Occupancy and N-mixture modeling applications in ecology: A bibliometric analysis

Laurentiu Rozylowicz[1*], Viorel D. Popescu[1,2], Steluta Manolache[1], Andreea Nita[1], Simona R. Gradinaru[1], Marian D. Mirea[1], Raluca I. Bancila[1,3]

[1] University of Bucharest, Center for Environmental Research, 1 N. Balcescu, Bucharest 010041, Romania
[2] Columbia University, Ecology, Evolution and Environmental Biology, New York, NY 10027
[3] Emil Racovita Institute of Speleology of Romanian Academy of Sciences, 13 Septembrie Road, 050711, Bucharest, Romania

*corresponding author: laurentiu.rozylowicz@g.unibuc.ro

Keywords

hierarchical modeling; n-mixture models; occupancy models; bibliometric networks; bibliometric review

Published as:

Rozylowicz, L., Popescu, V.D., Manolache, S., Nita, A., Gradinaru, S.R., Mirea, M.D. & Bancila, R.I. (2024) Occupancy and N-mixture modeling applications in ecology: a bibliometric analysis. Global Ecology and Conservation, e02838.

https://doi.org/10.1016/j.gecco.2024.e02838

Abstract

The rapid decline in global biodiversity underscores the critical need for comprehensive monitoring of wildlife distribution and abundance. This study explores the trends in applied hierarchical modeling, which is an important tool in addressing these conservation challenges. By analyzing a dataset of 697 peer-reviewed articles published between 2002 and 2022, we examine the taxonomic focus, detection procedures, study designs, and modeling choices within the field of population ecology. Our findings revealed that most studies concentrated on single taxonomic groups, particularly mammals and birds. Data collection methods included visual surveys, acoustic surveys, camera traps, and traps, with some studies combining multiple techniques. Notably, the United States dominated the geographical focus, accounting for 46% of published papers. In terms of modeling approaches, single-season occupancy was the most prevalent, followed by various other models, including multi-species occupancy and *N*-mixture models. While hierarchical modeling has gained popularity, citations for these articles remained relatively modest, with only a few achieving over 100 citations. Authorship analysis revealed a highly collaborative network of researchers, with key authors contributing significantly to the field's development and dissemination. Co-authorship and co-citation networks highlighted the importance of authors who can bridge differing scientific groups and those that have made substantial contributions to hierarchical modeling methods. Despite its growth, the field faces challenges related to standardization in modeling and reporting practices. While efforts to address these issues are currently underway, a cohesive framework for occupancy modeling in ecology is still in an emerging stage.

Introduction

The rapid decline in worldwide biodiversity underscores the critical importance of comprehensively monitoring species abundance and distribution (Bellard et al., 2012). Global, regional, and national policies acknowledge the significance of monitoring the abundance and distribution of plant and animal populations as a key step in halting biodiversity loss (Collen et al., 2013). Such policies frequently rely on the scientific community to develop robust and user-friendly tools for assessing the status and effectiveness of conservation programs (Gonzalez et al., 2023; Miu et al., 2020).

Population parameters estimates such as abundance or probability of occurrence are at the core of many conservation and management plans. The simplest method to estimate abundance in wild populations is through a complete census, i.e., counting every single individual within a specific area. Abundance estimations via census methods are not possible unless the geographic extent is small, the time frame is short (Henderson, 2021), and the target species is easy to survey and detect. At coarser scales and across large geographic extents or over long periods of time, biodiversity data are often collected as detection/non-detection data. Thus, it is more practical to estimate species occupancy, i.e., the probability of a species being truly present or absent at a site (MacKenzie et al., 2002; Tyre et al. 2003; MacKenzie et al., 2017). Both occupancy and abundance may be confounded when the species is not perfectly detected, i.e., when the detection probability, p, is less than 1 (MacKenzie et al., 2002). To address this issue in estimating occupancy, models have been developed to account for detectability based on detection/non-detection data of unmarked individuals, i.e., individuals that cannot be distinguished from one another, via repeated surveys (MacKenzie et al., 2002; Madsen and Royle, 2023). These models, known as occupancy models (MacKenzie et al., 2006; MacKenzie et al., 2017; Altwegg and Nichols, 2019), are particularly useful when it is not practical to detect or count all individuals, e.g., due to species characteristics (e.g., cryptic or rare species or species that move large distances) or logistical constraints (e.g., cost or access constraints, and skill differences among observers in the ability of detecting and identifying species) (Royle and Dorazio, 2008; MacKenzie et al., 2017).

For abundance estimation using unmarked animals, this challenge is commonly addressed using repeated counts, although alternative methods, such as distance sampling and double-observer sampling, are typically used. Abundance can also be derived from capture-recapture methods of marked animals (Nichols, 1992; Grosbois and Gimenez, 2010; McCrea and Morgan, 2015). Such methods involve capturing, individually marking, or photographing animals for identification, and releasing them at the capture site, and incorporate the probability of recapture to estimate demographic parameters and abundance. However, the intensive work of capturing, marking, and recapturing animals, which is often high cost and effort, limits applications at broad spatial scales. This has led to the emergence of abundance modeling approaches from repeated counts of unmarked individuals (Zipkin et al., 2014; Royle and Kery, 2007; MacKenzie et al., 2003). *N*-mixture models simultaneously estimate the abundance and detection probability of animals from repeated counts of unmarked individuals at multiple survey sites (Royle, 2004). Occupancy models and N-mixture models fall under the umbrella of hierarchical models, which separate the state process (e.g., occurrence or abundance of a species) from the observation (detection) process. For clarity, we will refer to them collectively as hierarchical occupancy-type models, emphasizing their incorporation of both occupancy and N-mixture models.

Over the last two decades, hierarchical occupancy-type models exploded in popularity as a low-cost/effort but powerful approach for estimating occupied and unoccupied sites using detection (presence) / non-detection (pseudo-absence) data (i.e., imperfect detection) and count data (i.e., incomplete census) of unmarked animals (MacKenzie et al., 2017; MacKenzie and Royle, 2005). Hierarchical occupancy modeling allows unbiased estimation of abundance or occupancy (or measures of population size, such as the relative abundance or density and the proportion of area occupied) and facilitates the inclusion of covariates to account for survey-specific detection probability (Royle and Dorazio, 2008). The increased interest in creating more robust and complex models to account for imperfect detection can also be attributed to the advancement of sampling technologies (Silvy, 2020). In particular, the availability of equipment, such as camera traps and bioacoustic recorders, and the advent and the cost-effectiveness of environmental DNA (eDNA) sampling and processing have motivated the development of many occupancy model variants for unmarked individuals. These models can answer a wide range of questions, from population and community assessment to interspecific interactions across many spatial and temporal scales (Zipkin et al., 2014; Royle and Kery, 2007; MacKenzie et al., 2003; Kellner et al., 2023; Kery and Royle, 2021; Kery and Royle, 2016).

The advancement of hierarchical modeling may also be attributed to the development of dedicated applications such *MARK* (White and Burnham, 1999) and *Presence* (Hines, 2006) and of the R program (R Core Team, 2023) packages available for occupancy modeling such as *unmarked* (Fiske and Chandler, 2011). New fitting strategies are available via packages *spOccupancy* (Doser et al., 2022), and complex and computationally intensive models may be built using implementations of the BUGS language, such as *NIMBLE* (de Valpine et al., 2017; Goldstein et al., 2021), *JAGS* (Plummer, 2003), and *BUGS* (Kery and Royle, 2016; Kery and Royle, 2021), or *Stan* platform (Carpenter et al., 2017), such as *ubms* (Kellner et al., 2021).

