OBSGESSION
Observation of Ecosystem Changes for Action

Deliverable D3.1 – Best practices for Detection Attribution Modelling

Lead Beneficiary: CNRS

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24/06/2025

Schweizerische Eidgenossenschaft
Confédération suisse
Confederazione Svizzera
Confederaziun svizra

Funded by
the European Union

UK Research
and Innovation

Prepared under contract from the European Commission

Grant agreement No.101134954

EU Horizon Europe Research and Innovation action

Project acronym:	**OBSGESSION**
Project full title:	**Observation of Ecosystem Changes for Action**
Start of the project:	January 2024
Duration:	48 months
Project coordinator:	Petteri Vihervaara

Deliverable title:	Best practices for Detection Attribution Modelling
Deliverable n°:	D3.1
Nature of the deliverable:	Report
Dissemination level:	Public

WP responsible:	WP3
Lead beneficiary:	CNRS

Citation:	Estopinan, J, Thomas, A, Gaüzère, P & Thuiller, W. (2025). *Best practices for Detection Attribution Modelling*. Deliverable D3.1 EU Horizon Europe OBSGESSION Project, Grant agreement No. 101134954

Due date of deliverable:	Month n°18
Actual submission date:	24/06/2025

Deliverable status:

Version	Status	Date	Author(s)/Reviewer
1.0	Draft	02 June 2025	Joaquim Estopinan, Anne Thomas, Pierre Gaüzère, Wilfried Thuiller CNRS
2.0	Review	06 June 2025	Sander Mücher, WR Jussi Mäkinen, Syke
3.0	Final	24 June 2025	Joaquim Estopinan CNRS

Summary

Detecting and attributing biodiversity changes is a multifaceted and demanding task. The first key challenge is gathering data on biodiversity metrics and the likely drivers that is sufficiently structured and aligned in space and time, and wide enough to cover the dynamical range of the target latent processes at play, enabling statistical inference. Demonstrating that a measure of biodiversity has significantly changed relative to a reference state — a reference which is often difficult to define due to a lack of past data — constitutes a second challenge. A third key challenge is designing an identification strategy that can isolate the contribution of multiple potential causal factors with statistical confidence.

The review comprising the deliverable D3.1 addresses these three key challenges in a coherent framework, meeting the task expectations. It is entitled *"Advancing Causal Inference in Ecology: Pathways for Biodiversity Change Detection and Attribution"* (Schrodt et al., Methods in Ecology and Evolution, under revision). This work was achieved in collaboration with the IMPACTS synthesis group of the French Foundation for Biodiversity Research (FRB). This text provides conceptual and practical guidance on taking advantage of existing causal methods to detect and attribute changes in biodiversity. There is an emphasis on how remote sensing data can mitigate pressing issues related to confounding factors that occur across scales.

By paying attention to the described challenges and relying on the suggested methods and workflow, the review introduces a solid basis to root biodiversity change studies in causal principles for better detection and attribution. The proposed manuscript is indeed highly interdisciplinary in its attempt to bring biodiversity studies closer to the science of attribution through causal inference from observational data. While this deliverable is fully autonomous, it is complemented by two perspective articles that are also under revision and a method decision tool that is under development. They cover related aspects of detection and attribution.

As deliverable D3.1 format is a scientific manuscript, it is provided in its most recent version in Annex 1 below.

Annex 1

Advancing Causal Inference in Ecology: pathways for biodiversity change detection and attribution

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Abstract

1. Understanding the causes of biodiversity change is essential for addressing environmental challenges. While causal attribution has advanced in other fields, ecologists remain cautious about causal claims or misinterpret predictive models as causal. With growing spatio-temporal data, computational power, and cross-disciplinary collaboration, discussions on improving attribution methods in ecology are gaining momentum. However, practical guidance remains limited for non-experts. Here, we identify the challenges and decisions involved in detecting and attributing biodiversity change and provide an overview of suitable methods based on available data and specific research questions.

2. The first challenge we address pertains to biodiversity and driver data. Unlike controlled experimental data in other disciplines, ecological data often stem from monitoring programs or field samplings with varying degrees of rigor, which complicates the analysis due to sampling biases, interacting drivers, measurement error, or spatio-temporal variations. We specifically outline how data structure (e.g., structured *vs*. opportunistic

data) and data coverage along the spatial and temporal scale impact detection and attribution.

3. The second challenge involves the ability to detect directional change in the system of interest, which is associated with numerous hurdles. We provide an overview of the most relevant approaches to deal with sampling variability, gaps and biases in the data, non-linearity in the temporal trends and to identify the most appropriate spatio-temporal resolution.

4. For the third challenge, causal attribution, we focus on data driven approaches. We review recent frameworks that draw on methodologies from other disciplines, offering analytical roadmaps and a step-by-step guidance for causal inference. These include constructing theoretical causal models *a priori,* full causal models based on data and theory, and *posterior* causal interpretation tailored to specific data and research questions.

5. Moving forward, it is essential to foster interdisciplinary collaboration to adapt and refine methodologies from other fields, ensure robust data collection and sharing practices, promote the integration of advanced computational tools, and improve the link between data-driven and theory-driven approaches. This approach will enhance our ability to make robust causal inferences, thereby improving our understanding of biodiversity changes and informing effective conservation strategies.

Keywords

Biodiversity change, detection, attribution, global impacts, anthropogenic drivers, causal inference, environmental change

Introduction

Better **attribution** and understanding of **causal relationships** (Table 1) in biodiversity change are needed to create realistic and fit-for-purpose **projections** (Table 1) and scenarios. Both are required for various applications, including informing policy (e.g., IPBES 2016; Nicholson et al. 2019) and increasingly nature markets and economic models (Ferraro, Sanchirico, and Smith 2019; Takahata et al. 2024; West et al. 2023), effectively allocating resources and conservation priorities, promoting accountability, and ultimately, improving our understanding of the consequences of environmental change and human actions on ecosystem functioning and human well-being (MacDonald, Larsen, and Plantinga 2019). Methods for causal **driver attribution** (Table 1) – the process of evaluating the relative contributions of multiple potential **causal factors** (drivers) to a detected biodiversity change, with an assignment of statistical confidence to the causal models used to estimate these effects (Gonzalez et al. 2023) – have been proposed in several fields (e.g., physics, climate sciences, economics, and epidemiology) (Hegerl and Zwiers 2011; Reich et al. 2021; Runge, Bathiany, et al. 2019; Pearl 2009). However, ecologists often remain conservative in making explicit causal statements and tend to rely on a limited set of causal **attribution** methods, such as Structural Equation Models. Some forms of predictive modeling are often misinterpreted as identifying causal **drivers**, even though their primary objective is not to establish causality (Stewart et al. 2023; Arif and MacNeil 2022a) but see Nichols and Cooch (Nichols and Cooch 2025) for a counter argument.

Two schools of thought exist regarding causal inference with imperfect data and prior knowledge (Grace 2025). Causal liberals favor pragmatic approaches, making causal claims from observational data and models despite untestable assumptions (e.g., exchangeability, no unmeasured **confounders,** Table 1) (Rubin, 2008; Pearl, 2009). While this allows for actionable insights, it risks overconfidence in weakly validated models (Hernán & Robins, 2020). Causal conservatives, by contrast, demand stronger evidence—such as randomized trials, quasi-

experiments, or instrumental variables—emphasizing the difficulty of verifying key assumptions in observational studies (Greenland, 2005; Angrist & Pischke, 2008). This divide is often obscured by overlapping terminology, creating confusion in the literature (Grace, 2024). Fundamentally, it reflects a trade-off between rigor and practical action, akin to balancing Type I and Type II errors in statistical inference. In ecology, a wealth of mechanistic knowledge from experiments and long-term studies can inform causal inference despite data limitations. Grace (2024) advocates for a multi-evidence approach, leveraging all available mechanistic insights to strengthen causal claims in ecological research.

Implementation of a conservative causal **attribution** approach in ecology presents four significant challenges due to the inherent complexity of ecological systems, data limitations, and the interplay of multiple interacting, often unmeasured factors. (1) Detecting directional change: change **detection** in either a **response** variable or its putative **driver** (see definitions in Table 1) is non-trivial, particularly given issues of data scarcity and non-random sampling. Both observational and experimental ecological data frequently suffer from incomplete spatio-temporal coverage, bias in data collection, and methodological inconsistencies (Dee et al. 2023). These challenges are further compounded by the scale-dependence of ecological processes, where changes observed at one spatial or temporal scale may not generalize to others (Estes et al. 2018). (2) Complexity of mechanistic understanding: the lack of direct measurement of many key **drivers** results in often limited mechanistic understanding and reliance on inferred or proxy variables. The high-dimensional nature of ecological systems means that **drivers** interact in non-linear and often unexpected ways, with biological **responses** exhibiting lags, feedback loops, and context-dependent effects (Essl et al. 2015; Myers-Smith et al. 2020). The spatio-temporal variability of both biotic and abiotic **drivers** complicates efforts to isolate the contribution of specific factors and even controlled experimental setups cannot fully account for all or potentially even the most important confounding variables (Dee et al. 2023), limiting their ability to establish mechanistic

understanding. (3) Methodological and computational barriers: the mathematical and coding expertise required for formal causal **attribution** approaches, is often perceived as a barrier to widespread implementation and can risk increased use of black-box approaches. On the other hand, this complexity and messiness of ecological data also results in data often failing strict statistical requirements of causal statistics (see Grace 2024 for a thorough discussion) (4) Defining baselines in a changing word: Determining appropriate baselines for detecting change is a critical but unresolved issue. Many ecological monitoring programs were initiated only after environmental degradation became apparent, meaning that true pre-impact conditions are rarely available for comparison (Knowlton and Jackson 2008; Soga and Gaston 2018). Furthermore, most long-term ecological monitoring efforts commenced after anthropogenic pressures had already altered ecosystems, making it difficult to disentangle human impacts from natural variability (Mihoub et al. 2017).

On the other hand, given the increasing availability of 'big data' in ecology, including biodiversity and **driver** data (Schrodt et al. 2024; Wüest et al. 2020; Bush et al. 2017; Farley et al. 2018), enhanced computational power, and open sharing of code among disciplines, there has been a resurgence of discussions on improving **attribution** methods in ecology. Several frameworks have been proposed to address some of the above-mentioned issues, also encouraging application of more comprehensive and sophisticated causal **attribution** methods in ecology (Laubach et al. 2021; Gonzalez, Chase, and O'Connor 2023; Dee et al. 2023; Ferraro, Sanchirico, and Smith 2019; Grace 2024). Laubach et al. (Laubach et al. 2021) and Ferraro et al. (Ferraro, Sanchirico, and Smith 2019) draw on methods from other disciplines, especially epidemiology and economics, providing an analytical roadmap for causal inference based on causal diagrams and structural knowledge of the system. Gonzalez et al. (Gonzalez, Chase, and O'Connor 2023), on the other hand, propose a framework based on the '**detection** and **attribution**' approach developed in climate sciences (Bindoff et al. 2014). This five-step approach starts with a

theoretical causal model guiding data collation, followed by estimating and detecting change in the target biotic variable, and, finally, attributing this change to a **driver** (Gonzalez, Chase, and O'Connor 2023). Grace (Grace 2024) on the other hand, proposes an integrative paradigm harnessing mechanistic understanding and fully utilizing evidence across different research studies. Yet, despite the developments of conceptual frameworks for causal inference, there is a lack of practical guidance to overcome the range of problems that ecologists face. Here, we address key challenges of biodiversity change **detection** and conservative causal **attribution** and propose solutions to overcome barriers in (1) *biodiversity and **driver** data characteristics, (2) detection of change within both data types, and (3) linking **driver** and biodiversity data for causal inference.* Specifically, we provide guidance on the choices to be made at each step of biodiversity change **detection** and **attribution**, offering a guide for selecting suitable methods based on the available data and the research question. To ease cross-referencing and understanding for non-experts, important technical terms are bolded throughout the text and defined in Table 1. For more detailed discussions on terminology, see: on discipline specific jargon (Siegel and Dee 2025), on definitions and interpretations of the term "causal" (Grace 2024), on use of causal terminology in Remote Sensing (Van Cleemput et al. 2025).

Challenge 1: Biodiversity and driver data

Several properties of data critically affect the ability to detect and attribute changes in biodiversity (Fig. 1).

The first general property is the level of structure in data collection and reporting of observations. **Structured data** (Table 1) typically come from standardized sampling protocols (referred to as "sampling structure" in Fig. 1), often with repeat sampling across years at the same location ('temporal structure" in Fig. 1, also referred to as "**longitudinal**" or "**panel**" **data**) and sometimes with a spatial sampling design ("spatial structure" in Fig. 1, Table 1) (Kelling et al. 2019). In

contrast, unstructured data consist of **opportunistic** observations (Table 1) compiled from uncoordinated data collection of independent surveyors.

The second property is data coverage: biodiversity and **driver** data can range from small to large spatial extents, short to long timeframes, and can target anything from a single species or environmental **driver** to comprehensive documentation of all species or multiple socio-economic, environmental, and biological **drivers** in a given location (Fig. 1). Further challenges emerge since multiple dimensions of biodiversity may change at different scales. For instance, a single metric of biodiversity can increase when considering certain spatial scales, times, and taxa, but decline in others (Dornelas et al. 2023).

Here, we highlight three main structure axes and three main coverage axes (Fig. 1), though the importance of each will depend on the type of change being detected and the **driver** and **response** in question. Below, we discuss the main challenges associated with data streams that vary with respect to these axes and highlight the key trade-offs that need to be considered for **detection** and **attribution**.

