

A decade of movement ecology

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Abstract

Movement is fundamental to life, shaping population dynamics, biodiversity patterns, and ecosystem structure. Recent advances in tracking technology have enabled fundamental questions about movement to be tackled, leading to the development of the movement ecology framework (MEF), considered a milestone in the field [33]. The MEF introduced an integrative theory of organismal movement, linking internal state, motion capacity and navigation capacity to external factors. Here, a decade later, we investigated the current state of research in the field. Using a text mining approach on > 8000 peer-reviewed papers in movement ecology, we explored the main research topics, evaluated the impact of the MEF, and assessed changes in the use of technological devices, software and statistical methods. The number of publications has increased considerably and there have been major technological changes in the past decade (i.e. increased use of GPS devices, accelerometers and video cameras, and a convergence towards R), yet we found that research focuses on the same questions, specifically, on the effect of environmental factors on movement and behavior. In practice, it appears that movement ecology research does not reflect the MEF. We call on researchers to transform the field from technology-driven to embrace interdisciplinary collaboration, in order to reveal key processes underlying movement (e.g. navigation), as well as evolutionary, physiological and life-history consequences of particular strategies.

Keywords: movement ecology paradigm, technology, text mining, biologging, interdisciplinarity

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Introduction: the rise of a field called movement ecology

Movement, defined as a change in position of an individual in time, has been studied for millennia, from philosophical (Aristotle’s *De motu animalium* 384-322 BC) and mechanistic perspectives (Galen’s *De motu musculorum* 129-210 AD) (Fig. 1), but more recently has diversified into several research fields, such as physics [20], physiology [16], data science [46], and ecology [12].

Around a decade ago, and as part of a PNAS’ special feature on movement ecology, a unifying conceptual framework for the study of movement was developed [33], aiming to promote “the development of an integrative theory of organism movement for better understanding the causes, mechanisms, patterns, and consequences of all movement phenomena”. The movement ecology framework (MEF) was born. In the same special feature, a literature review of movement research [22] revealed that, up to that time, studies had mostly focused on describing movement patterns and their links with external factors (e.g. the environment), neglecting the causal drivers and its consequences for individuals, populations, and communities. It highlighted the relevance of the MEF, and encouraged interdisciplinary work to make this possible. Technological and methodological advances were stated as main requirements to quantify the movement of individuals towards the study of movement in the new integrative framework [33].

Animal telemetry devices were first used in the mid 20th century [38]. Since then, and particularly in the last decade, loggers have become smaller, cheaper, and more reliable, allowing for more animals to be tagged from a large diversity of species and taxa globally, and data to be collected at ever finer spatio-temporal resolutions [25]. In the first few decades, studies using animal telemetry commonly neglected the very nature of the movement process: the essence of movement (i.e. the autocorrelation in space and time) was typically considered a nuisance [36], such that researchers ignored time, space, or sometimes both. More recently and particularly in the last decade, statistical methods that deal with space and time have become more accessible and popular in telemetry studies (e.g. [3],[18],[15]), allowing for statistically sound and data-driven research on actual movement. In addition, developments in human tracking devices have given rise to scientific literature on human mobility. Initially inspired by animal movement studies, human mobility science is now taking the lead in handling big volumes of data through the development of machine learning methods for telemetry [38].

The aforementioned changes in both ideas and technology are consistent with an acceleration in the number of publications in movement ecology that started about a decade ago, and coincided with a series of special issues related to movement ecology among leading ecology journals (Fig. 1).

Ten years later, it is timely to ask the question: how have these advances shaped the field of movement ecology? In this study, we examined this research field, taking a decade-long snapshot of its research topics, evaluating the impact of the MEF in the literature, and assessing changes in the use of technological devices, software, and statistical methods. We accomplished this task by reviewing > 8000 movement ecology papers from the literature, using a text mining approach. Consistent with Nathan’s concept of movement ecology, the papers considered here studied movement of organisms, including humans. Based on a quantitative assessment, we