The advancement of sampling technologies, coupled with the availability of ready-to-use models, contributed to an increase in scientific productivity in the field of occurrence and abundance modeling (Kellner et al., 2023; Iknayan et al. 2014; Madsen and Royle (2023). However, to our best knowledge, a review of the literature on the use of occupancy modeling to answer animal and plant ecology research questions is lacking. Other modeling options have been extensively studied, including by using bibliometric reviews. For example, de Rivera and McCrea (2021) conducted a review of removal modeling and concluded that the field becomes more complex yet remains accessible to applied ecologists. Similarly, Tourani (2022) explored uses, limitations, and progress in spatial capture-recapture modeling approaches.

With the advent and diversification of hierarchical occupancy model types and their implementation, we aim to evaluate their use in the peer-reviewed literature to identify target taxa and data types, study designs, and types of models adopted by researchers, as well as to examine scientometric trends. We aim to provide a general overview of hierarchical occupancy model types used by researchers for applied ecology questions in order to enhance and refine future applications by serving as a valuable reference for researchers in ecology and related fields. The objectives of the study are: 1) to provide a synthesis of taxa, geographic focus, scale, data types, and hierarchical occupancy model variants to date; 2) to identify key contributors to hierarchical occupancy literature and generate research insights using a scientometrical perspective and mapping the co-authorship network and co-citation network; and 3) to identify recommendations to promote occupancy modeling methods as a robust choice for biodiversity monitoring.

Methods

Literature search and inclusion criteria

We reviewed English-written scientific literature (i.e., peer-reviewed articles) published up to December 2022 (excluding early access articles) that apply hierarchical occupancy models to address research questions in population and community ecology, such as to understand patterns of species abundance, occupancy, co-occurrence of communities and meta-communities. Article selection was conducted according to the Preferred Reporting Items for Systematic Reviews and

Meta-Analyses (PRISMA) guidelines, which provide a transparent workflow to report systematic literature reviews (Page et al., 2021). The workflow is presented in Figure 1.

We searched Web of Science Core Collection (Clarivate Plc) by topic (i.e., abstracts, keywords, and titles) using the following Boolean search string: (((((((((TS=(occupancy)) OR TS=(N-mixture)) OR TS=(multi-state)) OR TS=(”multi state”)) OR TS=(multi-scale)) OR TS=(”multi scale”)) OR TS=(abundance)) OR TS=(co-occupancy)) OR TS=(co-occurrence)) AND TS=(hierarchical). To include papers from journals without keywords (e.g., Science, Plos One) or the terms mentioned above in abstract or titles, we completed the search with Keywords Plus terms ”occupancy” and “N-mixture”. The search was limited to the following citation topics: Zoology & Animal Ecology, Entomology, Marine Biology, Soil Science, Zoonotic Diseases, Phylogenetics & Genomics, Sustainability Science, Environmental Sciences, Climate Change, Statistical Methods, Applied Statistics & Probability.

Articles were screened by an author of the present paper and considered relevant if they applied hierarchical occupancy-type modeling for the analysis of ecological data (i.e., model occupancy/abundance and detection probability of at least one species) and used observational data. Studies that exclusively used simulation data or those that did not discuss the results obtained with observational data were excluded after confirmation by a second researcher. When disagreement occurred, consensus was reached through discussions between the two authors or by referring to a third researcher. The search yielded 5548 articles, of which 4854 did not meet the criteria listed above, resulting in a database of 697 articles focused on applied hierarchical occupancy-type modeling.

Importantly, we acknowledge that, given the goal of this study of evaluating general trends and patterns in the use of occupancy modeling in ecology, the constraints imposed by our defined keyword searches, the Web of Science indexing properties, and the ability of co-authors of this paper to classify a particular type of modeling as relevant for this synthesis, the list of papers considered in this analysis may not be exhaustive, and the results are not a complete research landscape ranking of authors and references.

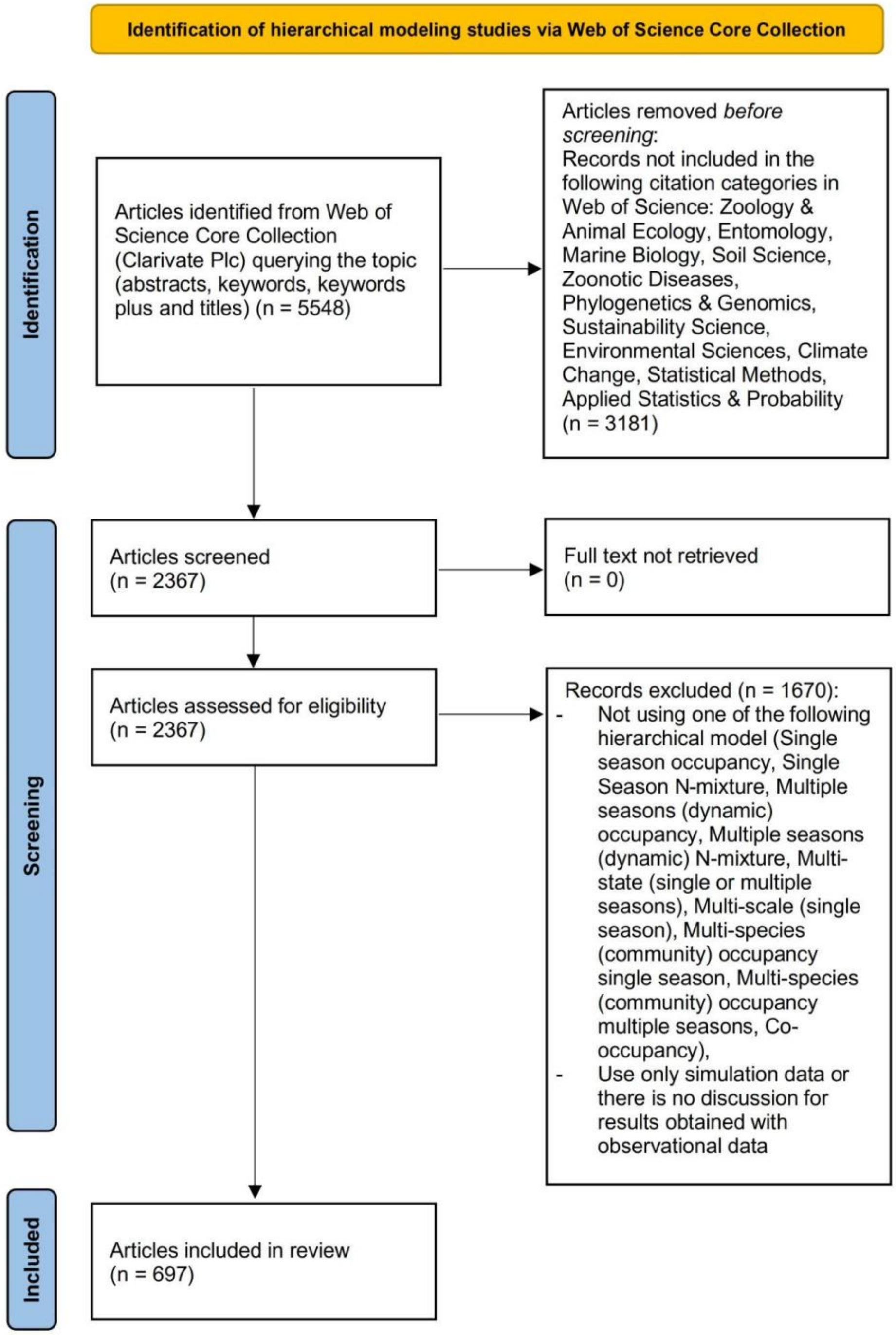

Figure 1 *PRISMA flow diagram of scientific literature search, screening, and selection process*

Data extraction and descriptive statistics

To understand the use of hierarchical occupancy-type modeling in ecology, we extracted several metadata for each relevant study, i.e., year of publication, location (country/countries/territories where that study was carried out), taxa (i.e., mammals, amphibians, reptiles, invertebrates, fish, birds), type of study (i.e., single-season occupancy, single-season *N*-mixture, multiple-season (dynamic) occupancy, multiple season (dynamic) *N*-mixture, multi-state (single or multiple seasons), multi-scale (single season), multi-species (community) occupancy single-season, multi-species (community) occupancy multiple season, co-occupancy), type of data (i.e., camera traps, tracks, acoustic surveys, visual surveys, eDNA, traps, interviews, online databases), study design (i.e., grid, transect, feature-based such as surveys at ponds or other discrete patches in the environment, territorial units such as counties or game management units, opportunistic collection), number of sampling units, and duration of study.