Challenge 1.1 - Biodiversity data

Data Structure

Whilst **structured data**, arguably the most desirable type of data for **detection** and **attribution**, remain rare, unstructured data are increasingly abundant due to online platforms like iNaturalist and data aggregators such as GBIF (Global Biodiversity information Facility), which involve reporting and aggregation of observations by experts and casual observers. Semi-structured data, such as eBird (Kelling et al. 2019), combine elements of **structured** and unstructured data, allowing variable data collection protocols but with improved documentation and interoperability. Finally, synthesis databases like BioTime (Dornelas et al. 2018), Living Planet Database (Loh et

al. 2005) or PREDICTS (Hudson et al. 2014), aggregate numerous independent studies, resembling semi-structured data: each study is internally standardized, but observations across studies vary in methodology and spatial-temporal resolution, with some minimum inclusion requirements and no *a priori* overarching protocol controlling which sites, species and times are sampled.

Structured or semi-structured data have many attractive features for monitoring and attributing trends since sampling variability is minimized or can be modeled with the available metadata (Bayraktarov et al. 2019). Repeated sampling at the same location (e.g., permanent or quasi-permanent plots), common in **structured data**, is ideal for detecting changes over time (Kapfer et al. 2017). However, **structured data** face trade-offs in spatial, temporal, or taxonomic coverage (see next section) (Isaac and Pocock 2015), which means that they are usually restricted in space and time and to select taxa (Estes et al. 2018), limiting their ability to capture ecological processes acting at larger scales (McGill 2019). Unstructured data, while abundant and broad in coverage, are prone to bias and require complex analytical approaches to isolate true biological signals from sampling variation and bias (Dobson et al. 2020; Rapacciuolo, Young, and Johnson 2021; Isaac et al. 2014).

Data Coverage

Coverage is critical for both **detection** and **attribution** but for different reasons. A broad coverage across a wide range of relevant species, ecosystems, and regions, or time, enhances the ability to detect change across broad systems and to characterize its mean and variance. For **attribution**, wide spatial and temporal coverage is essential to describe the **response** curve of a species to a **driver**, requiring sampling across a range of **driver** values (Thuiller et al. 2004). Moreover, **responses** to ecological thresholds can only be detected with sufficient sampling at

extreme values that surpass the threshold (Spake et al. 2022). Typically, there are trade-offs between the three coverage axes (Fig 1a), such as sampling many species in a limited area over a short period of time versus sampling a single species repeatedly over a large area over a long period of time. The coverage axes (Fig 1a) also trade-off with the level of structure. For instance, unstructured data from GBIF have greater spatio-temporal taxonomic coverage than **structured data**, which often cover narrower areas along the three axes. However, developments like the Biodiversity Information Standards (TDWG) ratifying the Humboldt Extension to the Darwin core (metadata standards for monitoring and survey data, including sampling effort/metadata), and GBIF's adoption of these standards have the potential to reduce these trade-offs, shifting unstructured data towards being semi-structured where possible (Sica et al. 2022).
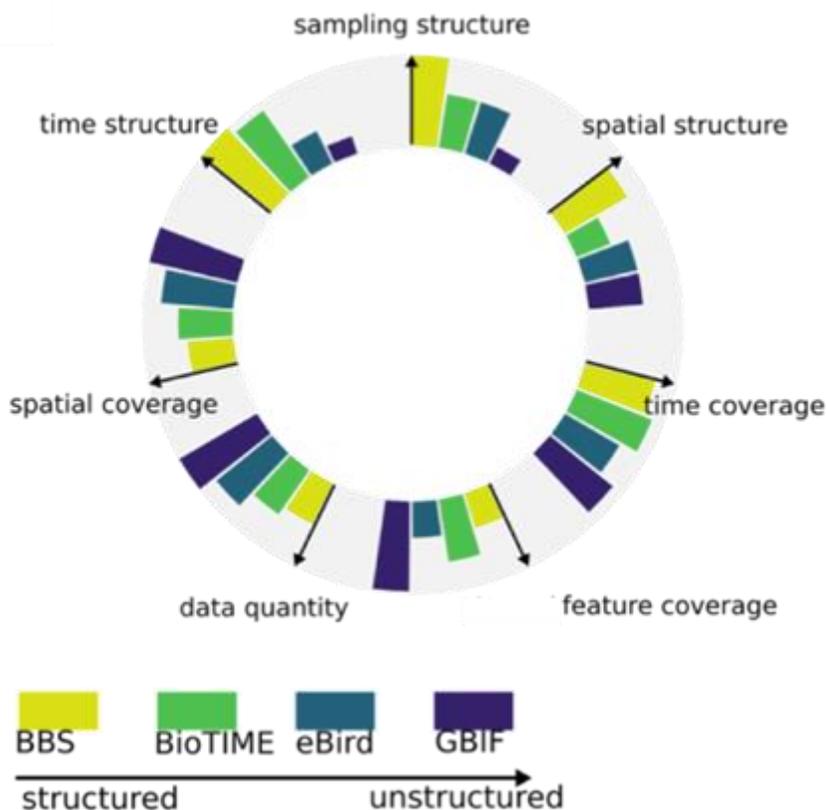
Figure 1 Existing biodiversity databases vary along seven major axes of structure and coverage. Biodiversity change **detection** and **attribution** data should ideally score highly on all of these axes. However, all databases (and sources of data, including from remote sensing) score low to medium on at least one of the axes. We illustrate such trade-offs on the example of four databases that were selected to follow a gradient in data structure (i.e., from a typical highly **structured** Breeding Bird Survey that is found in many European countries and the US (e.g. the British BBS, lime green) to the unstructured GBIF (purple) database). The height of the bars indicates the qualitative score along each axis for each database (indicated by colors) relative to the other databases based on published data and relative estimates. For example, the **time series** (Table 1) in BioTIME (green) may span over 100 years and be structured in time (high time coverage and structure) but is less structured in space (low spatial structure) and can be spatially limited to a single lake or forest patch (medium spatial coverage). In contrast, national breeding bird surveys (lime green) gather bird monitoring data with a high spatial structure over multiple years, but are limited in terms of spatial coverage, and citizen science platforms like eBird (blue) provide vast amounts of data (high data quantity) but for one taxon only (low taxonomic coverage) and with little temporal structure. Note that additional aspects that are of relevance, such as the data collection starting year and prior definition of study sites, are not shown in the figure. Semi-quantitative data informing this figure is presented in Table S2.

Challenge 1.2 - Driver data

Driver data on any natural or anthropogenic feature or process that could influence biodiversity, present unique challenges. While we do not aim to cover all the challenges, we here highlight some of the key considerations when dealing with **driver** data for the **detection** and **attribution** of biodiversity change. Similar to biodiversity data, **driver** data are often limited in spatio-temporal structure, resolution, and coverage (Joppa et al. 2016), likely leading to spatial and temporal

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mismatches between biodiversity and **driver** data or between research and policy on **drivers** (Mazor et al. 2018). For instance, a widely used 30m-resolution global deforestation database (Hansen et al. 2013) provides yearly data on forest cover yet many species monitoring programs (e.g., bird or mammal surveys) occur less frequently or at coarser resolutions (e.g., national park level). This causes spatial and temporal mismatches, as deforestation trends may show immediate habitat loss, but biodiversity declines often lag (e.g., species persisting in fragmented habitats before populations crash). Similarly, global fisheries data (e.g., Global Fishing Watch, FAO catch data) aggregates fishing effort at coarse spatial scales (~10-100 km) and annual intervals. However, species declines (e.g., sharks, tuna) are driven by localized, seasonally shifting overfishing hotspots (Kroodsma et al. 2018), making it difficult to link broad-scale fishing data to short-term species responses.

Additionally, we often lack variables capturing the actual **drivers** and use proxy variables that may be unsuitable for testing causality, or their value as a proxy may be scale-dependent (e.g., distance to major cities often used as a proxy of human disturbance and exploitation). Consequently, assessing the impacts of some **drivers** (e.g., climate change) is more straightforward than others (e.g., overexploitation). Remote sensing can provide opportunities to collect data on some **drivers** over continuous space and short time periods (Pettorelli et al. 2014; Lausch et al. 2019), but pose their own challenges, including confounding variables, **structured** or systematic and thus potentially highly problematic measurement errors and sometimes high uncertainty. Indeed, the number and range of confounding factors are multiplied at the large spatial scales reached by remote sensing products. Measurement error typically leads to regression dilution bias, whereby the effect of a **driver** on biodiversity would be underestimated. Therefore, their use should be accompanied by consideration of compensatory causal inference techniques to control for these biases and sources of error. For a thorough overview of the premise and challenges of using remotely sensed data for causal **attribution** in ecology see Van

Cleemput et al. (Van Cleemput et al. 2025). A number of ground-based **driver** databases (e.g., SoilTemp (Lembrechts et al. 2020), LUCAS (d'Andrimont et al. 2020)), provide granular and historical data but often with relatively low and highly biased coverage. Modeled databases (e.g., CHELSA for climate (Karger et al. 2020) or Soil Grids for soil physicochemical properties (Poggio et al. 2021)) are another rich source of **driver** information and now tend to provide uncertainty estimates to help account for the highly unstructured and low coverage input data these models are based on. Thus, although some workarounds exist, accessing highly **structured** *in-situ* or directly remotely sensed (rather than inferred) **driver data** with good spatio-temporal coverage remains challenging.

Data Structure

Driver data often suffer from a lack of systematic measurement, leading to biases and measurement errors similar to those in biodiversity data. For example, modeled climate data (e.g., CHELSA (Karger et al. 2020)) are based on *in situ* data from only a limited number of weather stations, often located in built-up areas, resulting in locally unreliable data in some parts of the world, particularly those also affected by a scarcity of biodiversity data (Daly 2006; Dinku 2019). Similarly, databases of *in situ* abiotic characteristics such as soil or geology, are often **opportunistic**, resulting in strong spatial and temporal biases (Schrodt et al. 2024). Temporal biases can also arise from changes in protocols, instruments, or observers over time (Somerton, Otto, and Syrjala 2002; Borges et al. 2024). Data FAIRness has not accelerated for **driver** data as fast as it has for biodiversity data, further limiting usability (Schrodt et al. 2024).

Land cover layers are based on machine learning **predictions** (Table 1) from remote sensing data, validated against a limited set of available ground truthing points, resulting in high uncertainty and substantial variability between different thematic classes. Yet, classification errors

from satellite data are rarely accounted for, although recommendations and approaches have been developed to account for measures of uncertainty/precision where available (Simmonds et al. 2022).

Data Coverage

Differences in the evidence base for **driver** impacts partly reflect differences in data availability and coverage. Although the situation continues to improve rapidly with new high-resolution, open-access satellite missions being launched and planned, some remotely sensed **driver** data remain inaccessible or expensive to use (Turner et al. 2015) or have too low resolution and grain size for ecological **attribution**. With satellite mission data only recently becoming publicly available and much *in situ* abiotic or socio-economic data not yet digitized, accessing historical data to match long biodiversity **time series** is challenging. Land use maps, for example, often present issues in temporal and thematic resolution (Daskalova et al. 2020) and lack the nuanced features needed to describe habitat quality or features important to different species (e.g., Lumbierres et al. (2022)). In addition, there may be socio-technical barriers to obtaining information on specific **drivers**. For instance, the resolution of human population density data (e.g.,CIESIN (2018)) typically matches political boundaries, which corresponds to relatively small areas in Europe, but large regions in Africa.

However, technological advances combined with state-of-the-art processing and interpolation methods (e.g. use of cloud-based processing solutions such as those offered on the OpenEO platform) are creating new opportunities to overcome **driver** data scarcity (Pettorelli et al. 2014), with improved mapping of land use intensity (Kuemmerle et al. 2013) pollution (Tóth et al. 2016; Pennock 2015), weather data across Sub-Saharan Africa (Kaspar et al. 2022), and remote sensing data on soils (Lausch et al. 2019), landforms (Lausch et al. 2020), and hydrology (Bauer-

Marschallinger et al. 2019). Ecologists are also exploring alternative data sources to complement remotely sensed, including ground-based imagery (Morueta-Holme et al. 2024), citizen and community science data (Davison, Rahbek, and Morueta-Holme 2024; Morueta-Holme et al. 2024), and broader geodiversity data (Schrodt et al. 2024).

Challenge 2: Detection of biodiversity change

In the **detection**-**attribution** framework, **detection** refers to the identification of directional change in the system of interest (Table 1). In biodiversity research, this step involves estimating annual or long-term trends in biodiversity metrics and assessing the degree of support relative to a historical baseline, a counterfactual state, or a no-trend scenario. The focus is generally more on estimating the magnitude and rate of change rather than a binary classification of change or no change. Trends may be estimated at the site level, but are more commonly generalized across multiple sites to derive an average rate of change that is representative of a wider area of interest. The method used to compile data significantly influences trend **detection** in biodiversity studies. Top-down approaches, which analyze global datasets using a standardized methodology, may be less sensitive to detecting biodiversity declines compared to bottom-up approaches, which synthesize local or regional studies through meta-analysis (Boënnec, Dakos, and Devictor 2024). This discrepancy arises because top-down analyses often aggregate coarse-scale data, potentially masking localized declines, whereas bottom-up approaches leverage high-resolution, context-specific data that capture finer-scale biodiversity changes. Furthermore, the choice between **structured** and unstructured **data** introduces distinct but overlapping challenges in change **detection**, influencing both the **sensitivity** and accuracy of inferred trends. Below, we explore some of these issues and present established and emerging strategies for the **detection** of biodiversity change whilst addressing these issues.

