Discovering new paths: Perspectives on causal discovery algorithms in ecology

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1 Abstract

Understanding the relationships between organisms and their environment is crucial for the conservation of species and ecosystems all over the world. In ecology, relationships between organisms and their environment are typically obtained from correlation-based analyses of observational data. However, understanding ecological processes and developing strategies to maintain them requires knowledge on causation rather than correlation. Since causality between organisms and their environment is difficult to study using observational data, ecologists may need advanced computational techniques to identify causal relationships. In particular, the field of causal discovery offers a smorgasbord of algorithms to establish causal relationships from observational data. Nonetheless, causal discovery algorithms have not yet been widely adopted in ecology. In this review, we (1) introduce the concepts of causality and causal discovery algorithms, (2) review the use of causal discovery algorithms in ecology, and (3) present a perspective on the use of causal discovery algorithms and the interpretation of causality in ecology, illustrated by the field of animal movement research.

So far, ecological studies have used causal discovery algorithms to establish causal relationships between organisms and meteorological factors, and to identify causal interactions between species. The most popular causal discovery algorithm in ecology is convergent cross mapping, which requires time series data. Ecological studies often study causal links to a single response variable of interest, whereas fewer studies consider causal links between more variables and create a causal network. Notably, ecological interpretation of causal links can be hampered by changes in the strength and effect (positive or negative) of the causal relationship over time or differences between observations.

To improve the interpretation of causal links in ecology, we identify three concepts that should be considered in ecological causality research: First, we argue for a network-based approach in which causal links between multiple variables are considered, because this could identify variables that modulate causal relationships between other variables. Second, we stress that causes may differ between time scales. Third, individual heterogeneity may hamper the interpretation of causal relationships. Overall, broader use of causal discovery algorithms in ecology can increase our understanding of the relationships between organisms and their environment, which could in turn help to conserve ecosystems.

2 Layperson's summary

As global biodiversity is declining, it is important to understand how organisms and their environment affect each other. Ecology studies the relationships between organisms, such as animals and plants, and their environment. The environment of an organism includes other organisms, but also non-living factors, such as rainfall or sunlight. For example, ecologists could ask whether plant growth increases or decreases when there is more rainfall. To study this, ecologists measure both the amount of rainfall and the amount of plant growth for a certain period of time. If the amount of plant growth always increases with the amount of rainfall, or the amount of plant growth always decreases with the amount of rainfall, there is a correlation between plant growth and rainfall.

Importantly, a correlation between plant growth and rainfall does not mean that plant growth increases *because* there is more rain, or rainfall increases because there is more plant growth. Indeed, there could be a third factor that causes both rainfall and plant growth to increase. Therefore, ecologists mainly report correlations between factors, instead of claiming that one factor causes the other. However, knowing which factors cause others to change is important to understand the functioning of an ecosystem, and to develop methods to protect endangered species.

Recently, computer methods have been developed that can tell whether one factor is a cause of another factor, based on measurements of the two factors. These methods are called causal discovery algorithms. Notably, causal discovery algorithms are not yet widely used in ecology. In this article, we aim to show how causal discovery algorithms can be useful in ecology, and what the advantages and disadvantages are. To that end, we first explain the concepts of correlation, causality and causal discovery algorithms. Next, we review how causal discovery algorithms have been used in ecology so far. Third, we discuss how the results of a causal discovery algorithm can be understood in their ecological context. Therefore, we take the field of animal movement research as an example.

Causal discovery algorithms in ecology are mainly used to understand how weather conditions affect living organisms and how living organisms interact with each other. Notably, ecological studies mostly look at causal relationships between two factors. However, ecosystems consist of many living and non-living factors. We argue that ecological studies should consider causal relationships between many different factors, to get a more complete image of the ecosystem. Moreover, we stress that ecologists should take into account the timescale of a causal effect. For example, the cause of daily movement of an animal may be different than the cause of annual migration. Finally, the causes of movement may differ between animals. Therefore, it is important to distinguish between causes of movement of an individual and causes of movement of a group. Overall, causal discovery algorithms are a promising new tool to understand causal relationships between organisms and their environment. This could help to develop methods to protect species and the ecosystems they live in.

3 Introduction

All life on Earth is shaped by the environment it lives in, and in turn affects its environment. Since ecosystems all over the world are facing biodiversity loss, it is important to understand the interactions between organisms and their environment [1]. In ecology, relationships between variables in an ecosystem are often studied by measuring correlations between variables in observational data, such as weather conditions, resource availability and animal behaviour [2]. Additionally, mechanistic models can be used to describe ecological phenomena based on assumptions or hypotheses about the interactions between organisms and their environment [3][4][5].

Notwithstanding the insights obtained from correlation-based analyses of observational data as well as mechanistic models, these methods do not provide insight into the causal relationships underlying ecological processes. Nevertheless, causal terminology such as 'drive', 'affect', or 'influence' is frequently used to describe a link between two correlated variables, implying a causal relationship without a theoretical underpinning [6]. Furthermore, modeling efforts may prioritize prediction of a response variable over identifying causation. Importantly, the best predictive model is not necessarily the model that describes the causal network underlying an effect [7]. Overlooking this could lead to claims of causation with a lack of theoretical foundations. Therefore, novel methods are needed to establish causal relationships in ecology.

