Towards a causal understanding of bidirectional effects in ecology and evolution

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Abstract

Feedback loops govern many processes in the natural world and are ubiquitous in ecology and evolutionary biology. Despite their prevalence in theory, however, feedbacks and other forms of reciprocal causation are rarely quantified by empiricists working with observational datasets. This divide has been brought to the fore by the causal revolution in the natural sciences. When researchers aim to quantify causal effects, the bi-directional nature of feedbacks seems incompatible with standard tools, such as regression, which begin by distinguishing between "response" and "predictor" variables. This seems to leave empiricists in ecology and evolution with few tools, if any, to quantify bidirectional effects. First, we highlight that, when ignored, feedback can lead to bias in common statistical analyses. We then present several methods that can help researchers quantify causal effects when feedbacks are present, including models with discrete cross-lagged effects as well as continuous time models, both of which are suitable for longitudinal data. We also consider instrumental variables, which can help to disentangle bidirectional effects from cross-sectional data. Focusing on examples from ecology and evolutionary biology, our aim is to provide a general primer on the challenges and opportunities for the quantitative analysis of bidirectional causation.

Keywords

Causal inference - bidirectional - feedback loop - statistical analysis - eco-evolutionary dynamics

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1. Introduction

Empiricists in ecology and evolutionary biology typically ask questions that are causal in nature. How does a predator influence prey behaviour? How is climate change altering community composition? How does social plasticity drive variation in reproductive success? Though the word "cause" is often not explicitly used, many observational studies answering questions like these imply causal relationships [1]. This lack of explicitly causal language stems from the well-engrained fact that *correlation does not imply causation*. However, in the past several years there has been a growing consensus that under a given set of assumptions, specific causal effects can be distinguished from other statistical associations (as is already very commonly done in the practice of using "control" variables). Sometimes termed "causal statistics" [2], this approach incorporates and relies on parallel methods for developing causal knowledge, such as the synthesis of evidence for relevant biological mechanisms. Inferring causation from observational data is increasingly recognized as an important and legitimate element of analysis in the broad fields of ecology and evolutionary biology [3–5].

This growing interest in identifying causal effects has important consequences for how empiricists quantify feedbacks (i.e. phenomena that are in mutual causation). Bidirectional effects are causal by definition, meaning that they cannot be captured by simple correlations. However, common methodological approaches to causal inference are often incompatible with bidirectional effects. For example, an increasingly common tool of causal inference, the directed *acyclic* graph (DAG), seems to exclude "cyclic" processes by definition. More generally, there is an incompatibility between feedback and the implied logic of standard analyses such as regression: that one trait (*response*) is the result of another (*predictor*). Here, it is often implicitly assumed that causation flows in one direction from predictor to response. Thus, there is a rift between the ubiquity of feedbacks in ecological and evolutionary theory [6–8], and the dearth of empirical work that quantifies them. Limitations in the ability to analyze bidirectional causation may be a barrier for understanding and managing natural systems.

Feedbacks have long been recognized as important processes in ecological and evolutionary systems [7]. They are also key to many new theoretical developments, for example, reciprocal causation between organisms and their selective environments plays a central role in the "Extended Evolutionary Synthesis" [8,9], while feedback between cultural and genetic change is the basis of gene-culture coevolution (i.e., how shared patterns of behaviour influence genotypes and vice-versa; [10]). Feedbacks are important in eco-evolutionary dynamics, where ecological and evolutionary processes influence each other over time [11,12]. Bidirectional links between state (e.g., body condition) and behaviour (e.g., boldness when foraging) are thought to underlie consistent differences in behaviour among individuals, i.e., personality [13,14]. While the importance of feedbacks in driving ecological and evolutionary dynamics is often difficult to quantify, feedbacks are known to impact a variety of processes as diverse as the dynamics of ecological communities [15], links between disturbance and biodiversity [16], the interplay of behaviour and microbiomes [17], and the pace of evolutionary change [18].

Similarly common in the ecology and evolution literature are calls to address feedbacks empirically [8]. For example, regarding eco-evolutionary dynamics, quantifying bidirectional causes between ecological and evolutionary processes has been highlighted as a key goal for future research. But how should one do this? While research in areas like density-dependent population growth or epidemiological modelling have incorporated feedback processes as central parts of their quantitative work, bidirectional processes are widespread and may be overlooked and/or incorrectly accounted for outside of these domains. To the extent that bidirectional effects drive ecological and evolutionary systems, empiricists face a stark disconnect between the standard analytic toolkit (such as regression and generalized linear models, which cannot handle reciprocal causation) and the natural phenomena they seek to explain. Here we apply and extend the paradigm of causal inference to clarify how bidirectional effects can be quantified. First, we highlight the pitfalls of ignoring potential feedbacks and how reciprocal causation can induce bias in standard statistical approaches, i.e., “simultaneity bias”. Next, we provide a primer on how causal feedbacks can be quantified using observational datasets, with a focus on cases relevant for researchers working in ecology and evolutionary biology. Our aim is to empower researchers to ask and accurately answer biological questions in the presence of bidirectional causation.

