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Context-aware movement analysis in ecology: a systematic review

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ABSTRACT

Research on movement has increased over the past two decades, particularly in movement ecology, which studies animal movement. Taking context into consideration when analysing movement can contribute towards the understanding and prediction of behaviour. The only way for studying animal movement decision-making and their responses to environmental conditions is through analysis of ancillary data that represent conditions where the animal moves. In GIScience this is called Context-Aware Movement Analysis (CAMA). As ecology becomes more data-oriented, we believe that there is a need to both review what CAMA means for ecology in methodological terms and to provide reliable definitions that will bridge the divide between the content-centric and data-centric analytical frameworks. We reviewed the literature and proposed a definition for context, develop a taxonomy for contextual variables in movement ecology and discuss research gaps and open challenges in the science of movement more broadly. We found that the main research for CAMA in the coming years should focus on: 1) integration of contextual data and movement data in space and time, 2) tools that account for the temporal dynamics of contextual data, 3) ways to represent contextualized movement data, and 4) approaches to extract meaningful information from contextualized data.

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KEYWORDS
Movement analysis; tracking data; environmental data; context; movement ecology

1. Introduction

Movement research has increased rapidly over the past two decades (Demšar *et al*. 2021). One of the main reasons for increased interest in the study of movement is the rising availability of movement data (in particular data from positional devices, such as GPS trackers) and the widespread growth in availability of environmental data from external sensors. Environmental data include both data from platforms like meteorological stations and satellites, but also data that are collected simultaneously with movement data, by bio-logging sensors located on tracking tags. One of the disciplines that benefited from this increased data availability is movement ecology, which investigates animal movement (Williams *et al*. 2020).

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Animal movement is a function of internal and external factors, which interact at different spatio-temporal scales. More specifically, movement is a product of physiological and environmental variability, which are dynamic across temporal scales ranging from seconds to years (Nathan *et al*. 2008). Some birds, for example, are known to migrate in response to changes in the intensity of sunshine and duration of daylight, which also cause physiological changes, such as the decrease in size of feeding related organs (Nebel 2010). The knowledge of how a specific contextual factor relates to different movement patterns is important for biodiversity conservation (Sutherland *et al*. 2013), wildlife management (Urbano *et al*. 2010) and animal epidemiology (Holden 2006). Considering these contextual factors when analysing movement can lead to inferences about the drivers of movement, contributing to a finer understanding and prediction of behaviour.

Contextualising movement in the analysis of human mobility is relatively easy, since participants can explain their motivations in travel surveys and tracking experiments. Data from such experiments represent a rich resource for contextualizing human movement (Thakuriah *et al*. 2020). However, the only method for studying animal movement decision-making and their responses to environmental conditions, is by analysing ancillary data which describe conditions at the location and time where the animal moves. In both the study of human and animal movement, the process of considering both movement and the conditions within which the movement occurred is termed Context-Aware Movement Analysis (CAMA) (Laube 2014).

Context has been described in many ways in the movement literature, but generally, it refers to factors that impact movement and therefore can help explain the reasoning behind it. However, terminology for context analysis differs widely and various frameworks have been proposed, that focus on either data or content, but not both. Additionally, CAMA and related research has been inconsistently labelled within and across different fields of movement research. As a consequence, it has been challenging to pull together a state of the science in CAMA. As ecology becomes more data-oriented (Cagnacci *et al*. 2010) and as methodological disciplines, such as GIScience, become increasingly interested in movement and spatial ecology (as demonstrated by this journal, the *International Journal of Geographical Information Science* – see for example many special issues on spatial ecology and movement analysis in the last few years, e.g Dodge *et al*. 2016, Long *et al*. 2018, Miller *et al*. 2020), we believe that there is a need to both review what CAMA means for ecology in methodological terms and to provide reliable definitions that will bridge the divide between the content-centric and data-centric frameworks.

In this review, we focus on the use of CAMA in movement ecology as one of the main research fields interested in contextualizing movement analysis. Our goal is to review the literature, summarize common themes, propose context definitions, and identify opportunities and challenges. The rest of the paper is structured as follows: first, we describe the methodology for our systematic review. We discuss the chosen criteria, identify results, and comment on individual trends. We then use these results to propose a new comprehensive definition of context and a general framework that merges three data-centric methodological frameworks with a content-centric framework from movement ecology. Finally, we identify several CAMA research gaps and challenges that can inspire further methodological research and lead to new interdisciplinary collaborations between GIScientists and ecologists.

2. Methodology for systematic review

We performed an electronic search in Scopus, Web of Science, Springer, IEEE, and ACM collections to identify the available literature related to context-aware movement analysis published between January 2000 and July 2020. We used one of the following terms: 'biological context', 'environmental context', 'geographic(al) context', 'geographic(al) embedding', 'influencing factors', 'modality context', 'motivation context', 'milieu context', 'covariates', 'context', 'context-aware(ness)', 'spatio-temporal context' or 'semantic geographic information' in combination with the term 'movement' and either the terms 'tracking', 'telemetry', 'GPS' or 'radio'. We refined our results by analysing the abstracts and discarding studies using handheld GPS devices or GPS coordinates of release and capture, because those data are usually not detailed enough to portray movement. In accordance with the publishing tradition in ecology, where journals are the main publication venue (See Section 5.2 of Demšar *et al*. 2021), papers published in conference proceedings were discarded and only journal articles were included.

We extracted the journal, year of publication, and publication type from each paper. We defined three publication types: 1) applied paper: studies that explore animal movement using contextual data and tracking data; 2) literature review: studies that review movement research literature and consider context-awareness; and 3) methodological paper: studies that develop a new method for performing context-aware movement analysis. In the next step, we extracted the terminology used to designate context, by categorising each paper according to how it called the contextual data. This resulted in five semantic groups, in which context was labelled using one of the following terms: 1) covariates; 2) ecological variables; 3) environmental context: this group includes expressions such as 'environmental factors', 'environmental features' and 'environmental variables'; 4) factors: this group includes expressions such as 'influencing factors', 'factors affecting' and 'proximal factors'; and 5) variable specific context: this group includes studies in which the contextual variable is referred by its specific name.