With the rise of big data analysis in the life sciences, the number of computational techniques available to biologists has expanded [8]. In particular, causal discovery algorithms have been developed to establish causal relationships purely based on observational data [9][10]. Indeed, this would enable ecologists to identify not only correlation but also causation from observational data, without the need for controlled experiments. Although causal discovery algorithms are extensively used in molecular biology, their applications in ecology have remained limited so far [11][12].

In this review, we aim to show the potential of causal discovery algorithms for ecology. To that end, we first provide a brief introduction to causal discovery. Second, we review the use of causal discovery algorithms in ecology so far. In the last part of this review, we present a perspective on the wider use of causal discovery algorithms in ecology. Therefore, we take a case of a field where causal discovery algorithms, to our knowledge, have not been used yet, but could be of great benefit: animal movement. Using animal movement as an example, we highlight three concepts to aid the interpretations of causal relationships in ecology.

4 Causality and causal discovery

The study of biology, as many sciences, is filled with associations between variables that follow from observational studies. Plant growth and daylight, heart rate and physical activity, humidity and bacterial growth might lead to neat diagonal lines when plotted against each other. Yet, finding a correlation between two variables does not answer any question other than whether the two variables are associated, while ever so often, the question of interest is a different one: Does variable A cause a change in variable B? [6]

Traditionally, causal questions in biology are studied using controlled experiments [13]. If a change in B occurs in the presence of a change in A, but not in the absence of a change in A, and all other factors are the same, then a change in A may be identified as a cause of a change in B [14]. Importantly, a controlled experiment adjusts for the possibility that A does not cause B, but both A and B are caused by a confounding variable C. Although setting up a controlled experiment can be feasible in molecular biology, relationships between organisms and their environment are difficult to simulate in a laboratory. Therefore, ecological research typically involves obtaining correlations between variables from observational data, and the possibility of confounding cannot be ruled out [6].

In lack of controlled experiments, causality between variables in ecology may be identified using causal discovery algorithms. (As the definitions and use of causal discovery and related concepts in literature differ, see Box 1 for an overview of the terminology used in this review.) Causal discovery algorithms aim to identify causal structures from observational data. Starting with a dataset with variables, the causal discovery algorithm infers whether the variables are causally related or not, and if so, what is the direction of the causality. Importantly, the field of causal discovery offers a wide range of causal discovery algorithms, that vary in terms of the computational procedures and assumptions underlying them [9][10]. To illustrate how causality could be established from observational data, we give an example of a causal discovery algorithm that requires time series data, convergent cross mapping, in Box 2. In general, convergent cross mapping states that if variable A is causally linked to variable B, then a trace of variable A should be found in the time series data of variable B [10]. However, it should be noted that other causal discovery algorithms can take very different approaches, and discussing all of them is beyond the scope of this review. For an extensive review of different causal discovery algorithms, the reader is referred to e.g. [9] and [11].

Box 1: Correlation, causality and causal discovery.

A **correlation** between two variables A and B implies that A and B tend to increase or decrease together (Figure 1a). Notably, correlation is not sufficient to establish a **causation**, nor is a correlation required to establish a causation. A causal relationship between A and B may be established if B changes in the presence but not in the absence of A, while all other variables that could possibly affect B do not change [14]. A causal relationship can be interpreted in terms of its **direction** (does A cause B, or does B cause A, or do A and B cause each other), its **strength** (what is the size of the effect of the causal variable on the response variable), and whether its **effect** on the response variable is positive or negative. If A and B correlate but are not causally related, the correlation between A and B is **spurious**. A spurious correlation can be a sign of **confounding**, in which a third variable C has a causal relationship with both A and B (Figure 1b). The causal relationships between variables can be shown in a **causal network** [9].

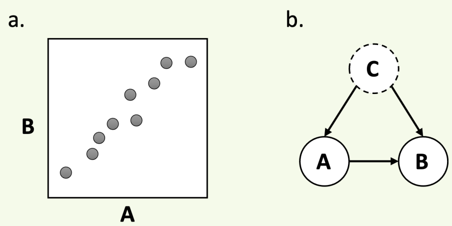


Figure 1: Inferring relationships between variables from observational data. (a) A correlation between variables A and B. (b) Arrows indicate causal relationships. A confounding variable C causes both A and B.

The aim of **causal discovery** is to infer causal relationships from observational data. Causal discovery is not to be confused with **causal inference**. Causal inference assumes causality between two variables in a data set and then tests the strength and the effect of the causal relationship, while causal discovery does not assume that any of the variables in the data set are causally related [15][16]. Although causal discovery generally refers to computational methods to infer causality from observational data, the terms causal structure discovery and computational causal discovery are sometimes used to describe causal discovery explicitly by means of computational methods [17][12].

Box 2: Convergent cross mapping.

Convergent cross mapping is a causal discovery algorithm that requires time series data. Convergent cross mapping is based on dynamical systems theory. Dynamical systems theory states that there is a causal relationship between two variables A and B in the time series data set if A and B originate from the same dynamical system. If A and B originate from the same dynamical system, A and B have a common attractor manifold [10].