2. Bidirectional effects and their pitfalls

Defining feedback and other forms of reciprocal causation

Fundamentally, bidirectional (or reciprocal) causation occurs when two or more entities are mutual causes of one another (See Glossary, Table 1). When causation flows in a loop such that a variable influences itself at a future time, the system can be considered a feedback loop, though for the purposes of this article we treat “feedback” and “bidirectional effects” as synonymous with respect to their impact on statistical analyses. Also encompassed by this is “coevolution”, which is often applied to instances of reciprocal evolutionary effects across species (e.g., predator-prey coevolution; [18]), but can also refer to bidirectional effects between sexes or between genes and culture, for example [6]. Feedbacks can be indirect, mediated through intermediate variables: for example, feedback between social structure and population density may be mediated through variation in fitness [19]. We also note a distinction between reciprocal causation and the related idea of reverse causation, when the opposite causal effect than expected occurs (e.g., when Y causes X) [20]. Feedback processes can be broadly categorized as either positive or negative, each of which has its own consequences for the dynamics and stability of the system

[7]. Positive feedbacks involve traits that reinforce each other through time, resulting in acceleration or exaggeration of change within a system, i.e., "runaway" effects. Note that positive feedback can result from bidirectional effects with a positive sign (+/+) or negative sign (-/-). Depending on the strength of the causal effects at hand, this can result in rapid transitions between alternate stable states. Generally, positive feedback processes will face ceilings or "brakes" that prevent infinite change – for example, morphological limits may restrict the extent of feedbacks between body size and behavioural traits [21]. In contrast, negative feedback involves effects of opposite sign (+/-) and often results in more stable dynamics, as each component of the loop regulates the other, though with time lags cycles can also occur.

Visualizing causal relationships through directed acyclic graphs (DAGs)

Causal diagrams are an important way to visualize and communicate assumptions about causal relationships in a study system. DAGs, a type of causal diagram, are an increasingly popular tool which have the additional benefit of helping to assert hypothesized causal relationships and then infer causal estimates under path analysis or the structural causal model (SCM) framework. In a DAG, variables are shown as nodes and arrows between them represent directional effects. For example, an arrow from A to B indicates that A causally affects B. Arrows in DAGs do not indicate the sign (positive vs. negative) of the effect nor its magnitude but are a key tool for causal inference in that they allow researchers to visualize confounds and other biases [22,23]. DAGs are theory-driven in that they are created based on domain knowledge, including expert opinion, previous studies and relevant literature. DAGs should include both measured and unmeasured variables required to depict the causal question at hand, and are only considered complete when all "common cause variables" (i.e., any variable that affects two or more variables in the DAG) are included [24,25].

Once a candidate DAG is created, researchers can apply the "backdoor criterion" to identify the variables that need to be controlled for to remove confounding, while also avoiding other forms of bias (see Glossary, Table 1). This includes overcontrol bias (e.g., including a variable on the causal path from treatment to outcome) and collider bias (including a common outcome, or "collider", of the treatment and outcome in a model; Table 1) [4,20]. In plain language, applying the backdoor criterion means identifying and blocking non-causal pathways that connect the variables for which one wants to estimate a causal effect. Software like *dagitty* can be helpful for computing the graphical rules of the backdoor criterion to more complex DAGs, where the potential backdoor paths can be less obvious [24].

Consider a hypothetical DAG linking marine protected areas (MPA), fishing activity, fish biomass, and coral cover (Figure 1; adapted from [26]). Estimating the effect of fish biomass on coral cover (blue arrow, Figure 1A) would require controlling the "confound" of MPAs, perhaps by including it as a covariate in a statistical model, thus “blocking” the backdoor path of association. This could also be achieved by other methods of controlling for confounding variables, such as matching methods, propensity scores, and stratification. Experiments with randomized treatments (e.g., randomized control trials or “RCTs”) remain gold standard of control [27], though even these approaches can be subject to causal biases [28,29]. Moreover, many studies in ecology and evolution rely on observational (non-experimental) data. Returning to our example, imagine that a researcher wants to estimate the effect of MPAs on fish biomass (via fishing). Here, including “coral cover” in the statistical model will actually induce bias, as it is a “collider” variable that opens a backdoor path between the variables of interest if included (Figure 1B; Glossary, Table 1). Though realistically complex DAGs will often involve more variables than shown here (see example in [30]), the backdoor criterion can be applied to help identify causal effects of interest. See [3,4,31] for additional detail.

The situation becomes more complicated if we imagine that fish biomass and coral cover influence each other reciprocally (Figure 1C). This causal diagram no longer fits the criteria of a DAG, as it includes simultaneous bidirectional effects. Though they still have a role to play, simple DAGs (e.g., Figures 1A, 1B) and the backdoor criterion alone are unable to provide causal insights about systems with feedback or other forms of reciprocal causation. To address this gap in methods, we present three widely applicable approaches for causal inference that can be applied in the presence of bidirectional effects.

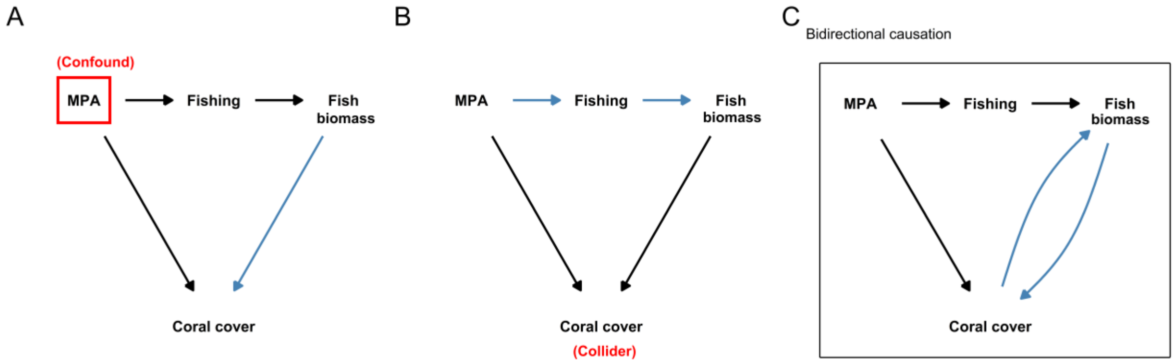

Figure 1 – Causal diagrams representing hypothetical relationships between marine protected areas (MPAs), fishing activity, fish biomass, and coral cover (adapted from [26]). (A) and (B) show examples of confounding and collider variables, respectively, contingent on the causal effect of interest (blue pathway). Note that (C) is not technically a DAG, as it includes simultaneous bidirectional or “cyclic” effects.