We also extracted from each paper the subject being studied, movement data collection method, method used to analyse contextual and movement data, contextual variables and their respective sources, temporal resolution of movement data, temporal resolution of contextual data, the total number of contextual variables used, the main goal of the study, the movement metric used for the analysis, and what interpolation method was applied to match movement data and contextual variable. Depending on how the authors displayed their results, we also classified the paper into papers integrating movement and context during analysis or papers summarizing movement by context. The first category includes papers with an exploratory approach: these integrate movement and contextual data during the analysis to then explore how they are related (exploratory approach).The second category is confirmatory: studies assume a priori that there is an effect and split movement data into groups defined by contextual variables, and then analyses each category separately.

Table 1 provides an overview of our categorisation. While it is not uncommon for studies to use multiple analysis methods, here we only note the main method used to analyse the relationship between contextual variables and movement. The movement metric is the measure used to match movement data and contextual data (for example, contextual data can be linked to points or to line segments).

Table 1. Criteria for categorisation of papers in the systematic review.

Categorisation criterion	Values
Publication type	Applied study Literature review Methodological study
Name for contextual variables (categories not exhausting, but as found In the papers)	'Covariates' 'Ecological variables' 'Environmental variables' 'Factors' Specific name for the variable
Subject of the paper	Taxon/species
Movement data type (categories not exhausting, but as found In the papers)	Acoustic telemetry ARGOS GPS telemetry Light geolocators Radar Radio (VHF) telemetry
Temporal resolution of movement data	< 1 minute ≥ 1 minute and < 1 hour ≥ 1 hour and < 1 day 1 day ≥ 1 day and < 1 week ≥ 1 week and < 2 weeks ≥ 2 weeks and < 1 month ≥ 1 month and < 1 year Irregular No information
Temporal resolution of contextual data	< 1 minute ≥ 1 minute and < 1 hour ≥ 1 hour and < 1 day 1 day ≥ 1 day and < 1 week ≥ 1 week and < 2 weeks ≥ 2 weeks and < 1 month ≥ 1 month and < 1 year Static Static (Appropriate)* No information
Analysis method (categories not exhausting, but as found In the papers)	ANOVA Descriptive statistics and tests Markov models Regression analysis Resource selection analysis Spatial analysis Visualisation
Goal of the study (categories not exhausting, but as found In the papers)	Corridors Foraging Home range configuration Home range use Life cycle analysis Methodological development Migration Prediction of behaviour Response to conditions Dominance analysis
Number of contextual variables	Min 1, max 10 (as found in the papers)
Name of contextual variables	Various possibilities (as found in the papers)
Source of contextual variables	As listed in the paper or not given
Movement indicator (categories not exhausting, but as found In the papers)	Activity rate Displacement Location point Home range Movement mode

(*Continued*)

Table 1. (Continued).

Categorisation criterion	Values
	Movement probability
	Potential Path Area (PPA)
	Speed
	Step length
	Stopover duration
	Tortuosity
	Trajectory
Temporal interpolation method to match movement and contextual data	Aggregation
(categories not exhausting, but as found	Average
In the papers)	ENV-DATA**
	Minimum
	Nearest-neighbour
	Percentage
	Range
	Unclear
How was context included	Integration during analysis
	Summarising movement by context

* Static (Appropriate) refers to the situation where context was represented by static contextual data and a static representation was compatible with the contextual variable at the given temporal scale, e.g. one land cover map for a study that lasted one week, or a topographic map for a study that lasted months.

**We are aware that ENV-DATA is a tool and not an interpolation method, however some studies state that the data was interpolated using ENV-DATA and do not specify the interpolation method applied.

3. Results

This section presents a meta-analysis and specific results. Further details are in Supplementary Information 1, which gives the list of all papers included in our systematic review and presents our categorisation of each paper as per Section 2.

3.1. Where were the papers published and what topics do they cover?

We found a total of 172 scientific papers (See Supplementary Information 1 for the full list of papers) published over a 20-years period (Jan 2000 – Jun 2020) with a five-fold increase in the number of published papers during the last decade (Figure 1). Most of the studies were applied (n = 155), eleven of them were methodological and five were literature reviews. They were published in 79 different academic journals, but more than a third of the studies (n = 60) were concentrated in the following seven journals: *the European Journal of Wildlife Research* (n = 15), *Movement Ecology* (n = 14), *Behavioral Ecology and Sociobiology* (n = 7), *Ecology* (n = 6), *International Journal of Geographical Information Science* (n = 6), *Landscape ecology* (n = 6) and *Mammal Research* (n = 6).

Tracking data were collected mostly with GPS telemetry (n = 86) and radio telemetry (n = 53), nine studies used the Argos satellite system, seven studies used acoustic telemetry, four studies used light geolocators and two used radars. Subjects were diverse, we broadly grouped them by movement domain (air, land or water) or by taxon when possible, which resulted in 26 categories (Figure 2). Almost 50% of papers studied birds (20.3%), cervids (17.4%), fish (8.7%), and the remaining 50% one of the other 25 different