Convergent cross mapping creates a manifold for the data points of A and another manifold for the data points of B (Figure 2). Thus, for every time index in the data set, a data point of variable A and a data point of variable B are found on the two manifolds, respectively. Next, convergent cross mapping assesses whether the time indices of points that are close to each other in the manifold of A can be used to find points that are close to each other in the manifold of B, and vice versa. This procedure is called **cross-mapping**. The estimation of B based on the time series values of A is evaluated by the **cross-mapping skill**, which is the Pearson correlation coefficient between the observed values of B and the values of B estimated using A. If A causes B, A can be estimated from the time series values of B [10].

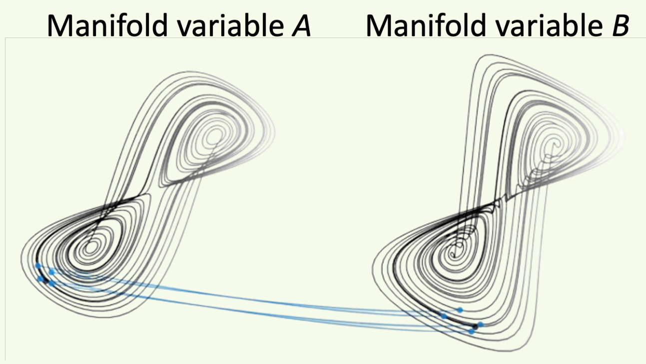


Figure 2: Manifolds of a variable A (left) and a variable B (right). The blue lines connect data points with the same time index. Modified from Sugihara et al. [10].

Importantly, **convergence** of the cross-mapping skill is crucial to establish a causal relationship between A and B. This means that the more data points are available, i.e. the longer the time series, the higher the cross-mapping skill for the estimation of A from B. The speed of convergence, i.e. the improvement in the estimate of B with an increase in the length of the time series of A, is a metric of the strength of the causal relationship [10].

5 Causal discovery algorithms in ecology

In molecular biology, causal discovery algorithms are a frequently used tool to uncover the causal structures underlying networks of gene expression [11]. In contrast, the applications of causal discovery algorithms in other fields of biology are much less explored. In ecology, causal discovery algorithms are occasionally used to reveal causal effects of meteorological factors ([18][19][20]) or to unravel interactions between species ([21][22][23]). Since observational data in ecology are often collected over time, convergent cross mapping is frequently used as a causal discovery approach [18][19][20][21][23][24]. However, a few studies use different causal discovery algorithms, such as fast causal inference and additive noise models, to infer causality from non-time series data [22][12]. In this section, we review the applications of causal discovery algorithms in ecology, highlighting the possibilities and challenges of the methodology.

5.1 Discovering causality using time series data

5.1.1 Causal effects of meteorological factors

As ecology studies the relationships between organisms and their environment, causal links in ecology could be identified between living organisms as well as between living organisms and abiotic factors, such as temperature, precipitation and sunlight. The direction of causality between organisms and meteorological factors is typically straightforward, e.g. sunlight may affect plant growth but the opposite is unlikely. However, establishing which meteorological factor causes a change in a biotic factor can be difficult, because seasonal change typically involves a change in multiple meteorological factors and biological processes concurrently. This can lead to spurious correlations, and to a high number of candidate causal variables for a seasonal biological process. In addition, laboratory experiments designed to isolate the effect of a single meteorological factor may fail to account for interactions between meteorological variables or seasonal change in a variable [19].

To reveal causal relationships between meteorological factors and biological processes, several studies have used convergent cross mapping [18][19][20]. For instance, Kitiyama et al. examined the effects of meteorological factors, such as air temperature and rainfall, on the seasonality of production of leaf litter in tropical rain forests [18]. Importantly, causing a change in a variable and causing seasonality of a variable are two different concepts. For example, a causal variable may cause a change in the response variable during a part of the year, but not be involved in seasonal changes of the response variable in the rest of the year. Therefore, establishing a causal relationship between two variables A and B is not sufficient to conclude that A is the cause of observed seasonal change in B. To find the cause of the seasonality of leaf litter production, rather than merely identifying variables that can affect leaf litter production irrespective of the seasonal pattern, Kitiyama et al. compare seasonality of time series of potential causal variables to seasonality in time series of leaf litter production. As a result, convergent cross mapping reveals air temperature, but not rainfall, as a cause of seasonality in leaf litter production [18]. This highlights the possibility of causal discovery approaches to distinguish between temporally correlated and causal factors, and to assess whether a causal variable is also causing the seasonal change of its response variable.

Even when two variables are causally related, the effect of a causal relationship may be dependent on a third variable. For example, Nova et al. use convergent cross mapping to find out if rainfall and temperature are causally linked to the incidence of dengue virus [19]. Both rainfall and temperature are identified as causal factors of dengue incidence, but only when the population of susceptible individuals is sufficiently large. This demonstrates that causal variables may be dependent on other variables to have a causal effect. Moreover, although increase in temperature had a small median positive effect on dengue incidence, increase in temperature could also lead to a decrease in dengue incidence. Likewise, rainfall had a median negative effect on dengue incidence, but could also result in an increase in the number of dengue cases [19]. Hypothetically, the effects of rainfall, temperature and possibly other factors on dengue incidence are coupled. In turn, the interactions between different causal factors might affect the net causal effect on dengue incidence.