We analyzed article metadata using descriptive statistics, including the frequency of articles per metadata category. Chi-square tests were performed to determine if observed frequencies in a category matched the expected frequencies. Furthermore, changes in frequencies across categories (taxa, data, and modeling choice) were visualized multi-dimensionally using alluvial plots. To quantify the strength and direction of the correlation between the number of citations and the year of publication, we used the Spearman rank correlation coefficient. We expect that the number of citations decreases as the year of publication increases for several reasons: (i) citations tend to accumulate gradually over time, (ii) seminal papers often continue to be referenced, while newer ones may focus on recent developments that are not yet widely recognized, (iii) with more papers published, new citations of any given article decreases, and (iv) older publications may benefit from increased availability and visibility over time, especially if they have become “go-to” references in the field.

These analyses were performed using the *base*, *dplyr*, and *ggalluvial* R packages (Wickham, 2016; R Core Team, 2023; Wickham et al., 2023; Brunson, 2020). Graphs, excluding network and alluvial plots, were generated using the *ggpubr* package (Kassambara, 2023).

Scientometric and network analyses

Authorship and citation data were analyzed using descriptive statistics, scientometric indices, and network analysis methods (Nita et al., 2019; Barabási et al., 2002; Aria et al., 2020). For scientometric data, we considered the following metrics: (1) the number of articles published by an author, (2) the number of citations received by the analyzed papers in Web of Science, (3) the local h-index of an author (indicating the number of publications for which an author has been cited by articles in our database at least that same number of times), and (4) the number of citations received by the analyzed papers from other paper included our database (Aria and Cuccurullo, 2017). We also calculated these metrics at the journal level (i.e., for papers included in the same journals).

To understand co-authorship and co-citation patterns, we used network analysis (Borgatti et al., 2018). We generated two undirected, unweighted networks: (1) a co-authorship network, where authors (nodes) are linked to other authors (edges) directly (if they co-authored at least a paper) or indirectly by bridge authors (two authors who have not written a paper together but have each co-authored a paper with a common third party author); the indirect connection can be two steps such as in the example mentioned above or more, and (2) a co-citation (co-references) network, where references included in a paper (nodes) relate to other paper references (edges) if they share at least one reference. Similarly with the co-authorship network, the links can be one step or more (Aria and Cuccurullo, 2017; Nita et al., 2019). The co-authorship network was used to identify network leaders, while the co-citation network highlighted the most important papers referenced in the field (van Eck and Waltman, 2023). For each of the two networks, we calculated two node-level centrality metrics: degree and normalized betweenness (Borgatti et al., 2018). Degree centrality of an author represents the number of direct connections that the author has with other authors in the network and helps to identify the most collaborative authors in the field of occupancy modeling (i.e., the authors with the highest number of connections). Betweenness centrality measures the extent to which an author lies on paths between other authors in the network otherwise disconnected (Nita et al., 2019). Such authors may be considered ”bridge” authors because they have the potential to influence the research landscape by serving as connectors between otherwise disparate research topics (Borgatti et al., 2018; Nita et al., 2019). Co-authorship and co-citation networks were calculated using *VosViewer* (van Eck and Waltman, 2023) and graphically represented using the *NodeXL* app (Smith et al., 2023). For visual representation purposes only, we used a cut-off for co-authorship network of minimum of 3 co-authored papers with at least 30 citations in Web of Science and for co-citation network of 20 articles from the database referencing the respective citation. Node-level metrics were calculated using R package *igraph* (Csárdi et al., 2023). Scientometric indices were extracted using R package *bibliometrix* (Aria and Cuccurullo, 2017).

Results

Hierarchical modeling of species occupancy, abundance, and co-occurrence was used to analyze biodiversity data in 697 articles published between 2002 and 2022 (median per year = 23, interquartile range IQR = 3 – 56) and indexed in the Web of Science Core Collection. Research in this field of applied ecology started at a slower pace (1 to 7 articles per yer between 2002 and 2009), surpassing the median of 23 articles in 2012 and reaching its peak in 2022 (116 articles) (Figure 2).

The majority of the published articles were focused on a single taxonomic group (96%). The proportions of focus taxa were skewed (chi-squared = 672.95, df = 6, $p < 0.001$). Mammals and birds were the most modeled taxa (40.46% and 34% of studies, respectively), followed by amphibians (10.47%), invertebrates (6.31%), reptiles (5.88%), fish (5.45%) and plants (2.15%). When more than one taxonomic group was modeled, the selected taxa included combinations such as mammals and birds, amphibians and reptiles, reptiles and plants, or the entire vertebrate community.

Studies also differed in the types of data used to model occupancy (chi-squared = 883.77, df = 7, $p < 0.001$). Almost half of the studies used data obtained from visual surveys (50.37%), followed by acoustic surveys (28.84%), camera traps (25.62%) and traps (16.69%). Less frequently used data were obtained by recording tracks (3.81%), online databases (3.66%), eDNA (1.76%), and interviews (1.76%). Nearly 29% of articles used more than one method for data collection. Most of such studies combined visual and acoustic surveys (145 out of 197 articles combining data collection methods), while the remaining studies combined camera traps and track or physical traps, camera traps with interviews, or visual survey and eDNA.