Bidirectional causation can induce bias in standard analyses

Before considering the ways that researchers can identify bidirectional causation in observational datasets, we address the issue that bidirectionality, when ignored, can introduce bias into standard analyses. It remains underappreciated in ecology and evolutionary biology that the presence of reciprocal causation results in biased estimates of direct, causal effects in regression analyses. For example, imagine that a researcher is interested in the causal effect of X on Y. Under a hypothetical DAG in which X causes Y with no other confounding relationships, the simple regression of Y on X will recover the effect (Figure 2A). However, this does not hold if the regression is reversed. In other words, the regression of X (response) on Y (predictor) will not recover the simulated causal effect of X on Y (Figure 2B). While this is the expected and correct behaviour of simple regression in this circumstance, the gap between the regression coefficients and causal effects highlights the importance of ruling out reverse causation even for even the simplest causal analyses. Correlational approaches are perfectly appropriate when the scientific question itself is correlational in nature. For example, "are bolder raccoons (*Procyon lotor*) larger?" can be answered with a simple correlation coefficient, even if size and boldness are reciprocal causes of one another. Similarly, "has natural selection occurred in a population?" can be answered without strict causal thinking – changes in allele frequencies map onto the covariance between fitness and a given trait regardless of the causes of their association. Quantifying causal relationships is not always necessary and depends on the scientific question at hand.

However, superficially similar, but causal, scientific questions, e.g., "what is the effect of boldness on body size in raccoons" will require separate methods. If two variables, X and Y, are reciprocal causes of one another (i.e., bidirectional causation or feedback), neither of the simple regressions will provide the direct effect of interest. For some combinations of simulated effects, this can result in effects that are of opposite sign of direct causes (Figure 2C). This issue has been acknowledged in parallel in other fields: for example, Paxton et al. emphasize that the social sciences often fail to address biases resulting from endogeneity (correlations between predictors and unexplained variance) given the presence of feedback loops [32]. More specifically, endogeneity bias resulting from reciprocal causation is sometimes referred to as "simultaneity". Simultaneity raises potential problems for seemingly innocent analyses. While researchers may sometimes recognize these issues, e.g., proposing cautious interpretation when feedback might be present, formal discussion of these biases have been largely absent from ecology and evolutionary biology.

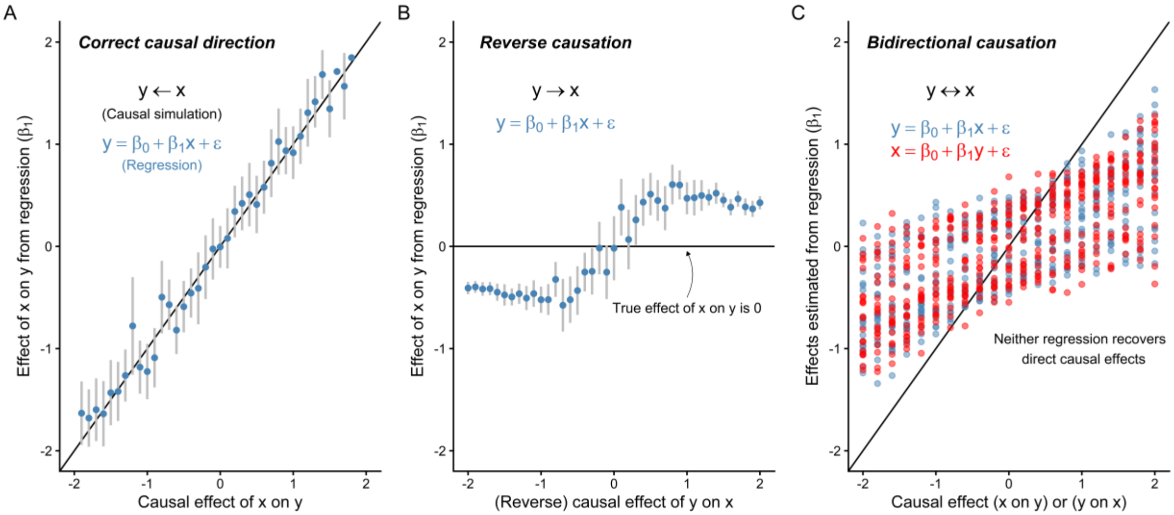

Figure 2 – Bidirectional effects can muddle standard regression analyses. Here we present a simple simulation where variables X and Y are generated from several different causal processes (shown by black text near top of each panel). **(A)** Across a range of simulated causal effects of X on Y, the coefficient of the regression of Y on X closely matches the true effect. Each point represents the point estimate of a coefficient from a model with a different simulated "true" effect, with grey lines showing 95% CIs of the estimate. **(B)** If we reverse the causation such that Y actually causes X, the same regression of Y on X often produces a non-zero coefficient even though X has no causal effect on Y. While it is unsurprising that the model picks up a statistical association, this example demonstrates the risks of failing to consider reverse causation when the aim is to infer causal effects. **(C)** When X and Y are reciprocal causes of one another, neither the regression of Y on X (blue) or the reversed model (regression of X on Y; red) reliably recover the direct causal effect of one variable on the other. See Section 4 of the supplement for a vignette detailing the code used to create this figure.

Table 1 - Glossary of key terms.

Backdoor criterion	A set of graphical rules applied to a DAG to identify sets of variables that, when conditioned on, allow for the estimation of specific causal effects. This is done by ensuring that all "backdoor paths" (i.e., non-causal paths) between variables of interest (e.g., X and Y) are blocked by conditioning on appropriate variables (e.g., adjusting for confounds, avoiding colliders). For example, a confound Z that affects both X and Y opens a backdoor path between them, which can be blocked by including Z in a regression of Y on X.

