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Shifting Trends in Tropical Ecology Research Over Six Decades

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ABSTRACT

The practice, geography and nature of tropical ecology have shifted substantially over past decades, but existing syntheses rarely resolve long-term, pantropical patterns across biomes. This gap is partly due to the challenge of analyzing vast and rapidly growing literature. The advance of large language models enables such analysis for the first time. We analyzed over 170,000 tropical ecology publications (1960–2023) to quantify long-term research trends across five major biomes, identify the most studied countries and leading contributors (based on first-author affiliations), and evaluate their relationships with national socio-economic indicators. Using GPT-4o mini to extract contextual location and biome data, we found that research output has increased across all biomes, but the rate of increase has been highest for tropical forests and lowest for grassy biomes, resulting in a growing dominance of forests and a relative decline of grassy ecosystems. Tropical coastal and freshwater biomes have seen modest relative increases, while oceanic biomes remain stable in relative effort. This relative decline is particularly concerning for Africa, where savannas cover ~70% of tropical land. Since 2010, 73% of tropical ecology papers have come from research hosted in ten tropical countries, led by Brazil (25%). China, India, Mexico, Indonesia and Malaysia are slowly rising to be powerhouses of tropical ecology. Conversely, early research featured broader African representation. This geographical disparity is more closely tied to socio-economic capacity than biome extent. Our analysis highlights both this encouraging shift and the remaining disparities, underscoring the need to strengthen research capacity in underrepresented tropical regions.

1 | Introduction

Tropical ecosystems host most of the biodiversity and ecological interactions on Earth. They are also major reservoirs of carbon, major shapers of regional and planetary hydrological cycles and play numerous other roles in the Earth system, including in mitigating climate change (Bouillon and Connolly 2009; Pan et al. 2024; Twilley et al. 1992). However, they are also increasingly threatened by climate change and other anthropogenic disturbances (Atwood et al. 2017; Exton et al. 2015; Mitchard 2018).

As such, research conducted in tropical ecosystems is key to understanding their functioning considering rising threats.

However, decades of research across ecology, conservation biology, and tropical science have shown that knowledge of tropical ecosystems is shaped by deep geographical, institutional, and socio-economic imbalances (Bruna 2025; Kainer et al. 2009; Stocks et al. 2008). At the broadest scale, ecology as a field remains dominated by temperate-region research and by high-income country scientific institutions

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(Culumber et al. 2019; Fazey et al. 2005; Melles et al. 2019; Nuñez et al. 2019; Parreira et al. 2017). Within the tropics, research is likewise unevenly distributed, historically concentrated in a small number of countries and field stations with long-standing ties to North American or European institutions, most notably Panama, Costa Rica, parts of Amazonia, and a few Eastern and Southern African sites (Stefanoudis et al. 2021; Stocks et al. 2008). Although tropical ecology spans a broad thematic range, it is often treated as a distinct sub-field within ecology. In contrast, temperate and boreal ecology are less commonly framed as separate sub-disciplines, reflecting the historically and institutionally constructed nature of this categorization (Bruna 2025).

Patterns of coauthorship and collaboration reveal similar inequalities. Tropical research is still often led by extra-tropical researchers, with tropical scientists underrepresented in leadership roles (Dangles et al. 2016; Mammides et al. 2016; Melles et al. 2019; Stocks et al. 2008; Tuyisenge et al. 2023). While tropical coauthorship has increased in absolute terms since the early 2000s, this partially reflects bigger teams rather than increased tropical leadership of research (Perez and Hogan 2018), and parts of Africa still show high rates of studies with no local coauthors (Mabele et al. 2023; Tuyisenge et al. 2023). While colonial history shaped early research geographies (Raby 2017), recent work suggests that contemporary foreign-led research is driven more by socio-economic capacity and researcher safety than by colonial legacy alone (Reboredo Segovia et al. 2020). In Amazonia, Brazil has become a major research leader, yet high-impact ecology and conservation research remains dominated by Global North institutions (Malhado et al. 2014). Overall, these studies examining patterns of authorship, collaboration, and research geography are informative but typically limited in scope (few journals/subfields) and time span.

Moreover, biome-specific research patterns in tropical ecology have not been assessed pantropically over long time scales. Prior syntheses largely track research locations at the country level. Besides, site-level analyses that exist have mostly focused on forests, especially Amazonia, and show strong accessibility bias, with studies clustering near long-term field stations, universities, and roads rather than areas of highest conservation need (dos Santos et al. 2015; Nelson et al. 1990). As a result, broader tropical biomes (savannas/grasslands, freshwater, and coastal systems) remain comparatively unexamined. This matters because conservation science globally shows pronounced biome-level research biases, where some threat-rich biomes receive disproportionately low effort (Caldwell et al. 2024). Whether similar mismatches exist within the tropics, and how research effort is distributed among tropical biomes or has shifted over time, remains unknown.

Much of what we know about tropical research patterns has been limited by the scale of traditional literature synthesis, which relies on manual review of individual studies. Earlier reviews typically analyzed a few hundred to a few thousand papers, often drawn from specialist journals (e.g., *Biotropica*, *Journal of Tropical Ecology*) (Perez and Hogan 2018) or a small set of top ecology/conservation journals (Caldwell et al. 2024; Melles et al. 2019), making pantropical, biome-resolved, multi-decadal assessments difficult (but see Bruna (2025), for a

large-scale keyword-based analysis). Recent advances in large language models (LLMs) now enable context-aware extraction of study locations, ecosystem types and other metadata from tens of thousands of abstracts (Berger-Tal et al. 2024; Gallois et al. 2025; Reynolds et al. 2024), outperforming keyword and conventional text-mining approaches that struggle with semantic ambiguity (Farrell et al. 2024). By leveraging long-range context (Vaswani et al. 2017), LLMs can distinguish true study sites from background mentions and infer biome identity from narrative descriptions, enabling large-scale, content-driven synthesis (Gougherty and Clipp 2024; Lin et al. 2024).

Here, we use an LLM-based pipeline to analyze over 170,000 publications in tropical ecology from 1960 to 2023, a dataset set two orders of magnitude larger than previous efforts. This uniquely large dataset allows us to examine long-term trends in tropical research across regions, biomes, and socio-economic contexts. Stimulated by 2024 marking the 60th anniversary of Association for Tropical Biology and Conservation, ATBC, we aim to address the following four questions:

1. How has the geographical distribution of tropical research changed over time?
2. How are patterns of first-author affiliation in tropical research associated with national socio-economic indicators such as Human Development Index (HDI), Gross Domestic Product (GDP), and population size (i.e., total number of people), which may influence national research capacity and the extent of local participation in leading the research?
3. How have research trends across major tropical biomes shifted over the past six decades?
4. Do country-level patterns of research align with the extent of tropical biomes within those countries?

Together, these analyses confirm and extend earlier work, offering the most extensive pantropical, biome-resolved, multi-decadal synthesis of tropical ecology to date. While our dataset is limited to English-language publications indexed in the Web of Science Core Collection (we will discuss bias and limitations of this below), it provides the most comprehensive view available of how the geography, equity, and focus of tropical ecology have evolved over the past 60 years.

2 | Methods

Figure 1 provides an overview of our workflow, including (1) retrieval of publications from the Web of Science Core Collection, (2) LLM-based filtering of irrelevant studies (disambiguation of “Savannah”), and (3) LLM-driven extraction of study country, biome, and climatic zone using GPT-4o-mini including the final filtering based on the extracted data. We describe each step in detail in the sections that follow.

