time, and reconstructions of deep-time biodiversity using fossil data provide critical insights into future biodiversity change. The fossil record, upon which these reconstructions are based, is known to be incomplete and unevenly distributed across the globe (1–4). Various geological, taphonomic, and anthropogenic factors have been shown to introduce biases into estimates of deep-time biodiversity, extinction and evolution, and decades of research have been dedicated to analytically mitigating their effects (5–8). However, considerably less attention has been paid to how historical, social, and economic factors influence the global distribution of fossil occurrences, and their consequent effects on studies of deep-time biodiversity.

The natural sciences were developed around an extractive process facilitated by European colonialism in the 19th century. When zoological and botanical specimens were uncovered during colonial expeditions, they were typically shipped back to the respective imperial capitals, to be housed in museums, which were rapidly increasing in numbers to accommodate the influx of material (9, 10). Fossils were no exception, and their collection was dominated by imperial systems and exchanges (11). For example, Charles Darwin aboard the HMS Beagle collected fossils in South America that were sent to London and studied by British paleontologists (12). These extractive research practices continue to this day within the natural sciences (13).

Compilations of modern biodiversity data show a clear association between knowledge production and wealthier, more politically stable countries, especially in Europe and Northern America (14). This asymmetry in research makes a clear case for 'scientific colonialism', whereby the centre of knowledge of a certain country is located outside of that specific country (15). Scientific colonialism is often equated with the term 'parachute science', where researchers, generally from higher income countries, go to other countries to conduct research and leave without any engagement with the local community, including local researchers (16). However, parachute science only represents a small part of this issue. Within scientific colonialism, the expertise of local researchers are often devalued and laws within these countries are often disrespected (17). This disjunct creates a dependency on foreign expertise in any field and hinders local scientific development, leading to an unfavorable power imbalance between those from foreign countries and those located 'on the ground'.

Here, we examine the evidence of scientific colonialism in paleontology by exploring the causal relationship between the global distribution of fossil occurrence data and the legacy of colonialism and associated socio-economic factors. We analysed paleontological publications from the last three decades (1990–2020) that have been collated within the Paleobiology Database (PBDB; `www.paleobiodb.org`) (See Material and Methods). The PBDB is used extensively in studies of deep-time biodiversity, especially with the aim of quantifying extinction risk as a result of climate change (18–20), thus representing a significant portion of deep-time biodiversity studies. We assess which countries are the main actors in driving global information asymmetry in paleontology, and whether the accumulation of paleontological knowledge is observed in certain countries or regions. Our goal is to advance discussions on the challenges of working with the fossil record, as it is critical to understand the imbalances in the production of paleontological knowledge and its exchange between geographical regions.

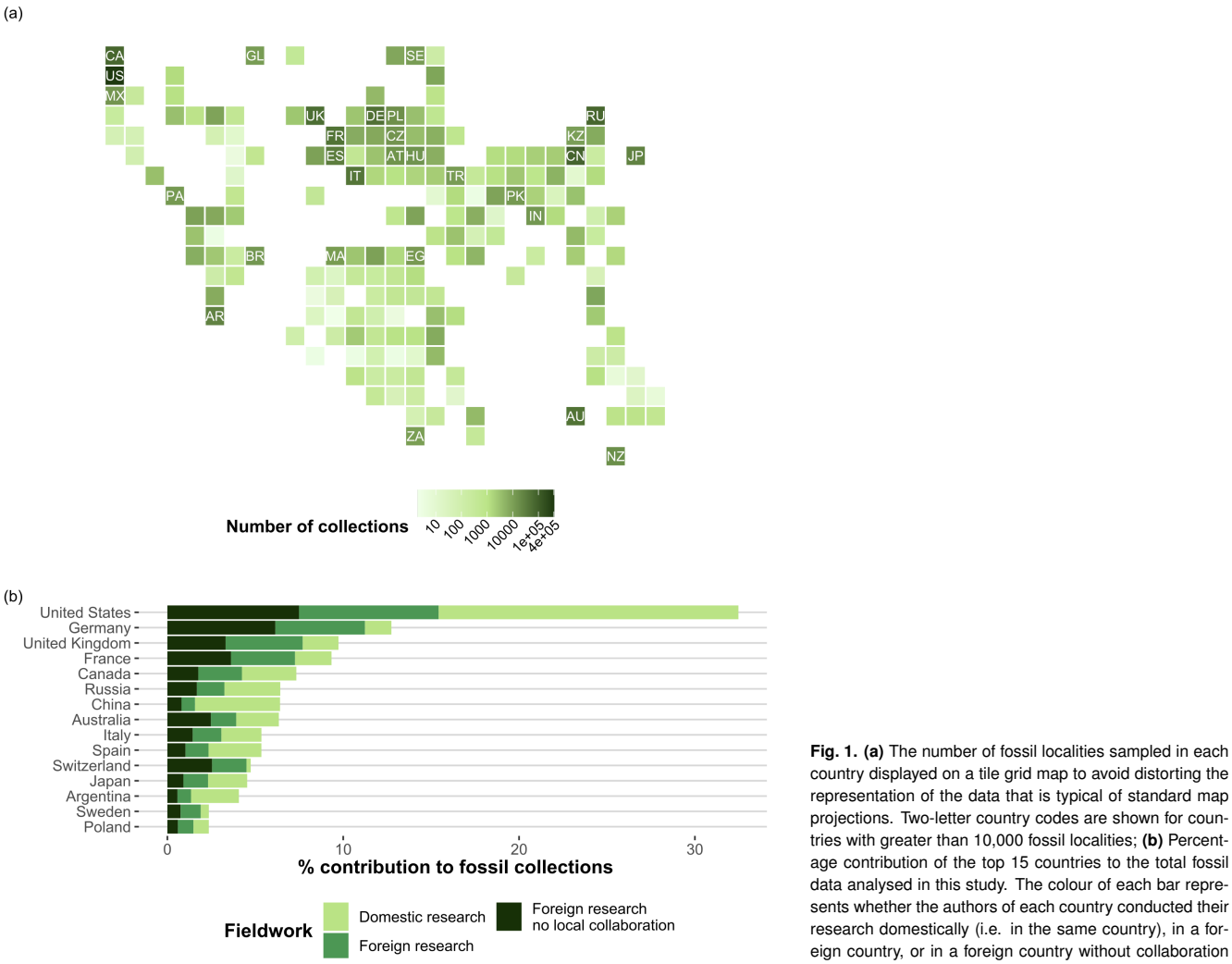


**Fig. 1. (a)** The number of fossil localities sampled in each country displayed on a tile grid map to avoid distorting the representation of the data that is typical of standard map projections. Two-letter country codes are shown for countries with greater than 10,000 fossil localities; **(b)** Percentage contribution of the top 15 countries to the total fossil data analysed in this study. The colour of each bar represents whether the authors of each country conducted their research domestically (i.e. in the same country), in a foreign country, or in a foreign country without collaboration with local palaeontologists.

## Scientific colonialism in paleontological research

We observe that paleontological research is predominantly carried out by researchers affiliated with institutions located in high or upper middle income countries; 97% of fossil occurrence data was contributed by authors based primarily in Northern America and Western Europe (Fig. 1). This pattern is unsurprising, given the history of the discipline and the position of the US and European Union as leaders in research and development expenditure (National Science Foundation 2020). Researchers in the US, who contribute over a third of the total fossil data (Fig. 1b), appear to conduct a similar amount of domestic (i.e. within the US) and foreign research (i.e. outside of the US by US-based authors). The next top three contributors are researchers in Germany, UK and France, who are each responsible for more than 10% of the total fossil data, and conduct a disproportionate amount of research abroad compared with domestic research, almost half of which did not involve any local researchers (Fig. 1b). Among the countries contributing to less than 10% of the fossil data, Switzerland stands out as a country with a high proportion (86%) of paleontological research conducted in foreign countries. Although the ratio of domestic to foreign research might look more even for countries such as the US, Canada, and Australia, these numbers may be misleading given the small proportion of researchers from indigenous and other marginalised groups in academic spaces (21–23). As such, fieldwork carried out by non-indigenous researchers on colonised or occupied territories (many of which are controlled by the state or federal government) could also be considered a case of scientific colonialism (24). This however cannot be quantified within the scope of this study, but, as a basic ethical requirement, should still be acknowledged by researchers undertaking such fieldwork.

At the other end of the spectrum, also among the top global contributors of fossil data, Argentina (66%), China (75%), and Japan (50%), tend to focus their research efforts domestically (Fig. 1b). In a skewed landscape, these countries may initially appear as unexpected outliers, but not when their paleontological research environment is further examined. These countries, along with India, Brazil and Mexico, are examples of 'regional hubs of paleontological knowl-

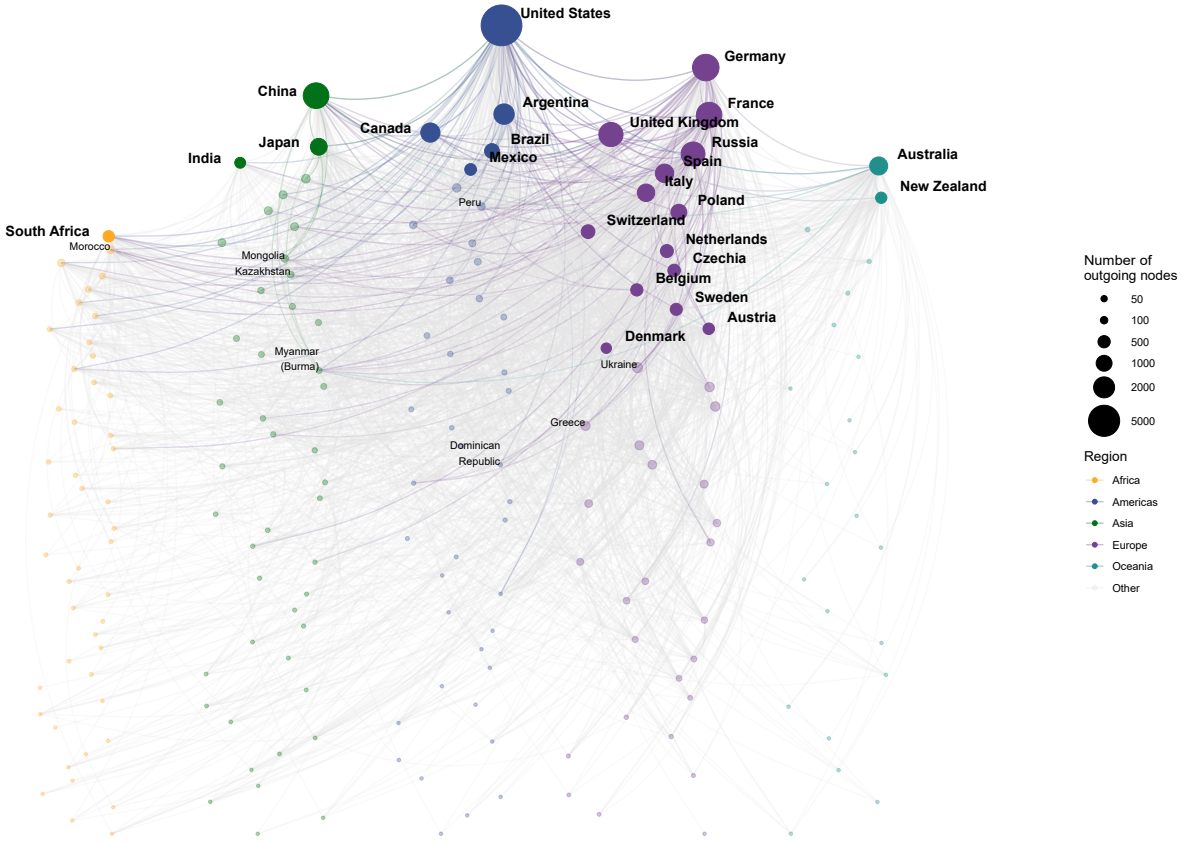


**Fig. 2.** Relationship networks among countries, coloured by region, showing the "research destinations" of researchers in paleontology. The chords represent connections between the country of authors' institutional affiliations and the country the fossil material has been collected from. The size of each country's circle represents the number of publications on foreign fossil material, also represented by the number of outgoing chords. The countries labelled in bold represent countries with more than 30 outgoing chords, i.e. the most popular "research destinations".

