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# The Evolution of *in vivo* Synaptic Plasticity Research in Learning and Memory (1987-2024): A Bibliometric Analysis

## Öğrenme ve Bellek Alanındaki *in vivo* Sinaptik Plastisite Araştırmalarının Evrimi (1987-2024): Bibliyometrik Bir Analiz

**Melek ALTUNKAYA[1], Nurcan DURSUN[2], Cem SÜER[2]**

*[1]Selçuk University Vocational School of Health Services, Konya, Türkiye*
*[2]Erciyes University Faculty of Medicine, Department of Physiology, Kayseri, Türkiye*

**ABSTRACT**

**Aim:** Synaptic plasticity forms the neurobiological foundation of learning and memory. Despite the rapid growth of *in vivo* electrophysiological studies, a systematic evaluation of global publication trends remains lacking. This study aimed to map the evolution, research themes, and scientific collaborations related to hippocampal plasticity.

**Materials and Methods:** A bibliometric analysis evaluated 2,348 English-language articles from the Web of Science Core Collection (1987-2024), extracted on October 2, 2025. To investigate systems-level dynamics, the exact topic (TS) query was TS= ("synaptic plasticity") AND ("hippocampus" OR "learning" OR "memory") AND ["long-term depression (LTD)"] OR "long term potentiation (LTP)" OR "LTP" OR "LTD" AND ("*in vivo*"). VOSviewer and Biblioshiny were utilized to analyze publication trends, thematic maps, co-authorship networks, and institutional distributions.

**Results:** Publications peaked in 2013 (130 articles) and have gradually declined since. Core keywords included synaptic plasticity, hippocampus, and LTP, while trending topics such as pathology, interleukin-1 beta and gamma oscillations indicated a shift toward clinical neuropathology. The most cited authors were Song S., Miller K.D., Abbott L.F., and Morris R.G.M. The strongest collaboration networks involved Rowan M.J., Bramham C.R., and Korte M. The United States, Germany, and China led the field, with Stanford and Northwestern Universities as top institutions.

**Conclusion:** Synaptic plasticity and hippocampal mechanisms remain the conceptual core of this research area; however, recent trends highlight a growing emphasis on neuroinflammatory and pathological processes shaping future directions in neuroscience.

**Keywords:** LTP, synaptic plasticity, hippocampus, learning, memory, bibliometric analysis

**ÖZ**

**Amaç:** Sinaptik plastisite, öğrenme ve belleğin nörobiyolojik temelini oluşturur. *İn vivo* elektrofizyolojik çalışmaların hızla artmasına rağmen, küresel yayın eğilimlerinin sistematik olarak değerlendirilmesi hâlen eksiktir. Bu çalışmanın amacı, hipokampal plastisite ile ilişkili gelişimi, araştırma temalarını ve bilimsel iş birliklerini haritalandırmaktır.

**Gereç ve Yöntemler:** Bu bibliyometrik analizde, Web of Science Core Collection veri tabanından 2 Ekim 2025 tarihinde elde edilen, 1987-2024 yılları arasında yayımlanmış 2.348 İngilizce makale değerlendirilmiştir. Sistem düzeyindeki dinamikleri incelemek amacıyla kullanılan kesin konu araması (TS) sorgusu şu şekildedir: TS= ("sinaptik plastisite") AND ("hipokampus" VEYA "öğrenme" VEYA "bellek") VE ["uzun süreli baskılanma (LTD)" VEYA "uzun süreli güçlenme (LTP)" VEYA "LTP" VEYA "LTD"] VE ("*in vivo*"). Yayın eğilimleri, tematik haritalar, ortak yazarlık ağları ve kurumsal dağılımların analizinde VOSviewer ve Biblioshiny yazılımları kullanılmıştır.

**Bulgular:** Yayın sayısı 2013 yılında zirveye ulaşmış olup bu yılda 130 makale yayımlanmış, sonrasında ise kademeli olarak azalmıştır. Temel anahtar kelimeler arasında sinaptik plastisite, hipokampus ve uzun süreli güçlenme, LTP yer alırken; patoloji, interlökin-1 beta ve gama osilasyonları gibi öne çıkan güncel konular, klinik nöropatolojiye doğru bir yönelime işaret etmiştir. En çok atıf alan yazarlar Song S., Miller K.D., Abbott L.F. ve Morris

**Address for Correspondence:** Melek ALTUNKAYA MD, Selçuk University Vocational School of Health Services, Konya, Türkiye
**E-mail:** melekbtkc@hotmail.com **ORCID ID:** orcid.org/0000-0002-6228-7831
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R.G.M. olmuştur. En güçlü iş birliği ağları Rowan M.J., Bramham C.R. ve Korte M. etrafında şekillenmiştir. Amerika Birleşik Devletleri, Almanya ve Çin bu alanda öne çıkan ülkeler olurken, Stanford ve Northwestern Üniversiteleri başlıca kurumlar arasında yer almıştır.

**Sonuç:** Sinaptik plastisite ve hipokampal mekanizmalar bu araştırma alanının kavramsal merkezini oluşturmaya devam etmektedir. Bununla birlikte, güncel eğilimler nörobilimde gelecekteki araştırma yönelimlerini şekillendiren nöroenflamatuvar ve patolojik süreçlere yönelik ilginin giderek arttığını göstermektedir.

**Anahtar Kelimeler:** UDG, sinaptik plastisite, hipokampüs, öğrenme, bellek, bibliyometrik analiz

## INTRODUCTION

Electrophysiological methods have played a critical role in understanding neuronal communication and the functional organization of the brain[1]. Following Lord Edgar Adrian's 1920s action potential recordings from single nerve fibers, the field reached a theoretical milestone in 1952 when Hodgkin and Huxley elucidated the ionic mechanisms of the action potential[2-5]. These advancements laid the groundwork for modern electrophysiological analyses. In 1966, Terje Lømo observed that high-frequency stimulation of the hippocampal perforant path led to a sustained enhancement in synaptic transmission[6]. These findings were confirmed in a seminal 1973 publication by Tim Bliss, which established long term potentiation (LTP) and represented a paradigm shift in synaptic plasticity research. Since the 1970s, direct recordings of synaptic transmission, particularly within the hippocampus, has gained substantial empirical attention in the literature[5,7-10].

