

# Trends and gaps in a decade of movement ecology

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<250 words for abstract. I had an idea for the abstract but I forgot my little notebook where I wrote it...

Keyword 1 | Keyword 2 | Keyword 3 | ...

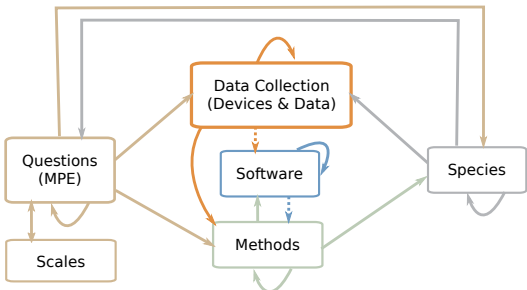
This section would be an introduction to movement ecology and the advances in the last 10 years. We'd mention the movement ecology special issue in PNAS, and particularly Nathan's paper in 2008 with the framework (or paradigm; we'll call it MEP as in other publications). Shortly describe Holyoak's paper in 2008 quantifying studies of movement and MEP by taxon. Some important things the paper says: There was a lack of studies of the different components of the MEP (most studies were describing movement and how it's influenced by the environment, conspecifics or others, but "we rarely know why spaces follow particular movement paths and how their mode of movement relates to short-term and long-term costs and benefits"), and called for more integrative (interdisciplinary) studies. They also mentioned some differences in taxa (studying movement), though they measure something different than us.

The idea of the paper is to assess the state of the field of movement ecology after Nathan's seminal paper and the special issue, by analyzing the text of all peer-reviewed scientific articles published between 2009 and 2018. We focus on several key aspects: the questions (express through the MEP), the species studied, the data collection, the software and the methods for analysis. Fig.1 represents the implicit dependencies between aspects (e.g. the choice of methods depend on the type of data to analyze). Generally speaking, movement ecology studies could be classified as organism-centered (i.e. the main goal is the gain of knowledge about a species) or process-centered (i.e. the main goal is to understand the processes behind movement in general: why, how, when and where movement is produced, and the organisms studied is a tool to get to that knowledge). We examine these two aspects (questions and species) first, as they are the main focus of movement ecology. Then, we assess the other three aspects and their connections with the questions and species. We also review and discuss how interdisciplinary is the field now and the challenges that we face now as a research community.

The statistics shown in this work were a result of the text analysis of 4417 movement ecology papers published between 2009 and 2018. The methods for selecting the papers and extracting the information are described in Supp. Mat. 1. We also conducted an online survey on movement ecologists asking about their perception of the field (Supp. Mat. 2). These perceptions are discussed in the following sections.

## The movement ecology paradigm: are we forgetting about the processes?

- Introduction to the MEP and the questions behind it (I think "why" is not only related to internal but also external factor.



**Fig. 1.** Key aspects for movement ecology: questions (represented by the movement ecology paradigm), species, data collection, software and methods for analysis. The questions have to take into account scales of movement. The arrows depart from the aspect that is needed to make a decision on the aspect at the other end of the arrow. Circular arrows indicate that this aspect can also be chosen by itself (e.g. the researcher's preference). Dotted arrows indicate some links that often happen but should not: the software is chosen because it is 'good' for some kind of data, or the methods are chosen because they are available in a software.

And so is when). And scales. - Mention the number of papers that refer to the movement ecology paradigm (or framework). Number of papers with scales in KAT (keywords, abstract, title) - Fig. 2: MEP and quantification of the links between components. This is tricky because the dictionaries were created for motion and navigation processes and not capacities. - Table 1: main "keywords" or categories for each component. - Discuss those results. We are still like in Holyoak's paper: mostly caring about external factor's role in movement. Why? Is everything else so difficult to quantify? Is it difficult to get data on motion or navigation? Are the methods not good for that? Are we not working with physiologists or physicists enough? (Invite to check next sections). Discuss "scale results". - Add stuff from the survey.