Bidirectional causation	When two measures of interest cause one another. There is no need for these causes to be direct, e.g., A and B exhibit bidirectional causation if A causes B (A –> B) and B causes C which causes A (B –> C –> A). This is synonymous with reciprocal causation. See *Feedback*.
Confound	A common cause of two variables for which a researcher wants to estimate a causal effect. For example, Z is a confound of X and Y if it directly or indirectly causes both X and Y. Confounds can be blocked by including them in a model to estimate the unbiased effect of X on Y.
Collider	A lesser-known causal pathology which is a common *outcome* of two variables for which a researcher wants to estimate a causal effect. For example, Z is a collider for X and Y if both X and Y cause Z. Unlike confounds, colliders should be excluded from a model to estimate the unbiased effect of X on Y.
Cross-sectional data	Data collected during a single period of time. Typically, cross-sectional data are collected across multiple sampling units (e.g., populations, sites, individuals).
Directed acyclic graph (DAG)	Tool for visualizing and analyzing causal relationships. Variables are represented by nodes while causal effects are represented by arrows. Being acyclic, DAGs cannot accommodate bidirectional arrows, but can represent bidirectional effects if they are made temporally explicit. One a DAG has been created, it can be used to guide model structure (i.e., which variables must be included and excluded from a model to identify a specific causal effect of interest).
Feedback	A special case of bidirectional causation where two or more variables are linked in a causal loop, such that a variable A influences itself at a future time. This can be a simple instance of bidirectional causation, as above (e.g., A -> B & B -> A at a subsequent time), but can also involve many interconnected variables [7]. For the purposes of this article however, feedback, bidirectional causation, and reciprocal causation are treated as mostly synonymous. See *Bidirectional causation*.
Instrumental variable	Variable that can be used to identify a direct causal effect in the presence of bidirectional causation, unobserved confounding, or other sources of endogeneity. Instrumental variables must satisfy several key criteria (see “Method 3” in main text).
Longitudinal data	Data with repeated measures of the same sampling unit (e.g., population, site, individual) over time. Longitudinal data are very useful for inferring bidirectional

	effects. Depending on the scale of the process of interest, this can include relatively short time periods as well as long-term, multiyear studies (e.g., long-term ecological research; LTER).
Reverse causation	When the true direction(s) of causation between variables is the opposite of what one expects. The "reversal" is relative to a researcher's belief about the system. This can involve situations of bidirectional causation, where a researcher expects solely that A causes B, for example, or situations with unidirectional causation, i.e., when a researcher expects that A causes B (A -> B) while in reality B causes A (B –> A).
Structural causal modeling	Framework for identifying causal effects including the formalization of assumptions using DAGs and the application of techniques like the backdoor criterion [33]. Crucially, this framework can be applied to observational data, allowing for causal inference without formal experimentation.

3. Approaches for inferring bidirectional effects in observational data

Method 1. Temporally explicit models with cross-lagged effects

Though bidirectional arrows cannot be represented in DAGs directly, unfurling the static causal relationship across time (with time-indexed measures of each variable) opens the door to formal causal inference in systems where traits cause one another. The resulting diagram will appear structurally similar to the statistical approach of "cross-lagged panel models" (CPLM; [34]), which are regularly used in the social sciences, but less commonly applied in ecology and evolution [35]. CPLMs allow one to estimate "cross-lagged" effects between variables of interest, made possible by expressing one variable (Y) at a given time (t) as a function of another variable (X) at a previous time ($t-1$). Simultaneously, X at t can be represented as a function of Y at $t-1$ (coloured arrows in Figure 3A). It is important to note that panel models do not necessarily provide causal insights, and are often used for more descriptive analyses, e.g., to identify temporal precedence between variables (i.e., if change in one variable tends to precede change in another). However, with an appropriately specified DAG, in some cases it is possible to interpret cross-lagged effects as causal.

Crucially, this temporally explicit approach means that bidirectional effects can be represented in DAGs without violating the requirement of unidirectional causes. These temporally explicit models often assume stationarity, i.e., that causal effects are consistent through time, but one can also allow cross-lagged and auto-regressive effects to vary at each step (e.g., [36]). Models with cross-lagged effects are especially suitable when there are clearly separable phases at which causal effects can be divided in time (e.g., seasonal effects or studies with consistent repeat measurements). Indeed, the scale of time gaps relative to causal effects are important for these models and can impact the results [37]. Mismatch between the timescale of measurements and the process of interest can result both in inaccurate estimates of effect sizes as well as misidentification of causal effects [38].

Returning to the example of a state-behaviour feedback, Figure 3A shows a temporally-explicit DAG where body size and foraging boldness influence one another through time. For illustrative purposes, we simulated a positive effect of boldness on body size, imagining that bolder raccoons gather more resources, but a negative effect of body size on boldness – perhaps larger animals are less motivated to take risks when foraging (See similar examples in [13]). First, "lagged" versions of each variable are generated, such that size at time t can be modelled as a function of size at $t-1$ (an auto-regressive effect) and boldness at $t-1$ (a cross-lagged effect). Reciprocally boldness at time t can be modelled as a function of boldness at $t-1$ and size at $t-1$. These sub-models can be estimated together in a bivariate framework, allowing for accurate estimation of the bidirectional effects (Figure 3B, 3C). We provide a simple example of this model implemented in the *brms* or *lavaan* packages in R [39–41] in the electronic supplementary material (Section 1.1). Similar approaches have recently been proposed for investigating reciprocal causation between biodiversity and productivity [42].