LTP refers to the long-lasting strengthening of synaptic connections between neurons in an activity-dependent manner and is regarded as the cellular basis of learning and memory[11]. Subsequent studies demonstrated that the sustained enhancement of synaptic transmission observed in LTP was not unidirectional, leading to the introduction of the concept of long-term depression (LTD) into the literature. LTD represents a long-term reduction in synaptic transmission strength following specific stimulation patterns. This process is considered critical for eliminating unnecessary information and maintaining network homeostasis[11]. Currently, *in vivo* electrophysiology remains one of the most robust techniques used to understand how the mechanisms of synaptic plasticity change under both physiological and pathological conditions, such as Alzheimer's disease, epilepsy, and depression[8,12-14]. In this context, the concepts of "synaptic plasticity", "hippocampus", "learning", "memory", and "*in vivo* electrophysiology" are frequently examined together in the literature. The dentate gyrus, CA1, and CA3 regions are the hippocampal structures most sensitive to synaptic plasticity forms such as LTP and LTD[15,16]. Over the past four decades, research has demonstrated that these concepts carry substantial implications not only in basic neuroscience but also in the context of clinical neurobiology[17,18]. In particular, electrophysiological investigations of learning and memory impairments such as those observed in Alzheimer's disease have contributed to the identification of potential therapeutic targets[19]. Currently, electrophysiological recordings related to synaptic plasticity are utilized not only to elucidate the neurobiological foundations of memory but also to reveal the mechanisms disrupted under pathological conditions. Therefore, bibliometric analysis of synaptic plasticity studies using *in vivo* electrophysiological recordings is important for elucidating the historical development, research intensity, prominent themes, and future directions of this field. Despite the large number of publications, comprehensive bibliometric mapping of global trends, leading countries, collaboration networks, and core themes in synaptic plasticity is lacking. Similarly, recent bibliometric reviews widely used in synaptic plasticity and related fields show that this method is one of the most effective ways to systematically map the increase in publication volume and categorize the contributions of countries, regions, and authors, and their relevance to research hotspots[20,21].

Accordingly, the present study aims to construct a systematic map of the research in this field by integrating the themes of synaptic plasticity, *in vivo* electrophysiology, the hippocampus, learning, and memory. The goal is to provide a guiding framework for understanding the developmental dynamics of the research area and to inform new research strategies, thereby offering valuable insights to both basic and clinical neuroscientists.

## MATERIALS AND METHODS

### Data Sources and Search Strategy

To specifically evaluate the functional dynamics of intact neural networks, the search strategy for this bibliometric analysis was restricted to *in vivo* approaches and foundational electrophysiological paradigms of synaptic plasticity, namely LTP and LTD. While the broader literature on synaptic plasticity includes extensive *in vitro* slice preparations, molecular biological assays, and non-invasive neuroimaging, incorporating these diverse methodologies would have generated a highly heterogeneous dataset. Such heterogeneity may obscure the specific evolutionary trajectory of systems-level electrophysiological research. By focusing strictly on "*in vivo",* "LTP" and "LTD", this study aims to robustly map research that directly links synaptic mechanisms to behavioral outcomes and clinical neuropathologies in living organisms.

Based on this established methodological framework, on October 2, 2025, data were retrieved from the Web of Science (WoS) database using the following topic search query: exact topic (TS) = ("synaptic plasticity") AND ("hippocampus" OR "learning" OR "memory") AND ("LTD" OR "LTP" OR "LTD") AND ("*in vivo*").

The selection criteria were limited to the document type "articles"; only publications indexed in the WoS Core Collection including the Science Citation Index Expanded (SCI-EXPANDED), Emerging Sources Citation index and Social Sciences Citation index were included. The search was further restricted to publications written in English. Most of the identified studies belonged to the field of Neurosciences, followed by multidisciplinary sciences, pharmacology and pharmacy, biochemistry and molecular biology, behavioral sciences, cell biology, clinical neurology, physiology, psychiatry, and psychology, with additional contributions from other related disciplines.

Prior to importing the dataset into VOSviewer and biblioshiny, a rigorous data preprocessing protocol was applied. Initial screening for duplicates yielded no redundant records, as the extraction was limited to a single database, no duplicate records were identified. Finally, the standardization of author names was manually reviewed to prevent the artificial fragmentation or merging of publication records. During this manual inspection, author name consistency was assessed by cross-referencing the authors' institutional affiliations and their historical co-authorship networks to resolve any potential ambiguities. This inspection confirmed a high level of consistency in WoS indexing of the major contributing authors and institutions, therefore, no significant manual unification was required prior to the co-authorship and citation network analyses. As a result, the search yielded 2,348 articles, with publication dates ranging from 1987 to 2024. The complete step-by-step process of literature identification, screening, and inclusion is visually detailed in the flow diagram, provided as Supplementary Figure 1.