edge' (Fig. 2). In these 'regional hubs' most domestic research is carried out by local researchers (Fig. S1), and the contribution of local researchers to these countries' research output has been increasing over the past 30 years (Fig. S2). Out of these countries, China is the most productive in terms of research output (Fig. 1b, Fig. S2). The establishment of paleontology in China can be attributed to rapid geological surveying and mapping initiated in the 1950s, the excavation of several world famous exceptionally-preserved Lagerstätten and, of late, the enforcement of laws to retain Chinese fossils within the country (Table S1). Similarly, paleontology is a long-established discipline in Argentina, Brazil and Japan (Table S1)—these countries have national paleontological societies, universities offering paleontology either as a standalone subject or as part of a wider programme, and national repositories for storing and curating these specimens on top of several funding opportunities for paleontological research (Table S1). These elements have a tremendous effect in shaping the culture and priorities in any discipline, paleontology included, by acting as a catalyst for its advancement (25). In the case of India, however, national funding agencies are less likely to provide funding for any work that involves fieldwork or research visits abroad (Table S1), which is in contrast to many other countries where such rules do not exist. This therefore represents a barrier to paleontological research, especially when many Indian specimens are housed in foreign repositories but are inaccessible to Indian researchers because of travel restrictions.

In many African countries, only a handful have these infrastructures in place for paleontological research, such as South Africa, and, more recently, Egypt (Table S1). As a result, many African countries have remained a target for parachute science (Fig. 3, Table S2). Most of the expertise around African fossils resides outside of the continent, with a clear link through colonial history to Western European countries (Fig. S2–S3). For example, one quarter of all research conducted in Morocco, Tunisia and Algeria was conducted by French researchers, 17% of research on fossils from Tanzania was conducted by German researchers, and 10% of research on South African and Egyptian fossils was conducted by British researchers. However, researchers from Western Europe do not restrict themselves to conducting research in their respective former colonies (Fig. S3). Rather, their scientific focus, along with that of the US, is spread globally.

Neocolonialism—whereby extractive research practices developed during European colonial expansion in the 19th and 20th centuries are maintained in the current century by other parties not previously involved in the colonising agenda—is

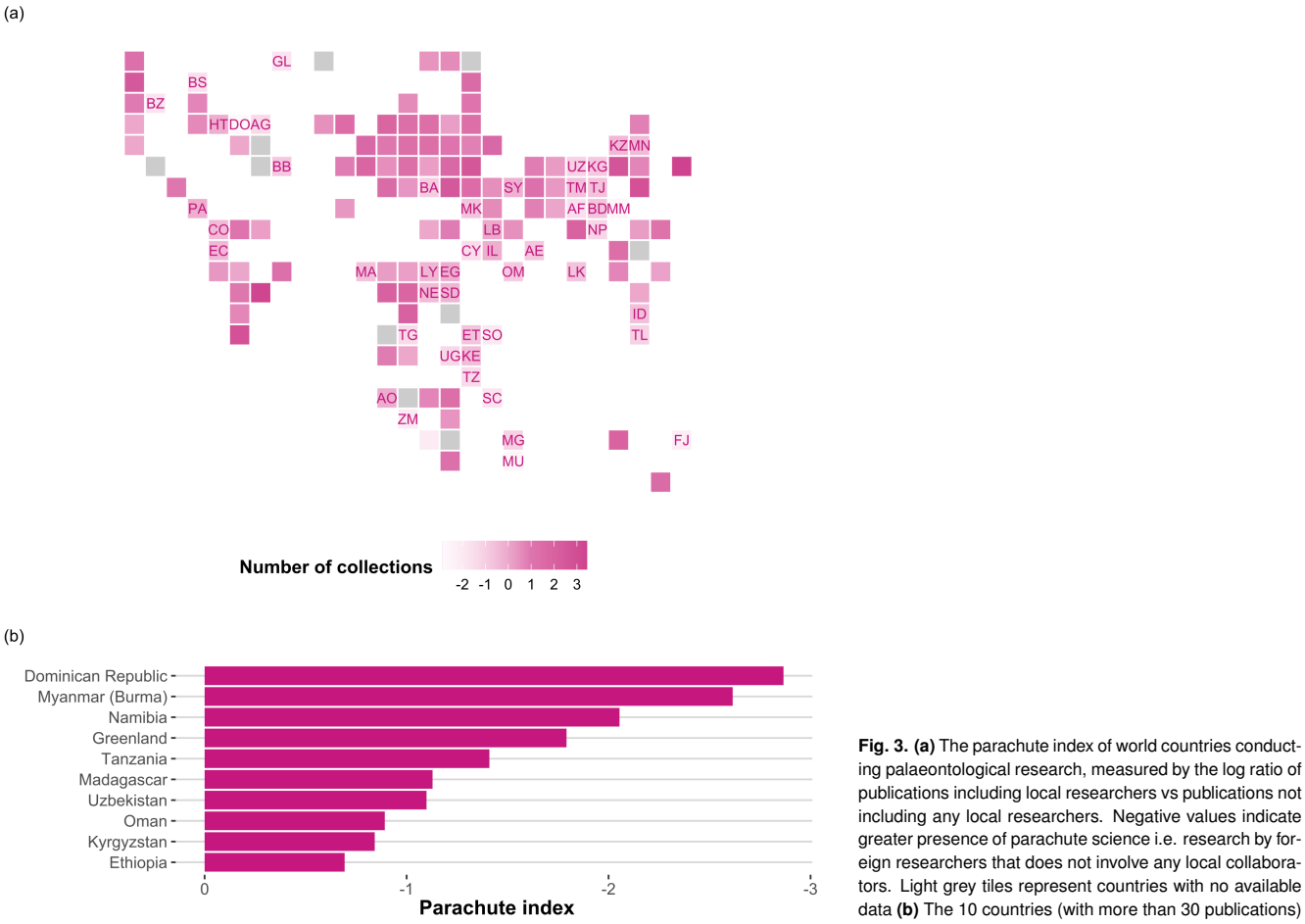


**Fig. 3. (a)** The parachute index of world countries conducting palaeontological research, measured by the log ratio of publications including local researchers vs publications not including any local researchers. Negative values indicate greater presence of parachute science i.e. research by foreign researchers that does not involve any local collaborators. Light grey tiles represent countries with no available data **(b)** The 10 countries (with more than 30 publications) that are the worst hit by parachute science.

also observed among the fossil data. For most of the past thirty years, China's focus has been domestic (Fig. S2). However, this focus has shifted in recent years, with a sharp increase observed in the number of publications on fossils collected abroad and no apparent local collaboration or engagement (Fig. S2). This switch can be linked to an increasing interest in Myanmar fossils, especially arthropods preserved in amber, by Chinese paleontologists (Fig. S4a, S5). Similarly, Japan has shown an increase in research on Myanmar fossils in the past ten years, although Japan's geographical focus has generally been wider than China's, with Japanese researchers conducting work not only in Asian countries (China, Mongolia, Thailand) but also in the US and Russia (Fig. S4b). In contrast, the paleontological interest of South African and Argentinian researchers has remained mostly regional, i.e. in Southern and Eastern Africa and South America respectively (Fig. S2, S4). Some publications by South African researchers on fossil specimens beyond the South African territory came as a part of collaborations with countries such as the US (conducted in Tanzania), and the UK and Russia (both in Botswana).

Countries such as Myanmar, the Dominican Republic, Morocco, Mongolia and Kazakhstan are some of the most popular 'research destinations', thereby being the greatest targets for 'parachute science' and scientific colonialism (Fig. 2). In the case of Myanmar and the Dominican Republic, the availability of commercial amber with fossil inclusions has increased the accessibility of this material to researchers in other countries (26), which has led to a high number of publications where there is no involvement from local researchers, indicating a clear example of parachute science (Fig 3, Table S2). In Morocco, Mongolia, and Kazakhstan, vertebrate fossils seem to be driving this same trend (Fig. S5). Vertebrates, whether modern or fossil, enjoy more popular interest than other groups, usually leading to larger financial incentives in terms of funding (27–29). As such, it comes as no surprise that vertebrate fossil deposits in many countries tend to attract the attention of foreign researchers. In fact, Mongolia and Morocco, along with other countries such as China, Mexico and Brazil, have been the victims of fossil trafficking and parachute research, especially vertebrate fossils, for decades (17). Similarly, issues of legality and ethics surrounding Myanmar amber have not deterred researchers from pursuing their endeavors in the field (26, 30, 31).

## Mechanisms causing knowledge imbalance in paleontology

Our results confirm that, on a global scale, socioeconomic and political factors are some of the dominant controls of pa-

leontological research output (Fig. 4). The human development index (HDI), which represents different socioeconomic factors, such as life expectancy, education and standard of living, has a significant positive relationship with research output ($r = 0.35, p < 0.05$; Fig. 4). In turn, HDI is directly linked to the Gross Domestic Product (GDP; $r = 0.71$, $p < 0.05$) of a country and its political stability (Global Peace Index, GPI; $r = -0.28$, $p < 0.05$) (Fig. 4). Increasing GDP often results in increased investment in different sectors such as health, education, and research and development, thus giving paleontologists from high-GDP countries a broader set of tools and resources to advance the discipline locally (Table S1). This has likely aided the establishment of regional actors beyond European and Northern American countries in the form of emerging economies such as China, India, South Africa, Argentina and Brazil.