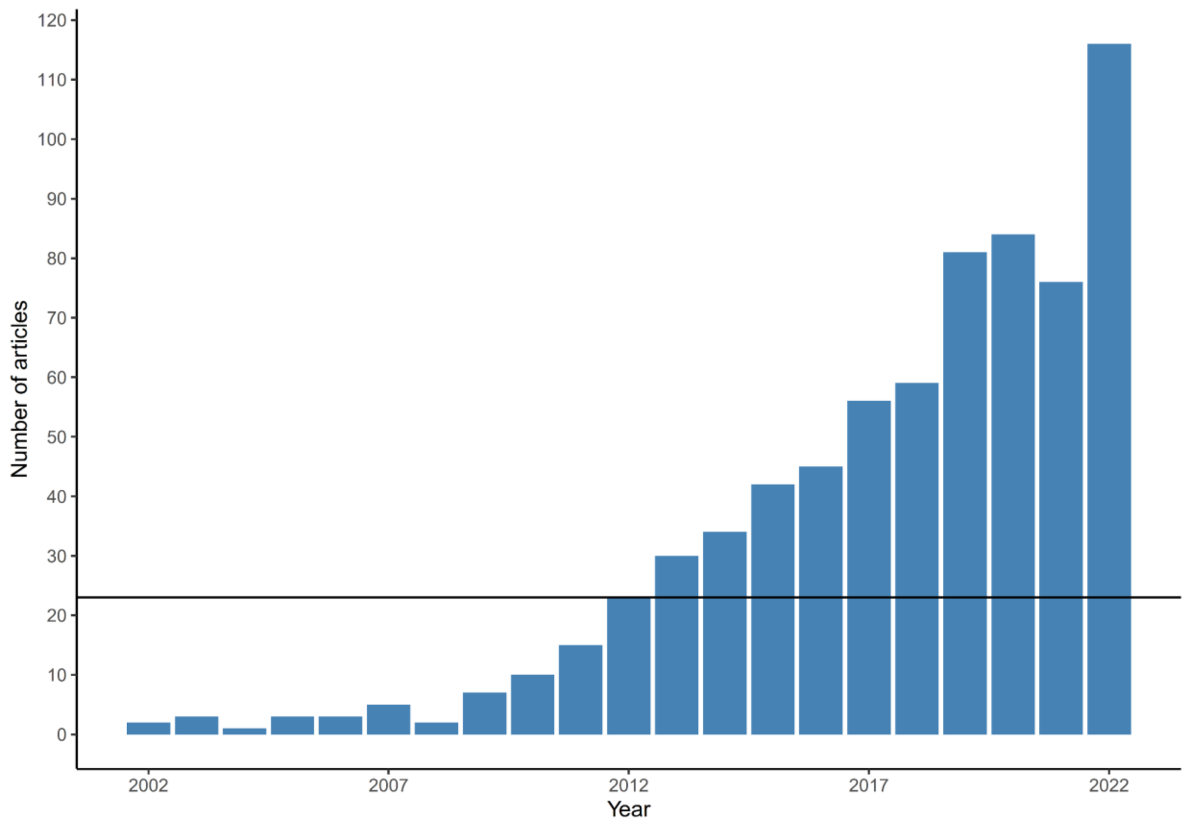

Figure 2 *The trend of annual scientific production using hierarchical modeling of occupancy, abundance, and species co-occurrence between 2002 and 2022*

The design of data collection is unbalanced (chi-squared = 243.56, df = 4, $p < 0.001$). Most data collection designs were identified as grids (39.74%), followed by transects (25.25%), feature-based (23.24%), opportunistic collection (11.91%), and territorial units (4.45%). Only 5% of articles combined study designs, with the most common combination being transects inside a grid or feature-based area. Only seven articles supplemented species data collected from a grid or transect with online databases or interviews.

Hierarchical occupancy-type modeling studies were implemented across 89 countries and territories (e.g., Antarctica). Notably, 46.20% of the published papers were conducted in the USA. The other countries in the top 10 list are Brazil, Canada, Australia, Argentina, India, South Africa, Spain, China, and France, each accounting for only 2% -5 % of the studies. Many of the studies focused on specific regions within a single country, with only 4% of papers involving research conducted in more than one country.

When analyzing the hierarchical modeling approach used in selected papers, we found a heavy focus on single species models (chi-square = 387.17, df = 8, $p < 0.001$). Almost 31% of studies employed single-season single species occupancy models, followed by single-season multi-species (community) occupancy (17.65%), single-season *N*-mixture (14.78%), multi-season (dynamic) occupancy (14.63%), multi-season multi-species (community) occupancy (9.04%), multi-season (dynamic) *N*-mixture (6.74%), multi-state (single or multi-season) (4.16%), multi-scale (single or multi-season) (4.16%), and co-occupancy 3.30%). Nearly all studies used only one hierarchical modeling approach, with only 5.73% (40 articles out of 697) involving a secondary method (e.g., occupancy and *N*-mixture models for abundant species).

Data collection methods were taxon-specific; most bird data were obtained from acoustic and visual surveys and analyzed using a wide range of models. Data for mammals were mainly based on camera traps and tracks and were largely modeled using single-season occupancy and multi-species (community) occupancy. Amphibian data were mostly collected via acoustic monitoring and visual survey and were modeled using the entire spectrum of models (Figure 3).

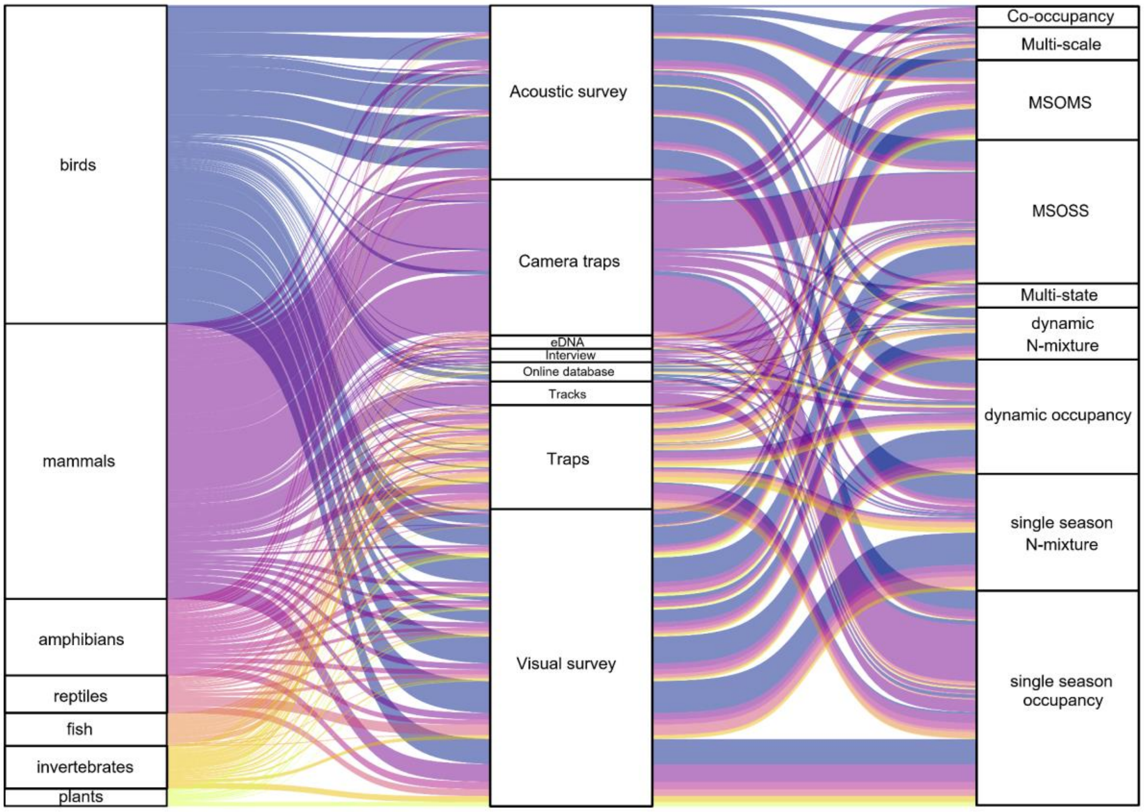

Figure 3 *Alluvial plot showing the frequencies of the relationships between taxa, methods for data collection, and modeling approaches used in the analyzed applied hierarchical modeling paper. The width of the colored lines is proportional to the flow quantity*.

The median number of citations received by occupancy modeling papers within our database is 8 (IQR = 2-17). Overall, the number of citations is negatively correlated with the year of publication (rho = -0.74, $p < 0.001$). However, as expected, several papers are more frequently cited compared to articles published in the same period (Figure 4). The most cited paper in our database is MacKenzie et al. (2002), with 3108 citations, followed by MacKenzie et al. (2003) with 1197 citations, Tyre et al. (2003) with 545 citations, Powney et al. (2019) with 359 citations, MacKenzie et al. (2004) with 312 citations, Mackenzie et al. (2005) with 309 citations, Soroye et al. (2020) with 304 citations, Royle and Kery (2007) with 302 citations in Web of Science, and Woodcock et al. (2016) with 265 citations. Other papers with more than 200 citations are e.g., Nichols et al. (2008), Dail and Madsen (2011), van Strien et al. (2013), and Zipkin et al. (2009).