2.1 | Literature Synthesis

We retrieved publication records from the Web of Science Core Collection (WoS CC, Clarivate Analytics), which is one

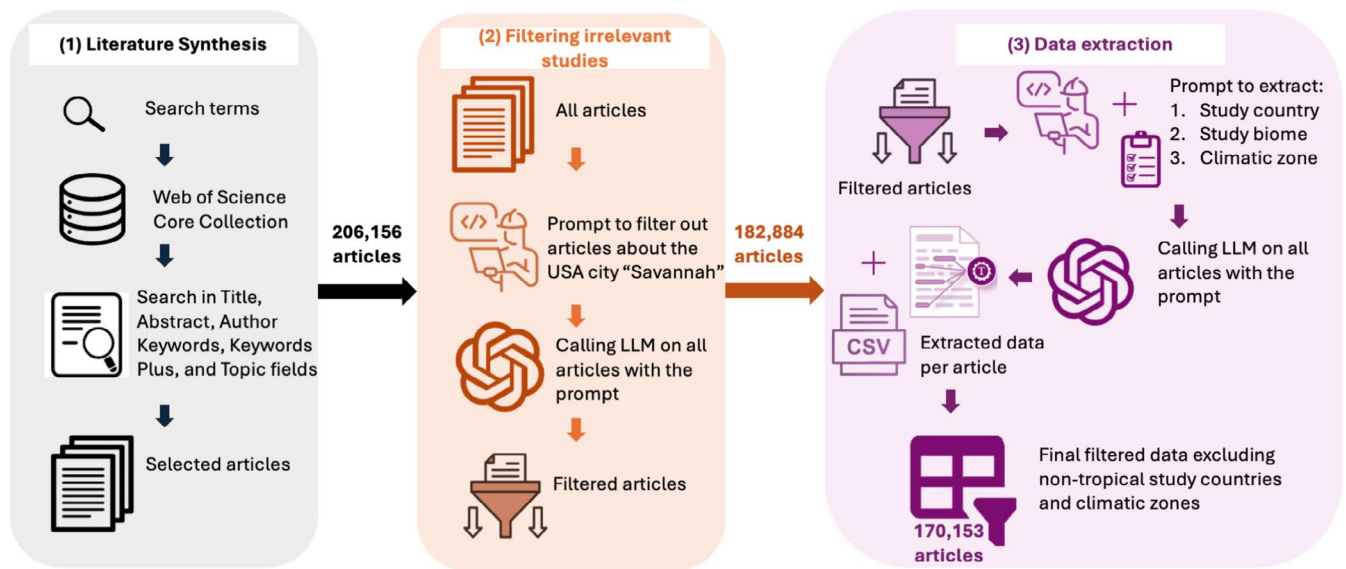


FIGURE 1 | Workflow illustrating the literature retrieval and LLM-based filtering, and extraction pipeline. A Web of Science Core Collection search yielded 206,156 records. An LLM filter removed nontropical and non-biome-relevant studies (including disambiguation of “Savannah”). GPT-4o-mini then extracted study locations, biomes, and climatic zones, resulting in a final dataset of 170,153 tropical studies.

of several databases within the broader Web of Science platform. The search was performed on 27 June 2024 and covered the years 1960–2023. We searched all available fields (Title, Abstract, Author Keywords, Keywords Plus, and Topic fields) using the following search terms: “Tropical ecosystems” OR “Tropical forests” OR “Savanna” OR “Savannah” OR “Cerrado” OR “tropical grasslands” OR “Tropical wetlands” OR “Mangroves” OR “Coral reef.” These terms were used only as a broad retrieval filter and might include papers that were not about tropical ecology. The main purpose of the step was to assemble the largest possible candidate set from which true tropical studies could later be identified using a LLM-based data extraction pipeline (Moorthy et al. 2025). The query returned 206,156 records, which we exported in batches of 1000 (the maximum export limit in Web of Science) and merged into a unified dataset for analysis.

2.2 | LLM-Driven Filtering of Irrelevant Publications

Of the 206,156 peer-reviewed publications, 28,500 publications were associated with the keyword “savannah.” We noticed the potential ambiguity between “Savannah” (the coastal city in Georgia, USA) and “savannah” (the tropical/subtropical biome). To address this issue, we specifically isolated the 28,500 publications containing the keyword “Savannah.” To distinguish between “Savannah” city references and “savannah” biome mentions, we deployed OpenAI’s GPT-4o mini model (accessed via the OpenAI API in Python) with a specialized prompt (see [Supporting Information](#)). The model was instructed to retain only those papers that referred explicitly to the savanna biome, excluding those focused on the city of Savannah, USA. We validated the model’s performance by manually checking a random sample of 50 abstracts. The model correctly classified all 50 cases, so no prompt refinement was required. Based on this classification, only 5228 of

the 28,500 “Savannah” records referred to the savanna biome; the remainder were removed.

2.3 | LLM-Based Extraction of Study Location, Biome and Climatic Zone

After removing records referring to the city of Savannah, we used GPT-4o mini to extract (i) ISO3 codes (three-letter country codes defined by the International Organization for Standardization [ISO] 3166-1 standard; e.g., BRA for Brazil) for true study locations, (ii) study biomes, and (iii) whether sites fell in the tropical vs. nontropical climatic zone, based on titles, abstracts, and keywords. Conventional keyword/Named Entity Recognition (NER) can detect place strings but generally cannot identify countries from local site names or distinguish true study site from background mentions (Farrell et al. 2024). The climatic-zone flag was necessary for countries spanning multiple zones (e.g., excluding clearly nontropical locations despite “tropical” terminology). We iteratively refined the prompt using 100 manually labeled abstracts. This helped us address indirect place references (e.g., national parks or mountain ranges) by assigning studies to the country (or countries) spanning the feature. Prompt refinement stopped once accuracy gains plateaued. Notably, for territories (e.g., Guam) the model returned territory ISO3 codes (e.g., GUM) rather than the governing country (USA).

For biomes, the model selected from nine predefined categories (Forests, Shrublands, Grasslands, Savannas, Mangroves, Wetlands, Coastal, Coral reef, Marine), which we aggregated into five groups for further analysis: Forests; Grassy (shrublands/grasslands/savannas); Freshwater (wetlands); Coastal (mangroves/coastal); and Ocean (coral reef/marine). The final prompt ([Supporting Information](#)) returned “NA” when location/biome could not be inferred (e.g., global studies or missing abstracts). We processed the resulting 182,884 abstracts to generate structured JSON (JavaScript Object Notation) outputs,

a standard format for representing structured data and commonly used as a return format from large language models. We then validated performance on an independent random sample of 200 abstracts (excluding the 100 used for refinement), consistent with standard practice in ecological LLM text-mining where large benchmark corpora are unavailable (Gougherty and Clipp 2024). Finally, we removed studies with nontropical study locations, yielding 170,153 abstracts for subsequent analysis.

2.4 | Data Analysis

All analyses were descriptive and aimed at characterizing large-scale, long-term patterns in tropical ecology research rather than fitting inferential or predictive statistical models. Accordingly, we used summary statistics, proportional trends, absolute publication counts, and Pearson correlations for bivariate associations.

2.4.1 | Geographical Distribution of Tropical Research

To track changes in where tropical research is conducted, we calculated, for each decade, the proportion of all tropical publications contributed by each tropical country. This allowed us to identify major research hosts, shifts in host geographical representation, and host countries with increasing or declining publication shares over time. Here, we define “research hosts” as countries where studies were conducted (i.e., study locations), irrespective of the nationality or institutional affiliation of the authors. If a study reported multiple study countries, each unique country was treated as a separate full-weight record, ensuring all host countries were credited for that publication.