## The species: are we focusing too much on some species?.

One or two lines of introduction on species studies in movement ecology. Then explain that we studied taxas and orders. -

### Significance Statement

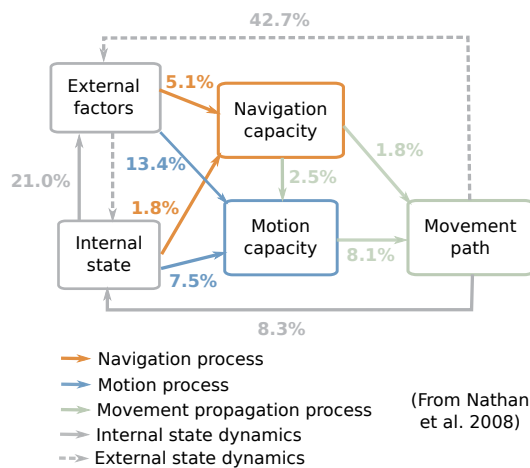
Authors must submit a 120-word maximum statement about the significance of their research paper written at a level understandable to an undergraduate educated scientist outside their field of speciality. The primary goal of the Significance Statement is to explain the relevance of the work in broad context to a broad readership. The Significance Statement appears in the paper itself and is required for all research papers.

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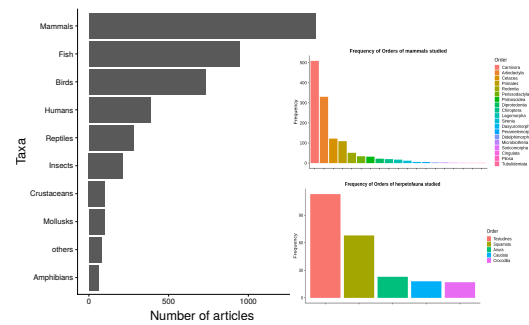
Please declare any conflict of interest here.

<sup>1</sup> A.O. (Author One) and A.T. (Author Two) contributed equally to this work (remove if not applicable).

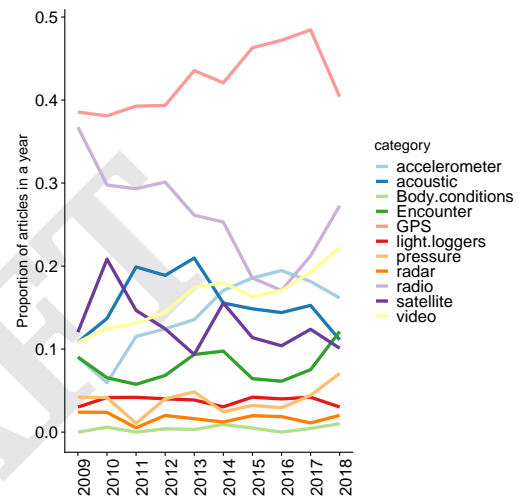
<sup>2</sup> To whom correspondence should be addressed. E-mail: author.twoemail.com



**Fig. 2.** Movement ecology paradigm (MEP) from Nathan et al. 2008. The values shown are the percentages of scientific papers (from which we extracted MPE information: 3750) that showed in the abstract that they were studying those components or links between components. Percentages in links with movement path correspond to papers only mentioning the components, which we infer is linked to movement (because those are movement papers).



**Fig. 3.** Left: Barplots of frequency of taxa studies. Top right: Barplots of frequency of studies of mammal orders. Bottom right: Barplots of frequency of studies of reptile orders. Click on the file to see it better.