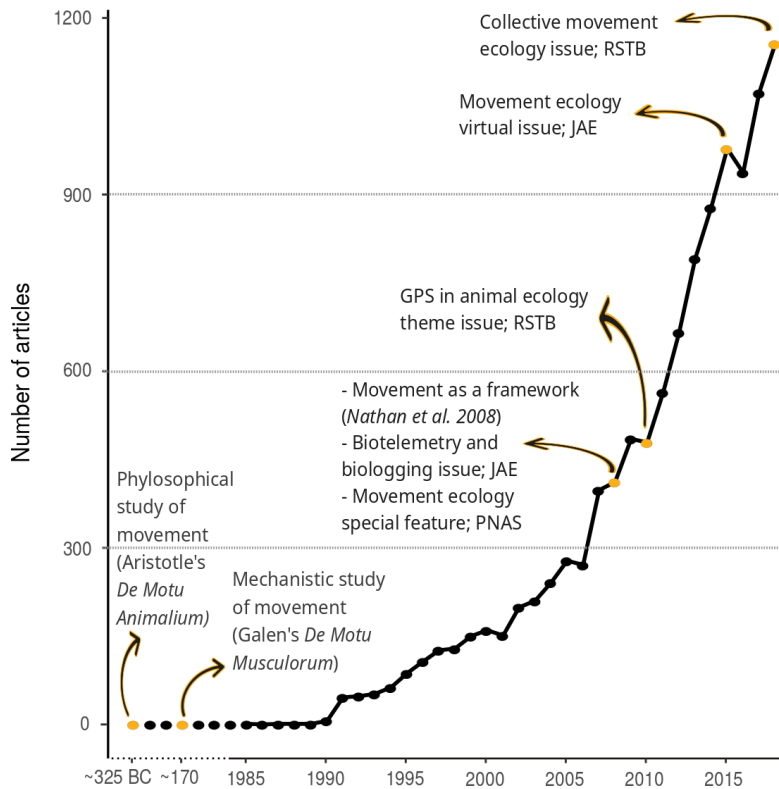


Figure 1: Timeline of movement ecology papers and milestones in the field

provide an integrative view of the state of the field, and open questions about its future directions.

Snapshot: research topics in movement ecology

We screened all abstracts from 2009 until 2018 to identify 15 broad topics from the words used (via Latent Dirichlet Allocation; see Material and Methods). We chose 15 topics as a reasonable number that would not be too large to prevent the interpretation of all topics, or too small that the topics would be too general (see discussion in the online Appendix section 3.1.2). These topics were, in descending order of prevalence:

- 1) **Social interactions and dispersal**, a broad topic encompassing interactions with conspecifics or the environment, as well as group movement, changes in population density and dynamics.
- 2) **Movement models**, encompassing any type of model (e.g. generalized linear model, model selection criterion, or even schematical models) that could be used to study dynamics, patterns, and populations.
- 3) **Habitat selection**, which encompasses choices in space use, influenced by resource availability or risks (e.g. natural predators or human disturbance), mainly in mammalian systems (Fig. 2).

- 4) **Detection and data**, focused on the collection of movement information and the required technological devices. This topic is also mostly related to mammal studies.
- 5) **Home ranges**, mostly focused on the identification of areas where animals live and develop their activities, and the geographical extent of this area.
- 6) **Aquatic systems**, involving the study of aquatic species, particularly fish, their migration, reproductive behavior and habitat, mostly for management purposes.
- 7) **Foraging in marine megafauna**, consisting of foraging strategies and behavior of marine top predators, mostly birds and mammals (Fig. 2).
- 8) **Biomechanics**, focused on body motion, swimming or flight power, and kinematics.
- 9) **Acoustic telemetry**, used to monitor animal movement (mostly fish), or in some cases, effects of anthropogenic noise on animal behavior.
- 10) **Experimental designs**, which involve analyzing behavioral and movement responses based on multiple stimuli, mostly on cattle and domestic animals.
- 11) **Activity budgets**, investigating—mostly using telemetry data—the effect of environmental conditions on the time allocated to different activities.
- 12) **Avian migration**, encompassing migration routes, orientation and flight strategies.
- 13) **Sports**, consisting of motion analysis of sports players for better performance.
- 14) **Human activity patterns**, mostly related to health and physical activity in children and adults, often sampled with accelerometers.
- 15) **Breeding ecology**, involving space use and movement corridors during breeding seasons; mostly, but not exclusively on turtles and whales.

While Sports and Human activity patterns are not strictly ecological topics, they are an integral part of the literature studying movement phenomena, and benefit from advances in movement ecology. For instance, works on Sports have tried to understand why and how certain individual and collective behaviors emerge in games, using principles from ecological psychology (e.g. [39]), focused on the interdependencies of humans and their environments [5]. Moreover, some studies related to Human activity patterns were also inspired from animal studies (e.g. [42]).

Social interactions and dispersal, Movement models, and Habitat selection remained the most relevant topics throughout the decade (Fig. 3). The prevalence of Home ranges studies decreased over the years. In contrast, Sports has become a more recurrent topic in the literature. The prevalence of the other topics has remained relatively stable in time. The division into research topics has revealed some distinction between marine and terrestrial realms, as four topics pertained specifically to breeding or foraging ecology in marine species.