The convergent cross mapping approaches discussed above do not explicitly consider the presence of unmeasured variables that influence the effect on the response variable. Importantly, unmeasured variables are not only potential causal factors, but they might also modulate the direction, strength or effect of the causal relationship between two variables. In the study on dengue incidence discussed above, rainfall could cause both an increase and a decrease in dengue incidence. Both high rainfall and water storage in times of drought could lead to more still-standing water, offering a habitat for the mosquitoes that transmit dengue virus [19]. Indeed, the effect of rainfall on dengue incidence could be mediated by a third variable, still-standing water, that is caused by rainfall as well as human behavior.

In addition, this example shows that causal links between variables could be worth studying even in the absence of a strong correlation. Namely, the effects of two causes may cancel out, so there is no net observable correlation between each of the causal variables and the response variable. For instance, if the effects of rainfall and water storage in times of drought cancel out, correlation-based methods may fail to detect an association between rainfall and dengue incidence.

So far, ecological studies using convergent cross mapping have mainly focused on discovering causes of a single response variable of interest [19][20][18][21]. To that end, the connections between the response variable and the other variables in the data set are studied, while connections between the other variables are typically not reported. However, understanding how an effect arises may require not only direct causal connections between the variable of interest and its causal variables. Indeed, studying the interactions and possible causal effects between the causal variables enables the creation of a causal network, providing insight into the causal processes underlying an observed effect. A causal network could also help to improve predictions of an effect, for instance because it might reveal a variable that modulates the effect of the causal relationship between two other variables.

Although convergent cross mapping is based on identifying whether two variables are causally linked, it can also be used to create a causal network. If a data set contains N variables, convergent cross mapping could assess all $N(N-1)/2$ variable pairs, and build a network based on the established causal connections [10]. This approach could be especially useful in cases where multiple variables have a causal relationship with the response variable, as that might suggest that the causal variables are causally related to each other as well.

Since the number of possible causal links increases exponentially with the number of variables in the data set, the amount of computational power required to analyse all possible connections between variables can greatly outweigh the amount of power needed to analyse only links connected to one variable. Further integration of ecology with expertise from big data analysis may be required to address the procedure in a computationally efficient and time-efficient manner. Importantly, some links between variables in the data set may not be relevant because they are ecologically nonsensical. Therefore, ecologists need to decide which connections to study based on prior knowledge or intuition. However, relationships between variables that do not make sense ecologically can still be useful as a control to confirm that the causal discovery algorithm finds no causal relationship. For instance, the causal discovery algorithm used in Nova et al. finds no causal effect of dengue incidence on rainfall [19]. Overall, explicitly considering interactions between variables other than the response variable of interest would be a logical step to do justice to ecological complexity and increase understanding of causality in ecosystems.

5.1.2 Causal discovery to create species interaction networks

The interactions between different species in an ecosystem, such as a predator and a prey species, have intrigued mathematical biologists for more than a century [25]. Although correlations between e.g. the abundance of predator and prey species are intuitive, inferring causality from species interactions is challenging. In this section, we discuss the applications of causal discovery methods to identify causal links underlying species dynamics, i.e. the abundance of species over time.

Notably, causal discovery approaches to reveal causal relationships between species typically involve more variables, and assess more interactions between variables, than studies on meteorological variables. Indeed, convergent cross mapping and other causal discovery algorithms are used to create networks of interactions between species rather than only establishing links directly connected to a single response variable of interest [21][22][23]. Species dynamics may traditionally be studied from an ecosystem perspective rather than from the perspective of a single species [26]. Therefore, it is logical to assess causal links between multiple species rather than only focusing on a single species of interest.

In contrast to the meteorological effects discussed above, species interaction networks describe connections where both the causal variable and the effect variable consist of living organisms. In particular, the species of interest are often animals, meaning that they have the cognitive and physical capacity to participate in complex behavioral patterns. This could be a reason why multiple causal discovery studies on species dynamics report that causal interactions between species change over time [21][23]. For instance, Ushio et al. analysed the interactions between fifteen fish species in a community in Maizaru Bay, Japan, using convergent cross mapping on data collected over twelve years [23]. Remarkably, the strengths of the interactions between the fish species generally follow a seasonal pattern, with weaker interactions during summer and stronger interactions during winter. The seasonal pattern might be explained by seasonal changes in primary production, species diversity, or behaviour [23]. The cause of the seasonality in interaction strength between the fish species could again be studied using a causal discovery algorithm. For instance, Kitayama et al. present an approach to study the cause of seasonality in a variable [18]. Following Kitayama et al., the seasonality in time series data on interaction strength between the fish species could be compared to seasonality in time series data of one of the proposed causal variables, such as fluctuations in primary production.