Of course, more complex biological datasets may involve more challenging DAGs, and may require conditioning on other covariates, the inclusion of varying or "random" effects, or approaches to deal with missing data. Crucially, the estimation of cross-lagged effects does not make an analysis immune to more typical causal issues. For example, if size and boldness (Figure 3) in fact have no causal relationship, but are each influenced by a time-invariant confound, ignoring this confound in a cross-lagged model will result in spurious estimates of bidirectional effects. Otherwise, there remains a lack of specific advice on adjusting for more complex causal pathologies in cross-lagged panel models. Static DAGs (i.e., without temporally indexed variables) may be a helpful starting point. For example, Heiman et al. apply a DAG to identify confounds for a cross-lagged panel model [36]. Perhaps the most straightforward approach is simply to incorporate known confounds into the temporally explicit sub-models (e.g., control for confound "c" at $t-1$; see worked example in electronic supplement, Section 1.2.2).

However, generating DAGs with at least two timesteps (and more if effects with lags longer than one time step are included) may be necessary to identify causal properties (e.g., confounding variables) of a system. For example, the inclusion of auto-regressive effects may block (i.e., resolve) certain types of confounding, but not others [43]. Given the potential complexity of temporally explicit causal diagrams, we expect that dagitty software, which can be used to evaluate temporally explicit DAGs, and the testing of simulated data will be most helpful for researchers seeking to infer causation with cross-lagged effects.

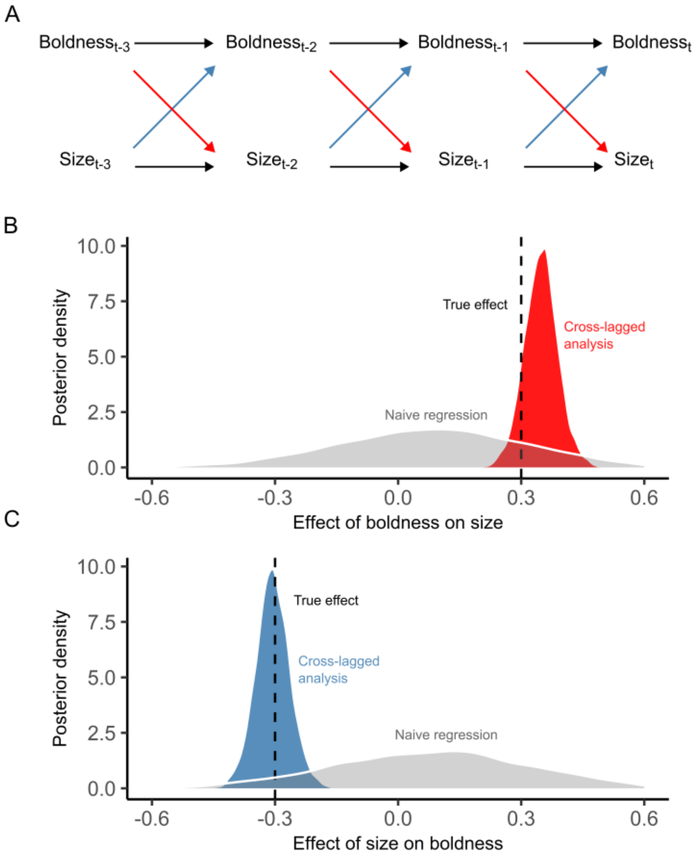

Figure 3 – Bidirectional effects can be identified using longitudinal data. **(A)** DAG representing reciprocal causation between variables X and Y over time. Coloured arrows represent reciprocal cross-lagged effects, which can be identified in a multivariate model. **(B)** Posterior of estimated effect of X on Y using a multivariate model with lagged effects alongside the true simulated effect (dashed vertical line) and coefficient from naive simple regression (grey). **(C)** Posterior of estimated effect of Y on X using a multivariate model with lagged effects alongside the true simulated effect (dashed vertical line) and coefficient from naive simple regression (grey).

Method 2. Continuous time models

A second approach to analyzing patterns of bidirectional causation uses ordinary differential equations to explain continuous changes in variables over time. Rather than representing how a variable changes over a specific time step (as in Method 1), ordinary differential equations express instantaneous change in one variable with respect to another, i.e., at infinitely small timesteps [44]. A classic ecological example of how this approach can incorporate bidirectional effects is the Lotka-Volterra equation which expresses predator (e.g., lynx; *Lynx canadensis*) and prey (e.g., snowshoe hare; *Lepus americanus*) populations as causes of one another. However, this general approach of using ODEs is highly flexible and is widely applicable for a range of ecological and evolutionary questions. A further benefit of this approach is that it can include mechanistic or "process" models, where specific biological mechanisms are represented mathematically. Despite this flexibility, developing differential equations for new research questions is challenging, and requires a familiarity with both mathematics and the potential mechanisms occurring in a system.

Once a system of differential equations has been developed to explain relationships between variables over time, one can use it to simulate possible outcomes, or fit it to data to estimate parameters of interest, including those representing bidirectional effects. In the first instance, comparing the dynamics of simulated data from models with and without bidirectional causation may suggest whether bidirectional causation is occurring (e.g., if cycles are evident, as in systems with negative feedback). For example, Pantel and Becks show how four alternate hypotheses of trait evolution across species can result in distinct patterns of biodiversity, which can then be compared to observed data [45]. More direct evidence for causal effects comes from fitting a continuous time model to observed data, i.e., estimating key parameters using a fitting algorithm (e.g., Markov chain Monte Carlo). Though this can be challenging, particularly in regards to the selection of "starting" parameters or priors, we direct the reader to worked examples based on lynx and hare pelt data [31,46].