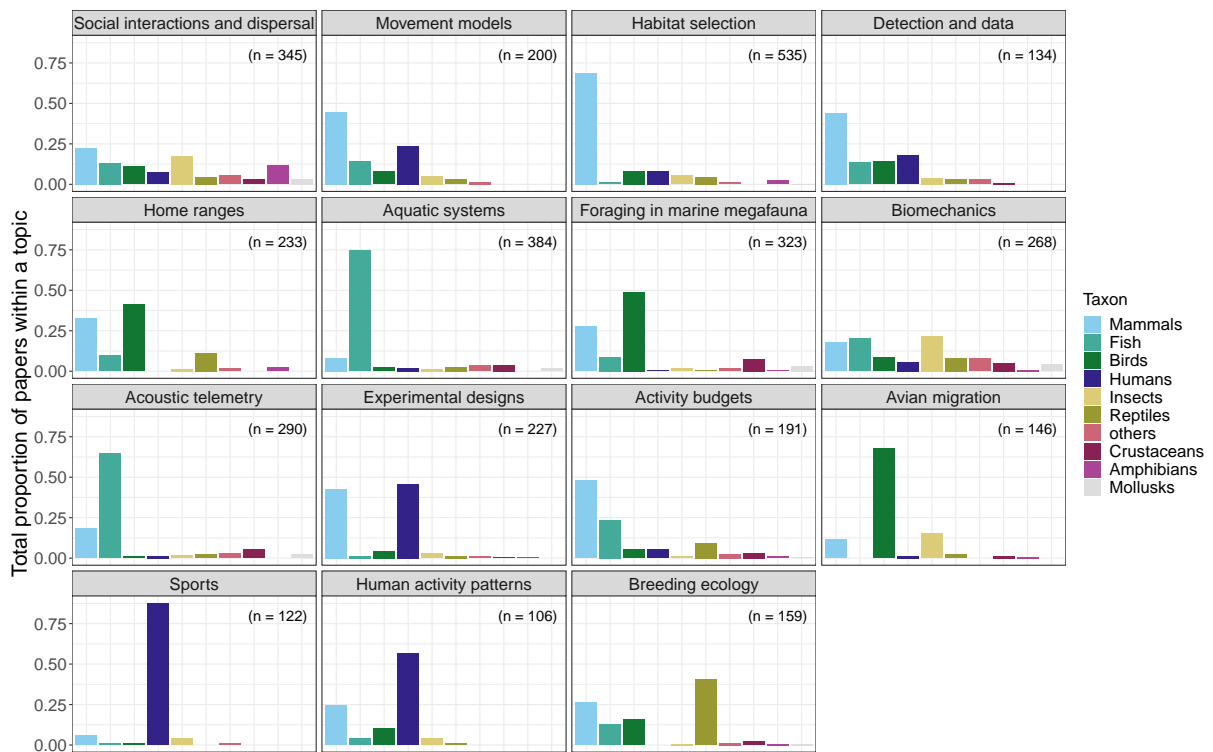


Figure 2: For each topic, relative frequencies of papers studying each taxonomical group. Only papers with more than 50% of association to each topic (γ , see Materials and Methods) are used for this graph.