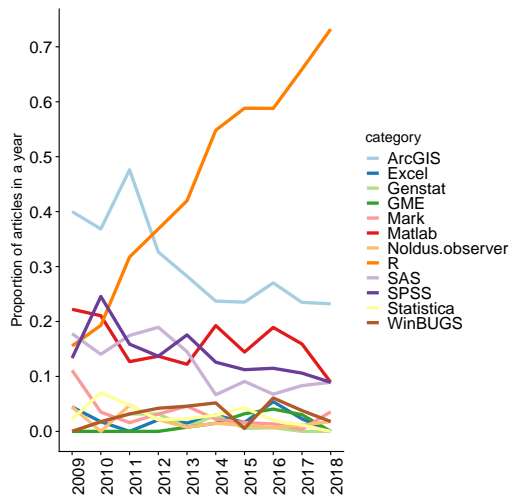
**Fig. 4.** Proportion of articles (per year) mentioning each type of device.

Fig. 3: Main figure: barplots of taxa. Smaller subfigures: barplots of orders (max 2 subfigures). - Comment results on taxa. Mammals historically easier to tag. Development of tags (see next section) is enabling tagging other taxa. But not all mammals' movement are being studied. It's mostly carnivores and ungulates. Why? Easier to tag? Longer life? More money behind? Are they becoming target species to develop more knowledge on processes? That would mean checking the studies of the framework on those orders and compare with the global results. - Other orders worth mentioning? Are there more studies on navigation or motion for certain orders? Are the spatial distribution of authors different? Is there something we can say about fish? - Studies on humans. [Ref1] mentions the study of humans should be included in movement ecology since they have effects in the dispersal of many organisms. Another paper (Thums et al 2018) discusses the potential of integrating human movement research in animal ecology (methods, software). Because of data availability, human research is developing platforms and methods to deal with big data, which is something that animal movement will need. Also, in the past, human movement studies have taken methods applied to animal movement first (e.g. random walk models). Here we included humans as the studied organisms; most of them analyzed as regular pedestrians or fishers - So... why are we studying some organisms more than others? Does it make sense? Should we break the trend? - Add stuff from the survey.

**Data collection: higher resolution to capture movement.** - One or two lines about tracking organisms and biologging. - Fig. 4: Ts of devices. - Check GPS and radio trade-off. Hebblewhite and Haydon (2010) offer a discussion on stuff we would be neglecting by choosing GPS instead of radar. - Talk about higher resolution for movement. Also shown by increasing use of accelerometer and video data. - What questions are these devices enabling to answer? What about the MEP? Or are we not collecting the right type of data yet? What do we want? Are the questions (i.e. MEP) playing a role in data collection planning? I think I read something

about that in Hughey et al (2018) though not about MEP. - Also, by going for higher resolutions, are we neglecting larger scale movement? - Remaining challenges in data collection. And even if we explore A LOT environmental factors role in movement, we still have the issue of having environmental data at different spatial and time scales than the movement data. How are we solving this? - Data sharing and standardization. The repositories. Challenges for databases. - What's next? (drones?) - Add stuff from the survey.

**Software: towards standardization and free access.** - One or two lines about software's importance for data processing and analysis, more now than before because of the volumes of data and the complexity of the methods. - Fig. 5: Ts of software. - Talk about software ts. Most software were never very much used (actually some French software are only used in French-speaking countries, see Supp. Mat. 3). The R trend which is a trend for standardization (everyone "speaking" the same language), not only in movement ecology but in science in general. Programming and also free access to codes will make science more reproducible. - Advantages and risks of everyone turning to R (talk about the packages and mention the R paper). - Emphasize need for integration and RopenSci as a peer-reviewed tool that forces packages to be developed for users. - Can other software appear in the near future?



**Fig. 5.** Proportion of articles (per year) mentioning each software. Only the top 12 most used software are shown. For the complete frequency table go to Supp. Mat...4?

Python? I just read on the news that facebook and Google are trying to develop new software to satisfy big data needs. - Add stuff from the survey.