Importantly, species interaction networks assess interactions between the collection of individuals of a species in a community rather than behavior of individual members of a species. Extrapolating interaction patterns at the level of the species to the level of the individual requires caution, because behavior can differ between individuals of the same species. Speculatively, behavior of a mere subset of individuals from species A might give rise to a causal effect on the dynamics of species B, while other individuals of species A do not participate in the behavior. Therefore, establishing a causal relationship between individual-level behavior and interactions between species may be challenging. Heterogeneity within the group of individuals from a species could result in variability in causal strength and type (positive or negative) of a possible effect of individual behavior on interactions between species.

5.2 Causal discovery algorithms without time series data

Most ecological studies using causal discovery algorithms analyse time series data, and therefore they can use convergent cross mapping. However, there are also causal discovery algorithms that can be used to obtain causal relationships from non-time series data. Yet, other causal discovery algorithms than convergent cross mapping are hardly applied in ecology [22][12]. Nevertheless, the few studies that do apply them offer promising results and perspectives for future research on causal discovery in ecology, so we include them briefly in this review.

To establish the direction of causality between generalism and abundance of species, Song et al. use cross-sectional data sets on fish, plants and hummingbirds collected at different locations [12]. Both causal discovery algorithms used, one based on an additive noise model and one based on information-geometric inference, identify generalism as a cause of abundance and not the other way around. Importantly, though, causality is assessed only between two variables - generalism and abundance - and possible confounding variables are not considered. A causal network with more variables could be created to identify possible confounding variables.

One approach to create a causal network from non-time series data is the causal discovery algorithm called fast causal inference [14]. Mielke et al. use a fast causal inference algorithm to identify causal relationships in freshwater ecosystems [22]. In contrast to convergent cross mapping, the fast causal inference algorithm takes a network structure of variables as a starting point. In a nutshell, fast causal inference starts with a network that connects every variable to every other variable in the data set, and then removes a connection if the variables are conditionally independent. Next, the direction of causality between the remaining connected variables is established. Notably, a causal link between two variables can also be bidirectional. Mielke et al. present an example of a bidirectional link between two plant species, which is interpreted as a sign of a confounding variable, water, that is causally related to both plant species [22]. However, in other cases, a bidirectional causal link between two variables may indicate a feedback loop rather than a confounding variable [24].

6 Conclusions and future perspectives

Traditional computational analyses of relationships between variables in ecology have been mostly limited to correlation-based approaches (Figure 3a, first panel). Recently, the field of causal discovery has been explored to identify causal relationships from observational ecological data, with convergent cross mapping as the most popular approach. Causal discovery algorithms, mainly convergent cross mapping, have been used in ecology to shed light on the causal links underlying the associations between species and meteorological factors as well as interactions between species and species dynamics. Interestingly, convergent cross mapping approaches have successfully unmasked causal relationships from data sets with many temporally correlated variables, such as meteorological data. This is a promising result, because ecological processes are often correlated with meteorological variables, and many fields of ecology have not yet exploited the potential of causal discovery algorithms to determine whether temporal correlation is underpinned by causality. Despite the fact that correlation is not a prerequisite for causality, correlations between ecological factors may serve as a good starting point to search for causal relationships.

Although causal discovery algorithms have successfully identified causal relationships between ecological variables, interpretation of the causal relationship can be difficult. For example, a causal variable can be positively associated to its response variable in one case but negatively in another [19], or the strength of the causal relationship can change over time [23]. To better appreciate the implications of a causal relationship between two variables in the ecological context, future work should focus not only on identifying causal relationships, but also on understanding the variability in strength and effect of the causal relationship over time or between individuals.

To aid the interpretation of causal relationships in ecology, we identify three concepts: (1) studying a causal network rather than a single variable of interest, (2) considering the time scale at which a causal effect occurs, and (3) accounting for individual heterogeneity within a group of organisms. We argue that these three concepts are widely applicable in ecology, including fields of ecology where causal discovery algorithms have not yet been applied. Notably, some ecological studies already use causal discovery algorithms to create causal networks [23][22]. However, to our knowledge, no ecological studies have explicitly assessed the implications of time scale and individual heterogeneity in the interpretation of causal links established by a causal discovery algorithm. Therefore, we illustrate the potential of these two concepts by means of a field where causal discovery algorithms have not been applied yet, but could be of great benefit: animal movement. As animal movement is a complex behaviour associated with many internal and external factors, causal discovery algorithms could help to understand what causes an animal to move.

6.1 Towards a network-based approach of causality in ecology

Remarkably, most ecological studies using causal discovery algorithms have focused on causal links to a single response variable of interest (Figure 3). Although this limits the required amount of data and computational power, focusing on causal relationships to a single response variable may hamper the interpretation of a causal relationship in its ecological context. For instance, the strength and effect (i.e. positive or negative) of a causal relationship can change over time, which is difficult to understand when the causal variable remains unchanged. A possible explanation for variability in strength and effect of a causal relationship could be the presence of an unmeasured variable that modulates the causal relationship. Alternatively, the identified causal variables in a study may not only be causally related to the response variable of interest, but also to each other.