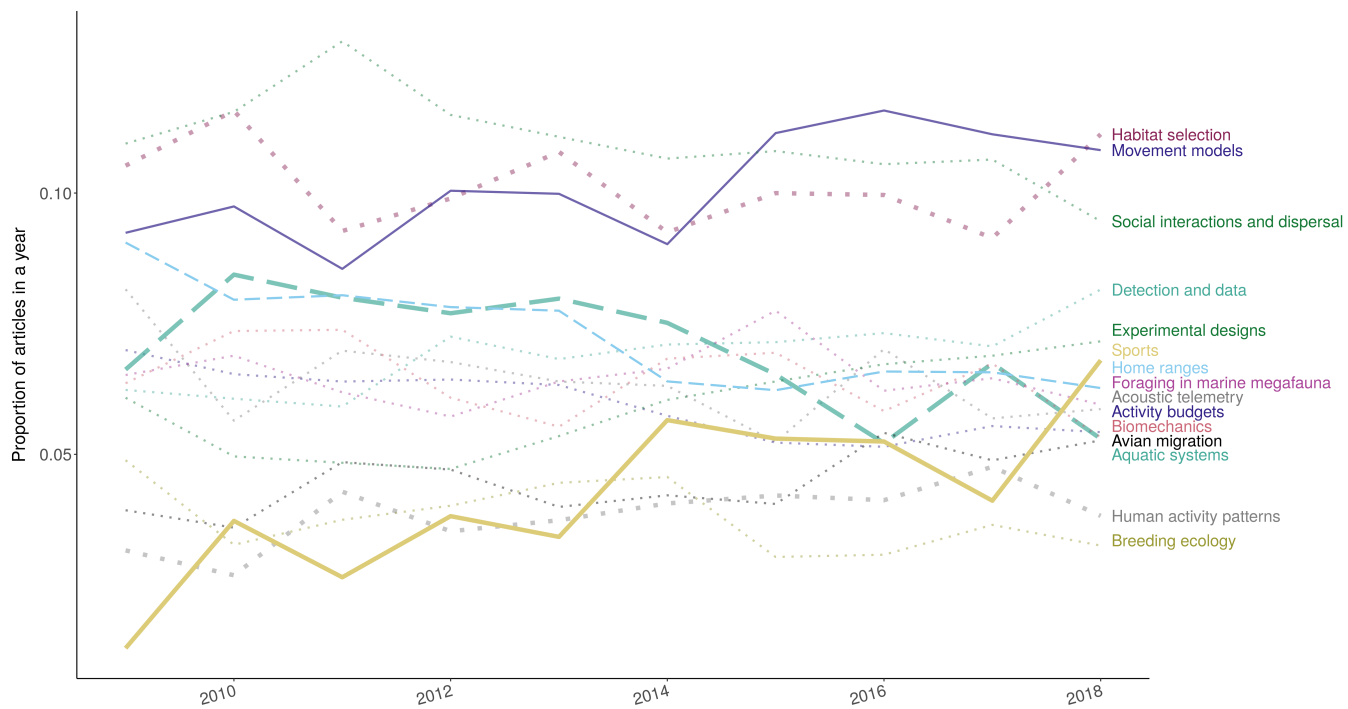


Figure 3: Time series of the relative prevalence of each topic every year. To improve readability, the topics with the most pronounced increases and decreases have been highlighted by continuous and dashed lines, respectively.

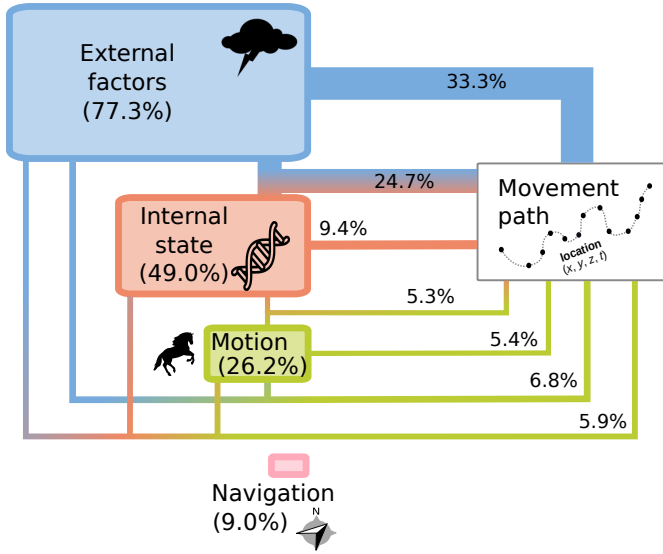


Figure 4: Representation of the components of the movement ecology framework and how much they were studied in the last decade: external factors, internal state, motion and navigation capacities, whose interactions result in the observed movement path. The size of each component box is proportional to the percentage of papers (in parentheses) tackling them irrespectful of whether they are only about this component or in combination with another one. The latter is specified through the segments that join the components to the observed movement path. One fill color corresponds to papers that only studied one component, while two or more colors correspond to papers that tackled two or three components, respectively (the ones from those colors). The width of the segment is proportional to the percentage of papers that studied that combination (or single component). Only combinations corresponding to $> 5\%$ of papers are shown; e.g. combinations involving navigation and papers studying navigation on its own had $< 5\%$ of papers each therefore they are not shown in the graph.

The movement ecology framework

The MEF introduced by [33] consisted of four components: external factors (i.e. the set of environmental conditions that affect movement), internal state (i.e. the intrinsic factors affecting motivation and readiness to move), navigation capacity (i.e. the set of traits enabling the individual to orient), and motion capacity (i.e. the set of traits enabling the individual to execute movement). The outcome of the interactions between these four components would be the observed movement path (plus observation errors). We found that, in the last decade, most studies tackled movement in relation to external factors (77%), while a minority of them studied the three other components (49%, 26%, and 9%, for internal factors, motion, and navigation capacity, respectively). For the most part, studies did not look into interactions between these components, except for external factors with internal states (25% of the studies; Fig. 4). Quite strikingly, this is the same overall pattern as in the decade before (1999-2008; Appendix section 3.3.1).