**Methods: from hypothesis testing to movement models.** - A phrase about methods being key to get from anecdotal observation to significant, representative scientific findings. Here we refer to statistical and mathematical methods; mostly statistical which are more common now (and the ones I know). - Holyoak mentioned in his paper that most papers were about hypothesis testing. Here we should show our statistics confirming that for this decade as well. So this is still true. Are we p-value dependent? Short discussion about p-values; their usefulness and their danger (to find good p-values and feel happy and ready to publish). - There is not a unique way to classify methods, and many could fall into several categories at the same time. For instance, regression trees could be considered machine learning, a multivariate technique and a regression method (strictly speaking, any method with more than one variable would be multivariate). A random walk could be a time series method or a spatio-temporal method depending if it considers a 2 or 3D component or not. Moreover, it is difficult to directly and automatically link a method to the MEP. Several methods could be used for the same question, and the choice of method also depends on the available data (and the preference of the analyst). Here we propose a classification based on methodological questions for movement ecology analysis.

Methodological questions would be: 1) Where, with a focus on spatial components; 2) why, focusing on identifying covariates that would explain the variable or process studied; 3) how, focused on the links between a variable and the others; 4) when, with a focus on the temporal dimension; 5) what, with the goal of identifying a latent variable (i.e. a behavioral pattern) that would be behind the observed movement patterns; and 6) with whom, focusing on the interspecific or conspecific interactions that would have an effect on movement. Table 1 summarizes these definitions with some mathematical notations and examples of methods that correspond to each question. A method could, however, be useful for several

**Table 1.** Main methodological questions in movement ecology and variables involved

Question	Variables involved	Examples of methods
Where?	$X; f(X)$	Geostatistics, home range methods
Why?	$Z \sim g(Z')$	Hypothesis tests
How?	$Z \sim g(Z')$	Mechanistic models
When?	$t; f(t)$	Time series models
What?	$Y \sim h(Z)$	Classification methods
With whom?	$g(z_i, z_j)$	Agent-based models

$t$  represents a time step and  $X(t)$  a given location in time. A continuous georeferenced variable in time (e.g. turning angle) would be denoted by  $Z_{x,t} := f(X_t)$ .  $Y$  is a latent variable that could be expressed as a function of  $Z$ .  $g$  is a distance function between individuals  $i$  and  $j$ .

**Table 2.** Main methods for each question

Why		How		When
word	count	word	count	word
random walk	282	Akaike's information	593	mixed effects model
density kernel	178	%ANOVA%	511	linear model
movement model	172	mixed effects model	483	random walk
minimum convex polygon	166	t-test	311	%GLM%
utilization distribution	141	linear model	288	regression model
tortuosity	66	%GLM%	209	linear regression
%SSF%	63	regression model	202	logistic regression
Brownian motion	58	linear regression	192	movement model
%BBMM%	52	logistic regression	172	%SSM%
sinuosity	37	%SSM%	168	%RSF%

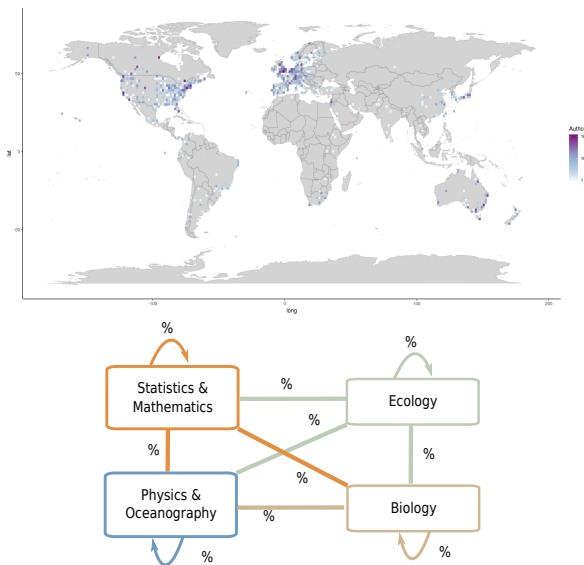
I have to edit the calculations to pass from keywords to methods. Also, I have to filter model selection criteria. And... this doesn't fit. Ideas?

questions; for example, a hidden Markov model links a hidden variable (what) to observed variables (why) in time (when) via conditional probabilities (how). Here we identified ~ 200 statistical methods and identified the questions they can answer (Supp. Mat. 5?).