European ideologies and culture permeate science (32). There are not only restricted to previous colonial powers but rather are ubiquitous across academic structures and political borders, leading to the discrimination and exclusion of marginalised groups that do not conform to this system (33). Our results show that this colonial legacy (measured here by a binary variable indicating if a country has benefited from colonialism; Table S3) has the greatest impact on research output in palaeontology ($r = 0.50, p < 0.05$; Fig. 4). This relationship is not unexpected, given the roots and history of the discipline. However, the fact that this is apparent in data collected in the last 30 years suggests that the power dynamics currently observed in the discipline are analogous to the ones that existed during the age of colonial plunder. Modern paleontology, like most of the natural sciences, was built on an exploitative system that was the European colonisation process – one centered on making highly asymmetric profits – which benefited the colonisers at the expense of the colonised (34). The colonial legacy that is reflected in the natural history collections of many of these countries has been at the forefront of many recent discussions (35–37). Some countries beyond Western Europe and Northern America, namely China and South Africa, also have their own (neo-)colonial legacy (Table S3). Also, in modern times, educational institutions and private companies, rather than the nation state, benefit from existing and new colonial structures (38, 39).

The relationship between proficiency in the English language (measured by the English Proficiency Index, EPI) and research output (Fig. 4) is another representation of how academic structures are rooted in the colonial process (40). Approximately 92% of publications recorded in the PBDB published between 1990–2020 are in English, with Chinese, German, French and Spanish making up the majority of the remainder (Fig. S6). English was established as the lingua franca of science as a result of the Anglo-American dominance after the second World War, and today 98% of scientific publications are in English (41). This monopoly of English disadvantages researchers for whom English is a secondary language or who are based in countries with low English proficiency (42, 43) and leads to biases in scientific research through the exclusion of non-English publications

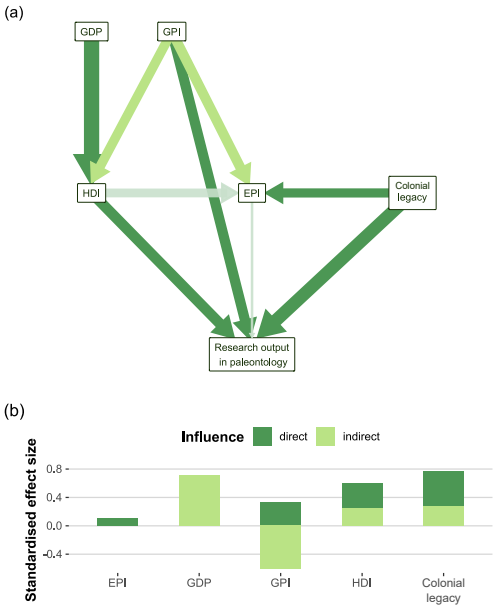


**Fig. 4.** **(a)** Path diagram of socio-economic factors and colonial legacy influencing paleontological research output. Dark and light green paths represent positive and negative influences, respectively. Paths for which p>0.05 are semi-transparent. Path thickness is proportional to the standardized regression coefficient. **(b)** Direct and indirect effects of each of these factors. Acronyms for socioeconomic measures: EPI, English Proficiency Index; GDP, Gross Domestic Product; GPI, Global Peace Index; HDI, Human Development Index.

(44, 45).

In several countries, national political and legal frameworks through the formulation and enforcement of fossil heritage laws have promoted local research endeavors (17). Many countries (e.g., Argentina, Brazil and China) restrict exports of fossils to other countries (Table S1), meaning that these specimens remain in local repositories that can be accessed more easily by local paleontologists for research purposes, as compared to when they are reposited in foreign collections. This is especially observed in the case of Brazil where the stricter enforcement of laws since the 2000s in an attempt to curb this issue has led to increased contributions in terms of the number of publications by Brazilian scientists (Fig. S2). In addition, there are laws that regulate research undertaken by foreign researchers, usually by stipulating a requirement for a local collaborator (Table S1). This has resulted in an increase in collaborations with local paleontologists in these countries (Fig. S2). However, in the case of Myanmar and the Dominican Republic, the commercialisation of amber with fossil inclusions has increased access to researchers from higher income countries in spite of the presence of legislation restricting amber or fossil exports, and restricts access for local researchers unable to afford the material (46).

## Outlook

The fossil record is fundamental to our understanding of the evolution and diversification of organisms through deep-time, and the spatial structure of fossil data has been the dominant factor distorting our interpretations of global biodiversity dynamics across the Phanerozoic (7). However, current com-

pilations of fossil occurrences across the world are far from global; there is discernible geographic variation in where fossils are recovered and reported from (2, 6, 47). As we demonstrate here, these spatial variations are directly related to our current research practices in paleontology, leading to an underrepresentation of researchers from lower-income countries in the discipline. While there have been significant improvements in the last years, with important and considerable contributions from researchers based in countries other than Europe or Northern America (e.g. Fig 1–2, Fig. S2), there is still much work to be done to curb the spread of scientific colonialism in paleontology. Our results show that efforts to mitigate effects of sampling bias to obtain a truly representative view of past biodiversity are not disconnected from the aim of diversifying our field. Spatial sampling biases are born not only out of geological and physical factors influencing the fossil record, but also from pervasive historical and socioeconomic factors. We thus need to examine these biases more deeply and consider how current research practices in paleontology are hindering efforts to increase diversity across all aspects of our discipline. This is especially crucial if paleontology is to play a part in providing a long-term perspective on Earth's biodiversity in order to sustain current biodiversity through conservation (48, 49).

The first step towards conducting research that is more equitable and ethical is to acknowledge that scientific colonialism is prevalent in paleontology and that knowledge production is driven by global power relations, as demonstrated here. In many field-based disciplines, where a portion of the work has been undertaken by local scientists, their contribution is sometimes acknowledged in the form of co-authorship. However, there is a significant lack of publications being led by local scientists (Fig. S9). Collaboration in this form may thus be a representation of subordination, as the privilege of first authorship usually goes to foreign researchers, rather than creating an equitable partnership. Moving forward, developing and advancing paleontological knowledge will require adopting a research culture where knowledge exchange between researchers from different parts of the world takes place on a level playing field. Many sets of recommendations have already been provided for other fields such as genomics, marine science, and ecology (16, 50–52). We include some of these here among our initial recommendations based on our results that should be adopted in paleontology to transform the discipline into a more inclusive and equitable one.

**Developing equitable and ethical collaborations.** Collaborations should ideally begin with input from each party to develop research agendas that are built on mutual trust and respect. No one party should dictate the line of research and researchers, especially foreign ones, should ensure that they are not impeding on the research goals of local researchers. As such, researchers aiming to conduct research abroad should aim to connect with local scientists early in the project design to allow for long and sustainable partnerships. Researchers should also take time to learn the regulatory and cultural landscape of a country where they intend to carry out field research to avoid potential conflicts. Local partnerships can be key to navigating bureaucratic requirements or to grasping local social and cultural norms, but should not be sought out for this purpose alone. Institutional exchange programs for students are not only a way to train the next generation of paleontologists to be research leaders in their countries without dependency on foreign expertise, but also to communicate critical perspectives on how research is carried out in different countries. Usually, discussions regarding the training of students and researchers focus on the capacity of Global North researchers to act as teachers and mentors, but fail to acknowledge how much these researchers can learn from their peers in the Global South, with regards to their local knowledge, expertise, and practices.

**New funding schemes.** Current funding schemes in the Global North, to which principal investigators from high income countries apply, are often nationally or regionally based (e.g. European Research Council). Researchers are typically employed at institutions in the same country or region as the funding body, where they are evaluated upon the amount of funding they receive and their research output (13). This individualistic nature of the current system can often deter researchers from collaborative capacity building (53). When strategic funding decisions are not made in consultation with local researchers in the countries where data collection is to be carried out, the research agendas and priorities of these researchers are overlooked. Even in the case of collaborations with local researchers, the dissemination of results usually will occur in the 'home base' of the principal investigators, leading them to speak on behalf of local researchers. Regional or international funding bodies should not only ensure long-term funding for paleontological research in countries where national funding is not available, but also provide joint funding schemes for researchers from different countries. Transnational funding partnerships, which already exist in global health research (53) could be applied to the natural sciences. Fossils are found all over the world, meaning paleontology in particular is ideally suited to these kinds of funding partnerships. Instead of competing with each other, paleontologists from different countries could pool their resources, expertise and efforts to explore a myriad of research questions that have global importance.

**Access, management and protection of data.** Investment is needed to enhance countries' and their institutions' capacity to collect, store and organise fossil collections and data locally. The establishment of such local repositories, as well as the development of institutional educational programmes, can serve as centers of training for both local paleontologists and foreign researchers wishing to build equitable international partnerships. Joint programs in developing collections and collection management between countries would also ensure that fossils are kept in domestic repositories that are accessible to researchers from all over the world. So far, many fossil collections remain confined to Global North institutions as a result of colonial plunder in the 19th and 20th centuries or scientific colonialism there-

after. Repatriation requests are a sensitive subject for many of these institutions (37). While these discussions are ongoing, the status quo is maintained and researchers from lower income countries continue to face additional barriers with respect to their research, such as financial or visa restrictions. Similarly, the academic publishing culture contributes to this scientific gatekeeping: high-impact publications may offer more visibility, but researchers from lower income countries are highly underrepresented on the authorship of high-impact paleontological and ecological publications (13, 54) due to factors such as language barriers, governmental expenditure on research and development, and parachute research (55). Academic paywalls and exhorbitant open access charges also mean that many scientific publications exacerbate existing inequalities by restricting access to scholarly resources (56).

Given the current patterns documented here, widespread systemic changes are urgently required to address ongoing global power imbalances in the discipline of paleontology that have persisted for more than two centuries. Researchers and their teams should also reflect on their current research practices and identify where their work contributes to scientific colonialism and how their impact on the global power imbalance within palaeontology can be mitigated. There is undoubtedly a need for a central framework that is adopted by funding bodies, research institutions, professional societies, scientific journals and individual researchers to ensure that existing unethical and exploitative research practices become a thing of the past.

## Material and Methods

**Affiliation data of researchers.** Our dataset consisted of references published between 1990 and 2020 that have been compiled within the Paleobiology Database (PBDB; www.paleobiodb.org). We chose to use data from the PBDB because it is the most popular out of the existing large fossil occurrence databases (Table S4) and is widely used in large-scale temporal and spatial analyses of biodiversity in the fossil record. As such, the references in the PBDB is a representation of whose research is visible and important enough to contribute to these analyses that provide information on many important topics related to climate change and biodiversity. However, it is important to note that the PBDB originated as a product of a working group based in the US, which later expanded to involve data enterers from various other countries. Yet, the core PBDB "community" still consists mostly of US and European researchers. As such, the data compiled in the database may present a skew towards these countries.