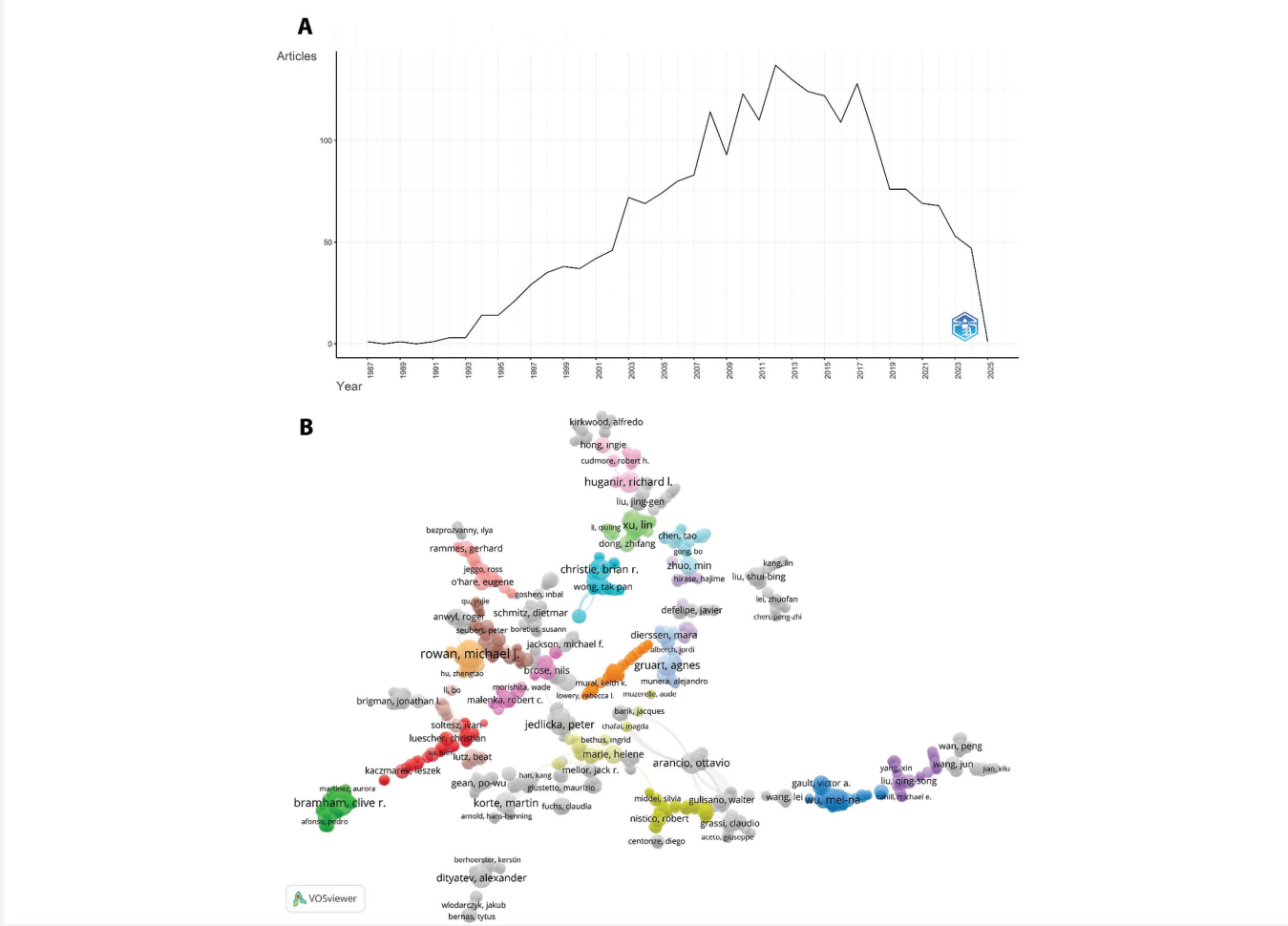


**Figure 1.** Annual publication counts and co-authorship network. (A) Distribution of annual publication counts from 1987 to 2024, (B) co-authorship network map of prominent researchers

### Statistical Analysis

The bibliometric data were exported in plain text format and analyzed using VOSviewer (v.1.6.20; Centre for Science and Technology Studies, Leiden University, Leiden, The Netherlands) and the Biblioshiny interface of the Bibliometrix R package (v.4.1.2)[22]. Descriptive analyses included publication and citation counts, annual publication trends, and productivity distributions by country, institution, author, and journal. To ensure the reproducibility of the results, specific thresholds were applied: for co-authorship analysis, a minimum threshold of one document and one citation per author was set in VOSviewer. To ensure the thematic significance of the results, the "Word Minimum Frequenc" parameter in biblioshiny was set to five, restricting inclusion to terms with at least five occurrences. Additionally, the "Number of Words per Year" metric was limited to three to identify the most prominent and representative keywords for each year. All network visualizations were performed using the "Association Strength" normalization method. Network analyses were conducted to visualize co-authorship, co-citation, and keyword co-occurrence relationships. Additionally, a thematic map was generated to identify major research themes and their interconnections. All bibliometric networks were visualized using VOSviewer's mapping and clustering algorithms. Ethical approval and informed consent were not required, as the study did not involve human or animal subjects.

## RESULTS

### Annual Publication Count and Co-authorship Analysis

Within the scope of the selected search terms, a total of 2,348 articles were published between 1987 and 2024, with an average of 62 publications per year. In terms of annual output, the fewest publications were recorded between 1987 and 1991 (1 article), whereas the highest number was observed in 2013 (130 articles). As illustrated in Figure 1A, the number of publications shows a declining trend after 2013. Based on the co-authorship analysis using VOSviewer, a network map, shown in Figure 1B, was generated to identify the most interconnected and collaborative authors. To ensure the significance of the collaboration network, the co-authorship analysis was conducted using a minimum threshold of one publication and one citation per author. A total of 2,348 articles were authored by 7,460 unique researchers, corresponding to a mean of 3.18 authors per article. The most highly cited authors were Song S., Miller K. D., and Abbott L. F. with 2,039 citations, followed by Morris R. G. M., with 1,722 citations, and Celnik P., with 1,686 citations. In terms of total link strength (TLS), the top three authors were Rowan M. J. (TLS: 87), Bramham C. R. (TLS: 87), and Korte M. (TLS: 85).

### Keyword Co-occurrence Analysis and Trend Topic Terms

From the 2,348 articles analyzed, a total of 2,760 keywords were extracted, comprising both Author Keywords and Keywords Plus terms indexed in the WoS database. The most frequently used keywords (Figure 2A) were synaptic plasticity (257 occurrences), hippocampus (256 occurrences), LTP (102 occurrences), Alzheimer's disease (94 occurrences), and memory (78 occurrences). Trend topic terms (Figure 2B), identified using a minimum word frequency threshold of 5, were primarily pathology, interleukin-1 beta, and gamma oscillations.