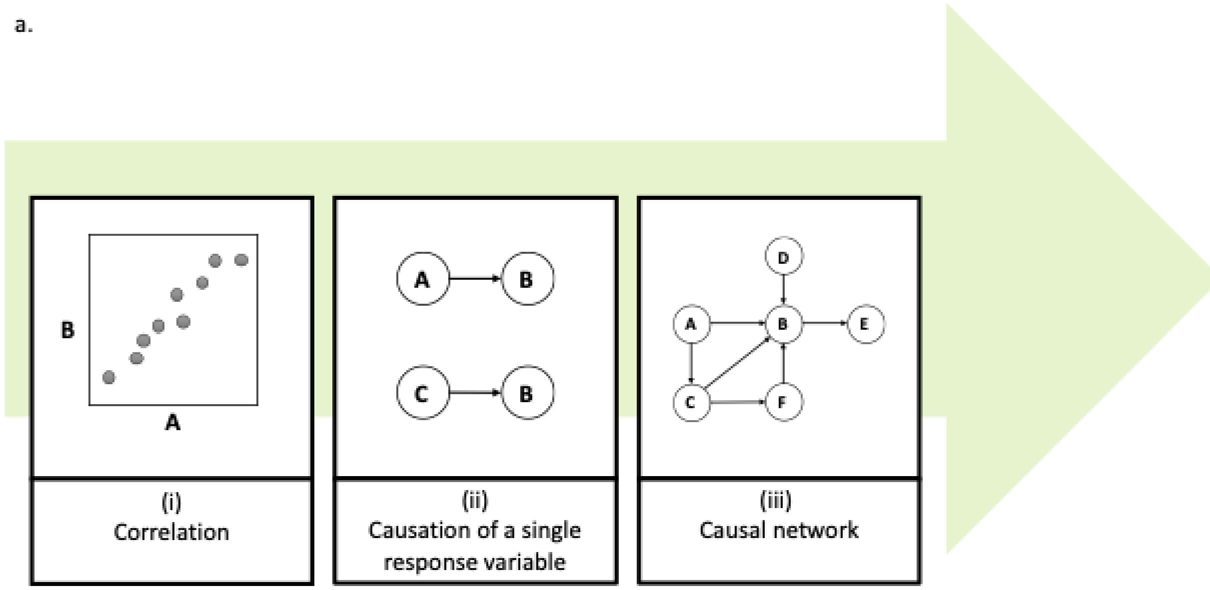
To address these challenges, we argue for a network-based approach to causality in ecology, that acknowledges the tight connections between ecological variables (Figure 3). To account for variables that are difficult to measure, causal discovery algorithms should be explored that can identify hidden or latent variables in a causal network, i.e. variables that are not in the data set [14]. Naturally, creating causal networks requires more data and more computational power than focusing on connections between one response variable and a few potential causal variables. However, integration of tools and techniques from the field of data science may help ecology to exploit the potential of the data that is already available [27]. Ideally, causal discovery algorithms should be added to the standard toolbox of data analysis strategies used by ecologists, to stretch ecological data analysis far beyond traditional correlation-based approaches. Moreover, future research should assess how correlation-based analyses, mechanistic models and causal discovery algorithms could complement each other, and provide a framework on when to use which approach. This way, ecological data can live up to its potential as a big data science, following disciplines like molecular biology in which big data strategies are widely adopted [27][11][8].

As with all interdisciplinary research, integration of data science methods in ecology comes at the risk of mutual misunderstanding. From the perspective of ecologists, causal discovery algorithms may lead to a black box effect in which a data set is put in and a causal relationship magically comes out. On the contrary, data scientists might overlook the complexity of ecological systems and the impossibility to fully capture biological organisms as nodes in a graph. Overcoming these challenges requires close collaboration between ecologists and data scientists, guided by clear communication and a willingness to learn about each other's discipline.

6.2 Moving forward: Causality in animal movement research

In the next sections, we discuss challenges in the interpretation of ecological causal relationships regarding the timescale of the causal link and individual differences between organisms. To our knowledge, these two topics have not yet been explicitly addressed in ecological causal discovery literature. To concretely illustrate the relevance of timescales and individual heterogeneity, we take the field of animal movement research as an example. First, we provide a brief background of the need to study causality in animal movement and how it has been studied so far. Second, we address challenges regarding the interpretation of causality from time series data. Third, we highlight the importance of individual heterogeneity within groups in interpreting causal relationships.

a.



b.

Approach	Causal discovery algorithm	Reference
Causation of a single response variable	Convergent cross mapping	[18]
	Convergent cross mapping	[19]
	Convergent cross mapping	[20]
	Convergent cross mapping	[21]
Causal network	Convergent cross mapping	[23]
	Fast causal inference	[22]

Figure 3: Strategies to understand relationships between ecological variables from observational data. (a) Correlation-based methods (first panel) are widely adopted in ecology. Causal discovery approaches are occasionally used, but mostly focus on a single response variable of interest (second panel). We encourage a network-based perspective on causal relationships in ecology (third panel). Black arrows indicate causal relationships. (b) Examples of ecological studies using causal discovery algorithms to study either causation of a single response variable (second panel in (a)), or to create a causal network (third panel in (a)).