In the PBDB, each record of a fossil occurrence is attributed to a reference, which are most commonly in the form of peer-reviewed primary literature, but also include books, field guides, and PhD theses (57). Using the download function, we downloaded all bibliographic references for the last 30 years (1990–2020), which comprised a total of 30,220 publications (latest download on 19th January 2021). Then, the affiliate countries of each author on these publications was compiled. This was achieved through (1) web scraping the landing page of the publication on the publisher's website (n=11,037) and (2) manual entry when (1) was not possible (n=16,660). In the event that the publication could not be accessed, because the online version was unavailable or behind a paywall inaccessible to us, we used alternative methods to infer affiliate countries of authors. These included obtaining the information from (i) another publication by the same author published in the same year as the one of interest with the assumption that no change in affiliation occurred during that year, (ii) personal websites of authors where online curricula vitae or similar were available, (iii) academic social networks such as ResearchGate or Academia.edu, (iv) published obituaries (in the event that the author is deceased). Note that this approach only provides us with information about where researchers are based, but not where they are from. However, institutional affiliations represent a proxy for the funding source of a researcher or working group, e.g. a non-German researcher based at an institution in Germany will likely obtain their funding from a German or European organisation. This thus represents one or more academic entities that allowed a particular research project to take place. Only 2573 (8.5%) of the downloaded references could not be accessed, and thus could not be assigned affiliation information. Of the 27,647 publications for which affiliation data was accessible for collation, 20,372 (73.7%) were written by more than one author, and 10,461 (37.8%) had two or more authors from different countries in the author list (i.e. represented international collaborations).

The final dataset comprised information on each publication (e.g. full title, year of publication, DOI if available, etc.), the affiliate countries of each author on a given publication obtained through the methods described above, and the country from which the fossil material described within the publication were sampled (hereafter "research destination") as obtained by the locality information provided in the PBDB. Publications describing fossil occurrences in more than a single country were recorded in the dataset for each country mentioned. All the country data was coded into three-letter codes to avoid any discrepancies between spellings (e.g. USA vs United States vs United States of America) using the *countrycode* R package (58).

**Socio-economic and -political data.** Research plays an important role in the socio-economic growth of a country and vice versa. There are several studies highlighting the link between research output and economic indices, the most popular one being the Gross Domestic Product (GDP) or GDP per capita (14, 59, 60). GDP data for our study were obtained from the World Bank (61). In addition, the amount of funding allocated for research and development per country is an important measure of research output in a country (60), however, as there is not enough information for funding information in the field of paleontology in different countries, we could not consider this variable in our study.

The Human Development Index (HDI) was created to emphasize that people and their capabilities should be the ultimate criteria for assessing the development of a country, not eco-

nomic growth alone (62). The HDI measures key dimensions in human development, namely health measured by life expectancy, access to education measured by expected years of schooling of children at school-entry age and mean years of schooling of the adult population and standard of living measured by the Gross National Income per capita. HDI data for our study was obtained from the United National Development Programme (62).

A strong association between English proficiency and research output has previously been documented in the literature (14, 63). While English proficiency is inherently not a cause for improved research output in different countries, studies show that non-native English speakers are less likely to have their publications accepted for publication than English-speaking countries such as the US or the UK (63, 64). As such, this has led to an over-representation of countries with high English proficiency, which also usually have strong research funding, and an under-representation of researchers from countries with lower English proficiency. For our study, we used the 2020 English Proficiency Index (EPI) which is based on test data from more than 2 million test takers around the world (65). As the EPI is not provided for English speaking countries, i.e. where English is the primary language used (Table S5), these countries were assigned the highest EPI (EPI=75). Countries which are listed as English speaking but were included in the EPI evaluations such as Fiji or Nigeria (66) were assigned their respective EPI scores rather than the highest score.

Finally, research productivity has previously been associated with political stability (14, 67). We used the 2020 Global Peace Index (GPI) as a proxy for political stability (Vision of Humanity 2020). The GPI is calculated by taking several factors into consideration such as number of and intensity of internal or external conflicts, related deaths, crime and imports or exports of weapons.

**Colonial legacy data.** We devised a binary variable to assess the influence of colonialism on research output in paleontology. Countries that have a history of colonialism or have profited from colonialism were assigned '1' and the remaining countries were assigned '0'. We use the term "colonialism" here to encompass a larger concept beyond the European expansion and domination over overseas territories and people (68). As such, the following criteria were used to categorise countries (listed in Table S3) as "1" if they practiced or were involved in:

(i) Setting up colonies beyond their territories

(ii) Exploitative colonialism: occupation of a country or region to exploit its population as labour and/or its natural resources as raw material

(iii) Settler colonialism: occupation with the aim of replacing the original population of the occupied territory

(iv) Internal colonialism: the exploitation of minority groups within a wider society leading to political and economic inequalities in a region or between regions.

(v) Surrogate colonialism: supporting the settlement of a non-native group on territory occupied by an indigenous population.

(vi) Colonial complicity: benefiting from colonisation by other countries without actively engaging in the colonialism process.

We use the signing of the Treaty of Tordesillas in 1494 as a cutoff point, before which any practice of or profit from colonialism was not taken into consideration. Imperial, or colonial, expansion and conquest was not unknown before this point. However, this treaty put the idea of global domination and power into a form which legitimised colonial possessions of territories and peoples as a political, economic and cultural right as well as the "civilising mission of the savages" (69).

**Data exploration and analysis.** Data manipulation, exploration and analyses were conducted within R version 4.0.1 (70) and various packages referenced in other sections. Plots were constructed using functions within the *ggplot2* R package (71)

**Determining the relationship between authors and research destinations.** For simplicity, we assumed that all fossil occurrences per publication were the result of direct access of the author(s) to the fossil material described in the publication, through (a) conducting fieldwork, (b) access to museum collections, or (c) purchase of fossil material. We created a global country network, in the form of a directed network, where each node represents a country ($G_{country}$) and each edge shows the number of publications authored by researchers in one country (country A) based on fossil materials collected in another country (country B). $G_country$ also includes self-loops, as fossil material in a country where an author is based should in theory be accessible to them. Country networks were also generated per continent and subcontinental regions of research destinations using the classification of the World Bank (Table S6). With the *igraph* R package (72), we used the network degree centrality and betweenness measures to identify countries which are the most influential countries in the network, thus, more likely to control the flow of information in the network (73). We also computed the "parachute index" for each country, referring to the term 'parachute science' (16). The "parachute index" compares the number of publications on a specific research destination carried out by foreign authors (i.e. those not based in the same country as the fossil material being published) as opposed to local authors (i.e. those who are based in the same country as the fossil material), measured as log-ratios.

**Quantifying causal relationships between authors and research destinations.** To obtain a more integrated picture of the direct and indirect influences on research output in paleontology, we conducted confirmatory path analysis (CPA) based on the piecewise fitting of different linear models using the *piecewiseSEM* R package (74). This allows the incorporation of both continuous and discrete variables (see Table S7) and applies a series of statistical techniques, such as mul-

tiple regression and factor analysis, to investigate the relationships between one or more variables. We have to emphasise that CPA itself does not provide a means of determining causal relationships but rather determines the strength of a causal relationship assumed by the analyst, in this case, us. Research output was first modelled as a function of all the above-mentioned socio-economic factors. However, before this was used in the path model, variable selection using a stepwise algorithm was applied to find the optimal model that minimises the Akaike information criterion (AIC). Similarly, HDI and EPI were also modelled as a function of all the variables and the same steps were applied to optimise each individual model. The final individual models were then added to the overall path model. The overall path model was evaluated using Shipley's test of directed separation (75), which yields a Fisher's C statistic that can be compared with a $X^2$ - distribution. If the resulting p-value is $> 0.05$, then the model can be said to adequately reproduce the hypothesized causal network.


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#### AUTHOR CONTRIBUTIONS

N.B.R and E.M.D, conceptualization, methodology, writing–original draft, investigation, data curation, methodology, formal analysis, visualization; T.M.K and P.S.N., investigation; all authors, visualisation, writing–review and editing.

#### DATA AVAILABILITY STATEMENT

Data and code for the analyses will be made available upon the publication of the peer-reviewed version of this manuscript.

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# Supporting Online Material:

## Colonial history and global economics distort our understanding of deep-time biodiversity

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The following section contains:

- Supplementary tables S1-S7
- Supplementary figures S1-S9

**Table S1.** Status of paleontology in selected countries

| Country | Fossil legislation | Funding | Paleontological society | University programs | Fossil repositories |
|---|---|---|---|---|---|
| Argentina | Paleontological sites with scientific interests are the property of the state and as such governmental authorisation is required for both exploration and research, and only reproductions of fossils can be exported. | Paleontological research makes up a big portion of research within the field of Earth Sciences, allocated to both early-career and senior researchers by several governmental agencies (76). | Asociación Paleontológica Argentina (Argentinian Paleontological Association) | Paleontology as a subject is available within geology and less often, biology degrees. Currently, only two universities provide a degree in paleontology. | Several museums and institutions serve as repositories of fossil specimens. |
| Brazil | Fossils are the property of the state of Brazil and as such are subject to the laws of the country. The collection of scientific data and materials in Brazil by foreigners is regulated and requires the participation of a local institution. (17) | Researchers in paleontology may claim funding from different Federal or State level scientific funding agencies. Financing by companies is also common, especially in the oil sector. | Sociedade Brasileira de Paleontologia (Brazilian Society of Paleontology) | Paleontology as a subject is available within geology, biology, and less often, ecology degrees. It is possible to specialize in paleontology in graduate programs. | Several museums serve as repositories of fossil specimens. |
| Mexico | Fossils are the property of the state of Mexico and as such are subject to the laws of the country. Collaboration with local researchers is recommended. (17) | Researchers in paleontology may claim funding from national scientific funding agencies. | La Sociedad Mexicana de Paleontología (Mexican Paleontological Society; SOMEXPAL) | Paleontology as a subject is available within geology, biology, and less often, ecology degrees. It is possible to specialize in paleontology in graduate programs. | Several museums serve as repositories of fossil specimens. |
| China | Vertebrates or any excavated “relics” are owned by the state. Fossils are explicitly protected under the law against exports. All materials to go abroad require an application from a Chinese national via a local institute to the County Level of the Department of Land & Resources (Liston and You 2015). | A large amount of funding is available, due to the extraordinary fossil sites present in China (77). | Palaeontological Society of China | A few universities offer paleontological courses (77). | Several museums serve as repositories of fossil specimens. |

| | | | | | |
|---|---|---|---|---|---|
| Japan | Many fossil sites are located either on public or private property and as such require permission for entry. Most fossils are protected by local public or administrative divisions (i.e. the city and village levels) Some fossils (e.g. dinosaurs, marine mammals, and Ice Age mammals) from certain areas are also assigned to 'natural monuments' and are protected under the 'Law of Protection of Cultural Property' (78). | A large amount of funding is available for research purposes (79) | Palaeontological Society Of Japan | Several universities offer paleontological courses, sometimes within Geology/Earth Sciences (80). | Several museums serve as repositories of fossil specimens. |
| India | It is recognized that the fossil sites and collected specimens belong to the country. However, there is no strict legislature to be effectively implemented. Sites of geologic importance are often used for mining and fossils are collected/exported without the knowledge of the local authority (81). | Paleontological research makes up a relatively small portion of research within the field of Earth Sciences, allocated to both early-career and senior researchers by several national funding agencies. Funding is limited for work conducted only in India. | The Palaeontological Society Of India | Paleontology as a subject is available within geology/Earth Science. There are no institutes within India that offer a standalone degree in paleontology. It is, however, possible to specialize in paleontology during PhD or MSc in the form of conducting specific research projects. | There is no single national research repository to house fossil specimens. Personal fossil collections belonging to academics are typically neglected upon their retirement and often lost without orchestrated curatorial efforts. |
| South Africa | All fossils are owned by the state and are protected under the Natural Resource Resources Act No. 25 of 1999. No fossil may be collected or exported without a permit. This Act also makes it illegal to own or sell fossils for personal gain. However, there are other provisional heritage acts that are specific to certain regions of the country, making South Africa one of the countries with the strictest fossil legislation in the world. | Paleoscience has various national funding channels. Other general sources include the French Embassy in South Africa which funds some paleoscience. Some universities supply seed money to departments that conduct paleontological research. | Palaeontological Society of Southern Africa | A degree in Paleontology is only offered at one university, the University of Witwatersrand. However, paleoscience research is offered in other universities but under different disciplines such as Anthropology, Botany, Entomology, Geology, and Zoology. | Several universities and museums serve as repositories of fossil specimens. |