Observational processes and sampling variability

Trend **detection** methods for **structured datasets** are relatively well-established (Dornelas et al. 2013; Martins et al. 2023), often using generalized linear models to describe long-term mean trends, or generalized additive models for fluctuations over time, or less commonly, threshold regression to identify abrupt changes (Chan, Yau, and Zhang 2015). However, there is still variation in how well observational processes (i.e., sampling variability) are modeled (Chadwick et al. 2024). Ignoring observational processes is possible if the sampling methodology does not vary over time (i.e., high sampling structure, Fig 1), although the noise caused by sampling effects can still reduce the statistical power to detect a trend. State-space models (SSMs) can effectively minimize the noise caused by sampling variation (Kindsvater et al. 2018). For instance, random walk models in SSMs can account for complex data structures and can be fitted in both frequentist (e.g., Kalman filters, Laplace approximation methods) and Bayesian frameworks (e.g., Metropolis-Hastings samplers; see Auger-Méthé et al. (2021) for a guide to SSMs).

Unstructured data typically require more complex hierarchical models to account for sampling variation over space and time. If sampling variation is not accounted for, biodiversity trend estimates could be driven by changes in sampling rather than true changes in species populations or distributions. Hierarchical models such as occupancy-detection models explicitly model factors affecting **detection** probabilities (see MacKenzie et al. (2017) for a guide to occupancy models) and have been used to characterize trends in a wide range of taxa that lack large-scale **structured datasets** (e.g., most invertebrates, (Outhwaite et al. 2020)). Other methods adjust for sampling variation in effort over space and time based on the frequency of benchmark species, such as the frequency local scaling method (FRESCALO; (Hill 2012; Eichenberg et al. 2020;

Auffret and Svenning 2022)). Using citizen science data, Isaac et al. (2014) found that occupancy **detection** models and FRESCALO are both efficient methods for detecting temporal trends from noisy ecological data. Other approaches, such as thinned point process models (PPMs), similarly attempt to model both factors affecting species occurrence and the **detection** of those occurrences (Bachl et al. 2019; Adjei et al. 2023), although they have primarily been used for spatial models (see Wiegand and Moloney (2020) for a guide to PPMs) rather than trend **detection** (but see Seaton et al.(2024)). Unstructured data can suffer from different types of measurement error. The above mentioned methods primarily aim to deal with false absences (i.e., when a species is present at a site but fails to be detected), but methods are emerging to deal with false positives (Kéry and Royle 2020).

Biases and data gaps

As illustrated above, biases and gaps exist in all types of biodiversity and **driver** data. Addressing these spatial, temporal, and taxonomic data gaps is critical to draw broad inferences about biodiversity change (e.g., Henriques et al. 2020), and some assessment and reporting frameworks for assessing bias are emerging (e.g., Boyd et al. 2022, ROBITT). Whether data gaps lead to biased trend estimates depends on whether they covary with the underlying distribution of true trends (Bowler et al. 2024). Solutions to potential spatio-temporal biases due to data gaps include subsampling, weighting or imputation techniques (Bowler et al. 2024; Nakagawa and Freckleton 2011). However, the strength and validity of such approaches are highly dependent on understanding the causes of data gaps and the quality and representativeness of the original data (Schrodt et al. 2015; Bowler et al. 2024; Ten Caten and Dallas 2023). Many "generic" imputation techniques assume the data are 'missing at random', an assumption that is rarely met in environmental change studies. For example, plant trait data available in databases are highly biased towards larger specific leaf area and larger seed mass, so bias correction methods need

to be able to address this specific type of non-random bias (Schrodt et al. 2015; Sandel et al. 2015; Thomas F. Johnson et al. 2021). Similarly, approaches have been developed to specifically address non-random taxonomic bias (Henriques et al. 2020; McRae, Deinet, and Freeman 2017). Mismatches between the availability of **driver** data and biodiversity data add to the challenge of data gaps and highlight the importance of considering the coverage of heterogeneous **time series** in all facets of biodiversity and environmental change (Duchenne et al. 2022; Courter et al. 2013) (see section below on process-based modeling for **attribution** of historical trends in biodiversity).

Appropriate resolution in time and space

Detecting a signal depends on the extent sampled along the axis of interest relative to the noise and the data resolution (Santini et al. 2017; Metcalf et al. 2021). Larger extents along the temporal or spatial axis facilitate trend detection despite the noise. Since the primary focus is often on identifying signals along environmental or anthropogenic gradients, the specific extent of the environmental gradient (e.g., variation in human impact) is more important than the spatial extent .

Temporally capturing peak periods of environmental change is challenging. For example, determining peak periods of land cover change requires attention to nuanced changes in land use intensity (Daskalova et al. 2020; Mihoub et al. 2017). Remote sensing products with higher spatio-temporal resolution can further increase statistical power and enhance signal detection within a given extent, however, increased resolution can also lead to increased noise, masking the true signal. Conversely, short temporal extents may not capture trends that reverse over longer periods of time, highlighting the need for appropriate temporal sampling resolutions and long-term studies that are aligned with ecological processes (Harte, Saleska, and Levy 2015). For example, for birds/mammals, a few sampling events during the breeding season are sufficient to assess

changes among years but taxa with strong seasonal variation in activity require sampling across the activity period (e.g., flight period for butterflies), in order to account for within-year patterns before attempting to detect between-year patterns.

Non-linearity

Mostly, **detection** of biodiversity change focuses on linear trends, which, for population or species abundance data, amounts to estimating mean annual population growth rates. Yet, growth rates naturally fluctuate over time (Duchenne et al. 2022; Rigal, Devictor, and Dakos 2020). For instance, several studies have documented the decline and subsequent increase of freshwater insect populations in Europe over the past 40 years (Outhwaite et al. 2020; Haase et al. 2023) Non-linear patterns can be more difficult to detect (Spake et al. 2022), but can have significant conservation implications. For example, a generally positive linear trend may not always indicate a growing population of no conservation concern if it is associated with a non-linear concave trend ('decelerating increase'), indicating a recent decline in abundance. In addition to non-linearity, non-monotony of trends also implies that the temporal extent of the data, particularly the baseline year, strongly impacts linear trend estimation (Duchenne et al. 2022; Daskalova, Phillimore, and Myers-Smith 2021). Similarly, a narrow temporal window increases the risk of capturing transient dynamics (e.g., Harte, Saleska, and Levy 2015). Recently, frameworks have been developed to characterize and classify non-linear trends (Rigal, Devictor, and Dakos 2020) and abrupt shifts (Pélissié, Devictor, and Dakos 2024) in **structured** time-series using polynomial effects and break detection methods, offering more consistent solutions to characterize the variability in trends. In the former, second-order polynomial functions are fitted to the trends using least squares regression and then summarised using metrics such as direction, acceleration, velocity and change points. In addition to the stable, linear and quadratic options defined in Rigal et al. 2020,

Pélissié et al. 2023 add an alternative by detecting step changes and selecting the best fit among the four models using the Akaike information criteria adapted for small **time series**.

Challenge 3: Attribution

Change **attribution** typically refers to the process of identifying and assigning causality to the factors, events or processes ('**drivers**') that lead to an observed biodiversity change or outcome ('**response**'). In other words, a **causal relationship** is a "situation where two variables are connected through some mechanism or means such that variations in one can propagate to subsequent variations in the other" [(Grace 2024)](#).

In most cases, the interest extends to quantifying the magnitude and direction of these **causal relationships.** Causal biodiversity change **attribution** combines insights from change **detection** with data on biological, environmental or anthropogenic pressure variables. Recent studies have introduced ecologists to causal inference methods commonly used in other disciplines [(Laubach et al. 2021; Dee et al. 2023; Ferraro, Sanchirico, and Smith 2019)](#). Here, we aim to contextualize causal inference methods within biodiversity change, discuss concepts that influence decisions, and outline possible workflows using different data types on **drivers** and biodiversity **responses**.

Analytical workflows for causal attribution of biodiversity change

Change **attribution** can be depicted as a multi-step process of data preparation/exploration, building the causal model (i.e., identification of the potential **drivers**, covariates, and the biodiversity metrics), followed by quantifying the **causal effect** of **drivers** on the biodiversity metrics, and finally model evaluation and interpretation (Fig. 2A). The choice of an **attribution** method depends on the direct **drivers**, potential covariates and biodiversity data characteristics,

the question being asked and the prior knowledge of the system. Methods vary along a continuum from more exploratory to knowledge-based methods, that may include several of the four steps (see Fig. 2B for some examples from published studies). Below we outline details of the considerations and choices that need to be made at each of these steps.
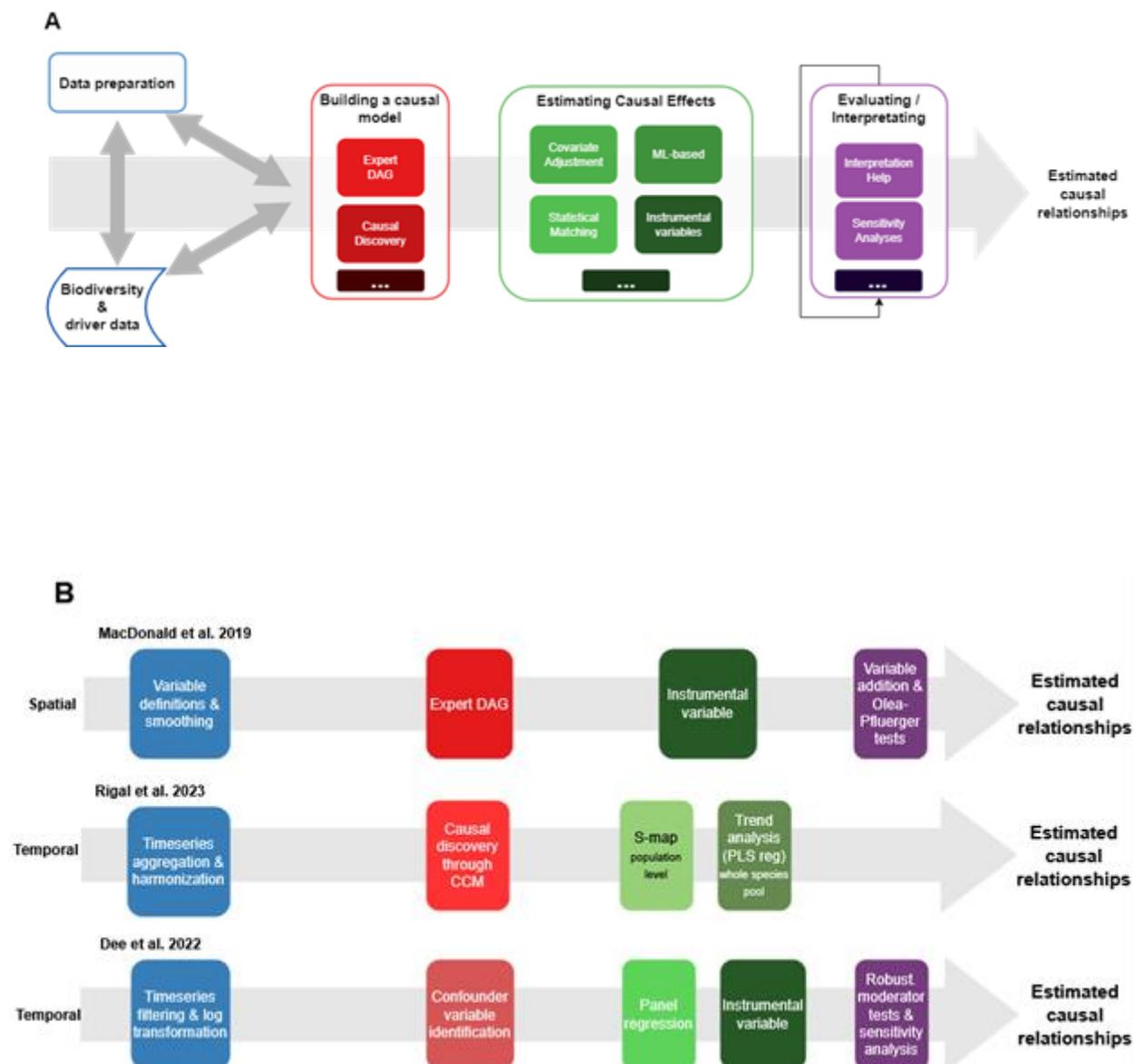
Figure 2 (A) Workflow from data to estimated causal relationships, providing key families of methods for each step. Depending on the data and knowledge available, the workflow may start with either data and their preparation (blue boxes) or causal model building (using either an expert DAG (dark red box) or Causal Discovery (light red box)), and several cycles of these steps may be required before continuing to the next one. Causal effect estimation can be performed using one or a combination of several methods (indicated by different shades of green boxes). The final step, evaluation and interpretation (purple boxes) is crucial for interpretation and should ideally be considered prior to causal effect estimation. Please note that the groups of methods shown here are only a few indicative examples, many others methods are available. (B) Key examples of applications of these steps in published ecological studies (MacDonald, Larsen, and Plantinga 2019; Rigal et al. 2023; Dee et al. 2023). Colors correspond to the steps outlined in (A), with different groups of methods indicated by different shading (e.g. dark green box = instrumental variables). Further examples can be found in Figure S3.

Step 1: Data preparation and exploration

In biodiversity change **attribution**, the task of data preparation and exploration often interacts iteratively with the task of building the causal model until all relevant **causal relationships** are identified (Fig. 2). For example, causal discovery methods (see "Data Driven Causal Discovery" below) require data that conform to specific formats and assumptions, which necessitates preprocessing before identifying relationships (e.g., dealing with data gaps, see Challenge 2). The identification of missing relevant variables or covariates may require additional rounds of data collection and preparation, including the identification of proxy variables if measured data for the missing variables are not available. If all relevant variables are known at the start of a project, data collection and preparation can take place in subsequent steps.