The ability to move from one place to another enables animals to find resources and reproductive partners, and to escape predators and extreme weather conditions. At the same time, animal movement plays a key role in seed dispersal, disease transmission and gene flow, and thereby in the maintenance of biodiversity [28]. Thus, animal movement is intertwined with many different biological processes at the individual level, the population level, and the ecosystem level [29]. Strikingly, animal movement is strongly linked to human action, with a reduction of mammalian displacement up to a threefold in areas heavily shaped by human activity compared to areas with low human activity [30]. Unraveling the causes of animal movement is required to reveal any causal relationships between human activities and animal movement. Consequently, understanding of the causes as well as the effects of animal movement may help to develop conservation strategies and maintain biodiversity.

At the individual level, animal movement can be studied by considering (1) the internal state of the animal, (2) motion, (3) navigation, and (4) factors external to the animal [31]. Using GPS tracking data, animal movement has been associated with internal factors such as heart rate and body size, as well as external factors like landscape and resource availability [32][33]. In addition to correlations obtained from observational studies, mechanistic models have been proposed to explain and predict movement patterns [4]. For instance, individual-based models simulating motion and navigation behavior have successfully predicted bird migration patterns [5].

6.2.1 Causality and time

To collect data on animal movement, animals can be equipped with a GPS tracker that follows their location over time. Animal movement can be quantified using different metrics related to speed, direction and displacement distance, such as the step size between two subsequent GPS locations in the data set [34]. As a starting point, convergent cross mapping may be used to find causality between an animal movement metric, e.g. step size, and a potential cause of animal movement for which time series data are available, such as resource availability or a meteorological factor.

Analysis and collection of time series data on animal movement come with a number of challenges (Figure 4). First, despite sophisticated GPS tracking technology, animal movement data frequently contains gaps. Therefore, imputation of missing values may be performed using strategies previously used to analyse movement data, or explore imputation methods specifically developed for causal discovery algorithms and applied in different fields of biology [35][36].

Second, data collection on animal movement raises the question of how much time there should be between two data points. Indeed, if an animal moves after the first measuring point but is back at its initial location before the second measuring point, the movement of the animal will not be registered. Hence, long time intervals between measurements can lead to an underestimation of the displacement distance. On the other hand, small time intervals may lead to indistinguishable GPS data points that are strongly affected by measurement errors [37]. Naturally, the maximum distance an animal can move within one time interval depends on the species. Hypothetically, the time interval between measurements could impact the patterning of the data set over time, and thereby whether a causal relationship can be established or not. Therefore, data thinning may be used to enlarge the time interval of an animal movement data set, and assess whether a larger time interval changes the outcome of the causal discovery algorithm [38].

Finally, the total duration of the study, i.e. the time span covered by the measurements, might affect whether animal movement and a variable of interest are causally linked. Importantly, movement patterns on shorter and longer timescales may not have the same causes. For instance, a cause of daily movement behavior is not necessarily a cause of seasonal migration. Moreover, causes of movement could change over time. One way to distinguish between movement behavior on different time scales would be to identify movement patterns from time series data (see [39] for methods) on different time scales (e.g. weekly, monthly, yearly). Following the approach of Kitayama et al., convergent cross mapping could be used to compare temporal patterns of animal movement to temporal patterns in potential causal variables, and possibly identify a cause of a specific temporal movement pattern [18].

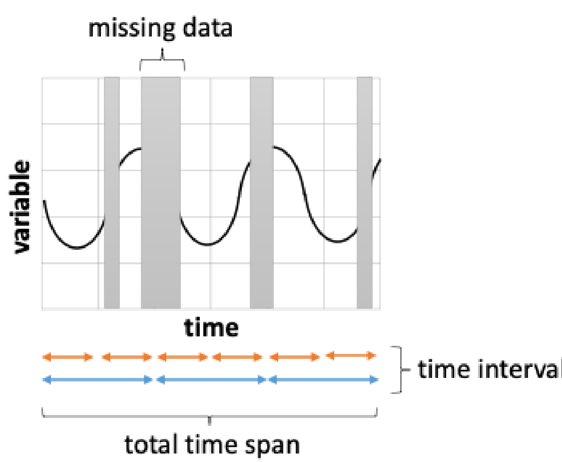


Figure 4: Time series data vary with respect to the total time span covered by the measurements, the time interval between measurements (colored arrows), and missing data (grey rectangles). The figure is not based on real data.

6.2.2 Individual heterogeneity in cause and effect

Animal movement is not only studied at the level of the individual, but also at the level of the group, where a group consists of multiple individuals (Figure 5a). Since animal movement within groups can be heterogeneous, extrapolating causality of individual movement to explain group movement could be incorrect [40][41]. Notably, the importance of individual heterogeneity in understanding group movement might depend on the spatial scale of movement. For instance, on a small spatial scale, individual movement heterogeneity could change the shape of a group because individuals move in different directions. Moreover, group and individual movement could have causal feedback on each other, e.g. because an individual adjusts its position to the shape of the group (Figure 5b). In this case, a change in group spatial position or shape would be both a cause and a consequence of individual movement. To test this, causal discovery algorithms may be used to analyse observational data on both individual movement and group movement, and assess causal relationships in both directions.