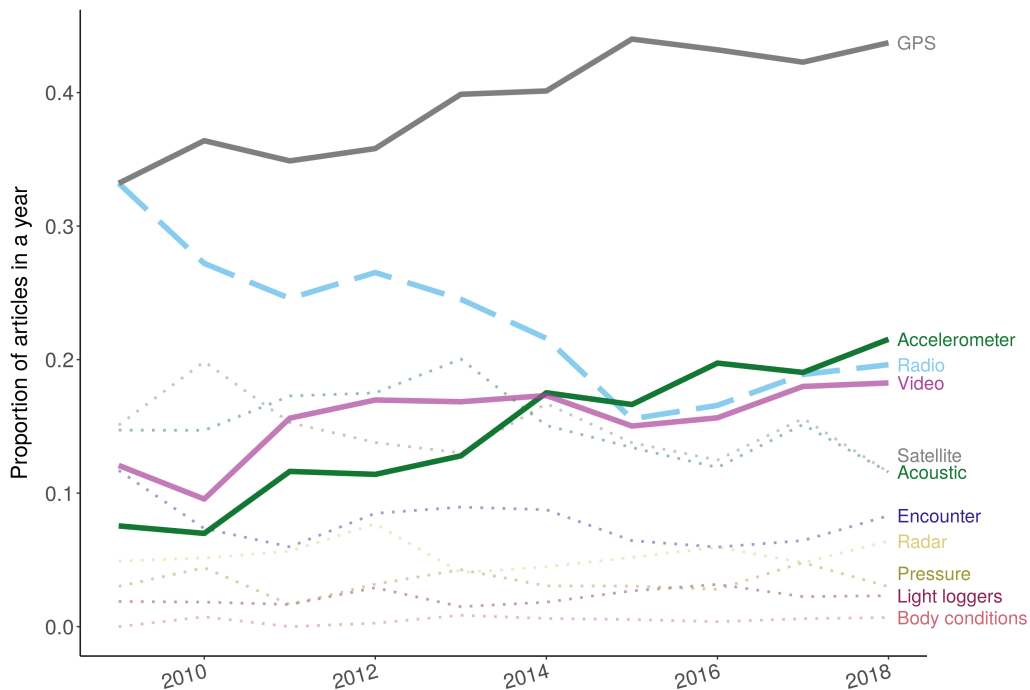


Figure 5: Proportion of papers in each year using each type of device. To improve readability, the devices with the most pronounced increases or decreases were highlighted by continuous and dashed lines, respectively.

Tools for movement ecology

Technology has been a major driver of trends in data collection and scientific publications in movement ecology. Past reviews have highlighted an increase in the amount and variety of tracking devices, which are becoming more affordable, with more efficient battery capabilities, and reductions in size (see [38], [25], [21], and survey to movement ecologists in Appendix section 4). Here, we categorized tracking device observations as accelerometer, acoustic telemetry, body condition measurements, encounter observations, GPS, light loggers, pressure data, radar, radio telemetry, satellite, and video/image (details of these categories and the analysis are in Appendix section 3.4).

Throughout the last decade, GPS has not only remained the most popular device in movement studies, but its popularity in relation to other methods has increased (Fig. 5). This is likely due to the development of cheaper, smaller and more efficient devices, which make them a feasible option for small and medium-sized animals [25]. While in 2009 radio telemetry was as popular as GPS, later in the decade GPS seems to have increasingly replaced radio telemetry [1], which has been experiencing a substantial decrease in parallel. The use of accelerometers and video is becoming more popular; the former allows for finer spatio-temporal resolution movement data (Fig. 5), opening avenues to exploring physiological aspects of movement like energy expenditure [45], while the latter gives us an animal’s-eye view of its local environment, providing information on visual cues used, foraging behavior and movement strategies [37, 24].