### Thematic Map of Research Themes

The conceptual structure of research on synaptic plasticity was further explored using the thematic map function in biblioshiny (Figure 3). To ensure a comprehensive yet focused representation, the analysis was conducted with a "number of words" parameter set to 250, allowing for a broad inclusion of terms. Additionally, the "minimum cluster frequency (per thousand docs)" was set at 5, which normalized cluster inclusion by requiring at least five occurrences per thousand documents. According to the map, the cluster consisting of the terms "LTP" synaptic plasticity, and *"in vivo*" is positioned among the basic themes (lower-right quadrant), representing the conceptual core and foundational framework of the field. In contrast, the cluster comprising the terms "dentate gyrus," "LTP," and "rat" falls into the specialized themes category (upper-left quadrant); indicating that while these topics exhibit relatively low centrality, they represent highly developed and well-established specialized sub-domains within the field. Furthermore, the cluster containing the terms "Alzheimer's disease" and "brain" is located among the emerging or declining themes (lower-left quadrant), suggesting that these neurodegenerative disease-related topics, while associated with synaptic plasticity studies, either represent newly emerging research directions or themes experiencing a relative loss of importance. Overall, the thematic map analysis indicates that the concepts of LTP and synaptic plasticity constitute the field's unchanging core research axis, while research associated with Alzheimer's disease forms a subcluster with strong developmental potential, and its integration into the field is ongoing.

### Co-citation Analysis of Cited Authors

Co-citation refers to instances where two or more authors or sources are cited together within the same publication. In the present analysis, authors with at least 20 citations were included. Figure 4A illustrates the co-citation network of authors. The most frequently co-cited authors were Bliss (321 citations), Malenka (201 citations), and Abraham W.C. (150 citations). However, as shown in Figure 4B, the annual co-citation rate demonstrated a declining trend after 2019.

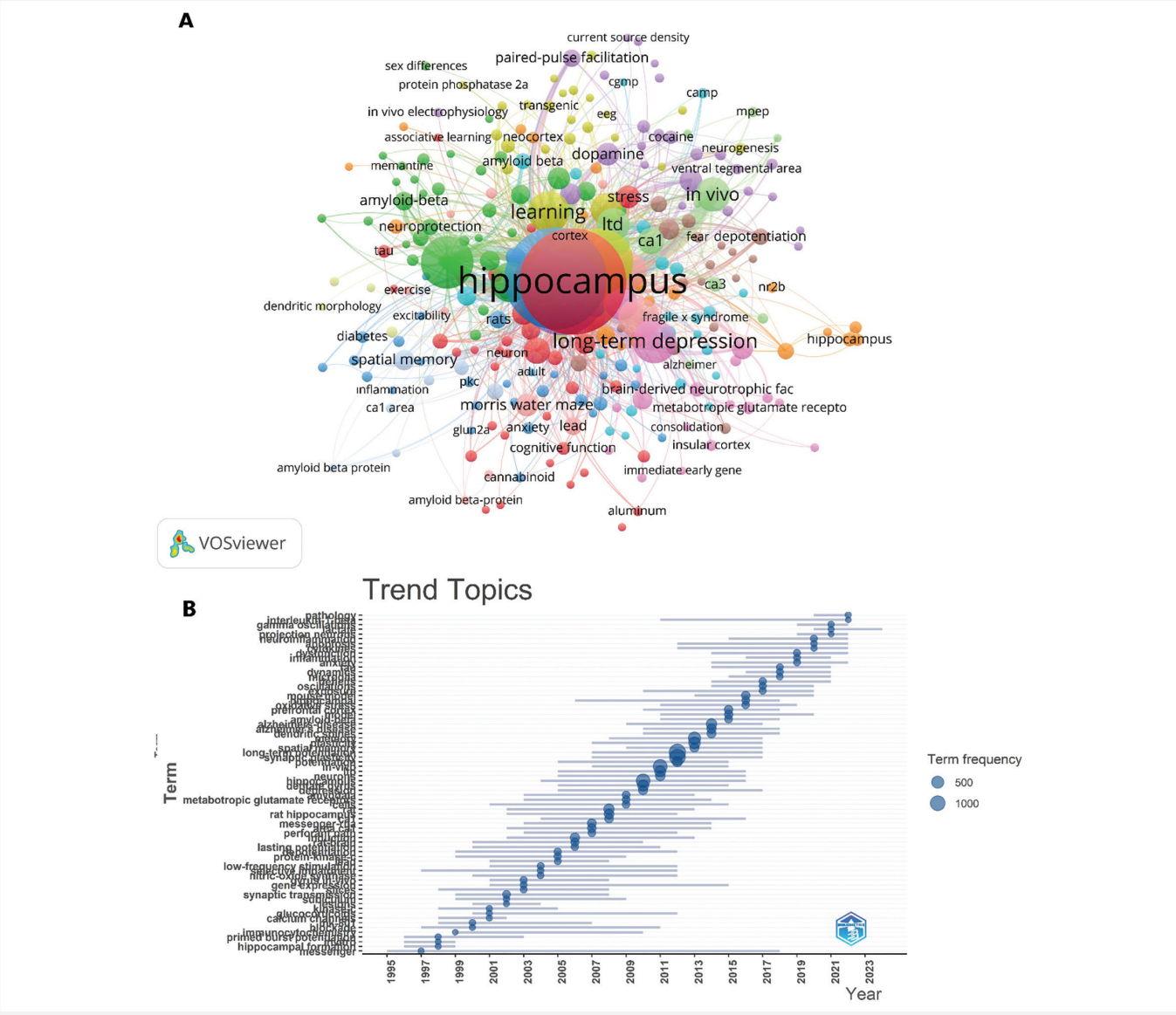


**Figure 2.** Keyword analysis and emerging trends. (A) Co-occurrence network of keywords showing the most frequent terms, (B) overlay visualization of trend topic terms

## Bibliographic Coupling of Organizations

To construct a network map of inter-institutional citation relationships, a bibliographic coupling analysis was performed. To ensure a comprehensive representation of institutional impact, the inclusion criteria were set at a minimum of one published work and one citation per organization.