Variable roles within biodiversity change attribution
Simple models, such as a linear regression between a change in species' population abundance and a change in temperature, often fail to capture the complex causality in biodiversity change due to multiple **drivers** acting simultaneously and influencing each other (e.g., temperature and drought (Bowler et al. 2020; De Palma et al. 2018)). Complex relationships among key variables

is common in the **attribution** of biodiversity change, which may explain why **attribution** is rather more challenging in ecology than in climate sciences. In climate **attribution** studies, radiative forcings are modeled as *exogenous* variables (external to the system), which greatly simplifies the inference of **causal effects** (Hannart et al. 2016). In biodiversity science, such exogeneity cannot be assumed because of the multiple cross-interactions between the variables of interest. It is thus key to a robust analysis to carefully identify the role of all variables in a study system before selecting the data and the appropriate model.

Within the framework of structural causal models, variables are classified into three main types: **confounders**, **colliders**, and **mediators** (Table 1; Fig. 3 (Laubach et al. 2021)). Ecologists have mainly focused on **confounders**, often overlooking the role of **colliders** and **mediators** due to a lack of awareness of their potential importance. Depending on the variable's role, different problems arise when the variable is excluded from the model (e.g., confounding, omitted variable bias) or included in the model (overcontrol, **collider** bias, M-bias, Table 2 fallacy) (Rinella, Strong, and Vermeire 2020). In ecology, a common modeling approach is to include all potentially relevant variables in a multiple regression model (a 'causal salad' regression) in order to control for potential confounding variables. However, this practice can lead to more biased estimates of variable effects than those resulting from potentially excluding key variables in an a priori selection (Cinelli, Forney, and Pearl 2020). Building a DAG (Directed Acyclic Graph) can clarify the roles of different variables and help identify which variables need to be included in a model for causal inference (e.g., Guzman et al. 2024; Fig. 3).

Confounders

Confounders occur when a third variable (Z) affects both the **driver** (X) and the biodiversity **response** metric (Y) ($X \leftarrow Z \rightarrow Y$; Fig. 3A). For example, a loss of species richness attributed to fragmentation alone could also be driven by habitat loss. Habitat loss confounds the overall effect

of fragmentation on species richness ('direct effects' in Fig. 3A). Similarly, the long-term recovery of plant and lichen species due to reductions in a specific air pollutant is difficult to attribute with certainty because of simultaneous declines in multiple pollutant intensities (particularly nitrogen and sulfur deposition), driven by concurrent pollution control policies ('indirect effects' in Fig. 3A) (Dise et al. 2011). Spatial and temporal analyses can differ in their susceptibility to confounding. Spatial gradients in **drivers** can be useful for **attribution** because they are typically stronger than temporal gradients over sampling periods (Oedekoven et al. 2017; Blüthgen et al. 2022), but they are also more likely to be confounded by other covariates (Viana, Keil, and Jeliazkov 2022). Studies using time-series can often better handle confounding factors because of weaker coupling of **drivers** and the fact that cause must precede effect.

Mediators

Mediators are variables (Z) that lie on the causal path between the **driver** (X) and the biodiversity metric (Y), creating indirect paths from exposure to outcome that break the flow of the information (X → Z → Y). They should not be conditioned when estimating a total effect, i.e., data should not be stratified to consider specific/individual values of the **mediator** variable. Including **mediators** in biodiversity change **attribution** within a 'causal salad' regression can lead to overcontrol, blocking indirect pathways. For instance, macroclimate change affecting species may be mediated by microclimate buffering from forest cover (De Frenne et al. 2021), while urban night lighting may mediate the effect of city regulation on insect abundances (Fig. 3B). In contrast, if the objective is to estimate the direct effect of city regulation, rather than the total effect of both night lighting and city regulation, indirect pathways should be blocked by conditioning on the **mediator**.

Colliders

Colliders (Z), or common effects, are shared effect variables of both the **driver** X and the biodiversity metric Y (X → Z ← Y). When conditioned on, these variables induce bias by opening up non-**causal relationships**, and consequently should not be controlled for, nor should their descendants. Generally, this occurs when a post-**treatment** variable (Table 1) is included in the model. For example, plant abundance may be a **collider** variable when studying the impact of ecosystem disturbance (e.g., a fire) on herbivores, since plant abundance can also be affected by herbivore abundance (Fig. 3C).
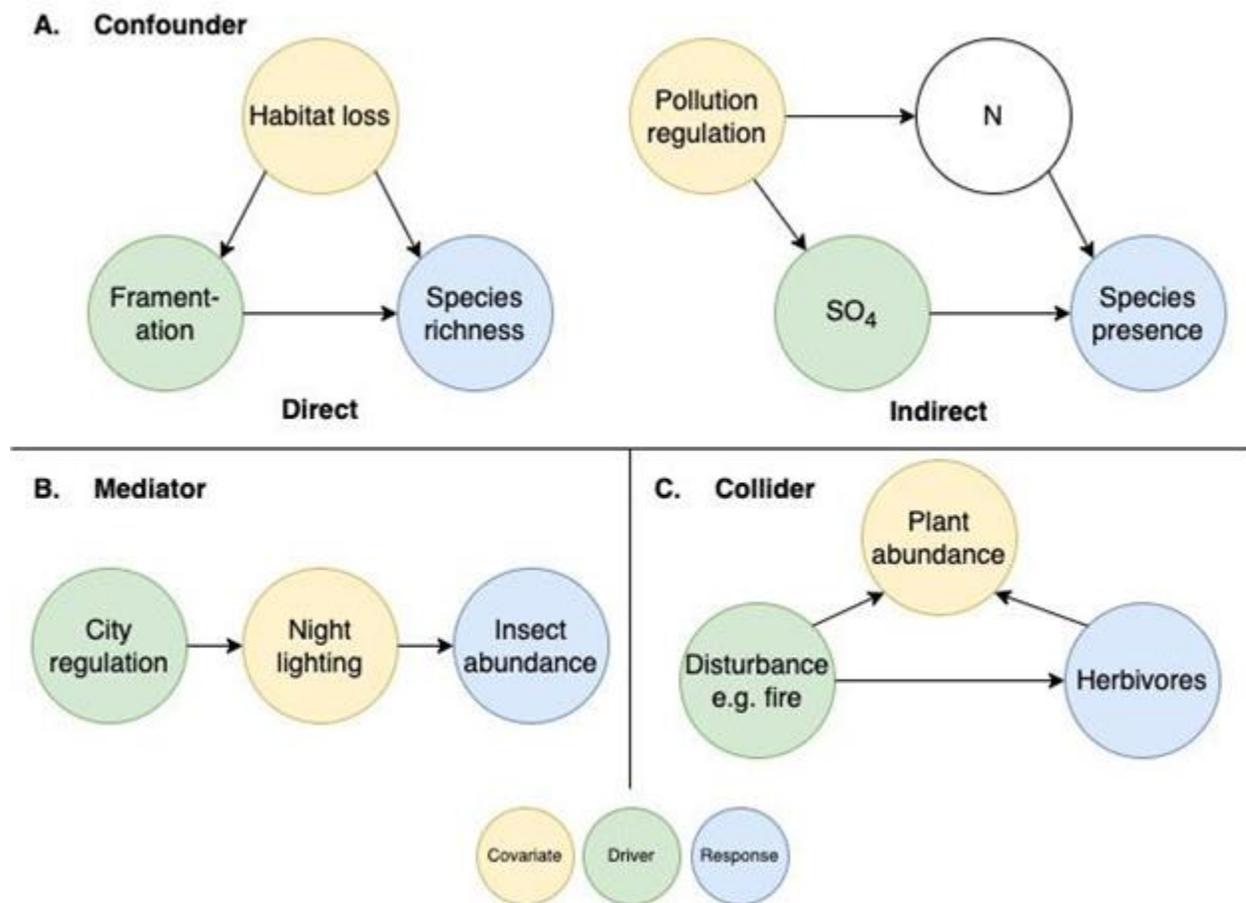
Figure 3: Examples illustrating the primary roles of covariates (yellow) interacting with a driver (green, the target of the causal effect estimation) and/or biodiversity response (blue). (A) direct (left) and indirect (right) confounders, (B) mediator and (C) collider covariates. In (A), confounding covariates must be included in the model to correctly estimate the causal effect of the driver. In (B), the mediating covariate could be included in the model to understand a possible pathway through which city regulation acts, but this would split the estimated total effect of city regulation. In (C), the covariate is a collider and should not be included in the model to estimate the effect of the driver.

Unobserved variables
The application of causal discovery algorithms necessitates the formulation of robust assumptions about the data-generation process, which in turn affects the data preparation. These assumptions typically include time-series causal **stationarity** (constant mean, variance and autocorrelation structure over time, Table 1) and causal sufficiency (the absence of **unobserved confounders,** Table 1). While some methods can deal with unobserved **confounders** under additional assumptions, identifying the target effect (i.e., the specific **causal relationship** or quantity we aim to identify, measure, or infer from our data) requires having access to variables measuring the processes that generate/cause the data. Whilst these processes are rarely fully known or accurately captured with ecological data, we can assume, infer and estimate them. Several methods have been adopted from other disciplines to do this using ecological data, including design adjustments (nested sampling and statistical designs) and causal diagrams (Byrnes and Dee 2024).

Lag effects
Finally, lag processes or "ecological memories" are ubiquitous in ecological systems but can be difficult to detect or incorporate. For example, forests may not show measurable **responses** to droughts until years after the drought event (**driver**) has occurred (Kuhn-Régnier et al. 2021; Pretzsch 2022). Moreover, time lags can lead to spurious feedback loops when constructing **causal graphs** (see Table 1 and Fig. S2/step 2 of the workflow). Similarly, lags can be of a spatial

nature, often considered in terms of spatial buffers or landscape-scale effects. For instance, in freshwater systems, **drivers** acting upstream may affect biological **response** measurements downstream, i.e. spatially removed from the **driver.** If these lag effects are not incorporated into a causal model, even very strong connections might be missed, or at least misestimated. Methods such as signal regression offer efficient ways to estimate how the effects of a variable change with spatial scale or temporal lag and can be fit with commonly used generalized additive models (Wood 2020).

Step 2: Building a causal model

Directed Acyclic Graphs (DAGs) provide conceptual representations of causal assumptions of a system (Arif and MacNeil 2022a; Laubach et al. 2021; Ferraro, Sanchirico, and Smith 2019). Highlighting direct and indirect pathways helps identifying variables as **colliders**, **mediators** or observed/**unobserved confounders** (Fig. 3), without first making assumptions about the variable distributions (normal, non-normal) or form of the relationships between the links (i.e., linear, non-linear, abrupt). It is recommended to include **unobserved** variables as incomplete DAGs may lead to inaccurate causal estimates/conclusions. In addition, the scale (temporal, spatial, organismal) at which phenomena are studied needs to be clearly defined, as mechanisms in biodiversity science are strongly scale-dependent. Climate influences land use at global and regional scales, but locally the microclimate is also strongly modulated by specific land uses and configurations, potentially reversing the main direction of causality (Fig. S1). Opposing directions of causality can create unwanted feedback cycles in DAGs which are acyclic by construction. Careful consideration of the space and time-scale for which the DAG applies can help clarify the most relevant direction of causality (see Fig. S2). DAGs can be built based on prior knowledge of the system ('expert DAG'), data-driven causal discovery algorithms, or a combination of both.

Expert DAG

In biodiversity sciences, there is often at least some basic domain knowledge about how variables relate to each other. The first step is therefore to put hypotheses down on paper in the form of a DAG, representing the variables present in the dataset and any other variables that are thought to be involved in the system, even if they are not initially connected to the graph. Second, a review of the literature should help to identify important missing covariates. Ideally, data matching the newly identified covariates can be collected and aligned with the existing samples to enrich the dataset (see 'Step 1'). If not, such covariates remain **unobserved** and will affect effect estimation. When working within the Structural Causal Model (SCM) framework, the causal Markov assumptions of the DAG need to be checked: are the (conditional) independencies drawn in the DAG verified in the data distribution? In other words, for any given relationship between a **driver** X and a **response** Y through a **mediator** M ($X \rightarrow M \rightarrow Y$), the full mediation model implies that Y and X are conditionally independent given M. Testing this assumption is difficult, especially in complex models. Statistical tests of the conditional independence (e.g., by simply regressing Y and X on M and assessing whether the residuals show non-zero correlation) are accepted as indicative (Textor et al. 2016). If the causal Markov assumptions are met, the DAG data are consistent and an effect estimation method can be applied. Otherwise, the DAG should be refined to reflect the interdependencies present in the data. See Arif and MacNeil (2022a) for a comprehensive review in an ecological context.

Overall, expert DAGs are intuitive, but are sensitive to prior knowledge, with the risk of, for example, missing relationships or recent discoveries, or being biased when translating findings from the literature to other systems.

Data Driven Causal Discovery

When researchers lack sufficient confidence in their representation of the data-generating process, or when little system knowledge is available, causal discovery or causal search can help identify pathways and directions of causality (Spirtes and Zhang 2016; Song et al. 2022). The choice of method depends on the type (**spatial/cross-sectional** or **temporal/longitudinal** (Table 1)) and sample size of the data, assumptions about the data-generating process (**stationarity**, **contemporaneous effects** (Table 1)), and the need to handle **latent** (**unobserved** but inferable) variables or **confounders** (Table 1). Conditional independence-based (or constraint-based) methods which start with an undirected graph linking all variables and then remove or redirect links based on conditional independencies in the data include the Peter-Clark (PC) algorithm (Spirtes, Glymour, and Scheines 1993), its flexible adaptations for time-series data (Runge, Nowack, et al. 2019), and the Fast Causal Inference algorithm (FCI (Spirtes, Glymour, and Scheines 1993)), which relaxes the causal sufficiency assumption.