The increasing volume and diversity of movement data obtained through these

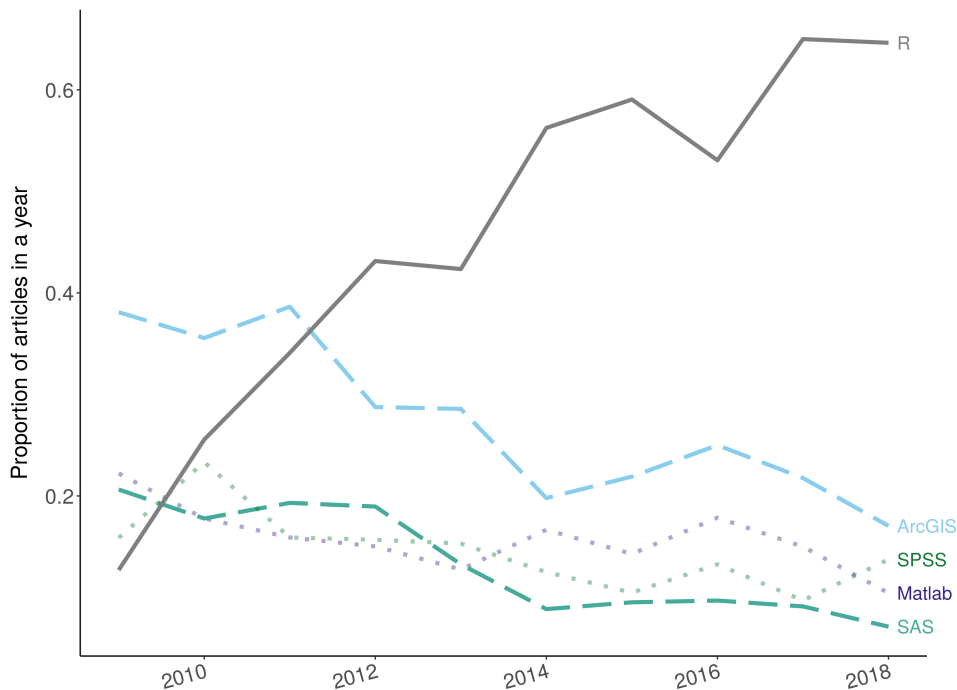


Figure 6: Proportion of papers of each year using each software package. Shown are the five most mentioned software packages. The ones with the most pronounced increases or decreases were highlighted by continuous and dashed lines, respectively.

tracking devices require appropriate software tools for data management, processing, and analysis [40, 23]. We evaluated the use of 33 software packages (see section 3.5 of the Appendix for a full list), and the five most popular through the decade were R, ArcGIS, Matlab, SPSS and SAS, in that order. Among those, R experienced a constant and strong growth in the last 10 years, while usage of all others substantially decreased, making R an undisputed preference in the field (Fig. 6).

In another study of ecology in general, the same pattern in reported R usage was observed [26]. According to both [26] and this study, the popularity of R ten years ago was low (used by $> 10\%$ of the papers), while the majority of articles published nowadays have reported its use, indicating a homogenization of not only movement ecology but ecology in general towards R. This success is likely due to the fact that R offers a free software environment to program and create new methods, share them, and improve them, facilitating transparency, collaboration, and reproducibility [28], and at the same time it can be extended with more than 50 specialized packages to process and analyze movement [23]. R also leverages other programming languages (e.g. C, python, Fortran, etc.) by allowing internal access to their use within an R workflow (and R syntax).

In parallel with the development and improvement of tracking devices and software, there has been substantial progress in the number and sophistication of quantitative methods for the study of movement (e.g. [3, 35, 2]). We investigated the use of statistical methods in the movement ecology literature (see Material and Methods, and Appendix section 3.6, for more details). Most studies (68%) used, at the least, generic statistical methods (i.e. with no explicit spatial, temporal or social interaction component in its definition) such as regression models. A smaller number

(57%) used at least one or more specialized methods, i.e. movement, non-movement spatiotemporal (e.g. spatiotemporal geostatistics), spatial (e.g. point process), time series, and social analysis methods (e.g. social networks). Our analysis reveals that researchers are not necessarily using movement-specific techniques to analyze movement (only 33% of the studies), and, in some cases (42%), not using spatial, temporal, or social analyses either.

While the availability of movement data and associated software tools and methods are increasing (see a summary list in [10]), the proportion of papers using movement-specific analytical methods does not show the same pattern (Fig. 7). Actually, the proportion of usage of generic methods is increasing. In addition, and based on a trigram analysis, we found that the most common methods were linear mixed models (Table in section 3.6.1 of the Appendix).

This raises the question: why were the majority of papers not using movement-specific methods? Certainly, not all studies require movement-specific methods; the choice of method should depend on the research question, assumptions, and data. Another reason for the use of non-movement methods could be related to many scientists coming-of-age in a time when autocorrelation in movement was considered a nuisance, or they do not possess the quantitative skills necessary to use these methods. Movement is a complex process, and in most cases, statistically noisy, nonlinear, and spatially and temporally correlated (28). Interdisciplinary work between ecologists and statisticians to “decomplexify” movement models (either making them more simple or usable for different datasets and situations) may still be a challenge to overcome [44]. Moreover, as we intensify data collection and processing, the use of movement models – for a statistical representation of movement and for population-level inference – can be expected to increase.

Open questions for the future of movement ecology

Technology has undeniably been driving research in movement ecology in the past decade. With access to numerous and diverse tracking data [4], and tools for data processing and analysis [10, 23], researchers have been able to sample spatiotemporal behavior and changes in physiology, to investigate subjects like social interactions, habitat selection, foraging behavior, physiological performance, and migration; topics that were revealed by our text mining analysis. However, the technological advances have not structurally changed the field of movement ecology: none of those research topics are new, and, we have not moved towards the integrative study of movement advised by the MEF.