| | | | | | |
|---|---|---|---|---|---|
| Egypt | All fossils (and other antiquities) are property of the state. The Supreme Council of Antiquities must be notified of fossil discoveries, and must be housed at the Council's museums. A license to excavate fossils must be sought from the Council prior to work commencing. Additionally, the law provides legal protection for geological features, by forbidding actions that would lead to destruction or deterioration of the natural environment (including the collection of objects such as rocks and shells). | There are various sources of funding from (inter)national funding agencies and universities. | Paleontological Society of Egypt | A vertebrate paleontology program is available at Mansoura University. Paleontological research programmes are offered at some universities, but under different disciplines such as Earth Sciences/Geology, Biology, Botany, and Zoology. | Several institutions and museums serve as repositories of fossil specimens. |

**Table S2.** Top 10 countries experiencing parachute science, the number of publications including local authors and the calculated parachute index.

| Country | **Region** | **Includes local authors** | | **Parachute index** |
|---|---|---|---|---|
| | | *Yes* | *No* | |
| Dominican Republic | Caribbean | 22 | 397 | -2.89 |
| Myanmar (Burma) | South-Eastern Asia | 56 | 765 | -2.61 |
| Namibia | Southern Africa | 5 | 37 | -2.00 |
| Tanzania | Eastern Africa | 21 | 86 | -1.41 |
| Madagascar | Eastern Africa | 32 | 100 | -1.14 |
| Uzbekistan | Central Asia | 14 | 42 | -1.10 |
| Oman | Western Asia | 25 | 58 | -0.84 |
| Kyrgyzstan | Central Asia | 28 | 64 | -0.83 |
| Ethiopia | Eastern Africa | 19 | 37 | -0.67 |
| Morocco | Northern Africa | 126 | 241 | -0.65 |

**Table S3.** Countries that practiced or profited from colonialism

| Country | Supporting claim | Source |
|---|---|---|
| Australia | Settler-colonialism: Establishment of British settler colonies which established control over the indigenous population. | (82) |
| Austria | Austria-Hungary (in the 18–19th century, extending from Northern Italy to Romania) was one of the countries present at the Berlin Conference of 1884–1885 to partition African territories among colonial powers. While it did not petition for any colonies in Africa, it benefited by securing docking rights and trade agreements in the colonies. During the Russian-Turkish War, Austria-Hungary annexed Bosnia and Herzegovina - a compensation from the Russians. The Austrian empire also fostered internal colonialism policies, marginalising and oppressing minority groups, including their political, religious and linguistic rights. | (83–86) |
| Belgium | Belgian imperialism led by King Leopod II's personal agenda led to the colonisation of Central African countries, including the Belgian Congo (modern day DRC), which laid the foundation for economic opportunities later on. | (87) |
| Canada | Settler-colonialism: Establishment of British settler colonies which established control over the indigenous population. | (82) |
| China | The subjugation of Tibetans in Tibet and the Uyghurs in Xinjiang has been equated to internal colonialism. China can also now be considered as a neocolonial power as its cultural, political, and economic reach increases in several countries across the globe. | (88, 89) |
| Denmark, Sweden, Norway, Finland, Iceland | Denmark and Sweden were the only two Scandinavian countries to have overseas colonies. However, all these countries have participated in the colonial project related to the production and dissemination of knowledge that maintained global hierarchies and thus practiced colonial complicity. These countries are also said to have shared similar ideas of power hierarchies and eugenics as colonial powers. | (90, 91) |
| France | France was part of a group of European countries that made territorial gains across the globe. | (92) |
| Germany | Unlike other European powers, Germany's colonial ambitions, as a result of 19th century imperialism, started late and were short-lived. It expressed territorial claims over several African territories and annexed a series of islands and peninsulas in the Pacific. | (93) |
| Israel | Surrogate colonialism: A consensus of the British Empire made the the legitimate settlement on Palestinian territories by Zionists possible, leading to the Palestinian occupation. | (94) |
| Italy | The Kingdom of Italy, only founded in 1862, was also late compared to other European powers. In the late 19th century and early 20th century, it took over Eritrea, Somalia, Libya and Albania. | (92, 95) |
| Japan | Imperial Japan took possession of several overseas territories in East Asia, including Taiwan and Korea, and the Western Pacific. | (96) |

| | | |
|---|---|---|
| Netherlands | The Netherlands was part of a group of European countries that made territorial gains across the globe. | (92) |
| New Zealand | Settler-colonialism: Establishment of British settler colonies which established control over the indigenous population. | (82) |
| Portugal | Portugal was one of the two countries that signed the Treaty of Tordesillas to divide South American territories between Spain and Portugal. It was the world's first global empire and also the longest lasting empire in world history (almost six centuries). | (97, 98) |
| Russia | Russian conquest of territories spreading across Europe and Asia occurred over many centuries. | (99) |
| South Africa | Settler-colonialism: Establishment of British settler colonies which established control over the indigenous population. This further transformed into a form of internal colonialism in the form of the apartheid system. Post-apartheid, South African firms rapidly expanded operations north of the continent resulting into trade inequity with regards to imports and exports on the continent. | (82, 100) |
| Spain | Spain was one of the two countries that signed the Treaty of Tordesillas to divide South American territories between Spain and Portugal. It was one of the most powerful empires in the 16th and 17th centuries. | (92, 98) |
| Switzerland | Switzerland never officially established any colonies. However, being surrounded by multiple imperial powers, it reaped the 'benefits' of colonialism by backing some powers. Swiss businesses were involved in the trade of textiles, agriculture and enslaved peoples. Access to colonies also resulted in the development of science and technology in the country. In the post-colonial world, Swiss stakeholders are able to secure opportunities with former colonies because of their unsuspicious neutrality and hidden colonial complicity. | (101–103) |
| Turkey | The Ottoman Empire controlled much of Southeastern Europe, Northern Africa and Western Asian between the 14th and 20th century. "Ottoman colonialism" emerged in the 19th century as the Ottomans ruling class adopted the ways of European powers as political and legal reforms consolidated power in Istanbul, neglecting peripheral areas of the empire. | (104, 105) |
| UK | Britain was part of a group of European countries that made territorial gains across the globe. | (92) |
| USA | Settler-colonialism: Establishment of British settler colonies which established control over the indigenous population. American imperialism: Establishment of cultural, political (through military actions) and economic influence and control beyond the territories of the United States. | (106, 107) |

**Table S4.** Number of hits returned by Google Scholar for large paleontological databases (as of 31st March 2021)

| **Keywords** | **Number of hits** |
|---|---|
| "Paleobiology Database" | 3260 |
| "Neotoma Paleoecology Database" OR "Neotoma Database" | 516 |
| "Neptune Database" OR "Neptune Sandbox" | 199 |

**Table S5.** List of counties that are considered to be English-speaking in this study

| Countries | Source |
|---|---|
| Antigua and Barbuda | (66) |
| Australia | |
| The Bahamas | (66) |
| Barbados | (108) |
| Belize | (66) |
| Canada | |
| Dominica | (66) |
| Grenada | (66) |
| Guyana | (66) |
| Republic of Ireland | (109) |
| Jamaica | (110) |
| New Zealand | |
| St Kitts and Nevis | (111) |
| St Lucia | (66) |
| St Vincent and the Grenadines | (112) |
| Trinidad and Tobago | (66) |
| United Kingdom | |
| United States of America | |

**Table S6.** Classification of countries per continent and sub-continental regions as defined by the World Bank (61).

| Continent | Regions | Countries |
|---|---|---|
| Africa | Eastern Africa | Burundi, Comoros, Djibouti, Eritrea, Ethiopia, Kenya, Madagascar, Malawi, Mauritius, Mozambique, Rwanda, Seychelles, Somalia, Somaliland, Tanzania, Uganda, Zambia, Zimbabwe |
| Africa | Middle Africa | Angola, Cameroon, Central African Republic, Chad, Congo - Brazzaville, Congo - Kinshasa, Equatorial Guinea, Gabon, São Tomé & Príncipe |
| Africa | Northern Africa | Algeria, Egypt, Libya, Morocco, South Sudan, Sudan, Tunisia |
| Africa | Southern Africa | Botswana, Eswatini, Lesotho, Namibia, South Africa |
| Africa | Western Africa | Benin, Burkina Faso, Cape Verde, Côte d'Ivoire, Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, Senegal, Sierra Leone, Togo |
| Americas | Caribbean | Antigua & Barbuda, Bahamas, Barbados, Cuba, Dominica, Dominican Republic, Grenada, Haiti, Jamaica, St. Kitts & Nevis, St. Lucia, St. Vincent & Grenadines, Trinidad & Tobago |
| Americas | Central America | Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama |
| Americas | Northern America | Canada, United States |
| Americas | South America | Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Guyana, Paraguay, Peru, Suriname, Uruguay, Venezuela |
| Asia | Central Asia | Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan |
| Asia | Eastern Asia | China, Hong Kong SAR China, Japan, Mongolia, North Korea, South Korea, Taiwan |
| Asia | South-Eastern Asia | Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar (Burma), Philippines, Republic of Vietnam, Singapore, Thailand, Timor-Leste, Vietnam |
| Asia | Southern Asia | Afghanistan, Bangladesh, Bhutan, India, Iran, Maldives, Nepal, Pakistan, Sri Lanka |
| Asia | Western Asia | Armenia, Azerbaijan, Bahrain, Cyprus, Georgia, Iraq, Israel, Jordan, Kuwait, Lebanon, Oman, Palestinian Territories, Qatar, Saudi Arabia, Syria, Turkey, United Arab Emirates, Yemen |
| Europe | Eastern Europe | Belarus, Bulgaria, Czechia, Hungary, Moldova, Poland, Romania, Russia, Slovakia, Ukraine |
| Europe | Northern Europe | Denmark, Estonia, Finland, Iceland, Ireland, Latvia, Lithuania, Norway, Sweden, United Kingdom |
| Europe | Southern Europe | Albania, Andorra, Bosnia & Herzegovina, Croatia, Greece, Italy, Malta, Montenegro, North Macedonia, Portugal, San Marino, Serbia, Slovenia, Spain, Vatican City |
| Europe | Western Europe | Austria, Belgium, France, Germany, Liechtenstein, Luxembourg, Monaco, Netherlands, Switzerland |
| Oceania | Australia and New Zealand | Australia, New Zealand |
| Oceania | Melanesia | Fiji, Papua New Guinea, Solomon Islands, Vanuatu |
| Oceania | Micronesia | Kiribati, Marshall Islands, Micronesia (Federated States of), Nauru, Palau |
| Oceania | Polynesia | Samoa, Tonga, Tuvalu |