Figure 5 delineates the citation relationships among institutions. The most represented institutions in terms of publication count were Tokyo University (30 publications), Stanford University (27 publications), and Johns Hopkins University (26 publications). The institutions affiliated with the most highly cited publications were Stanford University (5,159 citations), Northwestern University (3,613 citations), and the University of California, San Francisco (3,071 citations).

## Bibliographic Coupling of Countries and Journals

A network map illustrating citation relationships among countries was constructed based on the countries of origin of the publications. To ensure robust analysis of global interactions, the inclusion criteria were set to a minimum of one publication and one citation per country. Analyses of citation relationships were conducted for both countries and journals. Figure 6A shows the publication and citation connections among countries. In this network, the United States of America (USA) dominated both citation counts (51,108 citations) and

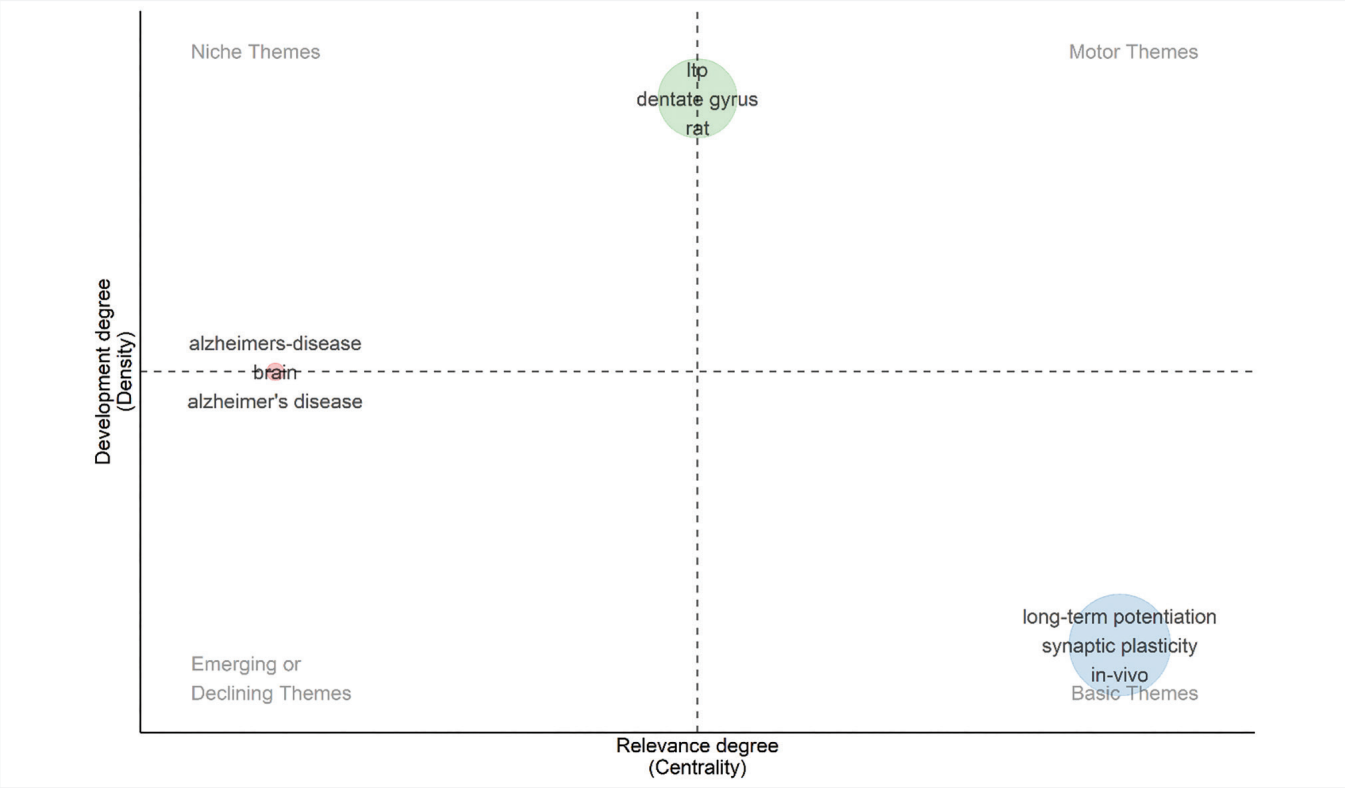


**Figure 3.** Thematic map of research themes. Visualization of research clusters based on centrality and density, categorized into basic, specialized, and emerging/declining themes

publication output (575 publications); Germany and China ranked second and third in citations, while China and Germany ranked second and third in publications. Figure 6 B shows the citation network of journals. The Journal of Neuroscience led the journal ranking, topping both citation counts (13,818 in the citation network) and publication numbers (132 in the citation network), with Nature Neuroscience (81 in the citation network) and the Proceedings of the National Academy of Sciences of the USA (44 in the citation network) completing the top three in citations and TLS.