2.4.2 | Lead Authorship

Using Web of Science affiliation metadata, we assessed shifts in tropical ecology leadership by comparing first-author affiliation countries in the pre-1980s versus post-2010s. We use first-author affiliation as a proxy for research leadership, as is common in bibliometric analyses, reflecting the location of primary analytical contribution. However, authorship conventions vary across fields and regions, and senior (last) authors may represent other forms of leadership not captured here. Because author–address mappings are incomplete before 2007, we used the pre-1980s subset (897 papers), extracted affiliation countries via a regex (regular expression; a method for identifying text patterns) parser, and manually verified all multi-affiliation cases (103/897), excluding 10 records where the lead-author affiliation could not be resolved. For post-2010 papers, where author–address links are explicit, we applied the same parsing approach to extract lead-author affiliation countries. In both periods, when first authors listed multiple countries, each unique country received one full credit. We then calculated each country’s publication share and identified the top ten leaders in each period.

2.4.3 | Temporal Trends and Biome-Level Patterns

To examine long-term shifts in research focus, we grouped all publications into five time periods: pre-1980, 1980–1990,

1990–2000, 2000–2010, and post-2010. Publications from the 1960s and 1970s were grouped together because early years contained very few records (e.g., 517 total abstracts in the 1960s).

For biome analyses, we used the five broad biome categories produced by our LLM pipeline (Figure 1): Forests, Grassy, Freshwater, Coastal, and Ocean. We quantified changes in both absolute yearly publication counts and proportional representation across decades. Because proportions alone may obscure overall growth, we also estimated exponential annual rates of increase in publication output for each biome (1960–2023) using log-linear models applied to yearly counts. When a publication was associated with multiple biomes, each biome was counted once with full credit.

2.4.4 | Biome Extent vs. Research Effort

To evaluate disparities in research output relative to biome extent, we focused on post-2010 publications only and restricted this analysis to the two major terrestrial biomes that dominate the tropics: forests and grassy ecosystems. Using WWF ecoregion boundaries, we estimated, for each tropical country, the area of forest (all tropical/subtropical forest types) and grassy biomes (tropical/subtropical savannas and grasslands). Although these ecoregion products are not perfect, for instance, savannas in Asia are sometimes misclassified as dry forest, they nonetheless represent the most comprehensive resource for globally comparing biome coverage across countries (Figure S1). For each country, we calculated a publication-to-biome-area ratio (share of publications/share of biome area). Ratios > 1 indicate higher-than-expected research output relative to biome extent, and ratios < 1 indicate underrepresentation.

2.4.5 | Socio-Economic Predictors of Research Hosting and Leadership

To evaluate whether countries with lower resource availability tend to host or lead fewer studies, we examined associations between post-2010 research metrics and national socio-economic indicators: HDI, GDP, GDP per capita, and population size. GDP reflects a country’s overall economic output, whereas GDP per capita captures average economic resources available per person. HDI integrates education, health, and income, and therefore provides a more direct and holistic metric of human development. Across countries, GDP per capita is correlated with HDI but with interesting outliers, whereas total GDP is only moderately related to HDI as country population size is a major factor (Figure S2), indicating that these metrics capture complementary but distinct dimensions of socio-economic context. We obtained HDI values from the United Nations Development Programme (2022) and GDP and population estimates from the World Bank. Because our goal was to quantify simple macro-level associations rather than test causal models, we used Pearson correlation coefficients to assess relationships between publication-to-biome-area ratios and socio-economic indicators and lead-author representation and socio-economic indicators. These analyses provide a descriptive assessment of whether national capacity and development correlate with tropical research hosting and leadership.

3 | Results

3.1 | Evaluation of Data Extraction Pipeline

We independently evaluated the OpenAI GPT-4o mini model's performance on 200 randomly selected abstracts and found an accuracy of 90% for extracting ISO3 codes and 88% for extracting biomes. Performance was highest when abstracts included explicit geographic references (e.g., country names, regions, province or national parks), with the model almost always returning the correct ISO3 code. However, ambiguous or broad references such as "Amazon" or "Africa," which spans multiple countries, often resulted in inconsistent outputs, with the model variably listing all, none, or only a subset of the relevant countries.

For biome classification, despite prompting the model to choose from nine predefined biome categories (plus NA), it occasionally produced other specific biome labels, resulting in 17 unique biome labels (e.g., "Woodlands" instead of "Forests"/"Grassy," "Salt Marsh" or "Estuary" instead of "Coastal") not included in our JSON schema. These deviations occurred in a small fraction of cases (~600 abstracts out of ~170,000) but necessitated a post-processing step. In this step, most model outputs could be reliably consolidated into the five broad biome categories, but ambiguous labels such as "Woodlands" (which occurred

only once and could plausibly refer to either forests or grassy biomes) or clearly non-ecological terms like "Agricultural" were assigned NA because their correct biome classification could not be determined without reading those abstracts in detail. Most classification errors were associated with abstracts on agroforestry, or policy papers or global analysis, which the model frequently mapped to major biomes like "Forest" rather than to NA. Nevertheless, the final accuracy, after post-processing, was sufficient to support large-scale analyses.

3.2 | How Has the Geographical Distribution of Tropical Ecology Research Shifted Over Time?

After excluding records with "NA" country codes, we analyzed 138,498 publications. The top ten post-2010 research host countries (i.e., countries ranked by their publication share after 2010) account for 73% of tropical ecology papers, up from 64% in 1960–1980 (Figure 2a). Brazil shows the strongest increase and now hosts 25% of all studies. Australia's relative publication share has declined since the 1980s but it remains the second most studied country; the USA (aside from a dip in the 1980s), South Africa and Colombia remain consistently prominent. China, India, Mexico, Indonesia and Malaysia's relative share show steady growth as emerging research hubs.