**Table S7.** Socio-economic variables used in the confirmatory path analysis (CPA)

| Variable | Abbreviation | Description | Source |
|---|---|---|---|
| Gross Domestic Product | GDP | A measure of a country's economic output | (61) |
| English Proficiency Index | EPI | The ability of a country's population to use and communicate in the English language with a certain level of accuracy | (65) |
| Human Development Index | HDI | A measure of average achievement in key dimensions of human development: life expectancy, education and living standard | (62) |
| Global Peace Index | GPI | A measure indicating the extent to which a country is involved in ongoing domestic and international conflicts. | (113) |
| Colonial legacy | - | Countries that practiced imperialism or profited from imperialism since the Treaty of Tordillas | Table S3 |

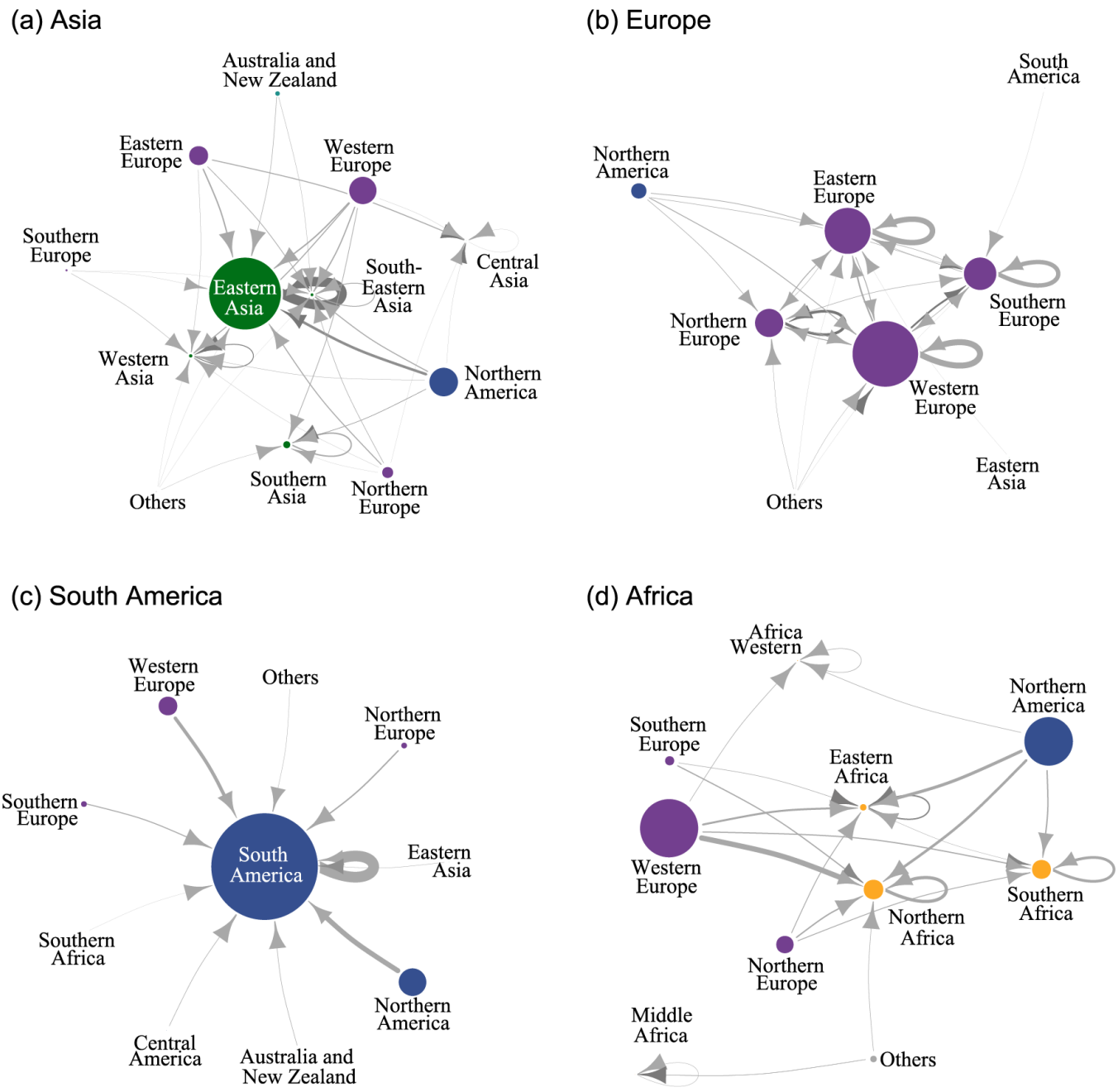


**Fig. S1.** Authors per region and their selected research destinations in **(a)** Asia, **(b)** Europe, **(c)** South America and **(d)** Africa. The direction of the arrows show the relationship between the region the author is affiliated with and the region where they carry out their research (i.e. the origin country of the fossil material described in the publications). Self-loops indicate publications concerning a specific region that were by authors from the same region, and the size of circles and thickness of the lines for each region are proportional to the number of publications by authors from the same region.

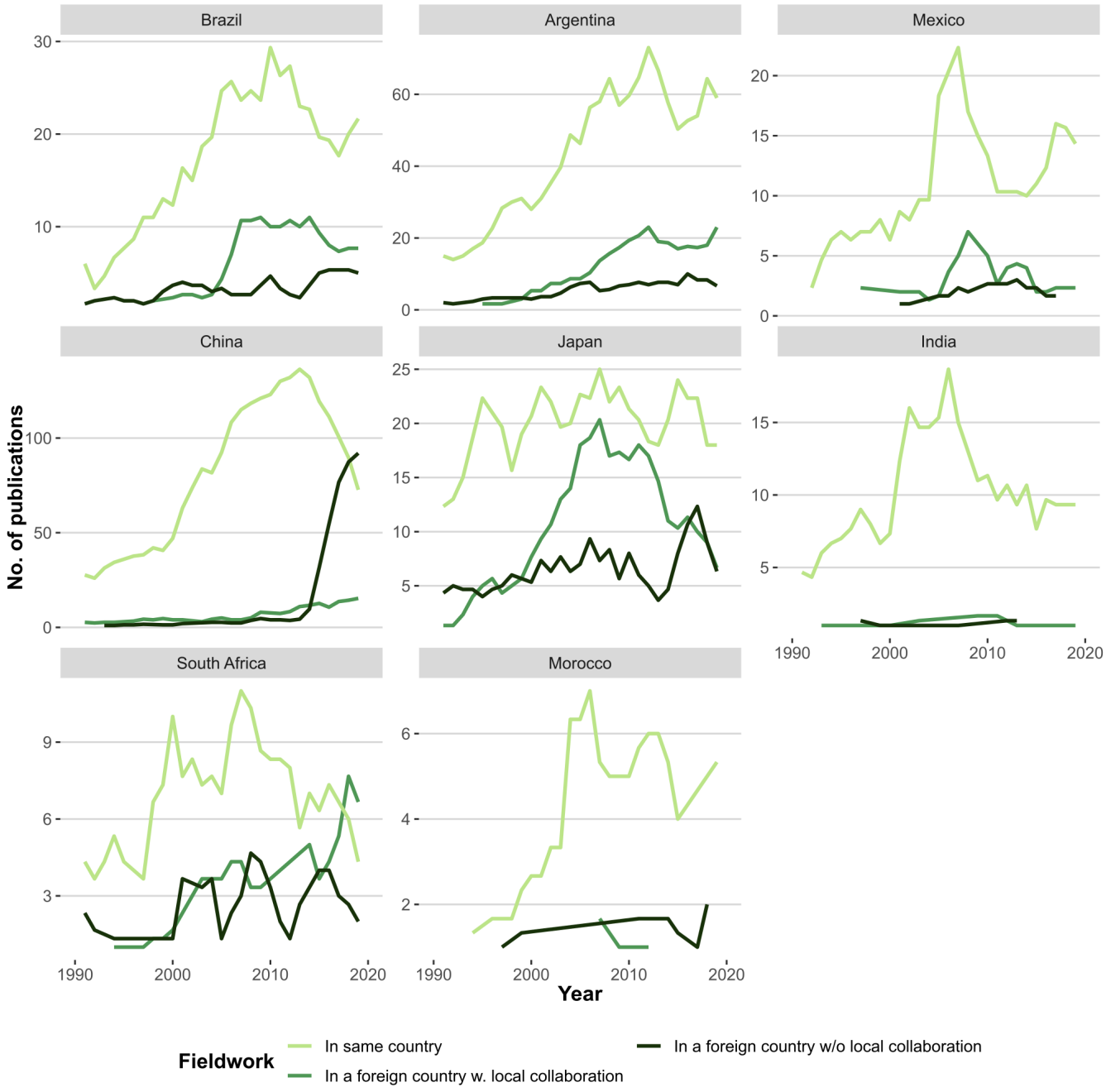


**Fig. S2.** The top eight countries in South America, Asia and Africa (i.e. regions of the Global South) in terms of the number of publications.