The movement ecology framework was a revolutionary idea: an integrating vision of the study of movement, represented by the interaction between the four components of the framework. As argued by [33], it is only through combining different components of the framework that we can gain a mechanistic understanding of movement, from the neurological and physiological drivers to the life-history and evolutionary consequences. While it has been recognized as a seminal, if not the most influential, publication in the field (with >1000 citations according to Web of Science), research in movement ecology has not translated into a relative increase in publications addressing the internal state, navigation, motion, or the interactions of the different components, than in the decade before. The findings in [22], that the majority of movement studies were “simply measuring movement, documenting

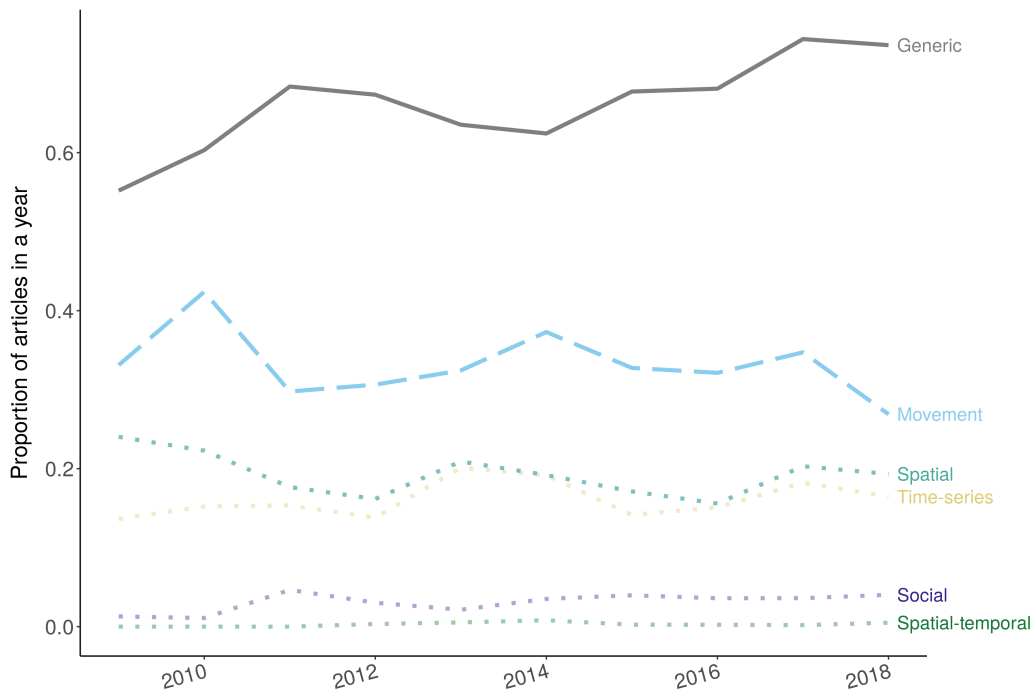


Figure 7: Proportion of papers of each year using each type of method. The types of method with the most pronounced increases or decreases were highlighted by continuous and dashed lines, respectively.

its occurrence, or describing how it was influenced by the environment”, still hold true. It may be for the simple reason that most researchers in movement ecology are most likely ecologists. Ecology is inherently focused on the environment; it is “all the comprehensive science of the relationship of the organism to the environment” [19]. It is logical that, in a field mostly populated with ecologists, research questions have been strongly related to the effect of external factors on animal movement and behavior. However, movement ecology as a science should pursue understanding of movement. The role of external factors on movement can only be understood in conjunction with the internal state, motion, and navigation capacities, even if these are closer to ethology, biomechanics, and neuroscience, respectively, and studying these may not seem as straightforward. Indeed, recent papers have addressed these issues (e.g. [16, 30, 32]) and opened perspectives for future studies.

What does this mean for the future of movement ecology? As in every field of science, there is a trade-off between data-driven and ideas-driven research (see an analogous discussion for physical sciences in [13]). It is likely that the development of tagging devices, statistical, and mathematical methods to describe patterns or model processes will continue to shape our field (see survey results in Appendix section 4). But will technological advances keep driving the field more than movement concepts? Or will science be driven more by new ideas to understand movement processes, inspiring the development and use of particular technologies and analytical methods? Movement ecologists need to decide where is the trade-off for their own research. If we continue with the trend of the last two decades we will eventually have to acknowledge the failure of the movement ecology framework as a unifying paradigm of movement ecology.

Movement ecologists can rather choose to break this trend, and transform the field into a more integrated science of movement. An integrated approach to movement, as suggested by the MEF, would require truly interdisciplinary efforts involving ecologists, biologists, neuroscientists, physicists, and statisticians, among others [22, 44]. It should aim at bridging the divide between human mobility research and animal movement ecology, and between aquatic, terrestrial, and aerial realms. These seemingly different fields may have questions and methods in common [27, 38, 31]; we could learn from each other and collaborate.