Tools such as the *ctsem* package, implemented in R, are particularly useful in that they allow users to use and customize a standard form of continuous time model [47], without needing to "start from scratch" with novel mathematical expressions. The *ctsem* package provides a general model framework to fit dynamic models incorporating auto-regressive effects and random effects. As a type of state-space models, they include both latent and observed variables that allow for the separation of process error, i.e., stochasticity that is not captured by deterministic aspects of the model structure, and measurement error, i.e., imprecision in the data sampling process [48]. Though *ctsem* can be used to fit models that treat time as a discrete sequence, as in the cross-lagged model in Method 1, it specializes in the use of differential equations to represent changes in continuous time. These continuous time methods are preferable when time lags between measurements vary (see [38] for further discussion on discrete vs. continuous approaches). The *ctsem* framework is well-suited for the incorporation of bidirectional effects over time.

For an illustrative example, we used *ctsem* to fit a system of differential equations to a simulated, idealized eco-evolutionary dataset with the primary aim of estimating the "crossed" effects of population density on trait evolution and vice-versa. For the purposes of this example, we imagine a population where a trait that influences growth rate (e.g., number of offspring produced) is subject to density-dependent selection. This could occur if selection favors individuals that produce more offspring (i.e., larger litters, clutches, more eggs or seeds) at lower densities, while at higher densities selection favors individuals producing fewer, higher-quality offspring, as competition between new recruits becomes increasingly important. This constitutes the "eco-to-evo" causal process, as an ecological process (density) influences subsequent evolutionary change (the distribution of the trait across the population). If these evolutionary changes feed back to influence population density, e.g., if individuals tend to produce fewer offspring, there will be an "evo-to-eco" effect, and the eco-evolutionary feedback is complete.

First, we simulated variables representing trait values and population densities over multiple timesteps, incorporating a negative effect of density on trait values, and a positive effect of trait values on density (See supplement, Section 2). Then, using a continuous time approach, we model dynamics of the simulated variables over time (Figure 4A), and most importantly, recover the "true" bidirectional effects, neither of which can be achieved using simple regression-type models (Figure 4D). And though we highlight an eco-evolutionary example here, continuous time methods are widely applicable to a range of natural systems where variables are measured over time.

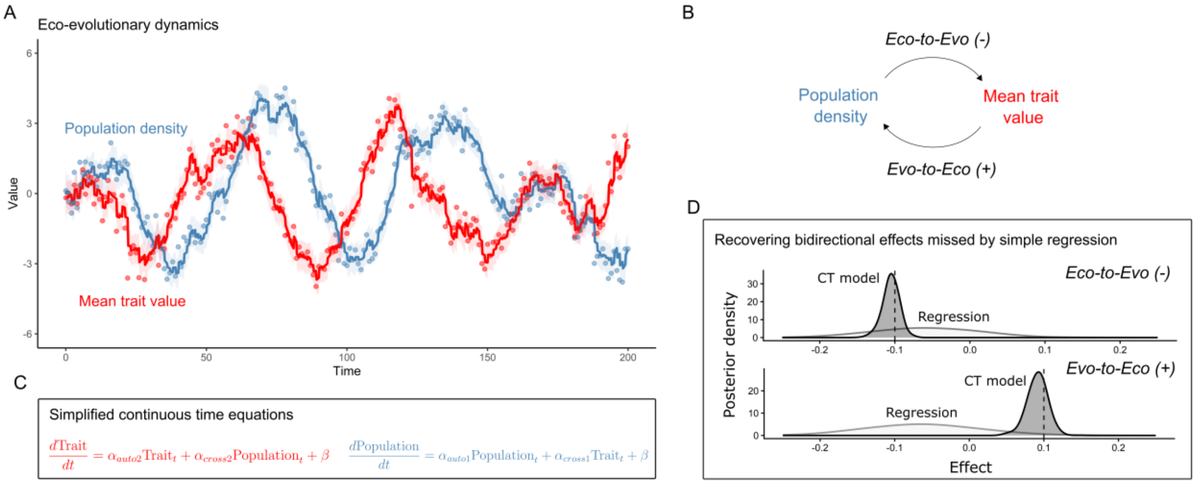

Figure 4 – Differential equations can allow for bidirectional effects to be estimated over continuous time. (A) Cyclic dynamics of population density (standardized) and a hypothetical life history trait from a simulated dataset (points), with fitted model predictions from overlaid on top (lines). Shaded

areas around each line represent uncertainty, incorporating both measurement and process error. (B) Causal diagram representing bidirectional causation between population density and the distribution of phenotypes in a hypothetical population. (C) Simplified equations representing how changes in two variables (population density, trait value) with respect to time can be simultaneously modelled as a function of each other (α_{cross}) and autoregressive effects (α_{auto}). Note that the β terms represent intercepts specific to each sub-model, and that these equations only represent the deterministic portion of the model, excluding additional noise parameters. (D) Posterior distributions of bidirectional effects estimated using a continuous time (CT) model (dark grey), which accurately recovers the true values (dashed vertical lines). Crucially, these positive and negative bidirectional effects are missed when simply regressing the variables on one another (light grey posteriors).

As in the previously described method, the reliability of inferred causal effects depends on the causal assumptions that are used to construct the model – potential issues like confounding and omitted variable bias may be important, depending on the goal of the analysis. For example, incorporating potential confounds as predictors may be necessary to accurately infer causal effects. Additional predictors can be specified as time-invariant (e.g., the latitude of a particular study quadrant, the sex of a study animal), or time-varying (e.g., a hurricane that impacts a subset of longitudinal data). Managing unmeasured confounding in continuous time models can be challenging, particularly if they are time-varying [38]. One approach to address unmeasured, time-*invariant* confounds is to incorporate random effects structures that can capture stable differences among units (e.g., individuals in a study). More formal links between ODEs and structural causal modelling have also been proposed, and may help in generating accurate causal inferences [49].