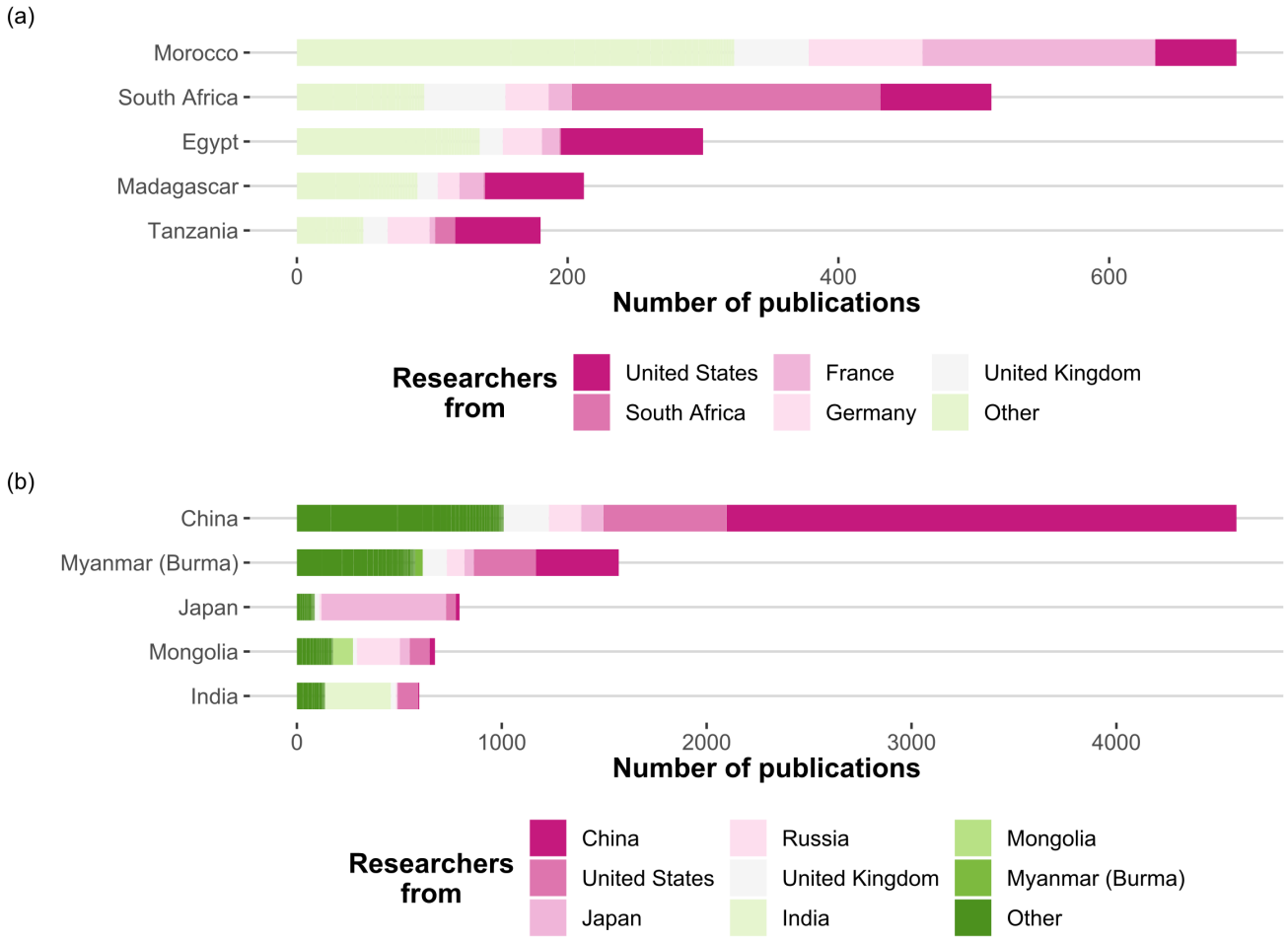


**Fig. S3.** The top countries in **(a)** Africa and **(b)** Asia where authors publish fossil material from popular research destinations.

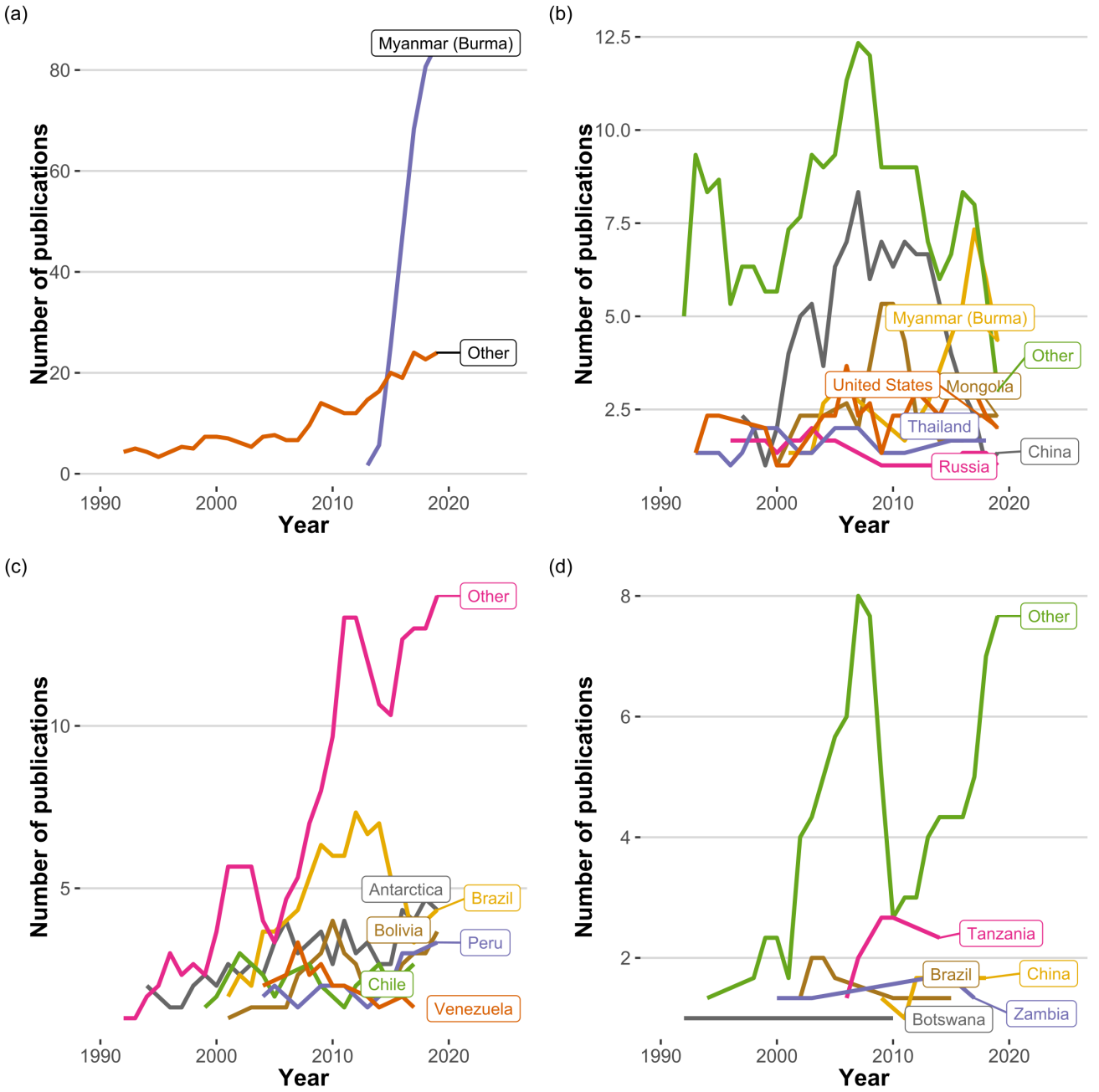


**Fig. S4.** Number of publications per year by authors in **(a)** China, **(b)** Japan, **(c)** Argentina and **(d)** South Africa, and the foreign countries in which the fossil material in their publications originates.

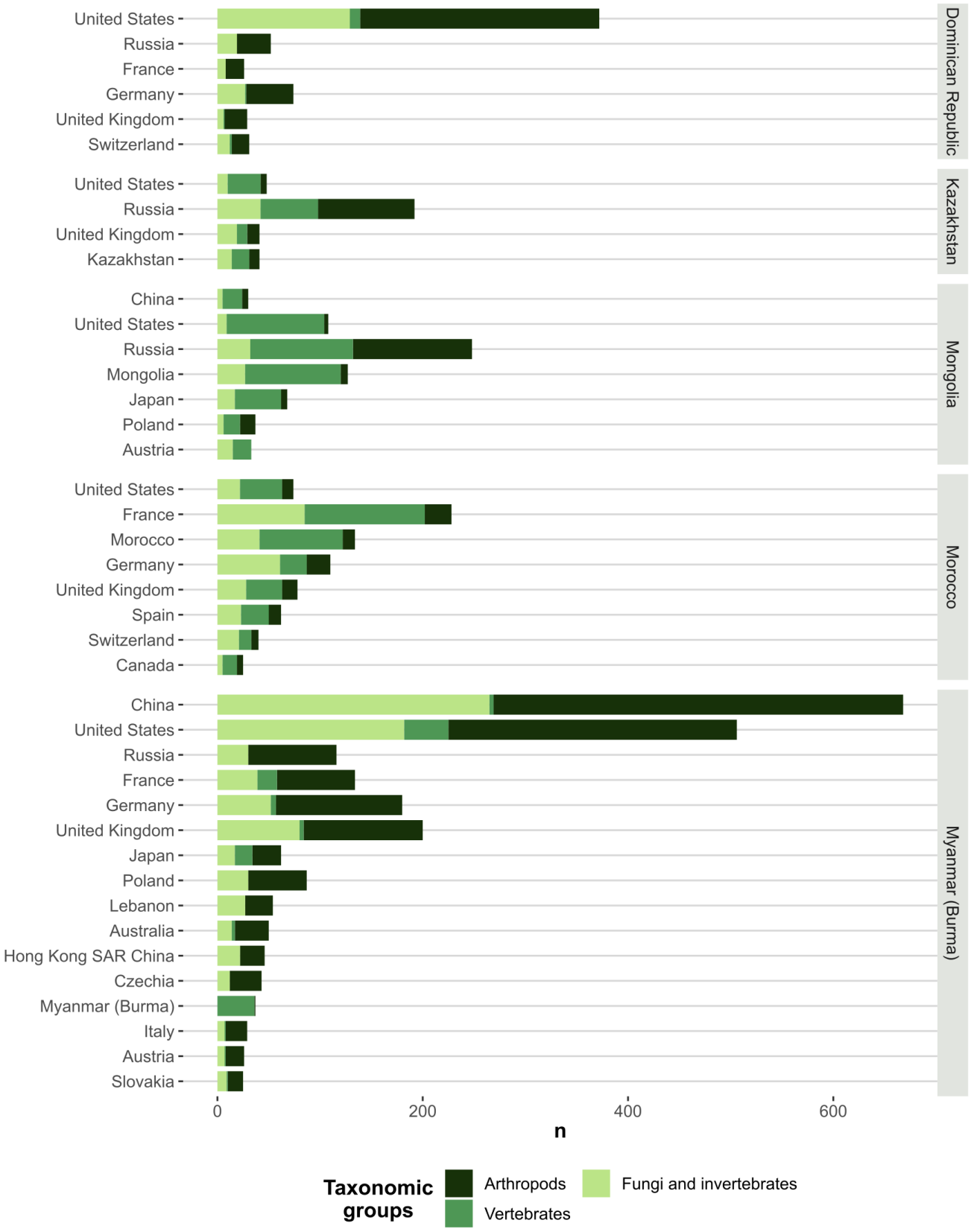


**Fig. S5.** Taxonomic groups by the country in which the fossil material originates (in grey boxes on the right) and by the countries that publish on them (on the left).