## DISCUSSION

This bibliometric analysis characterizes research trends from 1987 to 2024 focusing on *in vivo* electrophysiological studies of synaptic plasticity. The scientific framework of the field began to take shape in the 1980s, following the foundational discovery of LTP[6] in the previous decade and the subsequent standardization of electrophysiological techniques. During the first two decades of the analyzed period (the 1990s and 2000s), research was primarily marked by a focus on the hippocampus and its role in learning and memory[15,23]. Our findings confirm that historically, the concept of synaptic plasticity evolved strictly around the core phenomena of LTP and LTD, with the hippocampus receiving particular attention due to its critical role in memory processes. However, bibliometric indicators from 2010 to 2024 reveal a paradigm shift, with a growing emphasis on disease models (e.g., Alzheimer's disease, epilepsy, depression), neuroinflammation, and oxidative stress[19,24]. This thematic evolution provides crucial context for interpreting the observed decline in annual publication counts after 2013 in our dataset. Rather than indicating an actual decrease in scientific interest, this trend likely reflects an evolving terminology in the field. As research shifted toward specialized clinical applications and pathologies, authors may have increasingly utilized highly specific molecular, genetic, or disease-centric keywords rather than the broader, foundational terms ("synaptic plasticity" or "LTP/LTD") required by our search strategy. Furthermore, the diversification of the field toward advanced non-invasive neuroimaging or *in vitro* human-derived cellular models falls outside the scope of our strict *in vivo* electrophysiological criteria and has thereby reduced the retrieval rate of relevant studies in recent years.

Similarly, the reported decline in co-citation rates after 2019 should be interpreted cautiously. This trend represents a natural bibliometric phenomenon related to the citation time window; recently published articles inherently require a latency

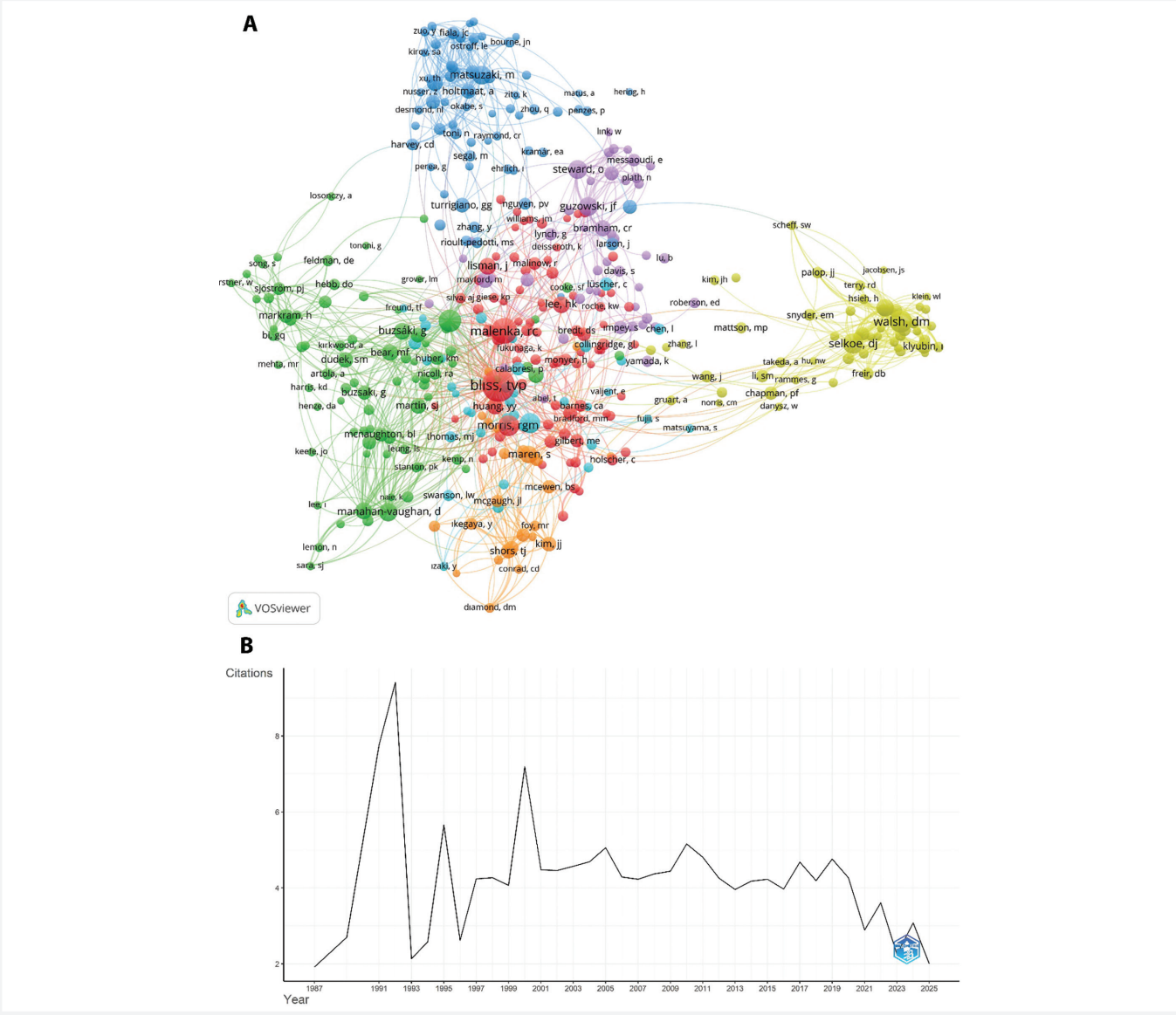


**Figure 4.** Co-citation analysis. (A) Co-citation network of authors (threshold: minimum 20 citations), (B) annual co-citation rate trends

period of several years to accumulate a substantial number of citations compared to older, foundational papers. Despite these terminological shifts and time-lag limitations, the high citation density of articles published in high-impact journals such as the Journal of Neuroscience, Nature Neuroscience, and Proceedings of the National Academy of Sciences of the United States of America indicates that *in vivo* synaptic plasticity continues to hold a central position in neuroscience research.

Supporting this evolving landscape, our thematic map analysis reveals that while the inclusion of "synaptic plasticity" and "LTP" constitutes a significant research effort, the relatively low centrality of "Alzheimer's disease" data suggests that the full incorporation of neurodegenerative data into the synaptic plasticity paradigm remains a matter of ongoing debate. Furthermore, the most significant thematic shift identified in the trend topic terms analysis is the transition from basic synaptic functions to the specific molecular drivers of these clinical neuropathologies[19,25,26]. In particular, the increasing prominence of emerging keywords highlights a multi-dimensional expansion in the field. This evolution spans from the molecular and neuroinflammatory levels evidenced by terms like interleukin-1 beta and pathology to systems level network dynamics, reflected by the interest in gamma oscillations. This trend confirms that understanding synaptic plasticity impairments now requires integrating immunological mechanisms with large-scale electrophysiological network activities[27-30].