Score-based methods (e.g., Greedy Equivalence Search (GES) (Chickering 2003)), Fast Greedy Search (FGS) (J. D. Ramsey 2015), or the Greedy FCI algorithm (Ogarrio, Spirtes, and Ramsey 2016)) are computationally more intensive because they add the causal links one at a time to increase a fit score. Another class of models are functional causal models such as the semi-parametric nonlinear additive noise models (Hoyer et al. 2008), that identify pairwise dependencies, or the linear LiNGAM method (Shimizu et al. 2006), which exploits the non-Gaussianity of the data. New methods recast causal discovery as an optimisation problem, benefiting from recent deep learning advances in neural combinatorial optimisation (X. Zheng et al. 2018; Pamfil et al. 2020; Zhu, Ng, and Chen 2019). For an exhaustive list of available causal discovery methods and software implementations, we refer the interested reader to Table 3 of the review by (Nogueira et al. 2022) and to (Glymour, Zhang, and Spirtes 2019) for a short illustrated review.

Complementary approaches, notably when assuming deterministic data processes and non-linear relationships, are state-space reconstruction approaches. The most widely used of the latter in ecology is Convergent Cross-Mapping (CCM [(George Sugihara et al. 2012)](#)), which assumes that in a dynamic system the exposure variable contains information about its causal predictor and thus allows cross-mapping within a reconstructed state-space. Whilst we distinguish between methods used for discovery versus those used for attribution, CCM can fulfill both purposes. CCM is based on empirical dynamic modeling and can help identify the direction of effects (discovery) but also quantify the strength of an effect via predictive power estimation (estimation). Many developments are available to tackle challenges present in ecological data such as short **time series** (multispatial CCM [(Clark et al. 2015)](#); Cross Map Smoothness [(Ma, Aihara, and Chen 2014)](#); latent CCM [(De Brouwer et al. 2021)](#), synchrony (Convergent Cross Sorting [(Breston et al. 2021)](#)), bidirectional coupling (Continuity Scaling [(Ying et al. 2022)](#)) or **cross-sectional/spatial data** [(Gao et al. 2023)](#). CCM can also be part of the estimation of **causal effects** (see 'Step 3').

Step 3: Causal effect estimation (causal inference)

Once a **causal relationship,** in form of a **causal graph** or **causal discovery** has been established, the objective is to estimate the associated **causal effects**, i.e., to quantify the respective magnitudes of **causal effects** acting on a given **response** variable. As described in the glossary, **causal effects** can be quantified using different metrics, depending on the scale, objective and methods of the study. In the following, we will adopt the generic term **causal effect,** as we believe that it is beyond the scope of this perspective to detail the different estimates associated with each method. It should be noted, moreover, that estimates depend on the assumptions made when constructing the graph. Ideally, graphs and estimates should be repeated over a range of likely assumptions to obtain robust results. Apart from repeatedly running the models, one can increase the robustness of the result and facilitate interpretation by

applying methods before (e.g., statistical matching, instrumental variables, see below) or after (e.g., **sensitivity** analyses, see next step and Table 1) the causal model. Some of the more commonly used methods are outlined below, with assumptions for causal interpretation and key considerations given in Table S2. For a near-complete list of available methods and software for **causal effect** estimation, see Table 12 in (Nogueira et al. 2022).

Covariate adjustment

Covariate **adjustment** (or selection) is the most widely used method for estimating **causal effects**. It consists of selecting the set of variables in a DAG to serve as model inputs in the next step. The Structural Causal Model (SCM) framework suggests rules for doing this, such as the backdoor criteria (Pearl 1995; Saavedra et al. 2022). This approach essentially means controlling for **confounders** (closing back doors) but not controlling for **colliders** (not opening the back doors) or for **mediators** (to avoid interrupting the information flow). Witte and Didelez (2019) review further selection procedures, which differ in their requirement for prior knowledge and/or the aim of the analysis. Once a set of controlling variables has been identified, the **causal relationship** can then be estimated using traditional modeling approaches (i.e., regression models) or, for more complex scenarios, machine learning approaches (random forest algorithms, neural networks etc). In the case of **unobserved** confounding variables, there are further approaches using variation within site or years (Byrnes and Dee 2024). The best set of controlling variables depends on the specific focal **causal relationship** of interest, which means that separate models might have to be constructed if there are multiple **causal effects** of interest (Guzman et al. 2024). For the same reason, it is important that the effects of the control variables are not interpreted as **causal effects**, to avoid the Table 2 fallacy (see Westreich et al. 2013 for further details).

Structural Equation Models

SEM is a methodology originally adapted from traditional path analysis that provides an explicit connection between data and theoretical ideas, allowing for complex ecological systems and causal networks to be modeled. This includes modeling direct and indirect pathways to the **response**, as well as constructing **latent** and composite terms. SEMs are evaluated using a theory-driven iterative framework that evaluates models through tests of parsimony. Prior to estimation, a conceptual model is constructed from selected variables using ecological theory, expert opinion and existing literature (i.e., the proposed model). Proposed models are then assessed for relative model fit (e.g., comparing the model-implied and observed covariance matrices), and pathways are re-evaluated if model fit is not satisfactory. Essentially, this process ensures all confounding pathways on endogenous variables are included in the model prior to estimation (see (Grace et al. 2010; Fan et al. 2016) for reviews)

There are several types of SEMs (e.g., covariance-based, piecewise, and Bayesian), each with strengths and limitations. For example, piecewise SEM can accommodate non-linear pathways (e.g., mixed effects) but cannot accommodate **latent** terms (Lefcheck 2016). Covariance-based SEM generally requires large datasets and may have limited scope for multi-level endogenous categorical variables due to model over-identification issues. These factors should be assessed and selected based on the data structure, target system, and research question at hand. As with other regression-oriented techniques, estimates of **causal effects** within SEM may be biased if predictors correlate with the error terms of the **response** variable, which could be addressed with tools such as instrumental variables (see below) where appropriate (Grace 2021).

Statistical matching

Matching methods allow the effects of specific interventions to be isolated by accounting for potential confounding issues due to selection bias (i.e., the fact that interventions are typically

non-randomly placed), prior to model application (Stuart 2010). These methods essentially adjust for differences in covariates between **treatment** levels to create a design that more closely resembles a randomized experimental design. Matching can also be used to improve the rigor of other quasi-experimental approaches, e.g., to select appropriate control units for difference-in-difference or BACI analyses . In ecology, such methods are already commonplace for assessing the effectiveness of protected areas (Schleicher et al. 2020). Often, such matching of **treatment** and control sites is done intuitively during study design (Redhead et al. 2022), but statistical matching methods also allow this to be done after data collection and are thus useful when relying on existing datasets/ databases (Emmons, Deel, and Davis 2022). This method involves deriving a propensity score (PS), defined as the probability of **treatment** assignment given the observed covariates, (D. S. L. Ramsey et al. 2019), which can be used to group similar control and **treatment** observations - even with high-dimensional covariates - and allow unbiased effect estimation under the causal sufficiency assumption. While originally developed for single binary **treatments**, there are extensions to handle continuous (generalized PS or GPS (Zhao, van Dyk, and Imai 2020)) or multiple **treatments** (McCaffrey et al. 2013). However, propensity scores do not always perform better than multiple regression as a way to control for **confounders**, at least with large datasets (Wilkinson et al. 2022).

Instrumental variables
In some cases, the **treatment** itself might be difficult to directly relate to an outcome, either because of possible reverse causation (i.e., if the outcome also affects the **treatment**) or omitted confounding variables (e.g., affecting both the **treatment** and the outcome). In these cases, an instrumental variable (IV) that explains **treatment** assignment but is not associated with other variables might be a better option to test for a **causal effect** of the **treatment** (Grace 2021; MacDonald, Larsen, and Plantinga 2019). An IV must satisfy two conditions (Kendall 2015), it

must: i) be a cause of the **treatment** variable of interest (*relevance*), and ii) have no **causal effect** on the outcome variable other than through the target pathway (*exclusion condition*). The second condition often severely limits the candidate instruments. IVs are then used in a two-step process consisting of, first, predicting unconfounded **treatment** levels and, second, estimating the **treatment** effect on the outcome based on the predicted **treatment.** However, the **causal effect** is only estimated from the subset of **treatment** that is actually affected by the IV (Dee et al. 2023)). Once identified, IVs can be integrated in different models, such as regression (Kendall 2015) or SEM (Grace 2021). While IVs are appealing, selecting variables that satisfy the above two conditions is challenging which has resulted in IVs not being used as much as other causal inference approaches.

Other quasi-experimental methods
When trying to estimate **causal effects** but facing confounding effects between **treatment** and outcome biases, quasi-experimental or natural experiments offer practical solutions to mimic a randomized experiment (Butsic et al. 2017; Larsen, Meng, and Kendall 2019). Before-After-Control-Impact (BACI) designs are appropriate when **longitudinal (time series) data** are available both before and after the **treatment** assignment; e.g., the implementation of a specific intervention in conservation science. The difference-in-differences method, a term more common in econometrics, focuses on the before-after change of the difference between control and **treatment** groups within a BACI design. The key assumption is that the before-after change of both groups would be the same in the absence of the **treatment** (the parallel trends assumption). For instance, such an approach has been used to study the effects of protected areas on species trends (Adams et al. 2015; Wauchope et al. 2022). The BACI design can be replicated retrospectively using statistical matching methods. Regression discontinuity (RD) design is a related approach but with different assumptions. RD is used when there is a clear breakpoint, or

discontinuity, in **treatment** allocation, either in space or time, that separates observations into control and **treatment** groups (Wuepper and Finger 2022). In ecology, this design has been used to test the effects of a wildfire by comparing burned and unburned areas (Butsic et al. 2017). The key assumption is that local randomization holds across '**treatment**' groups around the small interval of **treatment** allocation, which means that it most resembles a natural experiment; the **treatment** effect can then be estimated by comparing the **response** immediately below and above the breakpoint. If the effect of interest is measured across sites with repeated measures over time, fixed effects panel regression can be used (Jones and Lewis 2015; Larsen and Noack 2017; Ratcliffe et al. 2024), which uses site or time fixed effects to control for **unobserved** confounding effects that are assumed to be site-specific but time-invariant, or time-specific and common to all sites. In ecology, often random effects are included for site or year but these can lead to violations of the assumption that random effects are not correlated with any covariates, preventing unbiased estimates of causal factors (Antonakis, Bastardoz, and Rönkkö 2021). Fixed effects design variants adapted to different assumptions on the nature of observed and **unobserved confounders** are another option (Byrnes and Dee 2024).

Machine learning based methods
In addition to identifying **causal relationships** as seen in 'Step 2', machine learning algorithms can contribute to quantifying unbiased **causal effects**. This is not to be confused with the field of causal machine learning (Kaddour et al. 2022), where causal inference helps solve machine learning problems to achieve better predictive power and which is beyond the scope of this paper.

One family of techniques for estimating conditional **causal effects** (Table 1) are metalearners (Künzel et al. 2019), which decompose the task of estimating **causal effects** into basic algorithms such as random forests or neural networks. In ecology, these are especially useful for estimating spatially-varying effects of causal factors, or even just describing patterns of biodiversity trends

at fine spatial resolution (Fink et al. 2023). There are different metalearners, each adapted to specific data properties and assumptions (Caron, Baio, and Manolopoulou 2022). Double or debiased machine learning (Chernozhukov et al. 2018) allows for effect estimation in a two-step process based on the Frisch-Waugh-Lovell theorem: the **causal effect** is estimated separately from the nuisance parameters, i.e., the influences of the other variables on the outcome (Fink et al. 2023). Under the assumption of strong ignorability (i.e., causal sufficiency and overlap or positivity, meaning the **treatment** assignment probability is strictly between zero and one), causal forests (Wager and Athey 2018; Hahn, Murray, and Carvalho 2020) allow to obtain unbiased causal estimates. Finally, the benefits of supervised learning can be combined with the additional information provided by instrumental variables (Hartford et al. 2017).

Other methods

The Empirical Dynamic Modeling (EDM) framework is suited for **time series** data when separability of variables is not given (i.e., the influence of individual variables on an outcome can not be clearly distinguished and isolated) and interaction strengths or signs may change over time. Convergent Cross-Mapping (CCM), which we discuss in 'Step 2' as a tool to identify the existence and direction of a causal link between a pair of variables (possible **driver** and **response**), can be combined with Sequential Locally Weighted Global Linear Maps (S-maps) (G. Sugihara 1994; Deyle et al. 2016) to estimate the strength of the identified relationship. Compared to other similar **prediction** techniques for **time series** (i.e., DLM), ecosystem states are weighted based on their actual similarity, i.e., their distance in the reconstructed state-space, rather than their neighbors in time. However, to our knowledge, methods from the EDM framework do not have a proven ability to disentangle **causal effects** from **confounders** and **mediators**, as done in the SCM or potential outcome frameworks under precise hypotheses.

Invariant causal **prediction** methods (Peters, Bühlmann, and Meinshausen 2016) exploit the assumption of invariance, i.e., the cohesion of the direct **causal effects** on a **response** variable in subpopulations or changing environments, to identify and estimate causal structures. It relies on common concepts and methods, and helps address challenges such as non-linearity (Heinze-Deml, Peters, and Meinshausen 2018), **unobserved** variables (Peters, Bühlmann, and Meinshausen 2016) or sequential data (Pfister, Bühlmann, and Peters 2019).

Where continuous geospatial data are available, e.g., through remote sensing, using information theory in combination with causal methods can be useful (Vernham et al. 2023). For instance, temporal pattern analyses were used together with Markov models within a sliding window approach to attribute the impacts of ecological engineering and climate change on carbon uptake (Li et al. 2023).