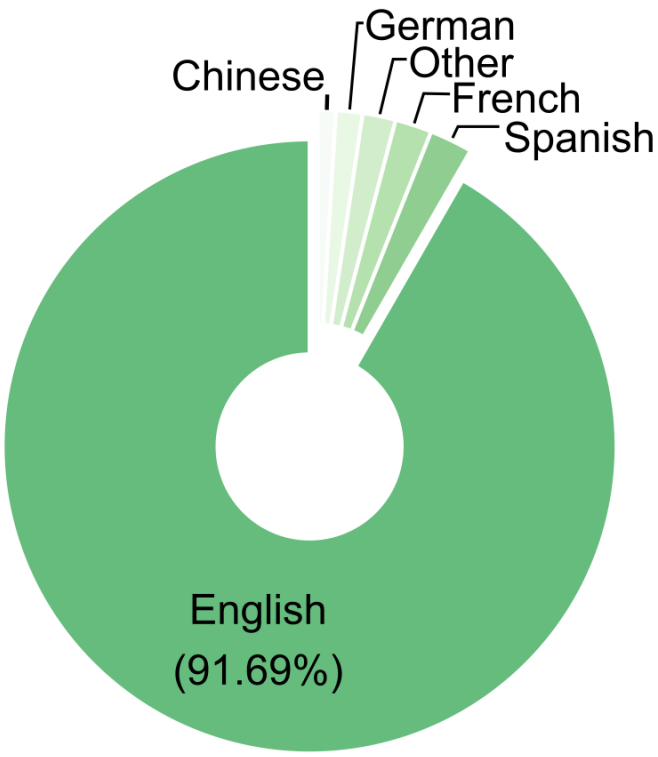


**Fig. S6.** Proportions of publications in the Paleobiology Database by languages.

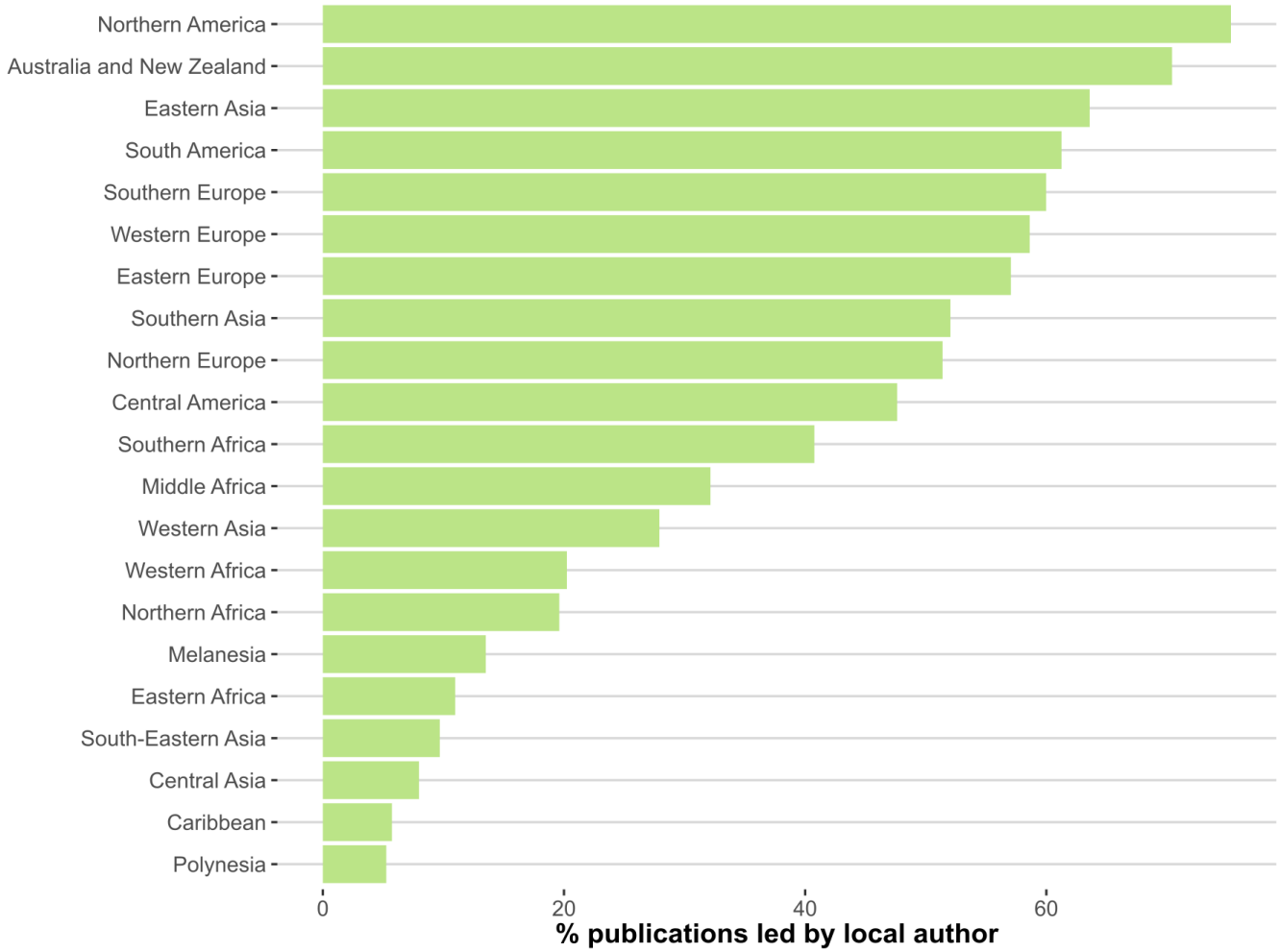


**Fig. S7.** Proportions of publications on fossil data in a specific country led by a local author, by region.

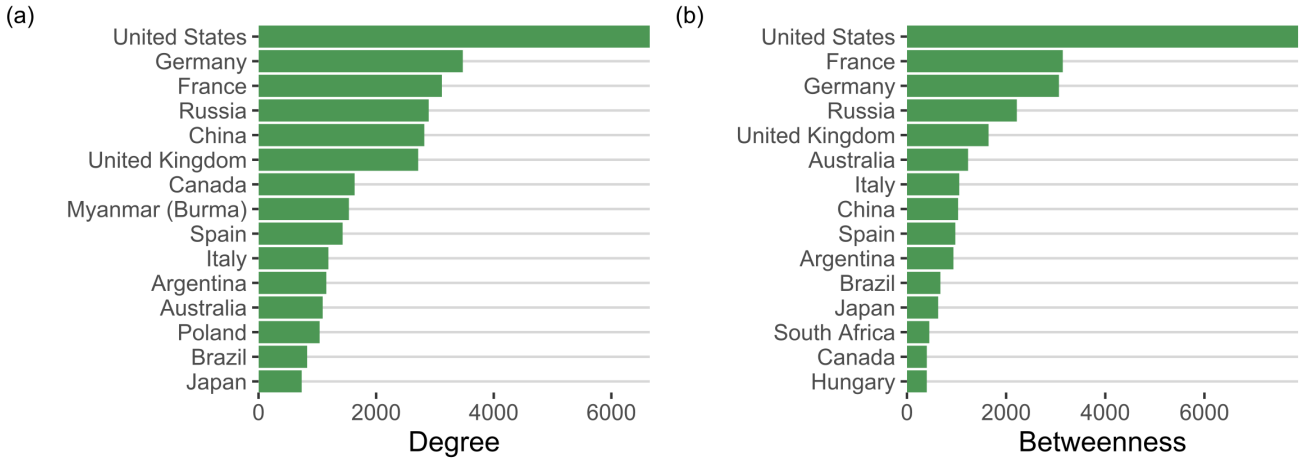


**Fig. S8.** Degree of centrality and betweenness of all regions combined.

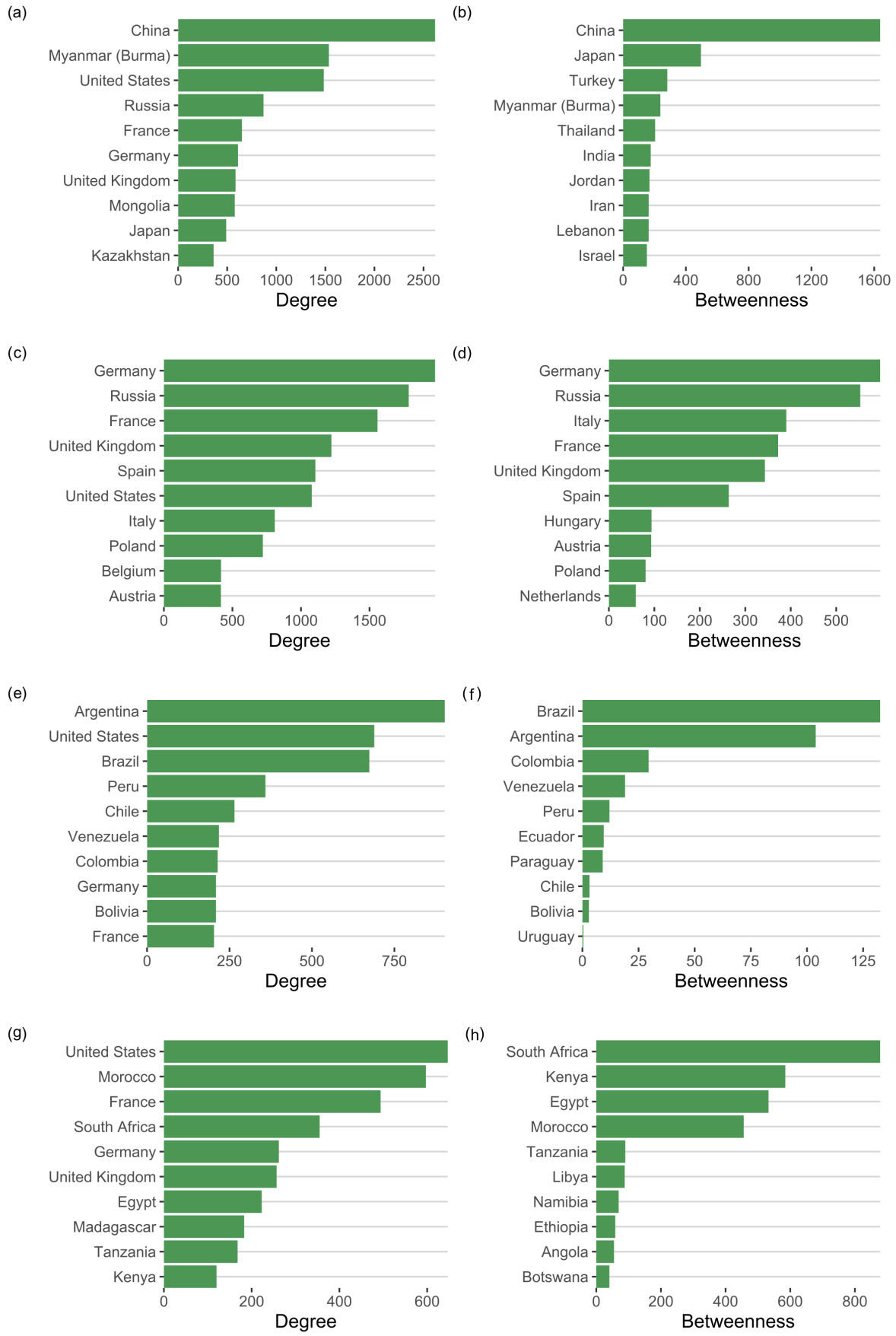


**Fig. S9.** Degree of centrality and betweenness per region: **(a)** Asia, **(b)** Europe, **(c)** South America and **(d)** Africa