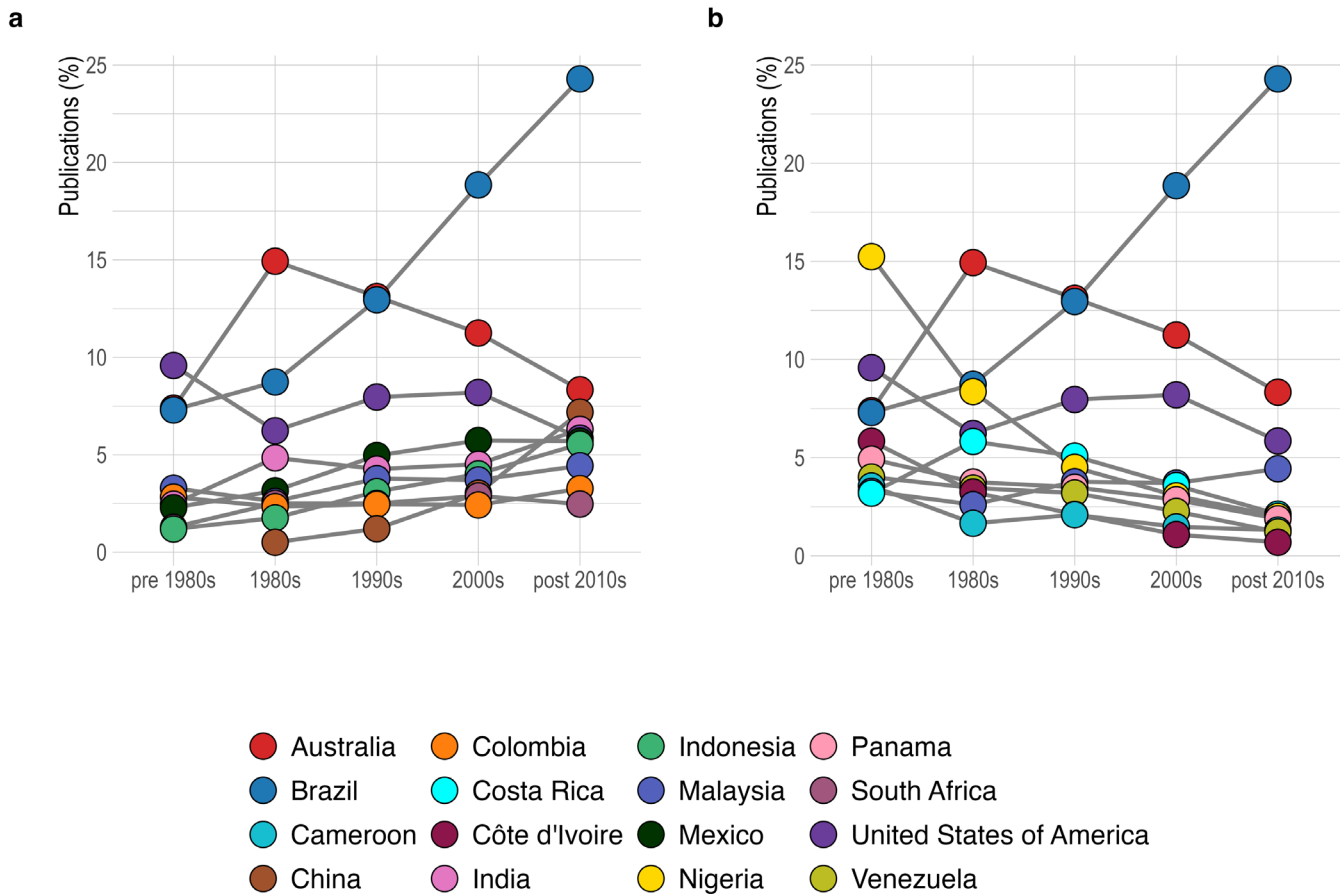


FIGURE 2 | Temporal changes in the relative contribution of countries hosting tropical ecology research. (a) Top 10 research host countries based on post-2010 publication volumes, showing how currently dominant hosts have increased or changed their relative share over time. (b) Top 10 research host countries based on pre-1980 publication volumes, illustrating how historically dominant hosts have changed, with several declining in relative importance. In both panels, each line represents a country and traces its proportion of total tropical ecology publications across decades.

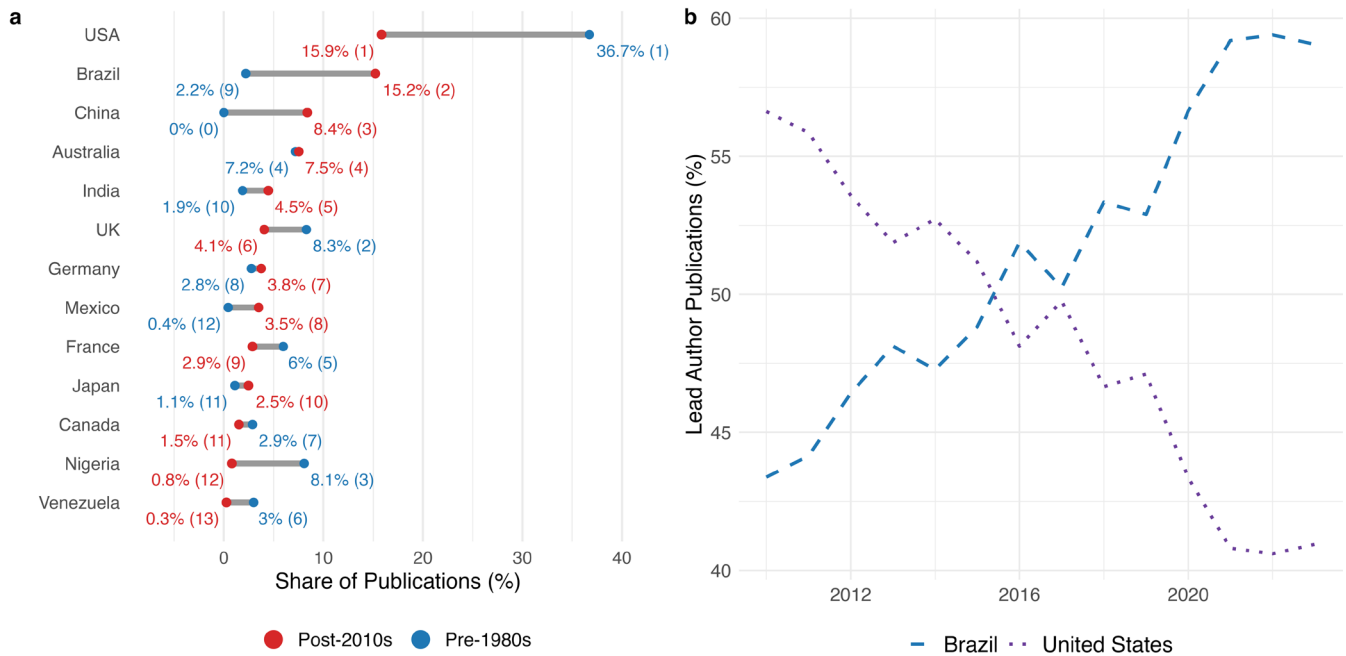


FIGURE 3 | (a) Dumbbell plot comparing the share of tropical ecology publications led by each country in the pre-1980s (blue) and post-2010s (red). Only countries appearing in the top 10 of either period are shown. Points indicate each country's proportional contribution (%), with ranks in parentheses, and horizontal gray segments show the magnitude and direction of change between periods. (b) Annual publication trajectories for Brazil (blue and dashed) vs. the USA (purple and dotted) post-2010, highlighting the specific timeframe in which Brazil's output overtook that of the USA.

We also assessed the top ten pre-1980 host countries, i.e., countries ranked by their publication share before 1980 (Figure 2b). While Australia, Brazil, the USA and Malaysia were already major hosts, several others have declined in their relative publication output markedly, most notably Nigeria (15% pre-1980 to 2% post-2010), along with Ivory Coast, Panama, Costa Rica and Venezuela.

We further examined the top five countries that serve as the current epicenters (post 2010) of research for the various biomes (Figure S3). Brazil dominates all biomes except ocean ecosystems, which remain centered on Australia and the USA. South Africa and Kenya are rising as grassy-biome hubs; India is prominent in coastal work; China is rising rapidly in forest and coastal research. Nigeria, formerly central for grassy-biome studies, continues to decline, while Indonesia shows strong growth across freshwater, coastal, and ocean research. Mexico appears among the top five hosts for forests and ocean systems, and Malaysia remains consistently among top forest hosts across decades.

3.3 | What Is the Geographical Pattern in Who Is Leading the Research in Tropical Ecology?

We further extended the analysis to determine which countries lead tropical ecology research, based on first-author affiliations, which is not geographically constrained. After excluding records without affiliation data and retaining only pre-1980 and post-2010 papers, we analyzed 121,859 publications (Figure 3a). Leadership remains concentrated but has diversified modestly: the top ten countries produced 79% of papers in 1960–1980 versus 68% post-2010. The USA, Brazil, Australia, and India appear

in both periods; Brazil overtook the USA in annual output in 2019 (“*ultrapassagem*”; Figure 3b). France, Germany, and the UK remain prominent leaders, while China and Mexico are rising and former leaders such as Nigeria and Venezuela have declined.

To explore drivers of contemporary leadership, we focused on countries leading $\geq 1\%$ of post-2010 publications (17 countries; Figure 4a–d). Only ten are tropical; the remaining seven are high-income countries outside the tropics. Across these 17, publication share correlates strongly with GDP and population ($R \approx 0.71$ and 0.70), whereas HDI and GDP per capita show little association, likely because HDI is uniformly high (≥ 0.7) in this group.

3.4 | What Trends Have Emerged in Biomes in Tropical Ecology Research Over the Past Six Decades?

We analyzed 168,114 publications (of 170,153 total) for which biome identity could be assigned. Across 1960–2023, forests have consistently been the most studied tropical biome, and their proportional representation has increased steadily since the 1990s. Freshwater and coastal biomes also show gradual proportional increases, whereas ocean ecosystems remain relatively stable across decades. In contrast, the proportional representation of grassy biomes (savannas, grasslands) has declined continuously since the 1960s (Figure 5).