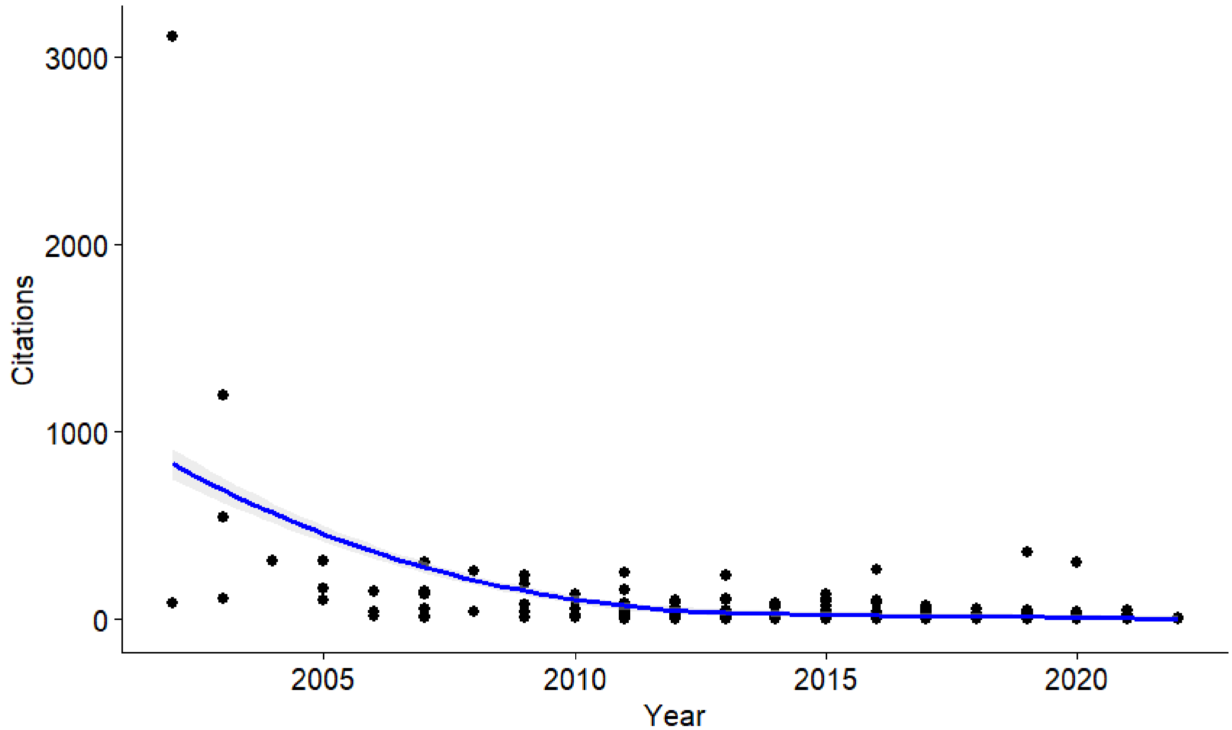

Figure 4 *The relationship between the number of citations of a paper and its publication year (blue line = LOESS regression curve; gray area = 95% confidence interval)*

The 697 papers on occupancy modeling included 2624 authors (median number of authors per paper = 3, IQR = 2-5). The top 10 most productive authors are listed in Table 1. Most authors (50.30%) were affiliated with institutions in the USA. UK (4.34%), Australia (3.65%), Canada (3.58%), Brazil (2.78%), Germany (2.66%), Italy (2.32%), South Africa (2.21%), Spain (1.94%), and France (1.82%) complete the top 10 countries by number of authors.

Table 1 *Most productive authors (>7 papers in our database) of applied occupancy modeling*

Authors	Number of articles in database	Local h-index	Number of citations	Year of first occupancy article published
Royle JA	19	16	4773	2002
Zipkin EF	13	10	588	2009

Kery M	12	9	818	2007
Nichols JD	10	10	5501	2002
Furnas BJ	10	8	204	2015
Hines JE	9	8	1803	2003
Miller DAW	9	8	390	2012
Macdonald DW	8	7	193	2012
McShea WJ	8	6	271	2016
Bailey LL	7	7	1122	2004
Siegel RB	7	7	144	2011
Gardner B	7	6	466	2009
MacKenzie DI	7	6	5099	2002
Rota CT	7	5	490	2009

When analyzing co-authorship using the network analysis (Figure 5), several authors have emerged as central in the network. These authors have either a high degree centrality (highly productive authors), betweenness centrality (collaborative authors that can bridge separate groups of authors), or both (Figure 6).

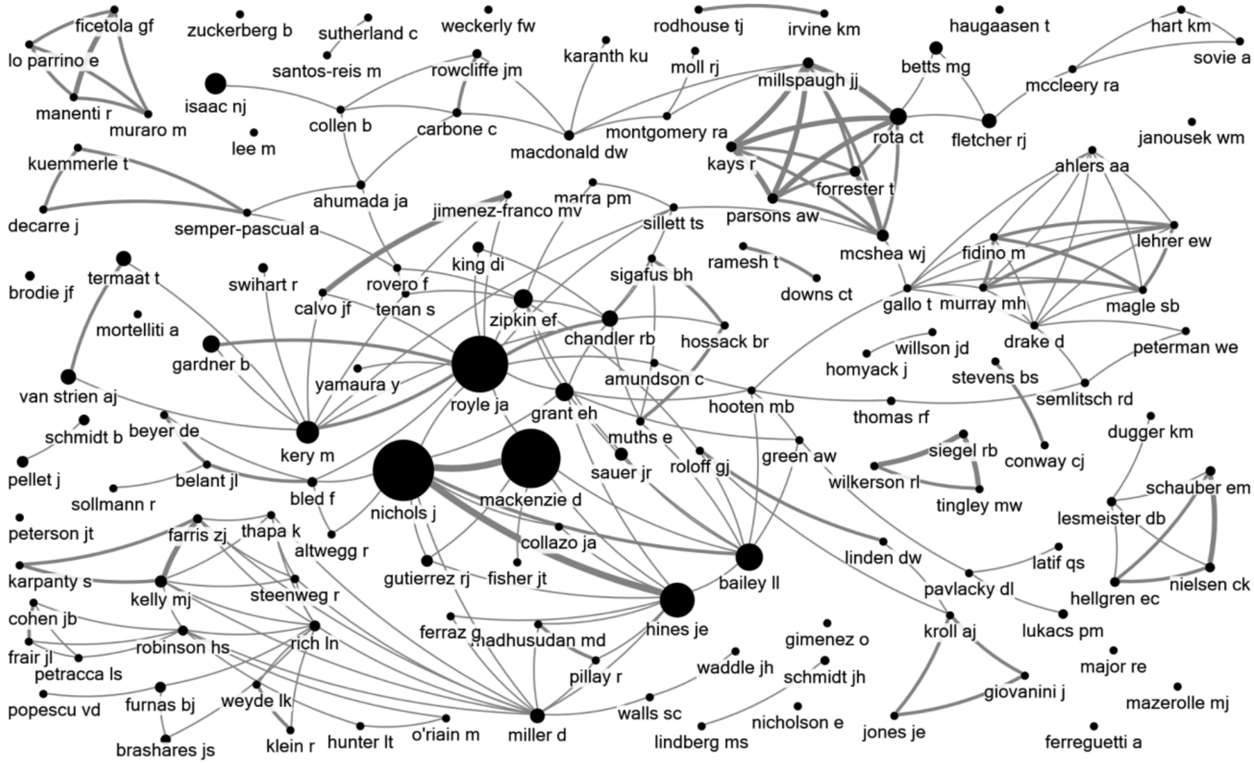

Figure 5 *Core co-authorship network in applied occupancy modeling papers. Authors are connected if they share the authorship of a paper. We included only the authors with a minimum of 3 papers in our database and at least 30 citations in Web of Science for the respective articles. Nodes (circles) size = the number of citations per author (max = 5476; min = 30); edges (lines) size = number of co-authorship. Isolated authors are directly connected only with co-authors who are not included in the core co-authorship network.*