The path towards interdisciplinarity comes with many challenges [14, 43], concerning the researchers as individuals (particularly regarding communication; [7, 29]) and as part of organizations that may not have structures that encourage interdisciplinarity [8], and, very importantly, the difficulties of obtaining funds for interdisciplinary research [9]. To face these challenges, movement ecologists should direct systematic efforts towards interdisciplinarity. The field of movement ecology would greatly benefit from exploring questions with multiple and integrated approaches, novel and emerging movement concepts. The path we choose to walk will be reflected on our research.

Materials and methods

We selected scientific peer-reviewed papers in English that studied the voluntary movement of one or more living individuals. We used Web of Science (WoS) as a search engine. Since very few papers mention “movement ecology” in their abstracts, titles and keywords, we did not use “movement ecology” as a search phrase. After a detailed testing phase, we came up with search terms within four groups of words: behavior, movement (e.g. motion, moving), biogging (e.g. telemetry, gps) and individuals (e.g. animal, human; we focused our efforts on Animalia). To be qualified, papers needed to use words from at least 3 of these groups in their abstract, keywords or title. Also, papers studying movement of objects other than whole organisms (e.g. cell, neuron), were filtered out. See more details on the search terms and their quality control in section 2 of the Appendix. More than 8 thousand (8,007) papers met our criteria. Results from the WoS (title, keywords, abstracts, authors, DOI, etc.) on these 8,007 papers were downloaded and used for most of the analyses. In addition, we used the `fulltext` package [11] in [34], using Elsevier, Springer, Scopus, Wiley, BMC, and PLOS one API keys to download full texts of 4,037 papers. Finally, using an automatic detection algorithm (see section 2.3 of the Appendix for a description), 3,674 “Materials and Methods” sections were extracted from this set of papers.

Topic analysis

Topics were not defined *a priori*. Instead, we fitted Latent Dirichlet Allocation (LDA) models to the abstracts [6]. LDAs are basically three-level hierarchical Bayesian models for documents (in our case, abstracts). Here we assumed that there was a fixed number of latent or hidden topics behind the abstracts, and that the choice of words in the abstracts were related to the topics the authors were addressing. Thus, an abstract would have been composed of one or more topics, and a topic would have been composed of a mixture of words. The probability of

a word appearing in an abstract depended on the topic the abstract was addressing. Here we used the LDA model with variational EM estimation [41] implemented in the `topicmodels` package [17]. More details about the practical aspects of LDA modeling and a short discussion on the number of topics can be found in section 3.1 of the Appendix.

From the fitted LDA model, we obtained 1) for each topic, the probability of the topic being referred to in each document (denoted by γ), and 2) for each word, the probability of appearing in a document given the presence of a certain topic (denoted by β). The β values were thus a proxy of the importance of a word in a topic. They were used to interpret and label each topic, and to create wordclouds for each topic, shown in section 3.1 of the Appendix. The sum of γ values for each topic served as proxies of the “prevalence” of the topic relative to all other topics and were used to rank them.

Taxonomical identification

To identify the taxonomy of the individuals studied in the papers, the ITIS (Integrated Taxonomic Information System) database (<https://www.itis.gov/citation.html>) was used to detect names of any animal species (kingdom Animalia) that were mentioned in the abstracts, titles and keywords. We screened these sections for latin and common (i.e., vernacular) names of species (both singular and plural), as well as common names of higher taxonomic levels such as orders and families. After having identified any taxon mentioned in a paper, we summarized taxa at the Class level (except for superclasses Osteichthyes and Chondrichthyes which we merged into a single group labeled Fish, and for classes within the phylum Mollusca and the subphylum Crustacea which we considered collectively). Thus, each paper was classified as focusing on one or more class-like groups; for example - mammals, birds, insects, etc. For the purpose of our analysis, we kept humans as a separate category and did not count them within Class Mammalia. See section 3.2 of the Appendix for more details.

Framework and tools

To assess the study of the different components of the movement ecology framework, we built what we call here a “dictionary”. A dictionary is composed of words and their meanings. Here, the words of interest were the components of the framework (i.e. internal state, external factor, motion, and navigation), and their meanings were the terms potentially used in the abstracts to refer to the study of each component. For example, terms like “memory”, “sensory information”, “path integration”, or “orientation” were used to identify the study of navigation. Similarly, the devices, software, and statistical methods used were also assessed through dictionary approaches. More details, including quality control of the dictionaries, in sections 3.3 to 3.6 of the Appendix.

Access to data and codes

We provide details on all data processing and analyses at <https://rociojoo.github.io/mov-eco-review/>, from descriptions of word search on Web of Science

and scripts to download the papers, up to the codes to reproduce every single plot in this manuscript. The website, hosted in the <https://github.com/rociójoo/mov-eco-review> repository, works as an online Appendix to this manuscript. The authors can be directly contacted for further development and questions about the dataset, which has not been released to respect Text and Data Mining rights of the publishers.

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