Absolute publication counts increased for all biomes, including grassy systems, across every decade (Figure S4). However, exponential annual growth-rate estimates (1960–2023) show that

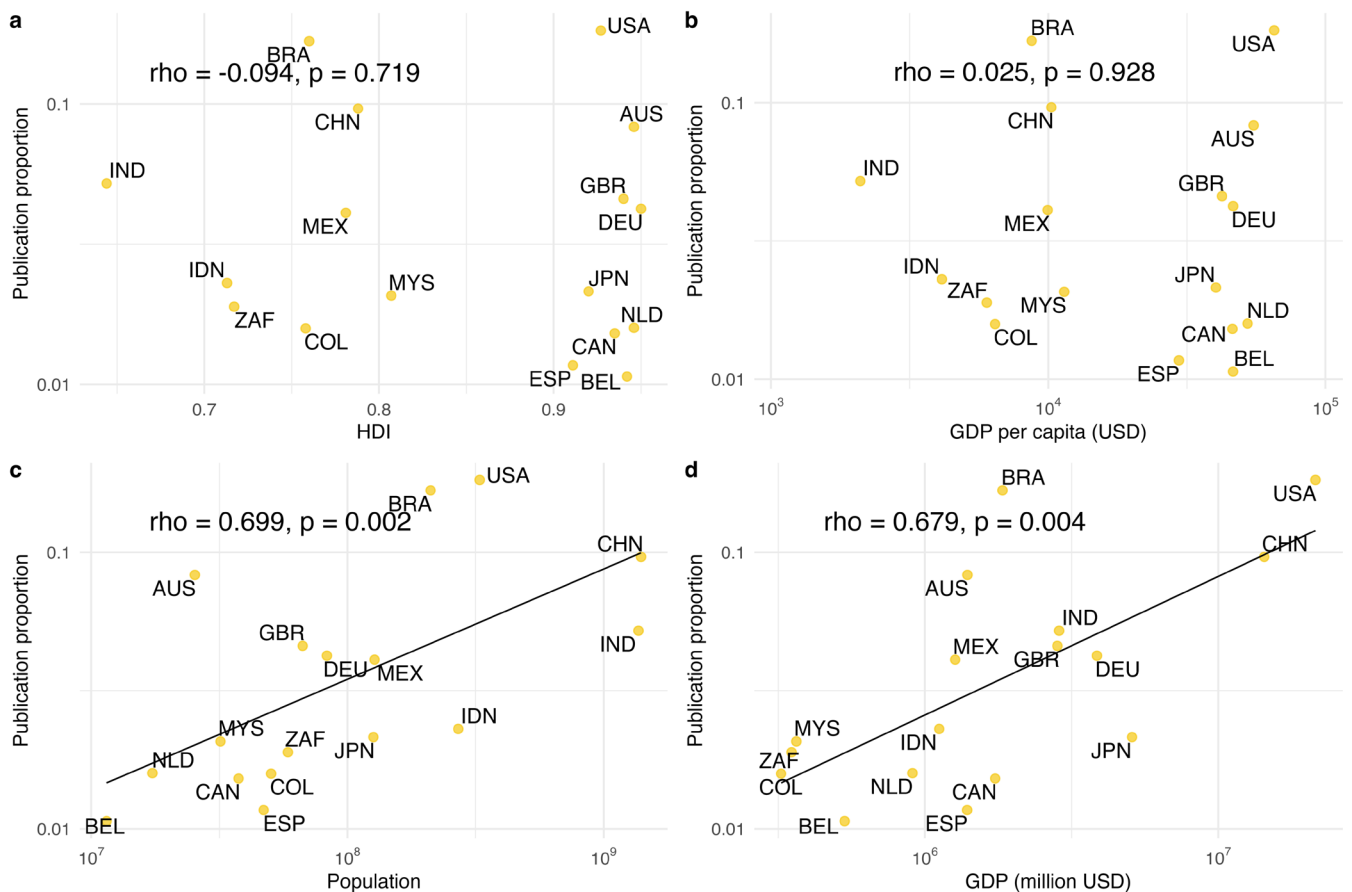


FIGURE 4 | Scatter plots the correlation between publication proportion of the top 15 leading countries (by post-2010 publication share) to three socio-economic indices, (a) HDI, (b) GDP per capita, (c) population, and (d) GDP. Each yellow point represents a single country.

grassy biomes have the slowest annual growth, whereas freshwater, forests, coastal, and ocean systems have expanded more rapidly (Figure 5).

We also examined how biome prominence varies across continents (Figure 5). In the Americas, tropical research has been consistently dominated by forests, with other biomes contributing smaller but relatively stable proportions over time. In Asia/Oceania, forests, coastal, and ocean biomes dominate, grassy biomes show a declining share, and freshwater systems show a slight increase. In Africa, grassy ecosystems declined in relative prominence as forest-focused research has expanded. Absolute counts increased for all biomes on all continents (Figure S4), and continental growth-rate patterns mirror global trends on most continents (except the Americas).

3.5 | Can the Disparity in the Geographical Distribution of Research Be Explained by the Country's Biome Coverage and/or Socio-Economic Indices?

We focused on post-2010 publications in the two major terrestrial biomes, forests and grassy ecosystems (53,562 records) and limited the sample to countries $\geq 1000 \text{ km}^2$ and holding $\geq 1\%$ of pantropical forest or grassy biome area to avoid artifacts from small countries. We first tested whether

a country's publication share scaled with its biome-area share (Figure 6a,b). Forest publications showed a moderate positive correlation with forest area ($R=0.58$), whereas savanna publications showed no significant correlation, indicating that savanna research is concentrated in a limited set of countries regardless of savanna extent.

We then compared research intensity using publication-share/area-share ratios (Figure 6c,d). Forests are generally studied more intensively per unit area than savannas. Brazil contributes 25% of forest studies, but this dominance largely disappears after normalizing by forest area, suggesting its forest research output is broadly proportional to its forest extent. However, Brazil exceeds all other countries in savanna research. Australia shows the opposite pattern, hosting more forest than savanna studies despite having disproportionately large savanna area, while South Africa and Kenya stand out for savanna research despite relatively small savanna coverage. To examine potential drivers of these mismatches, we related publication-to-area ratios to national socio-economic indicators (Figure 7a-h). Globally, HDI was the strongest (though modest) correlate for both forests ($R=0.37$) and savannas ($R=0.51$). GDP and GDP per capita were weaker to moderate correlates (forests: $R=0.29$ and 0.32 ; savannas: $R=0.42$ and 0.39), while population showed no relationship for forests and only a weak positive association for savannas ($R=0.32$). Many countries remain underrepresented despite relatively high HDI, indicating that no single index fully explains