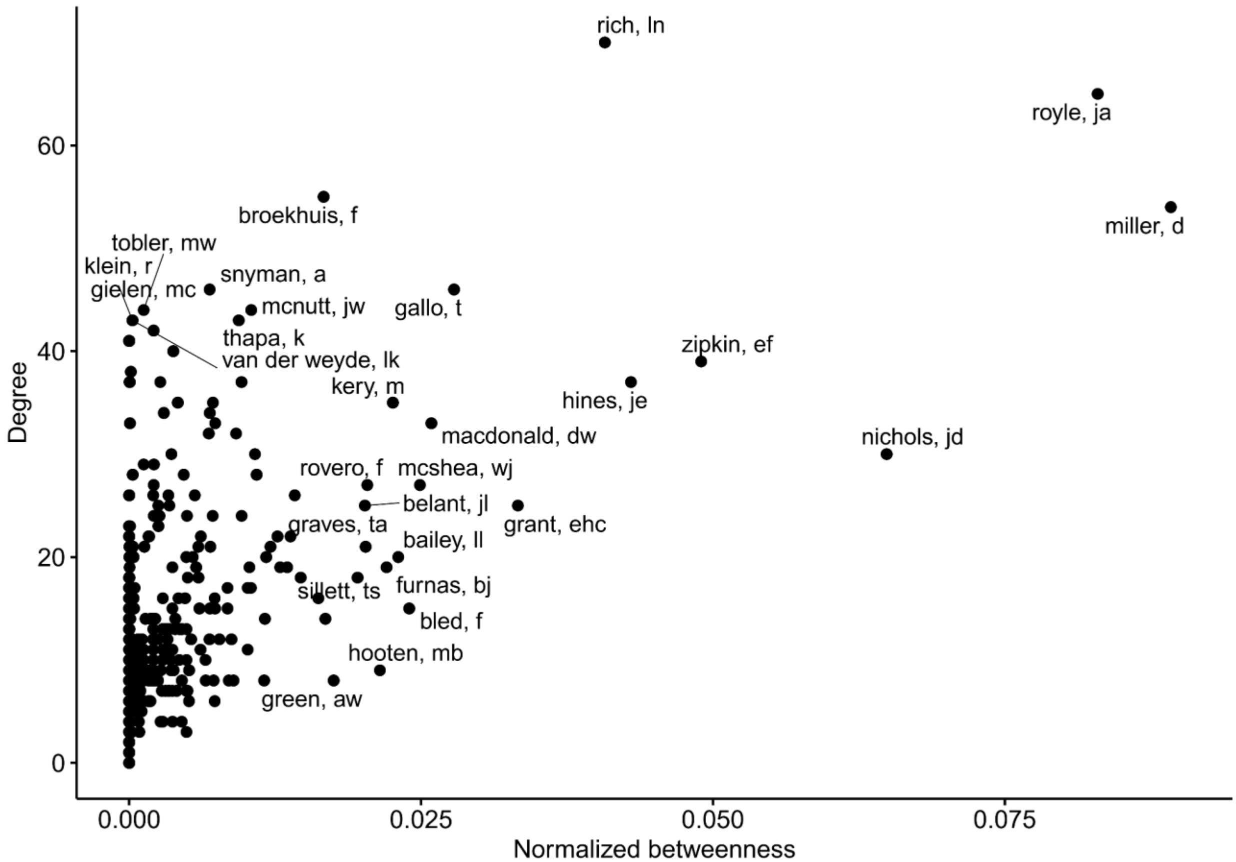

Figure 6 *Scatterplot of normalized betweenness and degree centralities of authors. Labeled authors have the highest degree (>41) and/or normalized betweenness centrality (>0.02) and can be considered highly collaborative and/or bridge authors in the field of applied occupancy modeling.*

The publishing venues are diverse, with 697 papers published in 143 different scientific journals. Of these, only 12 journals published more than 15 articles in this field (Table 2). *Diversity and Distributions, Biological Conservation,* and *Journal of Wildlife Management* published the highest number of occupancy-type articles (36 articles each). Articles published in *Ecology* and *Journal of Applied Ecology* were the most cited when considering the total number of citations. Furthermore, *Biological Conservation* has the highest h-index (21 articles cited at least 21 times).

Table 2 *Journals publishing more than 15 papers on occupancy modeling between 2002 and 2022*

Journal	Number of published articles	Total number of citations	Local h-index	Year of first article published
Biological Conservation	36	964	21	2005
Diversity and Distributions	36	640	17	2011
Journal of Wildlife Management	36	877	15	2005
Ecosphere	35	430	15	2011
Ecology and Evolution	31	315	11	2013
Plos One	30	706	15	2012
Journal of Applied Ecology	25	1705	15	2008
Forest Ecology and Management	24	277	11	2012
Ecological Applications	21	1090	12	2003
Ecology	19	5854	16	2002
Animal Conservation	16	242	10	2012
Landscape Ecology	16	200	8	2007

The analyzed papers include over 27,000 unique references, of which only 85 are cited by more than 20 papers in our database. When analyzing the co-citation network using the network analysis (Figure 7), several references clearly emerged as central in the network, highlighting their importance in the field. For example, several occupancy-related references cited many times together in the analyzed papers are MacKenzie et al. (2002), MacKenzie et al. (2017), Royle and Dorazio (2008), Fiske and Chandler (2011), MacKenzie et al. (2003), Royle (2004), Dorazio and Royle (2005), Kery and Royle (2016), Zipkin et al. (2009) and Royle and Nichols (2003). Furthermore, the popular references (references with a high normalized degree, i.e., number of links with other references in the database) and high betweenness (citations that frequently create the shortest path between different reference lists otherwise disconnected) reveal a list of 20 references that can be considered as key by the authors publishing in this field (Figure 8).