Bayesian networks offer another promising avenue for ecological applications. Bayesian networks, also known as belief networks or Bayes nets, are DAGs in which nodes represent random variables and edges represent probabilistic dependencies between these variables (Darwiche 2008). Bayesian networks can simultaneously integrate expert knowledge with statistically significant information learned from data, handle complex systems with many variables, and handle missing data, providing a scalable approach to modeling high-dimensional data (Borsuk, Stow, and Reckhow 2004). Another advantage is that they can model the effects of interventions (e.g., policy changes) on outcomes using 'do-calculus', which allows predicting the impacts of hypothetical changes, answering what-if questions, and thus supporting counterfactual reasoning. However, Bayes nets can be computationally demanding - as the number of variables and nodes increases, the complexity of computations for exact inference (such as marginalization and updating beliefs) can grow exponentially. A possible solution is either careful pre-selection of variables or application of distributed platforms such as DistriBayes (Ding et al. 2023). A potentially greater barrier that Bayes nets share with many other **attribution** methods is the

inability to integrate feedback loops and the reliance on conditional independence assumptions that may not hold in all real-world scenarios.

Finally, some methods are not strictly causal in the statistical sense but rely on predictability to infer or orientate causal links. The Granger causality framework (Granger 1969) does not directly provide an **attribution** in the mechanistic sense but instead tests a predictive relationship in **time series** data, i.e. whether one variable has predictive power over another, not whether X directly causes Y in a causal or mechanistic sense. Its utility thus lies in its ability to highlight potential **causal relationships** that warrant further investigation, often in combination with other methods that are more suited for **attribution**. Its main limitation apart from this is the requirement of separability, i.e., that the **driver** variable is independent from the **response** variable. Variants using random forests can deal with non-linear (Chen et al. 2004; Papagiannopoulou et al. 2017) or short multivariate time-series (Wismüller et al. 2021), while extensions relying on the time-frequency approach aim to identify periodic coupling (Detto et al. 2012) or anomalous events (Shadaydeh et al. 2019).

Step 4: Evaluation and interpretation

The **detection** and **attribution** of directional effects requires assumptions. The plausibility and strength of such assumptions should be assessed, where possible, using **sensitivity** techniques. This step is key to providing confidence in the significance of the estimated effects.

Sensitivity analyses
Sensitivity analysis is about assessing the robustness of the key assumptions behind the effect estimation methods. It evaluates how strong unconsidered **confounders** would have to be to explain away the association, i.e., how strong the confounding effect between the **treatment** and

outcome would have to be for the association between **treatment** and outcome to be non-causal (VanderWeele and Ding 2017). While the **overlap assumption** (Table 1) can be tested from the observed data, causal sufficiency can only be assessed indirectly. Testing how the results would be affected if the assumption of unconfoundedness is violated can provide confidence or necessary caution in the following interpretations. Various methods have been developed since the 1960s (Cornfield et al. 1959), including bounces for the **treatment** effect (Rosenbaum 2010) implemented in the rbounds R package (Keele 2022), but the more recent E-values and robustness values, from VanderWeele et al. (2017) and Cinelli et al. (Cinelli, Forney, and Pearl 2020) respectively, represent a major step forward by dropping strong assumptions about the nature of the unmeasured **confounders**, providing a clear reporting format to facilitate communication, and facilitating interpretation considering pre-existing domain knowledge (see also Table S1).

In addition, refutation methods test the robustness of the estimate by modifying the data and observing how the effect is affected. For example, adding an independent random variable as a common cause or replacing the data set with a randomly selected subset/bootstrapped samples should not significantly change the estimated effect. However, replacing the true **treatment** variable or the true outcome variable with an independent random variable (or placebo **treatment** and dummy outcome) should drive the estimated effect to zero. The R package DoWhy (Blöbaum et al. 2024) allows such tests to be performed with convenient functions and documentation.

Finally, partial identification consists of considering different assumptions and constructing confidence sets instead of precise point estimates based on possibly unverified assumptions (Tamer 2010). This **sensitivity analysis** can be seen as a step in uncertainty quantification where the implausible assumptions are relaxed and the causal model estimate is allowed to vary within its logical limits.

ML interpretability methods

When data-driven machine learning approaches are used to predict biodiversity patterns, traditional interpretability (explainable AI) methods can help to explain how model outputs depend on inputs (Moraffah et al. 2020). Such methods can disentangle the relative importance or the local contributions of **drivers** and their interactions. Global model-agnostic methods, e.g., Partial Dependence Plots (Friedman 2001) and Permutation Feature Importance (Breiman 2001; Fisher, Rudin, and Dominici 2018), can be used to explain the average behavior of **drivers** in the machine learning model. Local interpretability tools, including Local Surrogate models (LIME, (Ribeiro, Singh, and Guestrin 2016) and Shapley values (Lundberg and Lee 2017) can decompose the importance of **drivers** for individual **predictions.** Although derived from predictive tasks, these measures of **driver** importance are often interpreted as practical model proxies for **driver** effects on a given outcome variable. These techniques were indeed not designed for causal inference methods where the objective is to estimate a precise effect in an already identified data generating-process. However, when applied after careful variable selection informed by a causal diagram, confidence in the usefulness of these metrics can be increased. More recently, causal interpretable models have moved towards a new goal in counterfactual explanations which involve asking "what if" questions ("what if I had taken a different action, would the outcome have been different?") (Moraffah et al. 2020; Guidotti 2024). As such, counterfactual explanations are particularly valuable as they can provide actionable insights, e.g. in a conservation management context. This emerging set of models and interpretation techniques aims to bridge the gap between the importance and partial effect of variables in **prediction** tasks and effect estimation techniques.

Discussion

Rather than providing a fixed template for model building and parameter estimation, we have identified a general workflow using a selection of key methods and their requirements. The final choice for a **detection** and **attribution** approach must be made by the researcher, as it will depend on the characteristics and amount of data available, the objective of the study, the current understanding of the study system, the ecological question being addressed, and the modeling expertise available in the team. This selection can and indeed should be a dynamic process, moving back and forth between steps in the workflow and testing different methods until proceeding to the final analysis. Although it may be tempting to use some of the more advanced methods (e.g., causal discovery), they should not be used as a black box and results should not be interpreted blindly. Ultimately, causal inference and **attribution** are about improving understanding of the system, which includes awareness of model assumptions.

Causal model/DAG, facilitation beyond the analysis

Irrespective of the chosen methods and recognizing that this is not always strictly necessary, we encourage the construction and communication of a causal model, i.e., a DAG. Prior to analysis, causal models help to identify **confounders**, **colliders** and/or **mediators** and thus aid to select an appropriate method for robust analyses. A causal model can also aid decisions on data collection, as (confounding) variables may be identified that are worth collecting and/or integrating into monitoring programmes. The sharing of causal models could also support (cross-disciplinary) collaborations when links towards other disciplines become visible (Dolby 2021). Once published, a formalized DAG makes it easy to follow the authors' assumptions and rationale for including or excluding certain variables. It also facilitates the comparison between studies and verification that scientific (expert, literature) knowledge has been correctly integrated. However, it is important to note that the development of an expert DAG requires extensive knowledge of biological

phenomena, while in reality, our understanding is often superficial. This may lead to the omission of important links or **mediators** and thus to erroneous conclusions about causality. Moreover, DAGs may appear statistically sound but be fundamentally incorrect, thereby reinforcing our erroneous beliefs. Measurement errors, for example, might result in misinterpretation and biologically incorrect DAGs. They should therefore be used with care and a full understanding of the limitations and caveats inherent in DAGs.

Reporting uncertainty

Due to the complexity of ecological systems, a **detection** and/or **attribution** analysis will always involve some degree of uncertainty. This is either due to noise and bias, especially in observational data (Boyd et al. 2022; Moudrý et al. 2024; Chadwick et al. 2024), due to assumptions associated with model development (e.g., building a flawed DAG that meets modeling assumptions but may be biologically incorrect), or those associated with model selection (Copas and Eguchi 2020). The same holds for the spatial and temporal scales addressed in the study, as both trends and **drivers** depend on these dimensions (T. F. Johnson et al. 2024, Fig S2). Awareness of uncertainty and scale are key to robust interpretation of the results and should therefore be clearly stated (Gonzalez, Chase, and O'Connor 2023; Boyd et al. 2022; Pescott et al. 2022).

Bias-variance trade-off

When studying causal inference, one might assume that achieving an unbiased estimator with minimal variance is the ideal objective. This perspective contrasts with machine learning, where model selection is often driven by minimizing mean squared error (MSE) above all else.

However, in practice, causal inference does not strictly require unbiased estimators. In many cases, estimators with some bias but a lower MSE may be preferable. Grace (2024) introduced the concept of a **useful approximation** standard, which refers to estimates that are predominantly causal and at least exceed the likely degree of bias. The crucial consideration is not simply whether an estimator is unbiased but rather how its overall properties and trade-offs influence causal interpretation. For instance, in matching methods, the choice of the number of matches directly involves a bias-variance trade-off (Stuart 2010). Thus, causal inference requires a nuanced approach, balancing bias, variance, and practical applicability.

To attribute or not to attribute

While causal inference methods offer promising avenues for ecological and global change research, they are not always applicable, nor are they often the best possible choice among many possible inference approaches. In addition to the challenges discussed above, the complexity of certain phenomena is a major limitation. In real-world cases, variables may influence each other (undirected), or mechanisms may involve feedback loops (although there are approaches to deal with the latter (e.g., Wang et al. 2018; Bongers et al. 2016). These two relatively common cases violate the classical assumptions of DAGs, limiting the application of these methods. The reliance on proxy variables (e.g. use of human population density or travel distance to large cities acting as proxies for direct human disturbance/exploitation) and inappropriate resolutions (i.e. **driver** data not matching ecological **response** scales), further weaken analyses of **causal relationships**. Most importantly, DAGs can become overly complicated, making it impractical to test complex **causal relationships**. Here, again, inspiration ought to be sought from other, equally complicated systems in other disciplines, such as public health and economics that managed to establish a culture of practicing more robust **attribution** than ecology has so far.

Classical predictive approaches, such as model selection based on information criteria, have long been prevalent in ecology and frequently used to infer causality. However, increasing awareness highlights the limitations of such interpretations, as they can be misleading (Hone & Krebs, 2023; Addicott et al., 2022). Beyond potential biases arising from omitted variables and spurious correlations, a fundamental distinction exists between statistical and causal inference: while statistical inference prioritizes predictive accuracy, causal inference seeks to elucidate the underlying mechanisms driving observed changes. As a result, models incorporating all available variables may appear superior in terms of predictive performance yet remain misaligned with the structural relationships underpinning ecological processes (Arif & MacNeil, 2022a). A more rigorous validation framework is therefore essential, enabling model selection not merely based on predictive power but through explicit comparisons between causal inference methods and traditional predictive models applied without causal considerations (see workflow examples in Fig. S3). Such comparative analyses underscore the distinct objectives and divergent conclusions that emerge when causal **attribution** methodologies are explicitly incorporated into ecological modeling.

Causal inference, by contrast, is grounded in explicitly stated assumptions derived from prior knowledge or exploratory data analysis. These assumptions frame hypotheses that must be carefully formulated to avoid reinforcing pre-existing cognitive or methodological biases. Poorly constructed hypotheses—whether overly broad, incorrectly specified, or based on flawed premises—can obscure true causal mechanisms and skew inference. While causal inference methodologies rigorously define and test hypotheses about causality, they ultimately rely on classical statistical techniques for effect estimation. Consequently, their validity is contingent on both the robustness of the underlying assumptions and the appropriateness of the chosen methodological framework. Different causal inference approaches—such as Granger causality, convergent cross-mapping (CCM), and other **prediction**-based techniques—embed distinct

conceptualizations of causality, which may not always align with the specific demands of a given research question (McCracken & Weigel, 2014). Therefore, results must be critically interpreted within the context of the methodological definition of causality employed.

Simpler but well-designed correlative models may thus be a better choice, for instance, as a first step to understand a system when little is already known (Currie 2019; Nilsen, Bowler, and Linnell 2020). Such models create a first layer of scientific evidence of causal links in a system, including possible interactions of variables, which can then strengthen causal discovery or inference approaches as the data and knowledge grows. Correlative models may also be easier to interpret whilst providing similar results. For instance, propensity score matching may produce the same results as multiple regression in many, but not all, circumstances. Local experiments can further support intuitions where feasible. For more complex processes occurring on larger, less manageable scales, mechanistic models can complement correlative understanding by testing ecological processes *in silico*. Testing multiple causal inference models can offer additional support.

In conclusion, a comprehensive causal understanding of ecological systems requires both rigorous data analysis methodologies and a robust mechanistic framework (Grace, 2024). These components collectively enhance causal **attribution**, where simpler analytical approaches serve as foundational tools for refining complex causal models, revealing previously overlooked interactions, and improving inference precision (Shipley, 2016; Pearl & Mackenzie, 2018). By integrating mechanistic insights with advanced statistical techniques, researchers can more effectively disentangle direct and indirect ecological **drivers**, thereby advancing predictive and explanatory capacities in ecological research.

Perspective/outlook

A call for cross-disciplinary collaboration and method transfer

Some **attribution** methods, such as SEMs, are already well established in ecology, while others have great potential but are not yet routinely used in ecological studies (e.g., CCM). The focus of causal discovery research on high-dimensional and mixed data types is particularly promising for biodiversity data studies.

As many of these methods originate from other research fields characterized by different types and quality of data, future studies should test and compare these methods using simulated data representing hypothetical mechanisms under different ecological scenarios of change and/or *in situ* data from well studied and understood systems. This will allow us to assess their ability to capture **causal relationships**, their robustness to missing variables and noise in the data, and their data requirements in terms of resolution, coverage, and sample size. Crucially, we want to encourage curiosity about methods developed in other disciplines, and collaboration between experts in ecological data and systems and experts in **attribution** and **detection** methods.