In long-distance migration of a group, all individuals in the group simultaneously cover the same distance in the same direction. Yet, observing similar outcomes for individuals within a group does not mean that the cause is the same for all individuals in the group (Figure 5c). In theory, migration could be initiated by a few members of the group, while others simply follow. This could reflect heterogeneity of causes of movement within the group, where, for example, an internal factor causes movement of one or two individuals. That could in turn cause movement of the rest of the individuals, that may not even experience the internal factor that caused the others to move. Although this example is theoretical and is therefore not necessarily true for any case of group migration, it illustrates that heterogeneity in the causes of movement within a group should be considered, even if the effects are the same for all individuals (Figure 5c).

Traditionally, mechanistic models have been used to study heterogeneity within groups and feedback between biological levels [40][3]. However, mechanistic models generally seek for an explanation of the data rather than unraveling the causal structures that generated the data [42]. Causal discovery algorithms may help to identify causality between individuals and the group they belong to, e.g. between the shape of the group and the movement of an individual, and between the movement of individuals. Moreover, potential causal variables of movement should be studied in relation to different individuals in a group, rather than extrapolating findings for one individual to all individuals or taking the group mean. Indeed, a causal variable might have opposing effects on different individuals (Figure 5d). Hence, a weak or undetectable net effect of a causal link between two variables might be a sign of individual heterogeneity regarding the response to the variable.

To identify heterogeneous causes within a group, separate causal networks may be created for different individuals rather than creating one network based on the group mean of a movement variable. However, this approach is sensitive to measurement errors in the movement data of single individuals. Alternatively, observations from different individuals could be grouped beforehand based on the correlation coefficient of the movement variable with the potential causal variable of interest. Yet, an approach like this requires great caution as it decreases the sample size and comes at the risk of pushing the analysis towards a specific result, and future research should focus on exploring methods to study possible causal heterogeneity in animal movement.

6.3 Final remarks

Taken together, causal discovery algorithms are a promising tool to study causality in ecology. Causal discovery algorithms have already uncovered causal effects of meteorological factors and species interactions, mostly by means of convergent cross mapping. Close collaborations between ecologists and data scientists could explore the use of more different causal discovery algorithms in more ecological disciplines. To strengthen the position of causal discovery algorithms in ecology, future work should adopt a network-based approach to causality in ecology. Moreover, future research should explicitly take into account causality on different timescales and individual heterogeneity with respect to causes as well as effects. This could enhance our understanding of the complex relationships found in ecosystems, and help to conserve the variety of species found on Earth.

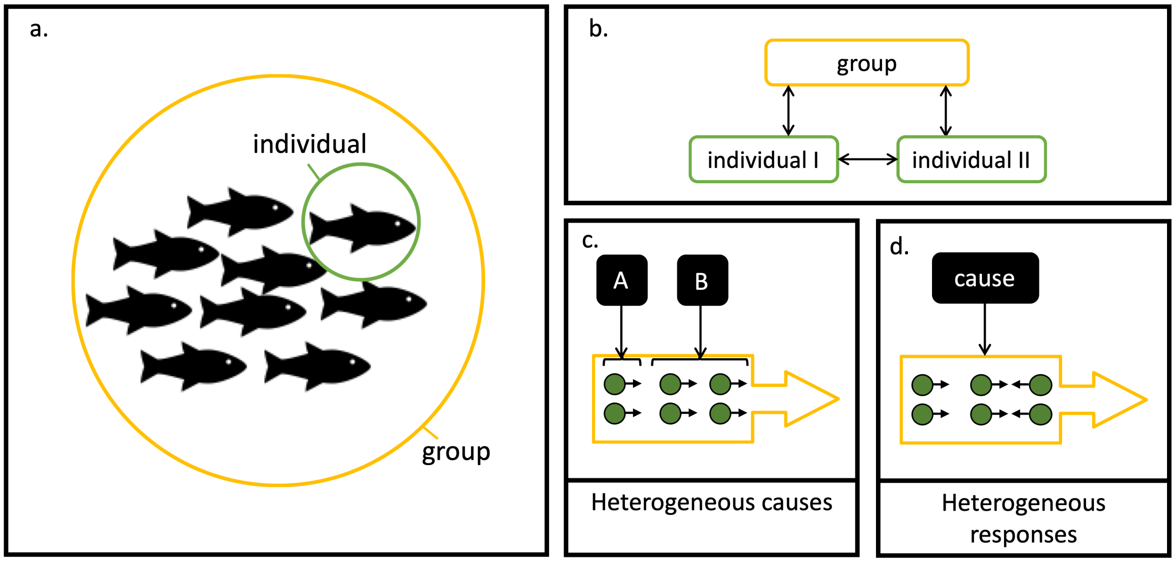


Figure 5: Animal movement at the individual level and at the group level. (a) Animals can be part of a group, for example a school of fish. (b) Group movement and individual movement could be causally related to each other, and individual movement can be causally related to the movement of other individuals in the group. (c) Causes (A and B, black boxes) of animal movement can differ between individuals (green circles) in a group, even if the effect is the same. (d) A cause of group movement does not necessarily have the same effect on all individuals in the group, e.g. because group movement (yellow arrow) reflects a net effect of individuals moving in different directions (green circles). In (c) and (d), vertical arrows indicate causal relationships, and horizontal arrows indicate movement.

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