Method 3. Instrumental variables – Inferring bidirectional causation without time series

Instrumental variables offer a distinct approach detecting reciprocal causation, and are especially useful in cross-sectional datasets, i.e., when time series data are unavailable. Instrumental variable techniques can also be used to identify a specific directional effect of interest when feedbacks are expected (e.g., if a researcher is only interested in the effect of X on Y but not Y on X). Underappreciated in ecology and evolution [50], this method requires the identification of “instruments”, which directly influence one variable of interest, but not the other. More specifically, to recover the direct, causal effect of X on Y, an effective instrument “I” must cause X, it must only influence Y through X, and it must not be causally related to any unobserved confounds of X and Y [31]. There are several approaches to fitting instrumental variable models, including two-stage-least-squares (“2SLS”), and bivariate (multi-response) models.

For an illustrative example, we draw on existing application of instrumental variable analysis for understanding the ecology of malaria and its relationship to habitat modification (see [51]). Imagine that a researcher wants to quantify the effects of deforestation on changes in the prevalence of mosquito-borne disease (e.g., malaria; *Plasmodium sp.*). The researcher has cross-sectional data on levels of deforestation and malaria prevalence at several sites in a given region. In particular, they are concerned that deforestation may boost levels of malaria, perhaps because the removal of forest ecosystems may create more suitable habitat for mosquitoes or perhaps reduce populations of their natural predators. If the researcher can safely assume that deforestation causes changes in malaria and not vice-versa (i.e., unidirectional causation), a simple regression will provide an unbiased estimate of the effect of habitat modification on malaria.

However, levels of malaria may also influence levels of deforestation via other mechanisms, for example, if high levels of disease interrupt or dissuade efforts to remove forest habitat. Without longitudinal data, these reciprocal causes will occur “simultaneously” to generate the observed data. In this instance, neither simple regression will reliably produce the desired causal effect. Now, imagine that the researcher also has access to commodity prices for lumber or downstream agricultural products that could make deforestation more lucrative. Assuming it satisfies the above criteria for instrumental variables, commodity prices can be used as an instrument to isolate the causal effect of deforestation on malaria (Figure 5). Similarly, the reciprocal effect of malaria prevalence on habitat modification can be quantified using a candidate instrument like temperature, which strongly influences observed levels of malaria. See Section 3 in the supplement for worked examples using the *ivreg* or *brms* packages in R [39,52]. It is important to note that identifying and reaching consensus on candidate instruments can be challenging – for example, there has been considerable debate on potential instruments relating to this above case study [51,53,54].

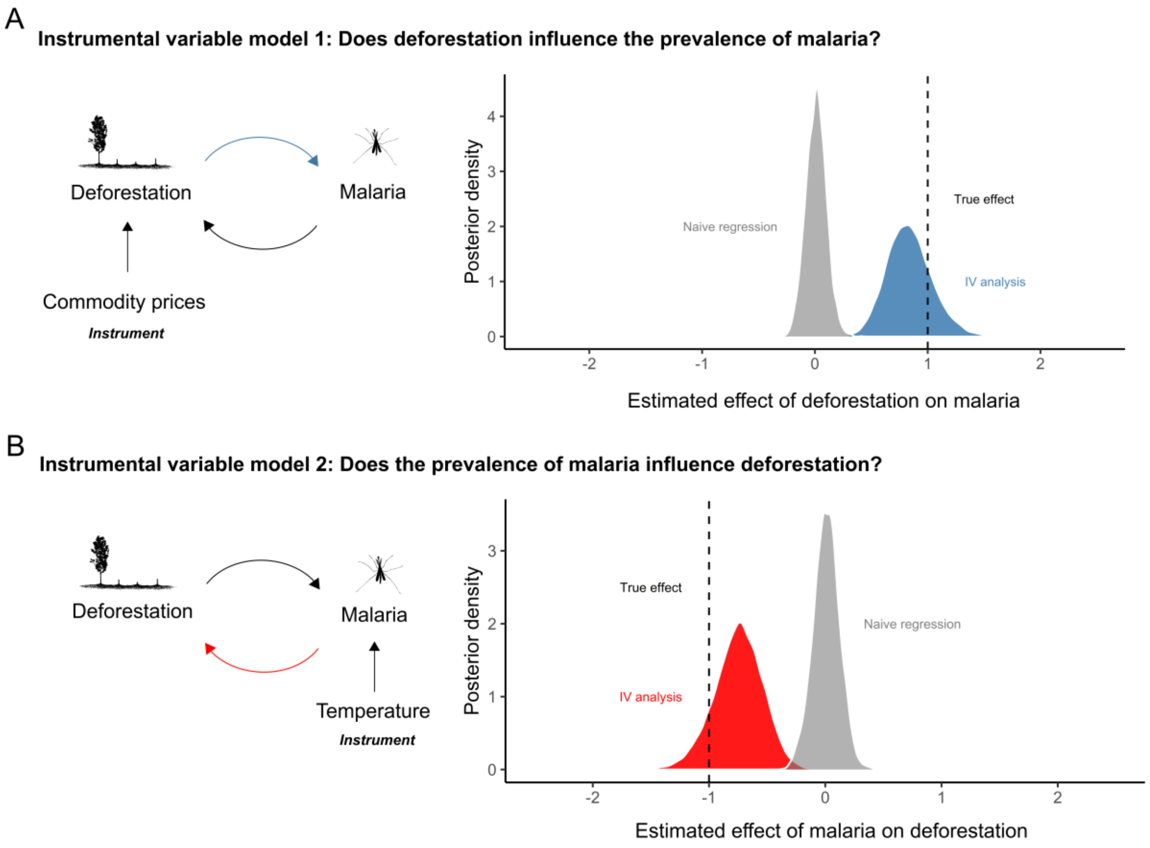

Figure 5 – Instrumental variable analysis can isolate direct effects when feedback is present. Here we simulate an simplified example where deforestation promotes malaria ("true" effect of +1) while the prevalence of malaria within a region reduces subsequent deforestation ("true" effect of -1). **(A)** First, commodity prices incentivizing the removal of forest and conversion to agricultural land serve as an instrument for estimating the effect of deforestation on the prevalence of malaria. While a naive regression of malaria prevalence on deforestation finds no relationship (grey posterior), the instrumental variable analysis successfully recovers the true (simulated) positive effect (blue posterior). **(B)** Temperature serves as an instrument for estimating the effect of malaria prevalence on deforestation. While a naive regression of deforestation on malaria prevalence finds no relationship (grey posterior), the instrumental variable analysis successfully recovers the true (simulated) negative effect (red posterior).