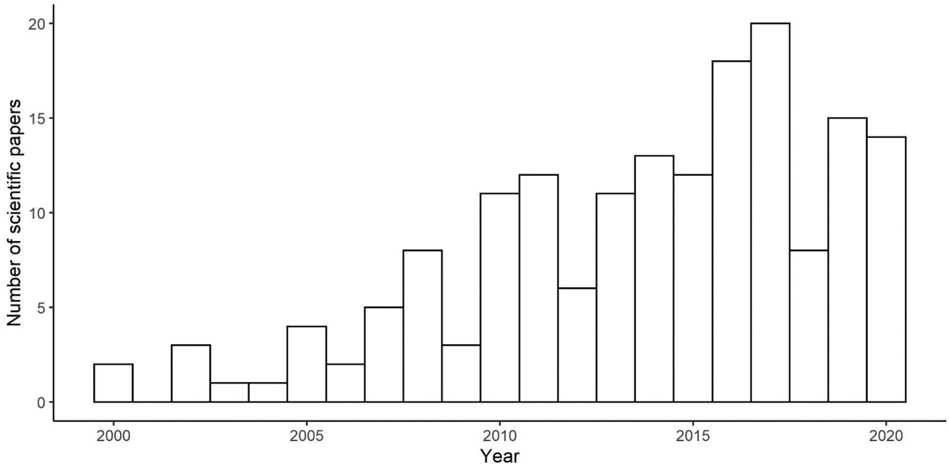

Figure 1. Context-aware movement studies published between Jan 2000 and June 2020. The search was performed in Scopus, Web of Science, Springer,IEEE and ACM.

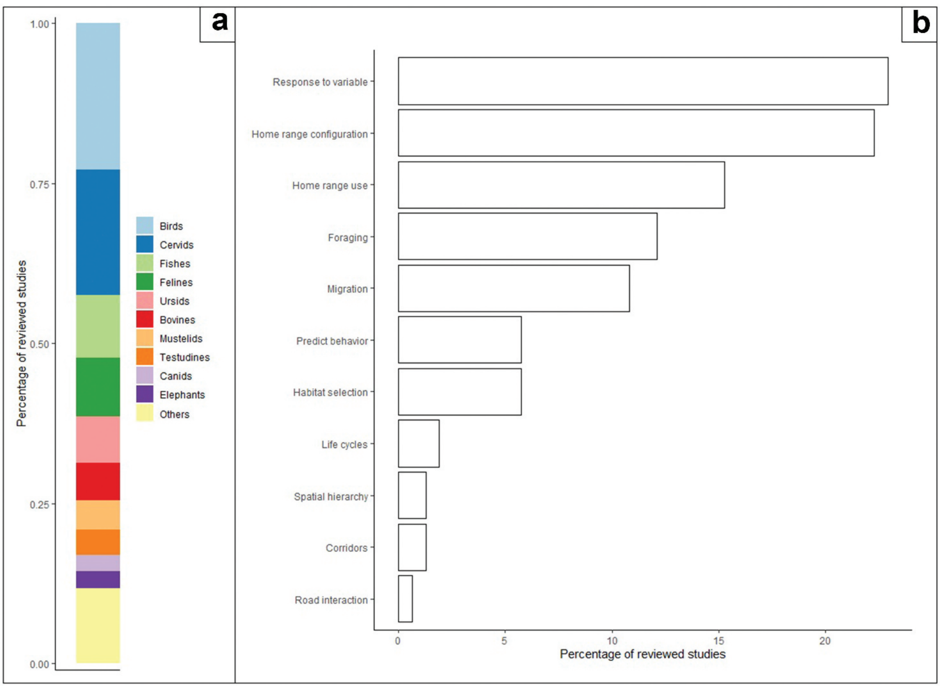

Figure 2. Distribution of studies by groups of subjects and by main goal of the research. A) Proportion of reviewed studies by subject group. The 'Others' group at the bottom of the graph includes species and groups for which there were less than four studies, such as mustelids, canids, elephants, swine, primates, snakes, and others. B) Percentage of reviewed studies by research goal.

groups of subjects (Figure 2(a)). More than 50% of the reviewed studies aimed to understand either the home range configuration, the response of the to a specific variable, or how the species is using their home range (Figure 2(b)).

3.2. Contextual variables and datasets

Most of the reviewed studies (n = 123) simultaneously considered more than one contextual variable, totalling 511 contextual variables of which 121 were unique. Figure 3 shows the frequency of the types of contextual variables and their distribution by source.

Land cover was the most used contextual variable, and it was typically obtained via remote sensing techniques, field campaigns, and maps. In this manuscript, the term map refers to the graphical representation of natural or anthropogenic features, which were not processed by the authors but acquired as secondary data. The variable land cover was sourced either in the form of maps (e.g. Sevila *et al*., 2014), as three dimensional LiDAR point clouds (e.g. MacNearney *et al*. 2016) or as NDVI (Normalized Difference Vegetation Index) images (e.g. Cornélis *et al*. 2011), which were often used as a proxy for habitat type, structure, and quality (e.g Bevanda *et al*. 2014, Whisson *et al*. 2015, Jansen *et al*. 2016). Interestingly, despite the multi temporality of movement data and regardless of the duration of the study, most of the reviewed studies use a single reference date for land cover data. That means that they assumed that there were no changes in land cover during the period during which tracking data were collected (e.g. Poole and Heard 2003, Martin *et al*. 2018). Only a few recent studies incorporated the idea of a dynamically changing landscape into the analysis by using land cover data collected at different times during the study period. This was common when land cover was inferred from NDVI (e.g. Cornélis *et al*. 2011; Avgar *et al*., 2013; Chynoweth *et al*., 2015, Brum-Bastos *et al*. 2020).

Seasonality was the second most common contextual attribute, and it was obtained either by field campaign or by performing a literature review for the study area. Seasons were used as a proxy for cyclical anthropogenic disturbances, vegetation abundance and food availability (e.g. Noyce and Garshelis 2011, Ordiz *et al*. 2017, Laver and Alexander 2018). Given this, we note that they could potentially be more accurately inferred from other sources than the literature, such as remote sensing images and maps.