Better (rather than more) data for detection and attribution

We have firmly entered the era of big data in ecology, as evidenced by the rise of semi-automated methods such as bioacoustics, camera trapping, eDNA and remote sensing, which will undoubtedly lead to even greater availability of ecological data in the future. But, as highlighted above, **driver** data at sufficient spatio-temporal resolution are lacking and are often a bottleneck for **attribution** studies, and biodiversity data gaps continue to limit the **detection** of change. We therefore need better, not necessarily more, data for **detection** and **attribution**. An easy win would be better collection, sharing and inclusion of metadata (e.g., eBird has fostered more detailed metadata collection than many other citizen science programs outside of **structured**

schemes), including change over time, and the collection of 'co-located data' on **drivers** and biodiversity (including individual attributes such as traits) at the same sampling locations. Constructing a DAG can help to identify limitations of the dataset/analysis and may also indicate where sampling efforts/ monitoring could be increased to collect the right variables and improve the model (Arif and MacNeil 2022a).

Linking causal and predictive frameworks

Predictive frameworks such as scenario models and digital twins are often process-based but currently lack the integration of statistical causal frameworks. This is unfortunate for several reasons. First, embedding causal models into predictive frameworks can help enhance our understanding of underlying causal mechanisms and thus reduce uncertainty around **predictions** of future states. Second, incorporating causal models in predictive frameworks helps to understand how different variables influence outcomes, providing a more robust basis for applying possible interventions in specific contexts (e.g., predicting the impacts of policy intervention on future biodiversity gains). By knowing not only what might happen, but also why, optimal strategies can be tailored to address root causes rather than symptoms. Finally, predictive models that incorporate causal frameworks can better anticipate unintended consequences and identify leverage points for interventions before consequences are realized, resulting in more robust and resilient management approaches. Better integration of **attribution** approaches with predictive ones will lead to more accurate **predictions**, better decision-making, and a more comprehensive understanding of ecological dynamics and human impacts. A range of causal predictive approaches are emerging, including causal forests and meta-learner algorithms (see 'Machine learning based methods' (Künzel et al. 2019)), that offer promise to tackle these challenges.

Acknowledgements

Table 1: Key definitions used in this manuscript.

Term	Definition	Category
Detection	The process of demonstrating that a measure of biodiversity has changed relative to a baseline or reference distribution characterizing undisturbed variation (counterfactual state), or an appropriate model-derived null expectation of biodiversity change in the absence of a human driver(s) (from Gonzalez et al. 2023)	G E N E R A L
Attribution	The process of evaluating the relative contributions of multiple potential causal factors (drivers) to a detected biodiversity change, with an assignment of statistical confidence to the causal models used to estimate these effects (from Gonzalez et al. 2023). Could also be defined as/referred to as causal inference.	
Causal Relationship	$X \rightarrow Y$ can be considered a causal relationship if there is reason to think that variations induced in X can propagate to subsequent variations in Y (from Grace et al. (2024)).	
Causal effect	For a given causal relationship, a magnitude measure quantifying how variation in the treatment impacts change in the outcome. Under key assumptions in causal frameworks (SCM, potential outcomes), this measure can be considered unbiased. Causal effects can be quantified with different metrics, depending on the study scale, objective and method applied. The most common are the overall average treatment effect (ATE), its restriction to treated units, the average treatment effect on the treated (ATT), and the conditional ATE (CATE), which restricts the ATE to a	

	subset of units that satisfy a condition on their covariates. The CATE refines the causal effect estimation when there is heterogeneity between units that blur the ATE. See **Nogueira et al. 2022** Section 4.1 *Causal effects* for mathematical definitions.	
Useful approximation	A simplified method or assumption that allows researchers to estimate causal effects when exact causal relationships are difficult or impossible to determine due to data limitations, unmeasured confounding, or complex causal structures. These approximations aim to provide reliable insights while balancing feasibility and accuracy (see Grace 2024).	
Projection	An estimate or forecast of future ecological trends or status based on analysis of current and past data on either the ecological response itself (e.g., forest cover) or associated drivers acting as proxies, and on boundary conditions that characterize future conditions (e.g., temperature change).	
Prediction	A probabilistic assessment of future trends or status based on current knowledge. Unlike projection, prediction is mainly influenced by our current knowledge, i.e. initial conditions, rather than future boundary conditions.	
Causal graph	Also **Directional Acyclic Graph** (**DAG**) or **path diagram**. A conceptual representation of the causal assumptions of a system in which all relevant variables are included (both observed and unobserved) and arrows indicate the direction of causality (from cause to effect). This allows variables to be identified as confounders, colliders or mediators and helps to select the optimal methods to be used.	C A U S A L M O D E L
Confounder	A third variable Z that influenced both the response and the driver variable. Its effect may be direct or indirect ($X \leftarrow Z \rightarrow Y$). Methods should always control for confounding variables to avoid attributing the wrong drivers.	
Mediator	A third variable Z, through which a driver variable affects the response and thus determines indirect effects ($X \rightarrow Z \rightarrow Y$). When estimating total effects, methods should not condition on mediator variables. Synonymous terms used in other disciplines are 'modifier', 'moderator' or 'modulator'.	
Collider	A third variable Z that is affected by both the driver and response variables ($X \rightarrow Z \leftarrow Y$). They should not be conditioned on when the total effects are estimated.	
Driver	Also **exposure variable**, **treatment variable**, or **causal factor** (see def. attribution). Process or feature that leads to a change in a response process or feature.	

Response	Also **outcome variable.** Variable upon which the *driver* has a causal effect (e.g., a biodiversity metric).	
Adjustment set	Collection of variables that need to be conditioned on (controlled for) to estimate the causal effect of a driver (X) on a response (Y) accurately. These variables help block confounding pathways that could distort the relationship between the driver and the response, ensuring a valid causal estimate. Adjustment sets are not necessarily unique, and multiple sets may be identified depending on the context and the causal structure of the problem.	
Estimand	A precise description of the treatment effect that a study aims to quantify, reflecting the specific scientific question of interest	
Treatment	Also intervention. A specific condition or intervention applied to a subset of the study subjects or experimental units, such as plots of land, populations, or ecosystems, to observe and measure its effects on ecological variables. A treatment might be active (e.g. application of nutrients, change of soil temperature in an experimental plot) or passive (e.g. decadal land-use change)	
Unobserved variable	Also **latent variable**, variable that plays a role in the data-generating process but is not represented in the data distribution for various reasons: overlooked, technically difficult to measure, unethical, etc.	
Overlap assumption	A requirement of many sensitivity analyses that, for each value of the covariates (i.e., characteristics or predictors), there must be a positive probability of receiving each treatment or being in each comparison group. In other words, every individual in the study population has a non-zero chance of being assigned to any of the treatment groups under consideration.	
Sensitivity analysis	Tests how strong the unmeasured confounding would have to be to explain away the association, i.e. how strong the unmeasured confounder would have to be associated with the treatment and outcome for the association between treatment and outcome not to be causal (VanderWeele and Ding 2017).	
Stationarity	A time-series is considered stationary if its mean, variance and autocorrelation structure remain constant over time. This implies the absence of a trend and periodic fluctuations.	T I M E S E R I E S
Contemporaneous effects	The effect(s) in question occur immediately, without any time lag. The causal relationship between two variables is thus 'contemporaneous'.	

		D A T A T Y P E
Cross-sectional data	Observation of subjects at one point or period of time, or for which the analysis has no regard to differences in time among the observations (Nogueira et al. 2022). In ecology, these data are typically spatial data. In causal analysis, cross-sectional data are used to examine how differences in one variable (e.g., an exposure or treatment) are associated with differences in another variable (e.g., an outcome) across subjects at the same time. However, since the data are collected at one point in time, establishing a clear cause-and-effect relationship can be challenging.	
Structured data	Data collected using a standardized and systematic sampling design to ensure consistency, comparability, and statistical rigor. These datasets are designed to minimize bias and maximize reproducibility, allowing for more robust ecological inference but are highly resource-intensive and thus not available in as large quantities as opportunistic data.	
Opportunistic data	Data collected without a standardized or systematic sampling design, often as a byproduct of other activities. Unlike structured monitoring programs, opportunistic data typically lack predefined spatial, temporal, or methodological consistency. Opportunistic data are extremely valuable and often available at larger quantities than structured data, but require careful statistical treatment to account for biases and limitations.	
Longitudinal / Panel data	Observations about several subjects at multiple points or periods of time, indexed in time order, and subject. Time-series are a particular case considering only one subject (Nogueira et al. 2022). Most typically called temporal or spatio-temporal data in ecology.	
Time series data	Observations about a single subject at multiple points or periods of time, indexed in time order (Nogueira et al. 2022).	

Table 2

Method	Assumptions for Causal Interpretation	Key considerations
	Correct model specification (all relevant paths and variables included)	SEMs assume the structure reflects causal relationships.

Structural Equation Modeling (SEM)	No omitted confounders Normally distributed errors Predictors don't correlate with error terms of the response Linear relationships (typically)	Model misspecification or omitted variables can bias estimates. Requires domain expertise for model building.
Matching / Weighting	Conditional Independence Assumption (CIA): all confounders observed Common support/overlap No hidden bias or unmeasured confounding	Balances covariates but does not control for unobserved confounders. Diagnostic checks (e.g. balance metrics , sensitivity analyses) are essential.
Instrumental Variables (IV)	Instrument relevance (strongly correlated with treatment) Instrument exogeneity (no direct effect on outcome, only via treatment) Exclusion restriction	Powerful for unobserved confounding, but finding valid instruments is difficult. Weak instruments bias estimates; validity must be critically evaluated.
BACI/Difference-in-differences (DiD)	Parallel trends (before-after change of groups would be the same in the absence of the treatment) Proper randomization No differential shocks (other than treatment)	Pre-trend testing and robustness checks are necessary. External validity can be limited
	Random effects are not correlated with any covariates	RDD gives causal effects near the threshold. Requires

Regression Discontinuity Design (RDD)	Precise knowledge of the cutoff No manipulation around the cutoff Continuity in potential outcomes at cutoff	careful bandwidth selection and validation that units just above and below cutoff are similar.
Bayesian Networks / DAGs	Correct graph structure Causal sufficiency/conditional independence assumption (no unmeasured confounders) Faithfulness and Markov assumption	Can handle complex systems and sparse data but depends heavily on expert input or data-driven discovery with strong assumptions. Can model effects of interventions.
Covariate adjustment (selection)	Known DAG and consistent with data No unobserved confounders Backdoors are closed	Effects of control variables must not be interpreted as causal effects (avoiding Table 2 fallacy)
Synthetic controls	Good pre-intervention fit No interference across units and consistent treatment definition No anticipation	Having sufficient pre-intervention periods to fit the synthetic control is key to the success of the method. Sensitivity analyses necessary.
Fixed effects panel regression	No interference across units and consistent treatment definition Within-units covariate variability	Ensuring that there is enough within-unit variation and that

	Site-specific but constant and/or time-varying but common unobserved confounding allowed	time-varying confounders have been included is key.
Metalearners	No unobserved confounders No interference across units and consistent treatment definition Good estimation of nuisance parameters	Cross-fitting of the nuisance (intermediate) parameters and choice of the metalearner suited to dataset
Empirical Dynamic Modeling (EDM)	Deterministic and stationary enough system Relevant dynamics observed: unobserved confounders of low influence Adapted sampling frequency	Suitable for time-series without separability of variables. Can't separate causal effects from confounders and mediators.
Invariant causal predictors	No unobserved confounders varying by environments Invariance assumption Multiple environments	Can handle non-linearity and unobserved variables shared between environments, needs variation across environments to identify non-causal associations
Granger causality	No unobserved confounders affecting the time series Stationary time series Prediction-based conception of causality	Time series should be pre-processed to be stationary and the sampling adapted to detect lagged dependencies