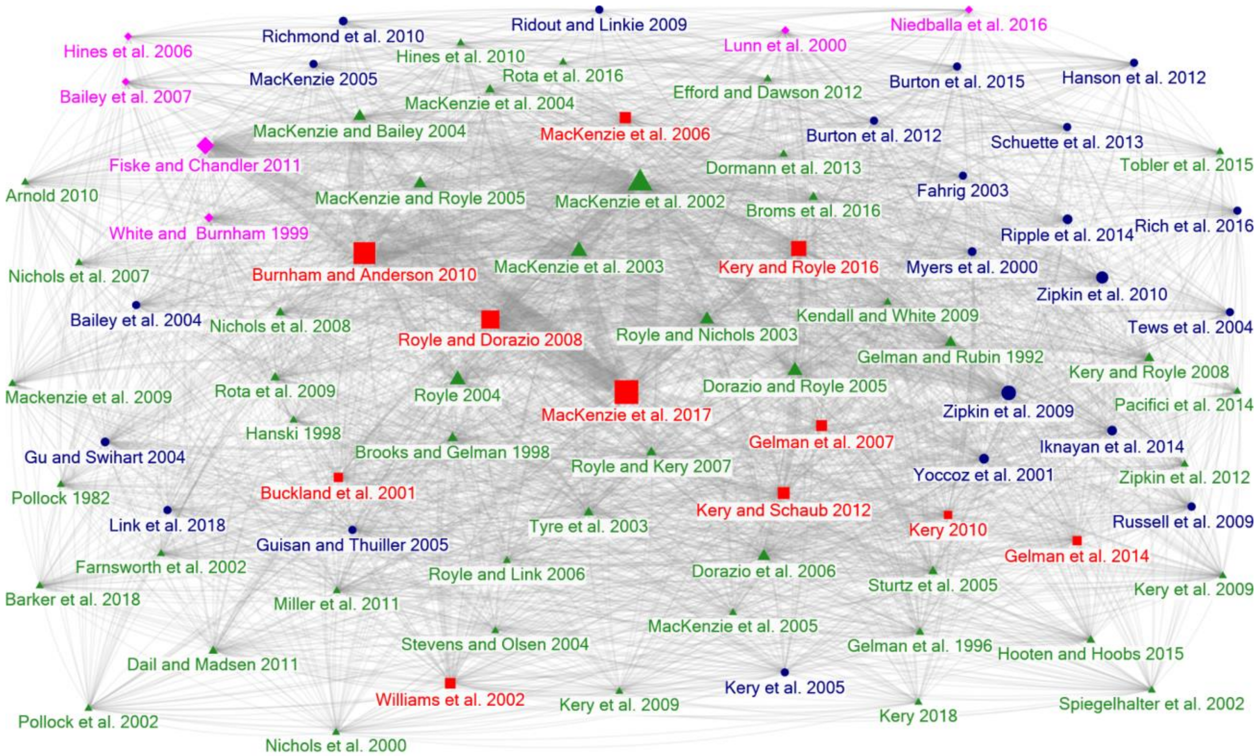

Figure 7 *Co-citation network extracted from analyzed papers (references included in more than 20 articles from the database). Nodes (circles and diamonds) size = the number of times the reference is included in the database (max = 283; min = 20); circles in blue = articles in journals, squares in red = books or book chapters, triangles in green = methodological papers, diamonds in magenta = software; edges (lines) size = number of times the two connected references co-occur in a paper (max = 126; min = 1).*

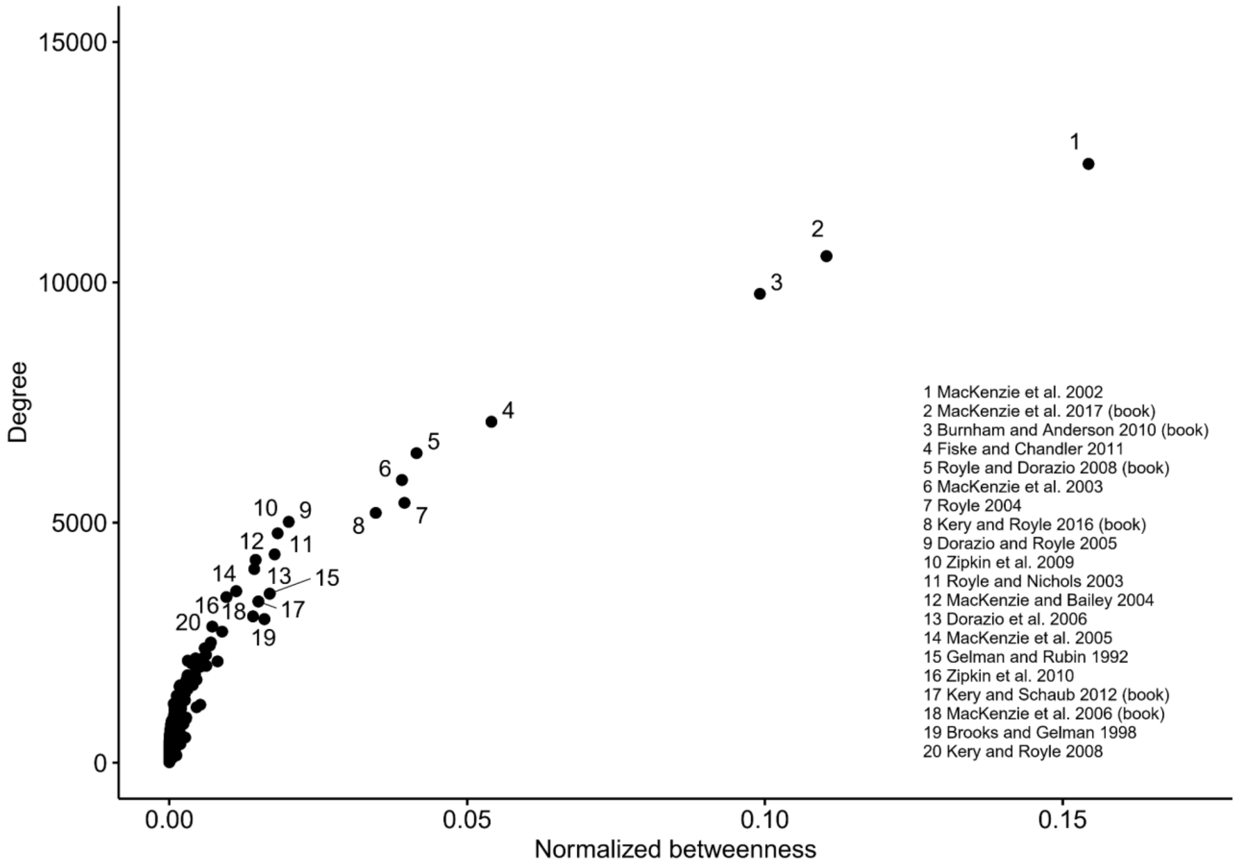

Figure 8 *Scatterplot of normalized betweenness and degree centralities of references included in the analyzed papers. References that are labeled represent those with the highest degree (>0.0096) and/or normalized betweenness centrality (>2975), and that can be considered important references in the field of applied occupancy modeling.*

Discussion

The analysis of peer-reviewed research implementing occupancy modeling of wildlife populations and communities worldwide indicates that this analytical approach is gaining prominence as a mainstream research field. This can be explained by improvements in the ease of implementation (e.g., via many R packages), high cost-effectiveness, and increased availability of data collection equipment such as trail cameras open platform bioacoustics monitoring such as AudioMoth (Hill et al., 2018). Our results also indicate that despite two decades of theoretical advances, software availability, and diversification of data collection methods, occupancy modeling of wildlife populations and communities remains a domain of highly specialized researchers from the developed world who use data from their own countries. To advance this field and create higher impact for biodiversity conservation and monitoring, there is a need for clearer syntheses of modeling approaches, as well as guidelines for study designs and parametrization of models that are accessible for a broader scientific audience. Furthermore, an increase in publications can be achieved through a better standardization of modeling nomenclature (e.g., model names) and standards for research conduct and reporting.

We found that researchers predominantly used single-season single species occupancy models, single-season multiple species occupancy models, single-season *N*-mixture models, and multi-season (dynamic) occupancy models. Collectively, these variants account for almost 80% of the studies. This finding can likely be attributed to the fact these model variants were among the initial models to emerge in the peer-reviewed literature between 2002 and 2004 (e.g., MacKenzie et al., 2002; MacKenzie et al., 2003; Tyre et al., 2003) and have the lowest data requirements. Furthermore, they were supported by standalone available software such as *Presence* (Hines, 2006) or *MARK* (White and Burnham, 1999). More complex models, such as multi-season multi-species (community) occupancy models, multi-season (dynamic) *N*-mixture models, multi-state models, multi-scale models, or co-occupancy, were less frequently included in the articles within our analyzed database. These variants built on the initial single-season and multi-season approaches (MacKenzie et al., 2002; MacKenzie et al., 2003; Tyre et al., 2003; Royle, 2004), and additional complexity was introduced through Bayesian implementations via the R programming and WinBUGS platforms (Royle and Kery, 2007; Royle and Dorazio, 2008; Kery and Schaub, 2012).

Birds and mammals emerged as the most extensively studied species, aligning with the traditional research focus on charismatic taxa or species of high conservation / management interest (Donaldson et al., 2017). This can also be explained by the predominant use of visual and acoustic surveys and camera traps for collecting occupancy-type data. The authors' taxonomic expertise is unlikely to account for the differences between taxonomic groups. Instead, the existence of open-source long-term datasets (e.g., North American Breeding Bird Survey) and the increased availability of camera traps and acoustics recorders (Mandeville et al., 2023) may explain this pattern. Relying on open-source long-term datasets for occupancy modeling highlights the collaborative and accessible nature of such initiatives, which foster a culture of data-sharing and community involvement in scientific research, emphasizing the overall importance of long-term monitoring. These findings may motivate researchers working on other taxa to establish similar initiatives at broad spatial scales (Lindenmayer et al., 2022); for example, initiatives such as Snapshot USA and Snapshot Europe (Smith and Alvey, 2023; Cove et al., 2021) or Urban Wildlife Information Network - UWIN (Magle et al. 2019) have started the creation of extensive camera trap-based databases focused on mammals (eMammal, MammalWeb). These initiatives are already leading to an upsurge in occupancy-type studies for inference at broad spatial scales and for multiple species (co-occupancy, multi-species occupancy).