Distance to a feature was another popular contextual variable. This was normally generated by either applying proximity analysis to maps, by conducting a field campaign, or from remote sensing data. Distances to features were used to determine the distance to roads, water bodies, edges of crops and human settlements (e.g. Keuling *et al*. 2008, Cornélis *et al*. 2011, Marshal *et al*. 2011, Martin *et al*. 2013). Distance was typically measured as a continuous variable, but also sometimes in a binary manner by using a buffer and determining if the feature was within the buffer distance or not. Distances to

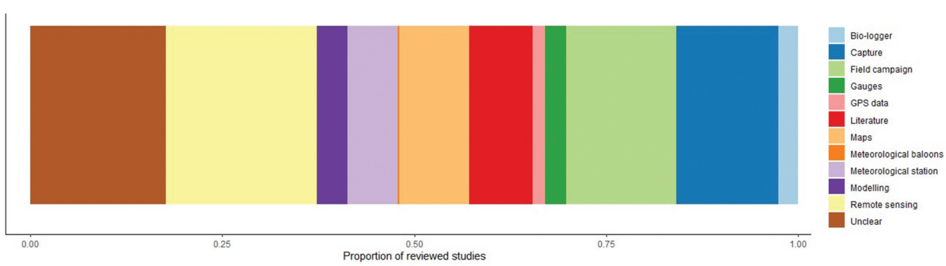

Figure 3. Sources of contextual data used in the reviewed studies.

features were commonly used to evaluate whether the subject was attracted or repelled by particular structures in the landscape, and also to test whether behaviour changed with the addition of a new structure, often a new road.

Temperature was obtained from meteorological station data, measured by sensors on bio-logging tags, observed in field campaigns, or through remote sensing and modelling. Temperature retrieved by bio-loggers was predominately a measurement of the subject's body temperature (e.g. Anders *et al*. 2017, Parlin *et al*. 2018), while field campaigns, modelling, meteorological stations and remote sensing were used to record the temperature of the environment (e.g. Coyne and Godley 2005, Homburger *et al*. 2015). The use of temperature from meteorological stations was often restricted to one site (e.g. Roe and Georges 2008, Gibson and Koenig 2012, Tini *et al*. 2017), which is problematic when working with large study areas because of how much temperature can vary across space. Similarly, precipitation was mostly acquired from meteorological stations and rain gauges (e.g. Bennetts and Kitchens 2000, Pigeon *et al*. 2016, Siers *et al*. 2016, Parlin *et al*. 2018), and was often restricted to one site, which again poses a problem for large study areas.

Human presence variables were either related to recreational activities (e.g. hunting, hiking) or to landscape changes caused by anthropogenic disturbance (e.g. MacNearney *et al*. 2016, Ordiz *et al*. 2017). Human disturbance was mostly obtained via field campaigns by measuring the animals reactions to the presence of the researchers (e.g. Goldenberg *et al*. 2017) or by extracting human-made structures from maps (e.g. Martin *et al*. 2013). The use of remote sensing data and modelling was not common for this variable, but we found a few studies in which these sources were used because of the absence of maps or other appropriate method. In some cases, this variable was retrieved by concurrent tracking of humans and wildlife (Olson *et al*. 2018, Marion *et al*. 2021).

The majority of studies used remote sensing data from one particular moment in time, i.e. they assume there were no changes in context during the study period (e.g. Poole and Heard 2003, Martin *et al*. 2018). However, times series data have been shown to be more accurate in representing and monitoring ecosystems (Lopes *et al*. 2020). Yet, only a few recent studies incorporated the idea of context changing dynamically into the analysis. This was typically done by using multiple data inputs to represent land cover at different timestamps along the study period (e.g. Cornélis *et al*. 2011; Avgar *et al*., 2013; Chynoweth *et al*., 2015). Moving beyond the static representation of context toward a dynamic representation can help detecting changes in context that influences movement and triggers specific behaviours (Neumann *et al*. 2015). Dynamic context is critical, for example, for the study of seasonality of movement in response to the level of landscape greenness (Bischof *et al*. 2012, Shariatinajafabadi *et al*. 2014). Meteorological variables, such as wind (Safi *et al*. 2013), are commonly represented as dynamic context by using hourly measurements from meteorological stations and gauges. The dynamic aspect of the weather is an intuitive concept for us because humans are directly influenced by it. However, the same does not apply for land cover, vegetation phenology and other variables that do not have large daily variations but vary across days, months and years. It is therefore important to evaluate whether the contextual variable has a large variation at temporal scales comparable to the study period and then establish if it should be represented as static or dynamic (which also depends on data availability).

Approximately 20% of the studies did not name the source of the data representing the contextual variable. In addition, most studies did not include a complete description of the contextual data with their respective characteristics and limitations, which is concerning from a reproducibility and replicability standpoint (Nüst *et al.* 2018). While ecology is at the forefront of open data use (Roche *et al.* 2015), ensuring that data sources are reported will foster data transparency and help to increase the speed of new developments in the field (McNutt 2014).

3.3. Temporal mismatch between movement data and context

The comparison between the temporal resolution of movement data and the temporal resolution of contextual data shows that approximately a third of the reviewed studies did not include information on the temporal resolution of either data types (Figure 4). Where we have this information, we found that more than 60% of the movement data were collected at sub-daily resolution, while approximately 80% of the contextual data were collected at a coarser temporal granularity. We also noticed that contextual data are often represented as static (Figure 4), however only about more than half of the time the static representation was appropriate (which we indicate by Static (Appropriate) in Figure 4). This category was assigned to studies where temporal resolution of contextual data could represent the changes during the timespan of the research. For example, using a single data set of vegetation coverage to contextualise movement can be