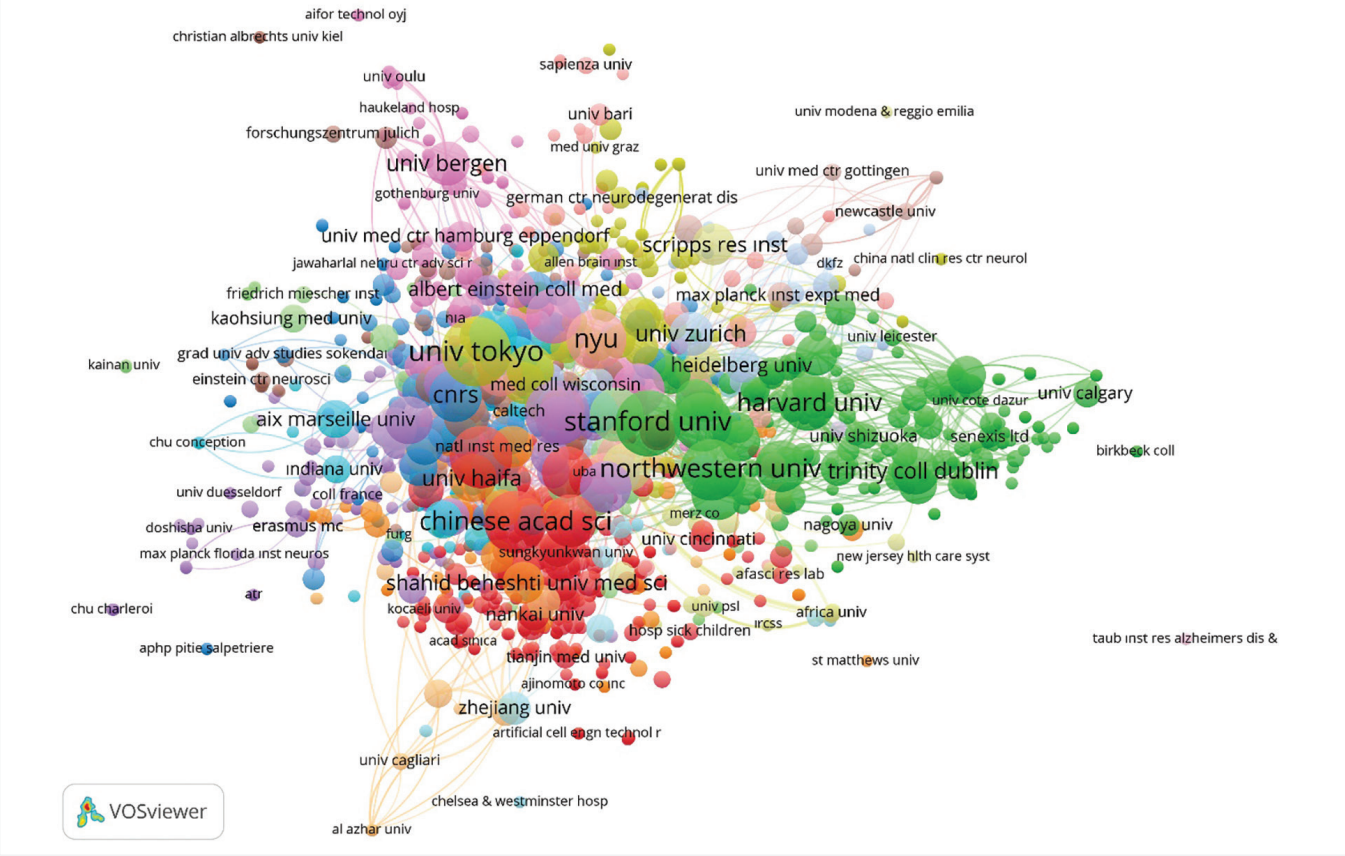


**Figure 5.** Institutional citation relationships. Network map depicting bibliographic coupling and citation connections among the most productive organizations

Analysis of author and institutional networks revealed that the United States, Germany, and China hold leading positions in research output and collaboration within the field. US-based authors achieved the highest citation rate, with 2,039 citations for the article titled "Competitive Hebbian Learning through Spike-Timing-Dependent Synaptic Plasticity"[31]. The notably high citation counts associated with Stanford University and Northwestern University indicate that these institutions have made influential contributions, shaping the direction of synaptic plasticity research. However, it was observed that most collaboration networks remain confined to regional clusters, with relatively few international partnerships. This pattern suggests benefits of promoting greater interdisciplinary and cross-national collaboration for future studies. In light of these observed trends, advancing the understanding of neural circuits and developing therapeutic targets for neurodegenerative and neuropsychiatric disorders may increasingly rely on multidisciplinary methodological integration.

## Study Limitations

Although this study provides a comprehensive bibliometric overview, it is limited to data from the WoS database and to publications written in English. One of its main limitations is the exclusion of research indexed in other databases, such as Scopus and PubMed, which may have led to the omission of relevant studies. Additionally, restricting the analysis to journal articles excluded other forms of scholarly output, such as conference proceedings and book chapters, which potentially limited the early identification of emerging research trends. Future research could broaden the global perspective of the field by incorporating multiple databases and publications in different languages, thereby providing a more comprehensive representation of *in vivo* synaptic plasticity research worldwide.