Environmental (eDNA) biodiversity inventories have become increasingly widespread, covering diverse habitats and taxa globally. However, a key limitation currently impeding the large-scale application of eDNA is the incompleteness of species' genomic sequences available in public databases, such as GeneBank. While some underrepresented taxa will benefit from the expansion of eDNA approaches (Valdez et al., 2023), others, such as insects, will probably be hindered by inadequate representation in genomic databases (e.g., for metagenomic-based multi-species studies) often linked to the lack of taxonomic expertise (Richards et al., 2018; Li et al., 2019). Artificial intelligence (AI) use in biodiversity monitoring is expected to grow with the advent of big and open datasets and provide an alternative tool for species identification in the near future. Similar to camera traps and eDNA data, invertebrate-derived DNA (iDNA or DNA collected via invertebrate 'samplers' such as mosquitoes, flies, or terrestrial leeches (Schnell et al., 2015; Ji et al., 2022) has emerged as a non-invasive and efficient monitoring technique for community-level biodiversity studies. iDNA has proved especially useful for arboreal species, smaller bodied species, and non-mammal species, which camera trapping, visual and acoustic surveys, and eDNA may fail to detect. Thus, to broaden the application of occupancy models to other taxa, there is a need to make new technological tools more accessible to researchers and develop more robust models for data collected in a less conventional framework (Gantchoff et al., 2022). For example, the occupancy framework has been extended to account for imperfect detection in eDNA studies and sources of error at the PCR stage (eDNAPlus; Diana et al. 2022).

Our analysis reveals that nearly half of the authors are affiliated with US institutions, and almost half of the studies are focused on US data. The prevalence of US-affiliated authors is not unexpected and is a common trend in other fields of natural sciences (Nita, 2019; Piguet et al., 2018). However, the low number of studies in megadiverse regions is a concerning finding. While the occupancy framework can accommodate biodiversity ”snapshot” surveys that can be conducted relatively inexpensively (Ji et al., 2022), data collection is just one aspect of this mismatch. To achieve increased representation of studies beyond the current Western Hemisphere / Northern latitudes, efforts are required to increase willingness to assist researchers from other regions in designing and implementing data collection designs and protocols suitable for occupancy modeling. Additionally, providing modeling training for researchers in less-represented countries/regions is crucial (Mammides et al., 2016; Maas et al., 2021).

Occupancy modeling in ecology is not a very popular research topic when compared with other topics such as species distribution modeling, joint species distribution modeling, and capture-recapture estimation. This is indicated by the relatively low number of citations received by articles in the Clarivate WOS database, given that few articles surpass 100 citations. This may be due to a topic-related issue. In most cases, highly cited articles from our database are methodological or involve larger scales of analysis than what would be addressed by the typical application of hierarchical modeling. Nevertheless, key authors in the field, as indicated by both co-authorship and co-reference network analyses, are overall highly cited, and the journals that publish occupancy-type studies are top journals in their fields (e.g., Diversity and Distributions, Journal of Wildlife Management, Biological Conservation). This may facilitate bridging occupancy modeling with more popular subjects (e.g., species distribution modeling, joint species distribution modeling, capture-recapture) and attract more researchers to the topic. Many top authors, recognized by their centrality degree (i.e., authors with an extensive network of co-authors) and betweenness (authors who can connect authors otherwise disconnected) have a robust statistical background; these authors also contributed to the development of the occupancy framework and model variants, including development of R packages and standalone occupancy software (e.g., Fiske and Chandler, 2011; Kellner et al., 2021; MacKenzie and Hines, 2022). Additionally, they have authored important papers and books for this field (e.g., MacKenzie et al., 2017; Royle and Dorazio, 2008; Burnham and Anderson, 2004; Kery and Schaub, 2012; Kery and Royle, 2021), securing their position as leaders of the co-citation network. This dual role of several top authors indicates that the field is still developing and has the potential for further growth, which may help fill the gaps in covering various taxa and regions.

The investigated papers undergo peer review, most of them being published in established journals and are methodologically correct, as indicated by the scarcity of comments and rebuttals. However, we faced challenges in categorizing modeling and study design approaches using a standardized nomenclature. Such challenges often arise when the field of study is relatively new (Davis and Kays, 2023). This is also because, despite the existence of several very well-cited methodological books and articles, this field lacks clear standards for modeling workflows and reporting the results. While several papers attempt to fill this gap, e.g., Kellner et al., (2023), Mackenzie and Royle (2005), Madsen and Royle (2023), more work and clear guidelines are needed for standardization (including naming of model types) given the diversification of data types and collection methods used in occupancy modeling and the increasing number of occupancy model variants. Additionally, there is a need for guidance on reporting metadata in hierarchical models, which should include details about studied taxa, study levels, type of sampling designs, study length, model results, and standards of accuracy (Araújo et al., 2019).

While comprehensive, our study has data-driven limitations. We relied on the Clarivate WOS database for extracting metadata such as unique authors and references, which, particularly in the case of references, needs corrections. Although we made efforts to correct the errors, the over 26,000 references likely included many redundancies. We corrected the most cited 50 references, and combining the co-authorship with co-citation analysis provides a less biased overview of top authors and references in the field of occupancy modeling. We reiterate that the final list of occupancy studies included in this analysis is the direct result of the keyword searches and may not be exhaustive, and we likely omitted some authors and papers. However, our study aimed to evaluate occupancy modeling applications as an emerging field, and the overall findings on patterns, trends, co-authorship, and leadership in the field did not change through several iterations of the analysis.

Our study highlights the growing importance of occupancy modeling in population and community ecology, providing a powerful tool for monitoring wildlife distribution and abundance. Despite significant growth, particularly since 2012, this field remains primarily driven by researchers from developed countries, with a strong focus on mammals and birds. Key findings emphasize the need for increased collaboration, especially with researchers from megadiverse regions, to ensure that this powerful set of tools reaches its full potential to contribute to our understanding and conservation of global biodiversity. Additionally, efforts to standardize modeling and reporting practices are crucial for increasing the impact of occupancy modeling studies. Although occupancy-type articles may not yet receive the high citation counts of studies in other subfields of ecology, key authors and journals play a pivotal role in bridging the gap between occupancy modeling and broader ecological topics. This suggests that continued growth and influence in the field are achievable. Ultimately, this research underscores the potential of this modeling framework to address critical conservation challenges. To maximize its impact, researchers, practitioners, and policymakers should work together to fully harness the potential of this valuable tool for the preservation of global biodiversity.

Funding

The research was supported by a grant from the Executive Unit for Financing Higher Education Research Development and Innovation (www.uefiscdi.ro), PN-III-P2-2.1-PED-2021-1965, Interactive tool for estimating abundance of wildlife populations (WildPop). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Acknowledgments

We would like to thank the three anonymous reviewers for their constructive comments, which helped us to improve the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Authorship

LR, VDP, and RIB designed the methodology; LR, SM, AN, and SRG collected the data; LR, SM, and AN analyzed the data; LR, VDP, and RIB led the writing of the manuscript; SM, AN, SRG, MDM contributed to the writing of the manuscript. All authors contributed to the drafts and approved the final version for publication.

Data Availability

The papers included in this review, authors' and journal citation metrics, co-authorship, and co-citation metrics are provided at https://github.com/rlaurentiu/review_hierarchical_modeling.

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