Supplementary Information
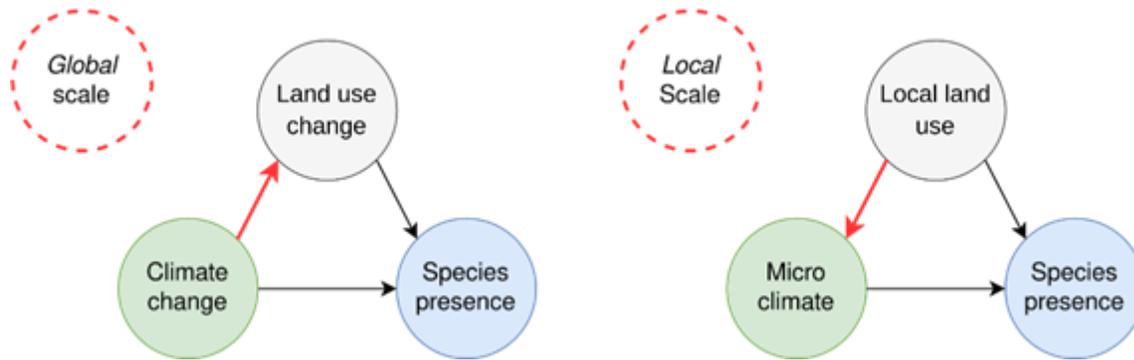
Fig. S1: Example illustrating the scale dependence of the direction of causality considering covariates (grey) interacting with a driver (green, the target of the causal effect estimation) and/or biodiversity response (blue). At the global scale, land use change should not be controlled for in order to study the total effect of climate change on species distribution, but, conversely, at the local scale, land use can be expected to influence microclimates and thus confound the relationship between climate and species presence (see also (Riva, Koper, and Fahrig 2024)).
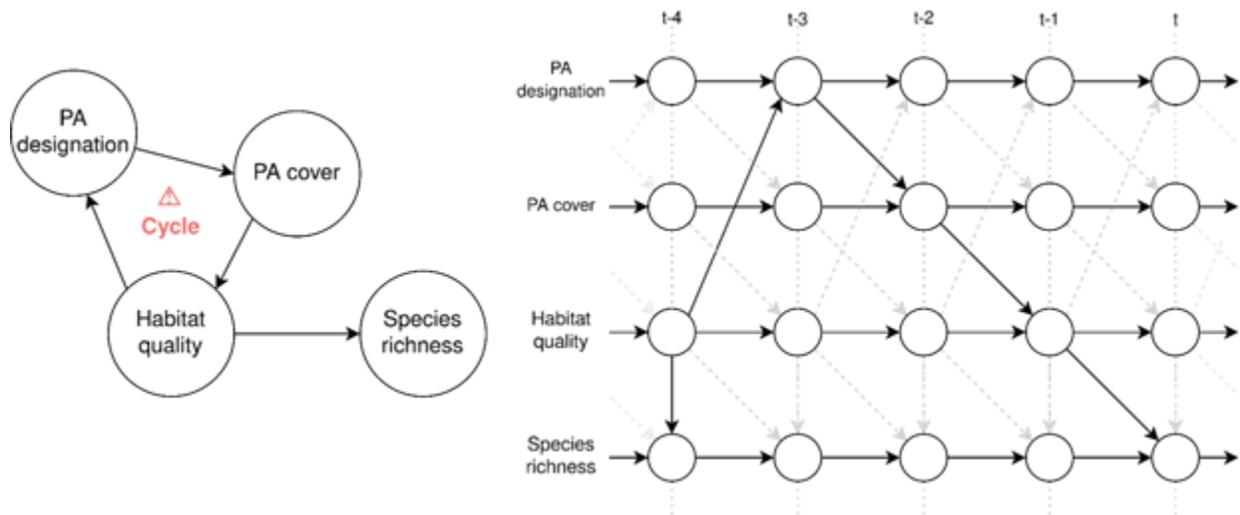
Fig. S2: When building causal models, cycles can prevent the identification of a DAG. They are often due to time lags between the variables involved. By explicitly integrating the time dimension, the variables can be disentangled and return to an acyclic graph. In this case, time-series are needed to identify and/or quantify average lag effects over time (Krich et al. 2020; Runge et al. 2023). Here, the inclusion of time illustrates how habitat quality directly affects species richness, but also the subsequent designation of protected areas (PAs), which in turn affects PA cover, and finally habitat quality.

Fig. S3: Illustration of the realisation of the attribution workflow steps identified in Fig. 1 by example studies in the field of biodiversity/ecology (Pearson et al. 2016; Rigal et al. 2023; MacDonald, Larsen, and Plantinga 2019; Dee et al. 2023; Arif and MacNeil 2023; Krich et al. 2020; Nova et al. 2021; Song et al. 2022). For each step, the applied method(s) are indicated.

Table S1: Non-exhaustive overview of programming resources and technical and non-technical entry points to the attribution methods discussed in section 3.

Step	Method family	R or Python package/ resources	Useful entry points/ explaining application	Reviews or technical details or applications
Causal Model	general	**dagitty Package** (R) - e.g., Verification of the causal Markov condition (Ankan et al. 2021) **DoWhy-GCM** (Python) - e.g., analysis of causal structures, verification of causal Markov condition (Blöbaum et al. 2024) **DAGitty** (webtool) - drawing and analysing		

		causal diagrams, verification of causal Markov condition https://www.dagitty.net/		
Causal discovery	general / various	**Causal-learn** (Python) - Classical and state-of-the-art causal discovery algorithms https://github.com/py-why/causal-learn Platform to benchmark causal discovery methods https://causeme.uv.es/	Documentation, getting started, examples https://causal-learn.readthedocs.io/en/latest/	(Y. Zheng et al. 2023; Runge, Bathiany, et al. 2019)
Causal discovery	PCMI, PCMI+, LPCMC	**Tigramite** (Python) https://jakobrunge.github.io/tigramite/	Blog post series https://medium.com/causality-in-data-science	(Runge et al. 2023) In particular the Method selection flowchart Fig. 2
Causal discovery	Information-geometric approach	Implemented in **Causal Discovery Toolbox**	Janzing et al. 2012 https://doi.org/10.1016/j.artint.2012.01.002	(Mooij et al. 2016)
Causal discovery	Independence tests,	**Causal Discovery Toolbox**	Documentation, get started and package description https://fentechsolutions.github.io/Causal	(Kalainathan, Goudet,

	graph and pairwise discovery, metrics	(Python) https://github.com/FenTechSolutions/CausalDiscoveryToolbox	DiscoveryToolbox/html/index.html	and Dutta 2020)
Causal discovery and estimation	ML-oriented reference guide	All programming languages	https://github.com/rguo12/awesome-causality-algorithms	(Guo et al. 2021)
Causal discovery and estimation	Bayesian networks	**CausalNex** (Python) - Documentation, tutorials, user guide https://causalnex.readthedocs.io/en/latest/index.html#	User guide https://causalnex.readthedocs.io/en/latest/04_user_guide/04_user_guide.html	(Darwiche 2008)
Causal discovery and estimation	Reference guide	All programming languages	https://github.com/AnaRitaNogueira/Methods-and-Tools-for-Causal-Discovery-and-Causal-Inference/tree/main	(Nogueira et al. 2022) In particular: Tab. 3 (discovery) and Tab. 12 (estimation)
Causal discovery & estimation	CCM	**fastEDM** (R, Python) - multispatial CCM & smap https://github.com/EDM-Developers/fastEDM-r **multispatialC**	Rigal et al. 2023 PNAS https://www.pnas.org/doi/10.1073/pnas.2216573120 (Application) Doi et al. 2021 https://royalsocietypublishing.org/doi/10.1098/rsbl.2020.0666 (Application in biodiv) Deyle et al. 2016	Continuity Scaling vs. Convergent Cross sorting (Bahamonde, Montes, and

		CM (R) - multispatial CCM https://rdrr.io/cran/multispatial CCM/man/multispatialCCM-package.html **Convergent Cross Sorting** (R) https://github.com/lbreston/CCS	- Quick intro & example case studies using EDM/ smap(https://royalsocietypublishing.org/doi/10.1098/rspb.2015.2258#d1e1249) **Video**: Introduction to Empirical Dynamic Modelling and the principle of CCM (https://www.youtube.com/watch?v=fevurdpiRYg&ab_channel=SugiharaLab)	Cornejo 2023)
Causal estimation	Covariate adjustment	**DAGitty** (webtool) -see 'Causal Model - general'		(Arif and MacNeil 2022b; Arif et al. 2022) (Arif and MacNeil 2022a)
Causal estimation	SEM	**piecewiseSEM** (R) https://jslefche.github.io/piecewiseSEM/ https://jslefche.github.io/sem_book/index.html **lavaan** (R) https://lavaan.ugent.be/ **semEff** (R) - calculate direct, indirect and mediator effect from a piecewiseSEM object https://murphymv.github.io/se	piecewiseSEM Lefcheck et al. 2015 https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210X.12512 Tutorial https://youtu.be/VT-gw_VVP1E?si=TJHJd1rni9q0af5z Book https://www.guilford.com/books/Principles-and-Practice-of-Structural-Equation-Modeling/Rex-Kline/9781462551910	(Fan et al. 2016)

		mEff/ **Semopy** (Python) https://semopy.com/		
Causal estimation	Matching/ PS	**MatchIt** (R) - many matching methods https://cran.r-project.org/web/packages/MatchIt/vignettes/MatchIt.html **Cobalt** (R) - Nice visualisation of matching results - many common methods https://ngreifer.github.io/cobalt **CausalGPS** (R) - Generalized PS score (multi-level treatment, continuous treatments) https://cran.r-project.org/web/packages/CausalGPS/index.html	Wu et al. 2020 (https://www.tandfonline.com/doi/abs/10.1080/01621459.2022.2144737) Ouyang et al. application in ecology	(Ribas, Pressey, and Bini 2021)
Causal estimation	Double /de-biased machine learnin	**DoubleML** (R, Python) - Documentation, user guide APIs and	User guide, blog post: https://matheusfacure.github.io/python-causality-handbook/22-Debiased-Orthogonal-Machine-Learning.html	(Chernozhukov et al. 2018)

	g	example gallery https://docs.doubleml.org/stable/index.html		
Causal estimation	Instrumental Variables		Grace 2021 Methods Ecol. Evol. SEM-IV https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.13600 Kendall 2015 Ecol. Statistics RegIV https://escholarship.org/content/qt5v21m05h/qt5v21m05h_noSplash_84105756a6bbfed2b85c95ccf7cd65f3.pdf	
Evaluation	Sensitivity analysis	**sensemakr** (R, Python, Stata) - Suite of sensitivity tools http://carloscinelli.com/sensemakr/	R vignette, useR! 2020 tutorial and software paper https://dx.doi.org/10.2139/ssrn.3588978	(Cinelli and Hazlett 2020)
Evaluation	Sensitivity analysis	**Evalue** (R, website) https://cran.r-project.org/web/packages/EValue/index.html https://www.evalue-calculator.com/	R vignettes, package paper https://doi.org/10.1097/EDE.0000000000000864	(VanderWeele and Ding 2017)
Effect estimation, interpretability	ML-based methods	**econml** (Python) - Heterogeneous treatment effects from observation data via ML https://github.com/py-why/EconML	Documentation, User Guide, tutorial https://econml.azurewebsites.net/index.html https://youtu.be/66LBrNG2un0?si=jw5hMs0DVCcIONvt	No package paper yet, references implemented listed here: https://github.com/py-why/EconML?tab=r

				eadme-ov-file#references
Effect estimation	Quasi-experimental designs	**Blogs with code** (Python, R) -Python: https://matheusfacure.github.io/python-causality-handbook/landing-page.html -R: https://www.r-causal.org/, https://bookdown.org/mike/data_analysis/		
Causal estimation	General/ various	**DoWhy** (Python) - Aims at integrating methods for all causal inference steps https://www.pywhy.org/dowhy/v0.11.1/index.html	General Overview, contains hints to R packages Reference CRAN Task view https://cran.r-project.org/web/views/CausalInference.html Getting started, user guide, documentation, examples, tutorial from ACM KDD 2018 https://causalinference.gitlab.io/kdd-tutorial/	(Sharma and Kiciman 2020; Blöbaum et al. 2024), both linked to Python package DoWhy.

Table S2: Semi-quantitative data informing diagrams in Fig. 1

	Biotime	eBird	British BBS	GBIF
Temporal coverage	1874-2024	2007-2024	1994 - 2024	1621 - 2024
Spatial coverage	35 biomes, 6 climatic zones	Global	UK	Global
Taxonomic coverage	Many taxa (incl. fishes, mammals, plants): 44 000 species	common/rare birds: 11 000 species	common / widespread species : 118 species	Most taxa: 2 600 000 species
Data quantity	15,602,025 (Shane Blowes, pers.comm)	1,000,000,000 (pers. comm Corey Callaghan)	8,138,900 (pers.com Ailidh Barnes)	About 3 000 000 000
Sampling structure		2	2	4	0
Temporal structure		2	1	2	0

Box S1: Key Considerations and steps for Causal Attribution in Ecology

Defining the Causal Relationship

- Identify the focal relationship of interest (e.g., X → Y).
- Clearly define and state your causal question.

Formulating Hypotheses and Predictions

- What types of evidence are available?
- How much evidence do we have and how consistent is the evidence?
- How strong is the agreement across different lines of evidence?
- How well does it apply to the context under consideration?
- Are there competing hypotheses, and how do their predictions differ?

Mechanistic Understanding and Data Contributions (see also Grace 2024)

- Does the data contribute to understanding causal mechanisms?
- Identify possible mediators and intermediate processes.
- Consider the depth of mechanistic understanding, including biological or social organization levels. E.g., if you were modelling a community response, think of the mechanism in terms of population responses, too.

Constructing Directed Acyclic Graphs (DAGs)

- Build DAGs based on causal knowledge and compare with DAGs based on available data.
- Clearly communicate which research you base your causal knowledge and assumptions on.
- Address key challenges:
    o Bidirectional arrows and feedback loops.
    o Temporal and spatial scale dependencies.
    o Stability of observed patterns over time and space.
    o Known and unknown, measured and unmeasured confounders, colliders and mediators

Adjustment Sets and Method Selection

- Determine the appropriate adjustment set (set of variables that should be controlled for based on the DAG for causal inference).
- Choose the right analytical method based on:
    o Nature of treatment variable (binary vs. continuous).
    o Nature of the data (spatial or temporal)
    o Confidence in identifying confounders and colliders.
    o Availability of data on confounders

- o   The number of confounders relative to the amount of data
- o   Hypothesized functional form of the causal relationship.
- o   Availability of instrumental variables.
- o   Feasibility of retrieving unbiased estimates.

Interpretation and Reporting

- Clearly state assumptions of any methods used for detection and causal attribution, and assess their robustness.
- Describe any potential measurement errors or biases and how they were addressed
- Provide details of sensitivity analyses or robustness checks performed to assess the validity of the results
- Discuss confounders, colliders and mediators and how they were controlled, including potential sources of bias (e.g., selection bias, reverse causality).
- Consider and discuss alternative explanations or competing causal pathways
- Do not interpret and report the effects of control variables as causal effects (Table 2 fallacy)
- Discuss the generalizability of the findings to other contexts, populations, or settings and, conversely, limitations related to the sample, design, or scope of the study that may affect the external validity.
- Clearly describe details if useful approximation approaches were applied (Table 1)

This structured framework supports rigorous causal attribution by integrating hypothesis testing, mechanistic reasoning, and methodological rigor.

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