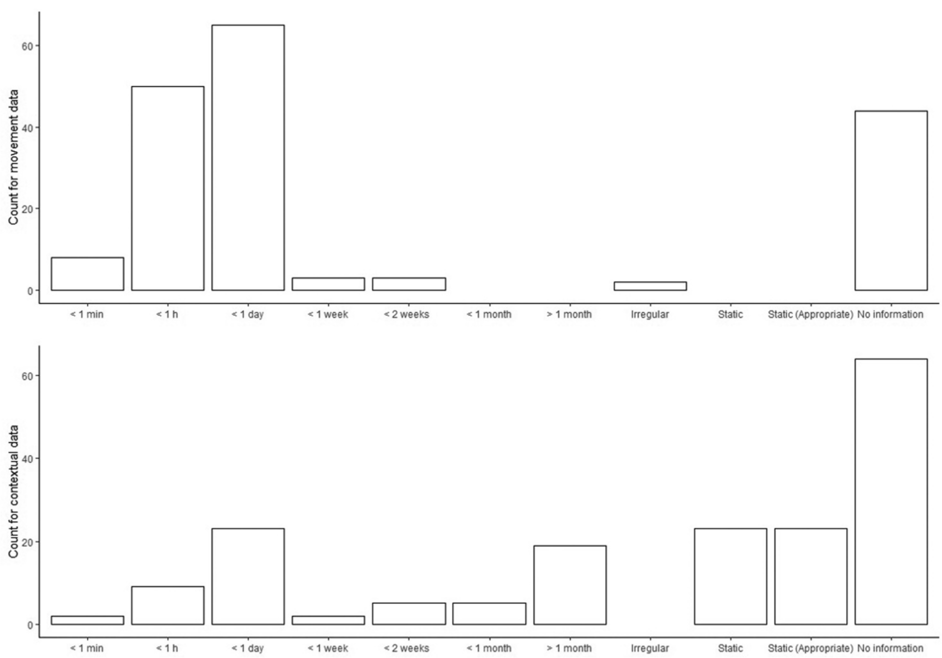

Figure 4. Comparison of the temporal resolution of movement data and the temporal resolution of contextual data. The labels on the x-axis refer to intervals between the value indicated in the label and the previous one, for example, '< 1 week' refers to temporal resolutions finer than a week and coarser or equal to one day. Static (Appropriate) refers to cases where the static representation of contextual information was appropriately used, i.e. the temporal resolution of movement data was suitable for changes during the timespan of the research.

appropriate for a study with a duration of a few weeks, but would likely not be appropriate for a study lasting a year or more because landscape changes occur at a shorter temporal period than one year. Using a static map could therefore misrepresent the actual conditions.

This not only highlights the known temporal mismatch between movement data and contextual data, but also highlights the need for new data fusion methods, which are capable to joining data from several sources to create environmental data at the same temporal resolution as movement data. This is typically done through interpolation in space and time and the results may vary depending on interpolation method used – this is yet another gap that we identified. Approximately 77% of the studies do not provide any information on the interpolation method and there is no information on how this gap between contextual and movement data was dealt with. The gap between contextual and movement data is a current relevant issue in the field (Dodge *et al*. 2013).

3.4. Analysis methods

The reviewed papers showed a low variety of methods to perform CAMA. Around 50% of the studies used regression models, 30% used descriptive statistics, 9% used ANOVA, 6% used spatial analysis, 3% used visualization and 2% used Markov chains.

Most papers employed traditional (and, of note, non-spatial) statistics, with linear regression the most used method. The use of descriptive statistics and tests was the second most popular analysis method, particularly for grouping movement data by context and testing the significance of differences between groups. Different types of analysis of variance, such as ANOVA and MANOVA, were used by almost ten percent of the studies to identify differences between movement patterns happening under distinct contexts.

Only 6% of the reviewed papers employed a spatial method to analyse movement within context, which was unexpected, considering that space and time are embedded in the concept of movement. This may be due to methodological challenges of including space and time into more traditional statistical methods and the lack of both tools and skills to use the tools – this has been identified as a problem in ecology (Pettorelli *et al*. 2014), but is now being addressed through initiatives that train ecologists in the use of spatial data and remote sensing, such as the AniMove.org summer school.

The reviewed studies used movement metrics such as activity rate, displacement, location, home range, movement mode, movement probability, potential path area, speed, step length, stopover duration and tortuosity. Using the size and shape of home range as the movement metric was the choice in approximately 40% of the reviewed papers, which reflects the continued popularity of home range analyses in ecology in general (Laver and Kelly 2008). In terms of how the studies used contextual data, less than 36% of the reviewed papers integrated movement data and contextual data as opposed to the 75% summarizing movement by types of context.

4. Use of context in movement ecology – context definition, a general framework and open challenges

We found a wide variety of definitions and terminology for context in our systematic review, but less variety in methodological and analysis terms. In this section we propose to unify the terminology and bring together frameworks for contextual analysis from GIScience and movement ecology to support wider understanding of similarities across movement studies. We also identify research gaps and open challenges that neither movement ecology nor GIScience have yet found a solution for, in spite of a long tradition of using contextual information to investigate movement.

4.1. A definition and taxonomy for context analysis in movement ecology

One of the goals of our review was to try to identify a common definition for context, not only as proposed by methodological studies, but also as used by the ecological community. Our conclusion is that there is no clear consensus on the definition – in particular, GIScience and computer science frameworks skew towards a data-centric definition (Dodge *et al*. 2008, Purves *et al*. 2014, Sharif and Alesheikh 2017), while the common movement ecology framework proposes a wider understanding of context as factors operating at internal and external levels (Nathan *et al*. 2008). We propose to merge these definitions in a more general one that is at an intersection of both perspectives. We therefore define context as *one or more variables that characterize the external or internal conditions that led to a movement decision or caused specific movement behaviour. These variables can be dynamic or static, depending on the temporal scale at which movement is being represented and on the temporal frequency with which the phenomenon represented by the contextual variable changes in space-time.*