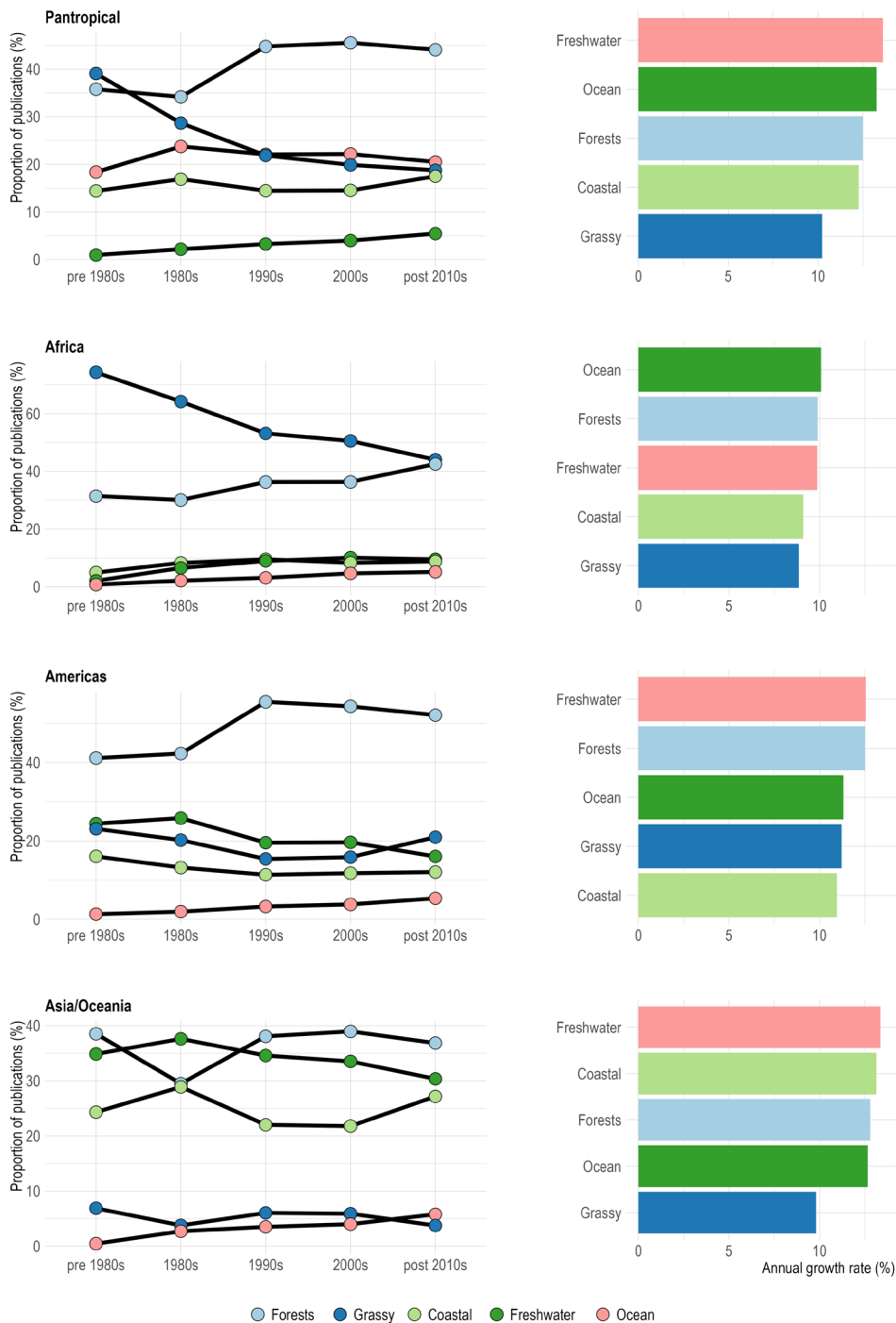


FIGURE 5 | (Left) Decadal trends in the most-studied biomes of tropical ecology, spanning the six decades from 1960s to 2023. The top panel (Pantropical) reflects biome-level publication proportions at the global scale, while the three lower panels focus separately on Africa, the Americas (Central and South), and Asia/Oceania. Each colored data series denotes a major biome, illustrating how research emphasis on different biomes has evolved over the past six decades both globally and within each continental region. (Right) Exponential annual growth rates (%) in publication output for the same five biomes, estimated from yearly publication counts (1960–2023). These bars quantify the rate at which research effort is expanding in each biome at the pantropical and continental (Africa, Americas and Asia/Oceania) scale.

global variation. Patterns strengthened when restricting to the top 15 biome-area holders. Among forest-rich countries, correlations increased sharply (HDI $R=0.86$; GDP $R=0.62$; GDP per capita $R=0.79$), implying that development and economic capacity more strongly predict research intensity among the largest forest holders. Among the largest savanna holders covering

mostly lower-HDI African nations, GDP and population were more influential, with GDP the strongest correlate ($R=0.67$), likely reflecting limited HDI variation in this subset. Malaysia and Mexico show higher-than-expected forest research given their socio-economic profiles, while Brazil (and to a lesser extent Nigeria) stands out for savanna research.

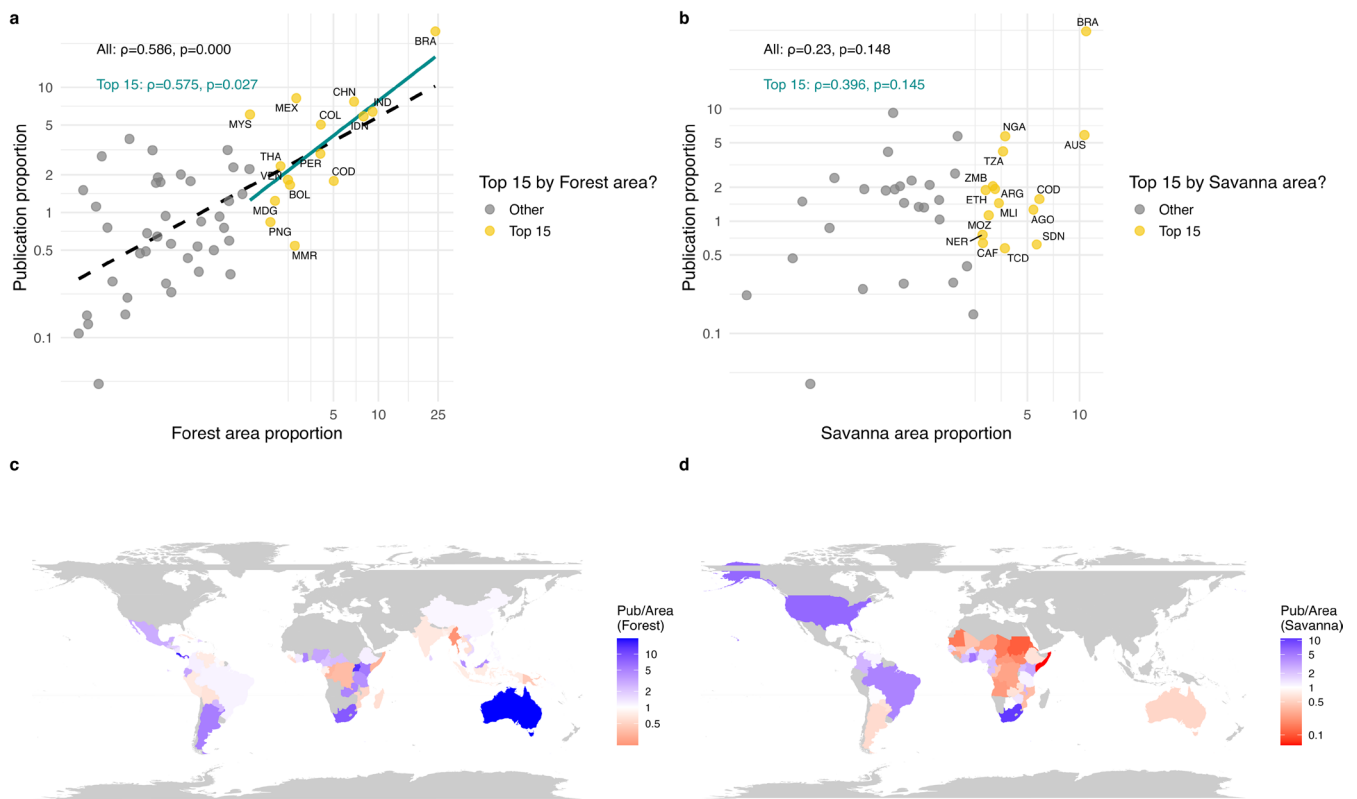


FIGURE 6 | Top row shows the scatter plots illustrating how each country's forest (a) and savanna (b) area share relates to its publication share, revealing whether simple area alone predicts research focus. Bottom row shows the global maps of disparity (publication share/area share) for forests (c) and savannas (d), highlighting which countries are over- or underrepresented in tropical research relative to their biome coverage.