Furthermore, the restrictive nature of our search strategy specifically the requirement for the terms "*in vivo*" and "LTP/LTD", constitutes a limitation and may introduce selection bias affecting the dataset's representativeness. Consequently, this study does not cover the entirety of research on synaptic plasticity. Substantial bodies of literature employing *in vitro*

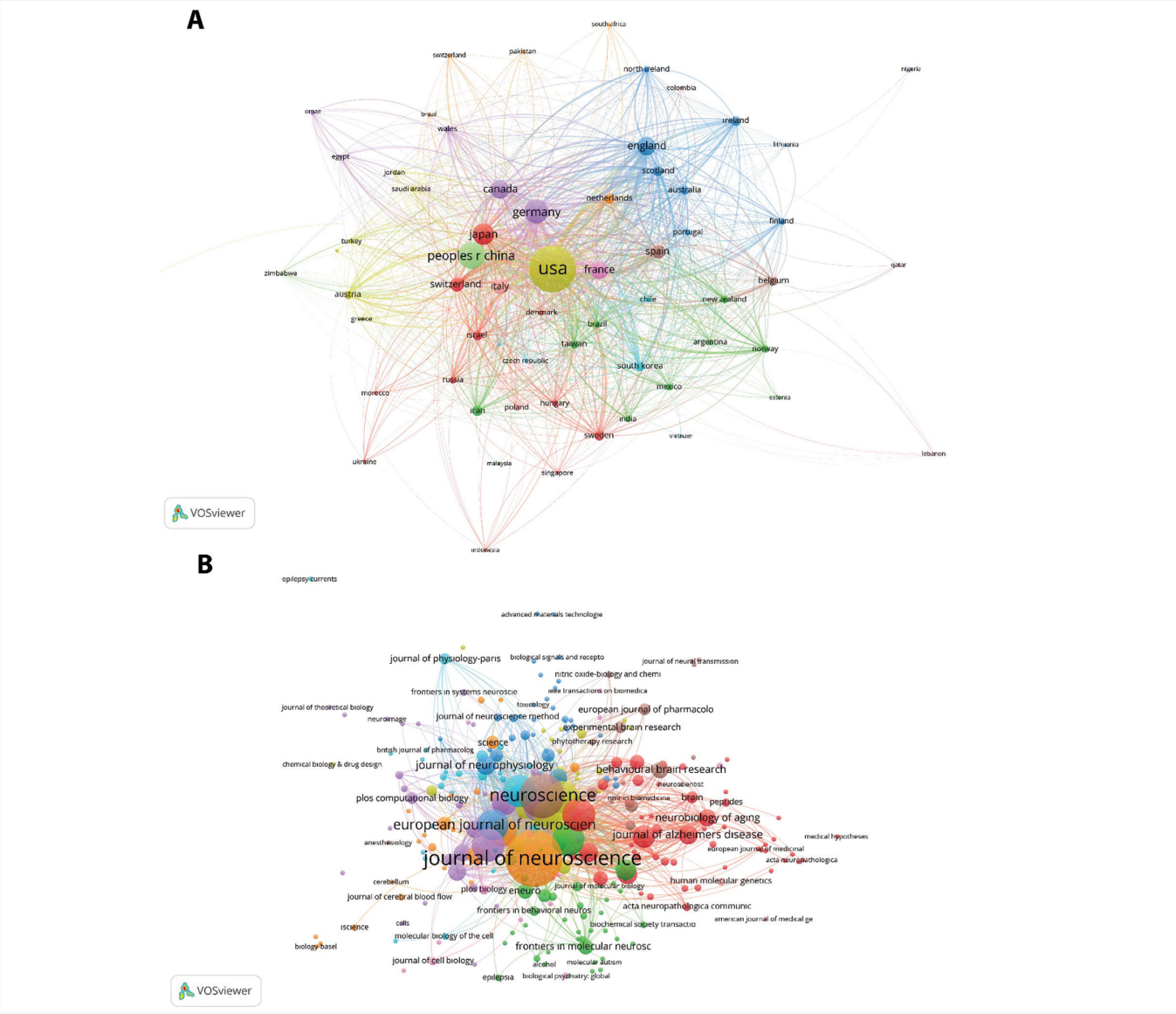


**Figure 6.** Global and journal-based citation networks. (A) Publication and citation connection maps for the most active countries, (B) citation network of leading journals in the field

slice electrophysiology, advanced cellular imaging, and broader molecular frameworks of plasticity were intentionally excluded. Therefore, our findings should be interpreted not as a universal map of all plasticity research but as a specialized bibliometric representation of systems level *in vivo* functional network dynamics.

## CONCLUSION

This study presents a bibliometric mapping of research on synaptic plasticity utilizing *in vivo* electrophysiological methods between 1987 and 2024. The results indicate that the field possesses a well-established core, while appearing to diversify through a growing focus on clinical pathologies and inflammatory mechanisms. Although LTP and LTD remain the central concepts of this research, bibliometric indicators from 2021 to 2024 suggest an increasing interest in specific topics including pathology, interleukin-1 beta, and gamma oscillations. This analysis provides an observational framework for understanding the historical dynamics of the field and highlights potential opportunities for future research and interdisciplinary collaboration.

### Ethics

**Ethics Committee Approval:** Our study did not involve any human or animal research and does not require Ethics Committee Approval.

**Informed Consent:** Ethical approval and informed consent were not required, as the study did not involve human or animal subjects.

## Footnotes

### Authorship Contributions

Concept: M.A., Design: M.A., Data Collection or Processing: M.A., N.D., C.S., Analysis or Interpretation: M.A., Literature Search: M.A., Writing: M.A., N.D., C.S.

**Conflict of Interest:** No conflict of interest was declared by the authors.

**Financial Disclosure:** The authors declared that this study received no financial support.

**Data availability statement:** The raw bibliographic data analyzed during the current study are available in the Web of Science (WoS) Core Collection database. The dataset can be fully replicated using the specific search query and inclusion criteria detailed in the Materials and Methods section.

**Supplementary Figure 1 Link:** https://d2v96fxpocvxx.cloudfront.net/cf9d60d6-523c-458a-a2e6-78728d3ffbb0/content-images/ffbc68d7-365a-4f8b-bcbb-97489c319f22.pdf

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