Our second goal is to provide a specific taxonomy for context analysis which will include both data-centric and content-centric perspectives and bridge the gap between CAMA in movement ecology and human mobility (Miller *et al*. 2019, Demšar *et al*. 2021). For this, we merge three data-centric taxonomies definitions from GIScience (Dodge *et al*. 2008, Purves *et al*. 2014, Sharif and Alesheikh 2017) with the content-centric taxonomy of movement ecology (Nathan *et al*. 2008) and define a new framework for context that spans all these taxonomies (Figure 5). The categories proposed by Nathan *et al*. (2008), Dodge *et al*. (2008) and Purves *et al*. (2014) are broad and for that reason have limited contribution toward data sourcing and methods development for CAMA. Sharif and Alesheikh (2017) present a refined categorization of context; however, compared to the results of our review, their classification is insufficiently comprehensive to reflect the complex nature of context in animal movement studies. In addition, Sharif and Alesheikh (2017) use the term 'movement context' to refer to quantitative parameters (e.g. speed and acceleration) that are commonly used to characterize movement patterns, while we use movement context to refer to other factors/variables that influence the movement process . In this, we follow Dodge *et al*. (2008), which lists variables that can be calculated from movement data (e.g. speed, acceleration, turning angle, direction) as parameters of movement. While movement parameters can help understanding behaviour, they do not describe context. Instead, they describe the actual movement and not the conditions that triggered or embedded movement. This is also in agreement with older scientific traditions. In kinematics (the origin of movement analysis), for example, movement is mathematically described and defined in terms of displacement, distance, velocity, acceleration, speed, and time.

Similarly, time is the basic dimension that underlies the dynamic of contextual variables as well as movement. As such, time is not contextual but inherent to both context and

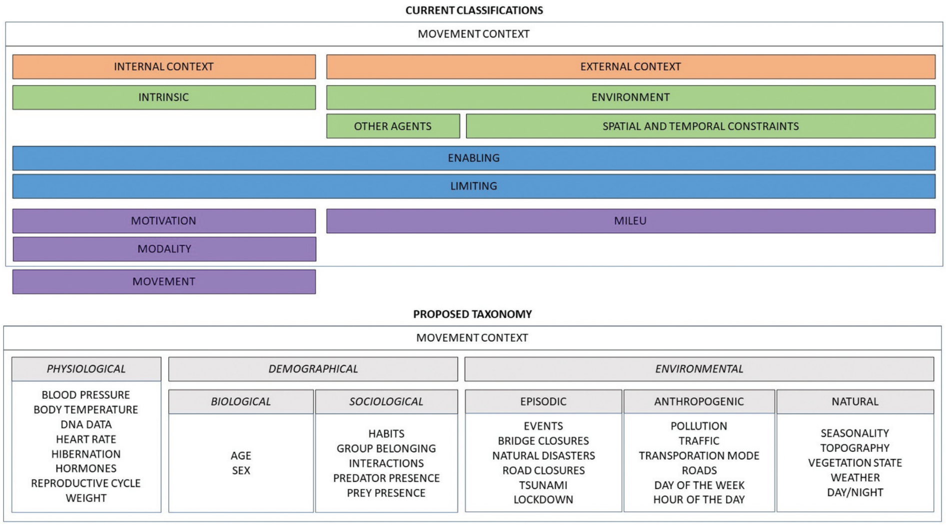

Figure 5. A new taxonomy for movement context with non-exhaustive examples of variables and how it relates to the classifications proposed by Nathan *et al*. (2008) (in orange), Dodge *et al*. (2008) (in green), Purves *et al*. (2014) (in blue) and Sharif and Elsheikh (2017a) (in purple). The movement category by Sharif and Alesheikh (2017) (in purple) is outside the movement context frame because, in agreement with Dodge *et al*. (2008), quantitative attributes (e.g. speed, acceleration), classified as 'movement context' by Sharif and Alesheikh (2017a), are considered movement parameters.

movement behaviour. However, some human-defined temporal concepts, such as working day/weekend and seasonality, can play a contextual role and explain changes in the movement patterns of wildlife (e.g. Li *et al*. 2020, Marion *et al*. 2021). For this reason we do not include time in the taxonomy but do list temporal concepts under the appropriate categories.

In Figure 5, at the top in orange, we have the division by Nathan *et al*. (2008) into internal and external context. To this, we map in green the division by Dodge *et al*. (2008), where their intrinsic factors match the internal context of the movement ecology framework, and their other agents and spatio-temporal constraints are mapped into environmental factors which correspond to Nathan's external context. The next two rows show the match between the other two frameworks (Purves *et al*. 2014, Sharif and Alesheikh 2017), while we propose a more detailed subdivision of context (the second box at the bottom in Figure 5), into physiological, demographical and environmental factors. Specifically, we classify *physiological* and *demographical-biological* context as internal factors, and *demographical-sociological* and *environmental* as external factors. In the following we define and explain all categories in the proposed taxonomy:

- **Physiological context**: these are variables inherent to the organism's regular functioning that can trigger a specific movement pattern. Unlike in human mobility, where participants can be interviewed about their motives, motivation for animal movement cannot be obtained directly – therefore we measure intrinsic characteristics, such as physiological variables and explore if and how they relate to movement decisions. For example, birds regulate temperature and circadian rhythms during migration, but not otherwise (Parr *et al*. 2019) and hormones regulate bird decision-making during migration (Eikenaar *et al*. 2020) and affect their stopover decisions (Goymann *et al*. 2017).

- **Demographical context**: these are variables inherent to the organism that facilitate a direct comparison to meaningful groupings of the population and might explain divergences in movement patterns among those groups. We identify two different sub-types of demographical variables:
  - *Biological context*: variables inherent to the organisms that do not depend on any other individual, for example age and sex (Widmann *et al*. 2015).
  - *Sociological context*: variables that describe the organism's relation and/or interaction to others or belonging to a specific group. For example, movement is affected by group belonging (Bode *et al*. 2015), by presence of predators (Fortin *et al*. 2005, Jarnemo and Wikenros 2014) and by the leader-follower relationship which has an effect on length of migration and therefore potential survival (Flack *et al*. 2018)
- **Environmental context**: this includes variables inherent to the movement's surrounding location, i.e. inherent to the place and/or time where movement is happening. The term surrounding is purposefully vague because the distance threshold to which environment influences movement depends on each case. For example, eagles can see a rabbit clearly as far as three kilometres (Grambo 1999) while rhinos cannot distinguish between a human and a tree at five meters distance (Matson 2012). Thus, the surrounding threshold for an environmental context that is visually perceived would be different between these two species. We further identify three different sub-types of environmental variables:
  - *Natural context*: variables inherent to the movement's surrounding location that describe the landscape and are not man-made, such as wind (Safi *et al*. 2013), temperature, vegetation (Pettorelli *et al*. 2005) and Earth's magnetic field (Benitez-Paez *et al*. 2021).
  - *Episodic context*: variables inherent to the movement's surrounding location that are irregular or infrequent at the temporal scale at which animal movement is being analysed, such as tsunamis, floods, earthquakes (Gething and Tatem 2011), road closures (Cole *et al*. 1997) and lockdowns (Rutz *et al*. 2020).
  - *Anthropogenic context*: variables inherent to the movement's surrounding location that are created or defined by human presence, such as pollution, traffic, hunting (Dowd *et al*. 2014), crop cycles (Monadjem *et al*. 2011) and variation in activities by day of the week (Marion *et al*. 2021).