4 | Discussion

Enabled by the advancements in the field of AI, we were able to identify large scale trends in the geographical distribution of research locations and the leading research institutions. This is the first study to examine such a broad scope of literature over multiple decades. We used over 170,000 publications to examine these trends over the past six decades, revealing prevailing disparities and identifying potential gaps and future research directions.

Our analysis shows a persistent geographic concentration in tropical ecology research. According to the official World Bank-approved boundaries, there are at least 156 tropical countries, territories and overseas departments. While the geographic coverage of research locations has expanded over time, studies remain strongly concentrated in a small set of countries, consistent with earlier syntheses showing similar clustering (e.g., 62% of tropical publications in ten countries during 1995–2004; Stocks et al. 2008). Brazil now stands out as the dominant research hub, with Australia and the USA remaining long-term focal countries (Malhado et al. 2014; Pitman et al. 2011; Murrins Misiukas et al. 2021; Stocks et al. 2008). Historically prominent locations, including Nigeria, Ivory Coast, Panama, Costa Rica and Venezuela, have declined sharply, likely reflecting the waning influence of colonial-era research infrastructures and long-standing international field stations rather than sustained local capacity (Clark 1985).

Our novel contribution is a pantropical, biome-resolved view of research effort, which is largely missing from prior syntheses

that either treat the tropics as a single unit (Stocks et al. 2008) or focus on one domain (e.g., forests, marine, or conservation) (Kainer et al. 2009; Murrins Misiukas et al. 2021; Partelow et al. 2020; Tuyisenge et al. 2023). The patterns observed here, particularly the disproportionate emphasis on forest biomes relative to other tropical systems, are consistent with evidence that moist broadleaf forests are over-sampled and over-cited, while drier low-tree-cover biomes remain under-sampled despite covering much of the tropics (Metcalf et al. 2025).

Our first-author affiliation analysis reinforces persistent leadership inequities reported across ecology and conservation (Mammides et al. 2016; Nuñez et al. 2019; Perez and Hogan 2018; Reboredo Segovia et al. 2020; Tuyisenge et al. 2023). Leadership remains geographically concentrated, though it has shifted in important ways over the past six decades. The United States, Brazil, Australia and India are the only countries that consistently appear in both periods, with Brazil now surpassing the USA as the single largest contributor, mirroring patterns reported in Amazon-focused analyses (Malhado et al. 2014). The decline seen in research leadership since the 1960s in countries such as Nigeria and Venezuela likely reflect decreasing state capacity for research over time. A limitation persists in modern records as affiliation-based metrics cannot distinguish Global South researchers publishing from Global North institutions (e.g., students from the tropics undergoing PhD training in the Global North), potentially underestimating positive trends in local scientific capacity. Author names do not provide sufficient resolution on

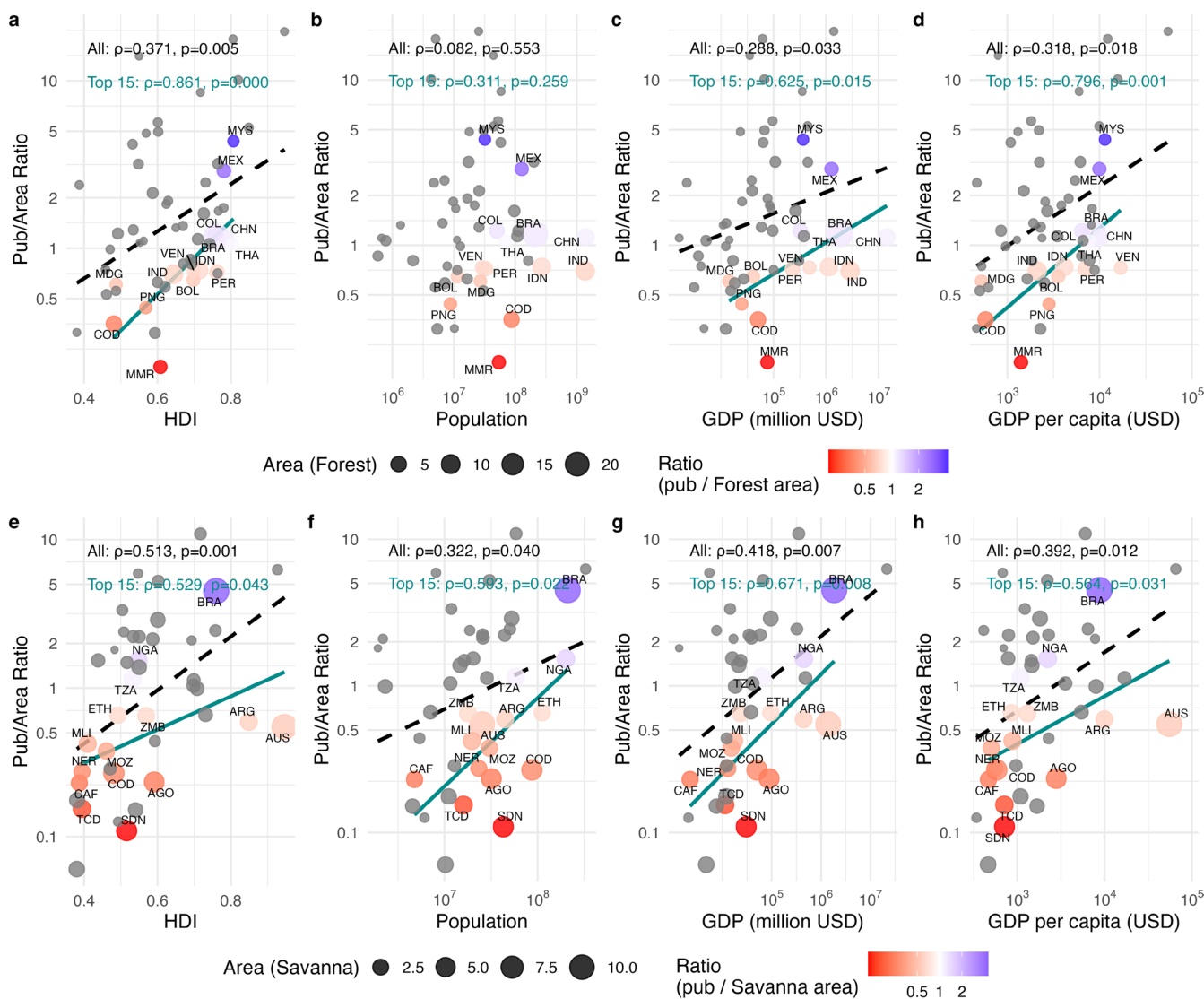


FIGURE 7 | Comparison of each country's publication-to-area ratio against three socio-economic indices: HDI (a, e), population (b, f), GDP (c, g), and GDP per capita (d, h) for forests (top row) and savannas (bottom row). Circles represent countries, sized by their respective biome area, with a red to blue diverging color scale indicating whether their ratio is below (red), near (white), or above (blue) 1. Each panel shows two best-fit lines, a black dashed line for all countries and a teal solid line for the top 15 biome-area holders, whose correlation values are noted above.

national backgrounds, as evidenced by the two Indian names of the authors of this study.

Among countries leading at least 1% of all tropical ecology studies published after 2010, only ten lie within the tropics, and no African country appears in the current top ten. Our analysis further shows that contemporary leadership correlates strongly with national GDP and population size, whereas HDI and GDP per capita show little explanatory power within this already high-HDI group. These patterns align with previous work demonstrating that scientific leadership depends on long-term institutional funding, political stability, and human capital more than on biodiversity or biome extent (Reboredo Segovia et al. 2020; Stocks et al. 2008). This is not surprising. At the same time, the rapid rise of Brazil, China, India, Mexico, and Indonesia highlights meaningful, regionally driven growth in tropical science in many of the tropical nations with larger economies.