Describe global results for the questions (Why: 1709, How: 1515, When: 859, Where: 842, What: 363, With whom: 215). Show Table 2 with the main keywords for each question. Discuss that when and where methods are not much used. Instead, it's more about why and how, driven by mixed models. While there may be some versions of mixed models that properly consider spatial and temporal components, most of them don't or add them as simple covariates. While it is good that researchers are using models (add here a statistic on how many abstracts use the word "model") not only to obtain a p-value (hopefully) but also to synthesize their knowledge of organisms' movement, since movement has a spatial and temporal component we should be movement towards more movement models. I need to quantify how many papers talk about movement models (so potentially spatiotemporal models like RWs, SSMs or HMMs). Also mention that there are several R packages for modeling movement. - Mention the reviews of methods for movement, mostly for movement models. Like Patterson et al. 2017. - Some challenges? Continuous movement models are not quite there yet. Patterson's review and McClintock et al. 2014. Do you see other challenges? - Add stuff from the survey.

RJ: This is what I think but I may be completely wrong.

RJ: Do you agree?



**Fig. 6.** Movement ecologists. Top: spatial distribution of authors of movement ecology papers. Bottom: interactions between researchers from different fields based on coauthorship.

Studies mention some challenges to actually go to manag. and conserv. such as team work with stakeholders, accesss to data of several species since management has to consider interactions in the ecosystem... so actually improving every single aspect of movement ecology that we've mentioned here could help for management and conservation. I should also mention somewhere the paper of Fraser et al (2018) comparing overall studies of movement ecology with actual use of them for conservation (but their study makes no sense by searching for "movement ecology" in any part of the text of a paper).

**Summary: future directions.** Wrapping up. No idea of what to put here. Oh, yeah: add stuff from the survey.

## Materials and Methods

Please describe your materials and methods here. This can be more than one paragraph, and may contain subsections and equations as required. Authors should include a statement in the methods section describing how readers will be able to access the data in the paper.

**Subsection for Method.** Example text for subsection.

**ACKNOWLEDGMENTS.** Please include your acknowledgments here, set in a single paragraph. Please do not include any acknowledgments in the Supporting Information, or anywhere else in the manuscript.

## Interdisciplinarity for movement.

RJ: I keep forgetting the differences between inter, multi and transdisciplinarity. Help?

- Movement ecology as a multidisciplinary field. If we want to understand movement processes better, we need ecologists, physiologists, statisticians, mathematicians, geophysicists, meteorologists, oceanographers, software engineers (am I forgetting some people?) to interact and push the field forward. - Here I should show results that I don't have yet on the diversity of journal with movement ecology papers, and on researchers' affiliations. - Imaginary table 3: it would show results on journals. I've got papers from 264 journals. We should come up with categories for classifications. How about ecology, biology, general, fisheries, methodological (mainly statistics, maths, data processing, GIS), physics (can oceanography be included here?), human (e.g. transportation, behavior research, human kinetics, sports). Does it make sense? Consider that this is to show if we are studying movement ecology from many disciplines. Also, I don't quite get the difference between ecology and biology so I need help with that (sorry).

- Fig. 6 would be composed of a map of affiliations and blocks of 'professions' (ecologist, biologist, physicist, stat/mathematician) and a quantification of their interactions. Like in the example.

- Discuss results. Are we interacting more than before? Is it still an issue? What's missing? Talk about conferences of biologging or movement ecology. Also ISEC and... biometrics? Ecological conferences (are the other people going?).

**Movement ecology for management and conservation.** This is the only application I found from the topics results (and the only way I found to add some of the topics results). We would show that among topics, this is the most popular one (Table in Supp. Mat), so there are efforts to respond to management and conservation needs with movement analysis. There is actually framework proposed by Allen and Singh (2016) to link movement ecology and wildlife management and conservation.