4.2. Research gaps and open challenges

We identified four main research gaps that pose methodological challenges for contextual analysis in movement ecology.

Challenge 1: How to match (integrate) contextual data and movement data across space and time?

The mismatch in spatial and temporal resolution between movement data and contextual data is a major barrier to performing CAMA (Dodge *et al*. 2013, Demšar *et al*. 2015 and see Section 3.3.). Further, there are currently no recommendations or best practice guidelines on how to deal with spatio-temporal incompatibilities between movement and contextual data. Movement data and contextual data are collected for different purposes and by diverse sensors, which results in structural and spatio-temporal mismatches between these data types. Movement data are collected pointwise with metric accuracy and at temporal resolution varying from seconds to days. Contextual data are collected in diverse forms, from raster imagery to point and areal data, with varying accuracies and at temporal resolution either ranging from seconds to minutes to days or sometimes without temporal information (static data). For ecology, the main question in this challenge is the integration of trajectories with environmental raster, point, or areal data. This is in contrast with disciplines tracking human movement, such as human mobility and transportation science, where contextual data are typically other objects (such as activity locations or places of interest and road networks, e.g. Yan *et al*. 2013, dos Mello *et al*. 2019).

The main source of contextual data for ecology are data from satellite remote sensing or other field data (Pettorelli *et al*. 2014, De Groeve *et al*. 2016). A typical example is the use of NDVI data from the MODIS sensor (Bischof *et al*. 2012, Shariatinajafabadi *et al*. 2014). It is not uncommon to find studies in which trajectories are integrated with MODIS NDVI data by interpolating multiple pixels to calculate the value at the exact point where movement data were collected, leading to a classical MAUP (modifiable areal unit) zoning problem (Jelinski and Wu 1996). MODIS NDVI data have a 250 m spatial resolution, which means that the value in each pixel is the average of a 62500 m^2 area. It is well known in remote sensing, that spatial interpolation algorithms cannot create more resolute data than the original data (Singh and Prasad 2014). The best practice in these cases would be the use of the value of the pixel in which the movement data point falls within, as any other interpolation technique would be trying to create more information than the original data set contains (Neumann *et al*. 2015), especially when using coarse spatial resolution images.

In terms of temporal interpolation, wind and temperature are examples of contextual variables with high temporal variability in values, yet they are often processed using the same interpolation methods as variables with lower temporal variability (e.g. land cover). That is, interpolation methods are chosen without considering the characteristics and scale of each contextual variable. In order to better deal with the temporal incompatibilities in CAMA there is a need to compare current temporal interpolation methods and their implications, and also develop new methods that take into account temporal profiles and characteristics of contextual variables in a way more suited to natural progression of contextual phenomena, as well as consider accuracy and uncertainty in both contextual and movement data.

4.2.1. Challenge 2: How can CAMA methods properly account for the temporal dynamics of contextual data (e.g. contextual factors that change over time)?

The representation of context should, whenever possible, match the nature of contextual phenomenon. In other words, dynamic context should be represented by dynamic contextual data. We found that studies in our review are often restricted to a single source of contextual data, which is commonly a pre-processed contextual variable with either no temporal variability or else temporal variability at an often coarse temporal scale (Urbano and Cagnacci 2014, Bühne and Pettorelli 2017). The use of multi-source data, particularly satellite data, to represent contextual variables can improve our capacity to capture the dynamics of the phenomenon that is providing context and its changes at a higher level of both spatial and temporal detail. For example, recent studies employ a multi-source analysis, where NDVI products from several satellite sources and across spatio-temporal scales are used (Berman *et al*. 2019, Brum-Bastos *et al*. 2020). Multi-source data can also enable analysis for which contextual data are required at higher temporal resolution and level of detail than what is readily available. The main advantage of this approach is that it can be applied to any contextual variable. It is common in movement research to simultaneously need contextual data with both a high temporal and spatial resolution, particularly for studies in heterogeneous environments. A multi-source approach could help provide these data. Multi-source methods are well developed in other research areas (e.g. environmental monitoring, battlefield surveillance, automatic target detection (Zhang 2010)) but currently remain limited in their application to movement modelling (but see Brum-Bastos *et al*. 2020).

4.3. Challenge 3: How do we represent contextualized data?

Representing movement data is a challenge given its multidimensional nature (X, Y, Z and time) but it becomes even more complex when incorporating context. Commonly, movement data are represented as trajectories, that is, time series of coordinate points (Laube 2014). Each trajectory point is then often annotated with several context variables which represent static or dynamic properties of the respective point. The result is a highly dimensional time series. Alternatively, context can be used for annotation in a so-called semantic trajectory model (Yan *et al*. 2013), which again results in a time series of highly-dimensional points, with the difference that the semantic points have first been identified as significant places or movement segments from the original raw trajectory (Siła-Nowicka *et al*. 2016).