Our biome-level results show persistent imbalances in tropical ecology. Although publication counts have increased across

all biomes, forests have become increasingly dominant, while grassy ecosystems have declined in relative share and show the slowest growth. Coastal and ocean ecosystems, despite covering extensive tropical areas, remain comparatively understudied (Caldwell et al. 2024). In Africa, grassy ecosystems have also lost share despite covering most tropical land area (Aleman et al. 2019), a concerning trend because forest-centric views of savannas can encourage large-scale tree planting in these non-forest ecosystems, potentially causing irreversible loss (Parr et al. 2024). When research effort is compared with terrestrial biome extent, we assume that an unbiased distribution of effort would scale with biome area; deviations therefore indicate relative over- or under-representation. Only a handful of large tropical countries (Brazil, Australia, India, China, and Indonesia) show this pattern, while major biome holders in Africa, such as the Democratic Republic of Congo, remain underrepresented. By contrast, Panama and Costa Rica host disproportionately high forest research relative to forest extent, consistent with long-standing ties to Global North field networks. However, country-level equivalence does not imply

spatially representative sampling, as research is often concentrated in a few well-established field sites. Such site-level biases cannot be recovered from abstracts alone and would require geolocated full-text analyses. Recent studies likewise show that sampling locations often reflect accessibility or institutional history rather than ecological threat, so highly threatened or remote ecosystems may still be overlooked (Caldwell et al. 2024; dos Santos et al. 2015; Lin et al. 2024; Nelson et al. 1990).

Our synthesis offers a large, standardized view of tropical ecology publication trends, but it is not a complete census. Because we rely on English-language records in the WoS CC, we likely underrepresent locally published and non-English scholarship, as well as books and other gray literature (see Pitman et al. 2006 for the importance of systematically capturing such sources demonstrated in Amazonian landscape). WoS CC indexing has also expanded over time, and some journals and early volumes (including *Biotropica*) are incompletely represented for earlier decades. In addition, biome and location assignments are inferred from titles, abstracts, and keywords rather than full texts, and leadership is proxied using affiliation countries, limiting our ability to resolve within-country sampling biases or researcher positionality. These constraints mean our results should be interpreted as the most comprehensive biome-resolved picture available from a single consistent indexing source, rather than a complete account of tropical ecology knowledge production.

Taken together, our results reveal both encouraging progress and persistent inequities in the global landscape of tropical ecology. Research locations have become somewhat more geographically dispersed over the past six decades, yet many tropical countries, particularly in Africa, remain underrepresented. Leadership patterns show an even sharper shift, with Brazil, India, China, Mexico, and Indonesia now playing more prominent roles in directing tropical research. Yet high-impact work continues to be disproportionately cited from institutions in the Global North (Figure S5), and research leadership still correlates most strongly with GDP and population size. These gaps are not explained by biome area but instead mirror broader socio-economic gradients and the uneven distribution of scientific capacity worldwide. Large-scale, data-driven assessments such as ours offer one pathway to monitor that progress, reveal persistent blind spots, and inform the strategic investments needed to build a more inclusive, representative and collaborative global tropical ecology.

Author Contributions

Conceptualization: Yadvinder Malhi. Methodology: Yadvinder Malhi and Sruthi M. Krishna Moorthy. Formal analysis, Data curation, Validation and Visualization: Sruthi M. Krishna Moorthy. Writing – review and editing: Sruthi M. Krishna Moorthy and Yadvinder Malhi.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the codes can be downloaded from the following link: https://github.com/sruthimoorthy/LLM_TropicaEcology_Analysis. All the datasets used for the analysis can be downloaded from the following link: <https://doi.org/10.5281/zenodo.15324252>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Map of India's WWF-designated tropical dry forests ecoregions, highlighting how recent studies suggest that the Central, East, and South Deccan areas (Ratnam et al. 2019) may function more as savanna ecosystems than true dry forests. This illustrates a broader issue in parts of Asia, where standard biome classifications risk conflating savanna-like grass-woodland mosaics with officially labeled dry forest ecoregions. **Figure S2:** Pairwise relationships among national socio-economic indicators across countries (\log_{10} -transformed GDP, GDP per capita, and population). Points represent countries, with linear fits (blue lines) and 95% confidence intervals (shaded). HDI shows a strong positive correlation with GDP per capita, but only a moderate association with total GDP, indicating that economic scale and average economic resources capture different dimensions of development. Pearson's r and Spearman's ρ are reported for each relationship. **Figure S3:** Current top five research epicenters for each major tropical biome, showing how these leading host countries have evolved in their publication shares over time. Inset pie charts show the proportion of total tropical research attributable to each biome from pre-1980 through post-2010. Forest, coastal, and ocean shares have remained comparatively stable, while grassy ecosystems show a slight decline and freshwater exhibits a modest rise. **Figure S4:** Figure

illustrates the absolute publication counts per biome across five time periods. The total number of tropical ecology publications increased markedly in every biome over the past six decades. Forests show the largest growth in absolute publication numbers, followed by coastal, grassy, ocean and freshwater biomes. These absolute trends confirm that all biomes have experienced substantial increases in research output. Values shown represent the number of unique publications assigned to each biome in each decade. **Figure S5:** Top 10 countries currently producing high impact research in the field of tropical ecology. The countries are ranked in the descending order of average citations per publication in the post 2010 era. **Figure S6:** Global maps illustrating each tropical country's share of all tropical ecology publications for five consecutive decadal periods (pre-1980, 1980s, 1990s, 2000s, and post-2010). The color scale indicates the percentage of total publications hosted by each country in that decade, highlighting how research activity has expanded or shifted geographically over time. **Figure S7:** Africa-specific maps illustrating each African country's share of all ecology publications coming from Africa for five consecutive decadal periods (pre-1980, 1980s, 1990s, 2000s, and post-2010). The color scale indicates the percentage of total publications hosted by each country in that decade, highlighting how research activity has expanded or shifted geographically over time. **Figure S8:** (a) Top 10 current research hosts in Africa (based on post-2010 publication volumes), illustrating how their relative shares in tropical ecology research have shifted over time. (b) Top 10 African research hosts prior to 1980, many of which have declined or remained stable since the 1960s and 1970s. Each colored line traces a single country's publication share across the decades. **Figure S9:** Americas-specific maps illustrating each North/South American country's share of all ecology publications coming from the Americas for five consecutive decadal periods (pre-1980, 1980s, 1990s, 2000s, and post-2010). The color scale indicates the percentage of total publications hosted by each country in that decade, highlighting how research activity has expanded or shifted geographically over time. **Figure S10:** (a) Top 10 current research hosts in the Americas (based on post-2010 publication volumes), illustrating how their relative shares in tropical ecology research have shifted over time. (b) Top 10 North and South American research hosts prior to 1980, many of which have declined or remained stable since the 1960s and 1970s. Each colored line traces a single country's publication share across the decades. **Figure S11:** Asia and Oceania-specific maps illustrating each Asia and Oceania country's share of all ecology publications coming from the two continents for five consecutive decadal periods (pre-1980, 1980s, 1990s, 2000s, and post-2010). The color scale indicates the percentage of total publications hosted by each country in that decade, highlighting how research activity has expanded or shifted geographically over time. **Figure S12:** (a) Top 10 current research hosts in Asia and Oceania (based on post-2010 publication volumes), illustrating how their relative shares in tropical ecology research have shifted over time. (b) Top 10 research hosts from Asia and Oceania prior to 1980, many of which have declined or remained stable since the 1960s and 1970s. Each colored line traces a single country's publication share across the decades.