One of the new approaches to incorporate context directly is the use of a sequence-based representation of movement (Dodge *et al*. 2012, De Groeve *et al*. 2016, Brum-Bastos *et al*. 2021). Sequence-based representation enables the representation of all contextual dimensions in relation to time, but only keeps the locational component in its temporal and semantic sense, i.e. geographic coordinates are disregarded in this representation but the temporal sequence of points they represent is still preserved and context is added in form of a categorical sequence of different contextual values over time. Using sequence-based representation opens the possibility of analysis methods not yet widespread for movement data, for example, the basic sequence analysis from bioinformatics to represent one contextual variable (De Groeve *et al*. 2016), its multi-channel version to include several contextual variables (Brum-Bastos *et al*. 2018) and a combination with data-driven methods such as eigen decomposition (Brum-Bastos *et al*. 2021). Sequence analysis methods provide new possibilities in understanding responses of moving individuals to environmental context and can do so for many contextual variables simultaneously.

4.3.1. Challenge 4: How do we extract meaningful information from contextualized data

One of the unexpected results of our review was the limited variety of methods used for analysis of contextualised data: the vast majority of studies used traditional confirmatory statistical methods (regression, ANOVA, descriptors), while only a few used spatial analysis. Given the spatial nature of wildlife movement data, we were expecting to see more exploratory methods, data mining, and/or machine learning approaches, but this was not the case. This is surprising compared to human mobility. There, a typical analysis flow would be to create semantic trajectories (Yan *et al*. 2013) and then apply data mining or machine learning to identify clusters or groups of objects moving similarly and responding to the environment in a similar way (Pelekis and Theodoridis 2014, Sila-Nowicka 2016). Further, human mobility is also capitalising on the newly popular methods in machine learning (ML) and artificial intelligence (AI). While ML/AI methods are not new and have been used in the movement context for decades (see for example Black 1995), there is a newly-found popularity of ML/AI methods for contextualisation of human movement (e.g. Fan *et al*. 2018, Wang *et al*. 2018). While ML/AI methods have been recently used in ecology, their use is primary in classical applications, for example image classification of camera trap images, (Norouzzadeh *et al*. 2018).

There are two possible explanations for this discrepancy. One potential cause for the lack of ML/AI methods in movement ecology is that ecology has a strong tradition of confirmatory statistical analysis, and this is reflected in the results of our review. Animal movement data are still difficult and costly to obtain and are typically collected as part of localized studies (although this has started to change in the last year or two with the new satellite tracking system ICARUS, depositing data into online repositories such as Movebank.org or similar initiatives). For such data, traditional statistical analyses are sufficient as they provide an inference toolset that allows interpretation of results in a well-established manner and allow for prediction. For example, regression analysis not only enables the discovery of the direction, magnitude, and significance of the effects of a variable on the subject’s movement, but also allows to predict how the movement would be affected by projected scenarios, which becomes very useful at a moment where climate and environmental change are driving many changes in animal behaviour. In contrast to this, ML/AI methods require a large amount of data to be trained and produce results that are often difficult to interpret and replicate any inherent bias in the data. As we cannot find out from animals what their motivation for movement is, it is therefore difficult to find sufficient ‘ground truth’ information that would feed into the ML/AI methods and ensure that the trained methods produce biologically feasible results. The second potential cause is that there may be a lack of awareness in ecological community about these methods (Demšar *et al*. 2021). This can be addressed either through methodological training or through interdisciplinary collaboration with data scientists and methodological researchers (Miller *et al*. 2019).

5. Conclusion

In this paper we performed a systematic review of the use of CAMA in movement ecology, one of the principal disciplines interested in contextualized movement analysis. We identified patterns in data and methodological use and proposed a unified terminology and definition of context in movement analysis studies by merging frameworks for contextual analysis. We have also identified the four main challenges for the future research agenda of CAMA.

We found that most of the reviewed articles did not provide complete information about contextual data (such as sources, formatting, specifications, and pre-processing) nor information on whether and how the spatio-temporal differences between movement data and contextual data were addressed. These are critical issues because they limit the reproducibility and replicability of movement research, particularly when it comes to matching the different spatio-temporal scales of movement data and contextual data (Konkol *et al*. 2019). As scientists, we must start addressing the lack of clarity regarding contextual data by stating sources and detailing the characteristics of the variables being used in our studies, and as peer-reviewers, we should reinforce the need for these details during the peer-review process.

The use of static data to represent dynamic contextual variables was another issue revealed by this literature review, particularly in studies that lasted a year or more. We found that land cover, for example, was predominantly represented by a single map or satellite image, which is problematic in many situations as the land cover map is a snapshot of the landscape at a particular time. In movement analysis, using static data to represent a dynamic environment leads to potentially new sources of errors as certain conditions may be incorrectly associated with movement patterns. This not only highlights the known mismatch between movement data and contextual data, but also reinforces the need for new multi-source data-fusion and interpolation methods, which will be able to create representative data at a sufficient spatial and temporal resolution. The development of new data fusion tools, (e.g. Dodge *et al*. 2013, Benitez-Paez *et al*. 2021) are beginning to provide solutions to this problem.

The reviewed papers show that most of the studies employ traditional (non-spatial) statistical methods and that spatial analysis has not been used as frequently. One of the reasons for this may be the complexity of applying spatial analyses to data with three or more dimensions. Further integration of the GIScience, remote sensing, human mobility, transportation, computer science and the movement ecology communities (e.g. Miller *et al*. 2019, Demšar *et al*. 2021), will support the adaptation and development methods able to efficiently handle space, time, and context.

Authors' contributions

VBB conceived the original idea, performed most of the literature review, and drafted the original manuscript. ML performed parts of the literature review. JL provided theoretical support for designing the literature review, conceptual discussions, and manuscript writing. TN provided theoretical support for designing the literature review, conceptual discussions, and manuscript writing. UD also drafted the original manuscript, provided theoretical support for designing the literature review, conceptual discussions, and manuscript writing. All authors contributed to critically revising the manuscript.

Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

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