Beyond the criteria mentioned above, instrumental variables must have a relatively strong causal effect for accurate inference [50]. Testing for potentially problematic "weak instruments" is straightforward and simply requires examining the regression of the explanatory variable in question on its putative instrumental variable [55]. Based on this regression, a commonly used rule-of-thumb is that instruments with an F-statistic less than 10 are considered weak [56]. Otherwise, for Bayesian implementations in particular, standard diagnostics of model convergence and fit are necessary for ensuring accurate inference.

One advantage of instrumental variable approaches is they inherently adjust for common types of confounding between two variables of interest, such as the presence of unmeasured confounds (see worked example in [31]). Returning to our example, any common causes of both deforestation and malaria prevalence (including unmeasured confounds) would be accounted for by the use of either instrument, and would not bias the estimates of bidirectional effects. As before, the use of DAGs can help to guide modelling decisions with instrumental variables. For example, causal diagrams may reveal "conditional instruments", variables that satisfies all criteria to be an instrument *when* controlling for another variable [57]. Suppose that instrument (I) that causes X also influences the outcome of interest (Y), but solely through a mediating variable (Z). In this case, (I) can be a valid instrument if Z is included (i.e., controlled for) in the instrumental variable model [26], assuming other criteria are met.

To summarize, instrumental variables are a powerful tool for uncovering causal effects in the presence of bidirectionality and other potential sources of bias (e.g., unmeasured confounds). The main challenge in implementing this approach is the identification of measured (or measurable) instruments that meet all of the necessary criteria. It is also worth noting that while the instrumental variable approach can identify reciprocal causation, it may not offer much insight into the dynamics of feedback systems, or into whether the causal effects themselves vary over time. Nevertheless, wider adoption of this method is likely to be useful in ecology and evolutionary biology. See [58] for a worked example where canine distemper serves as an instrument for predator-prey cycles. This and the other methods we present are summarized in Table 2 and Figure S1, with code vignettes available in the supplement (Sections 1-4). When possible, drawing together evidence from multiple approaches can help to strengthen causal inferences. For example, Dee et al. use lagged effects, instrumental variable analysis, and additional models testing for specific mechanisms to resolve the potentially bidirectional links between biodiversity and productivity in grasslands [59].

4. Special considerations for bidirectional effects in ecology and evolution

Eco-evolutionary feedback loops

One of the most exciting areas of development in ecological and evolutionary theory is eco-evolutionary feedbacks. Spurred by evidence that evolutionary processes can occur on relatively fast timescales

[60,61], the central idea is that effects of ecological phenomena on traits or gene frequencies (termed "eco-to-evo") can occur simultaneously with influences of trait or gene frequencies on ecological phenomena ("evo-to-eco"), opening the door to bidirectional dynamics. These dynamics are thought to be an important process shaping genetics and density within populations [62–64]. Eco-evolutionary feedback can be studied in experimental systems, such as the feedback between population size and genes linked to cooperative behaviour in microbes [65]. Most often, eco-evolutionary feedback is inferred from separate demonstrations of eco-to-evo and evo-to-eco processes, i.e., each half of the reciprocal causal system is present. While this "two halves" approach can reveal the *potential* for causal feedback, it offers little insight into how these effects work together to sculpt the ecological and evolutionary dynamics of wild organisms. Indeed, it is widely acknowledged that theory on reciprocal dynamics in eco-evolutionary systems has outweighed empirical evidence, due in part to difficulties in both data collection and analysis [45,66,67]. Accordingly, it remains difficult to know whether reciprocal influences from evolution to ecology (termed "evo-to-eco") are important in natural systems [11]. To the extent that these natural systems are generally studied using observational data, the methods discussed open new opportunities for simultaneously estimating effects between ecological and evolutionary phenomena.

Feedbacks across phylogenetic histories

Bidirectional effects can play an important role in macroevolutionary theory, where sets of two or more traits are expected to influence one another over long periods of time. For example, positive feedback processes have long been hypothesized to influence trait covariance between species (e.g., coevolution between plants and pollinators [68,69]), as well as within species (e.g., coevolution of slow life history and social bonds in cetaceans [70]). This is also an area of research where "what came first" is often an important question as it pertains to the specific evolutionary pathway in evolutionary history. As with other standard analyses, traditional comparative methods are unable to disentangle the direction(s) of causality when traits influence each other over time [71]. Pagel developed one solution for interrogating this "correlated evolution" which has been applied to coevolution of traits in human populations [72], including lactose tolerance [73], and systems of inheritance [74]. Less commonly, this method has been applied to nonhumans, revealing, for example, that sexual size dimorphism evolved first in pinnipeds, subsequently triggering feedbacks with polygynous group size [75]. This method treats a phylogenetic tree as a time series to identify temporal patterns of the emergence of different traits in phylogenetic history**.** Still, most studies of "coevolution" use techniques that assume unidirectional causation, leaving possible bidirectional influences as speculative hypotheses (e.g., [76,77]). One reason for this is that available tests for causal coevolution have been limited to consideration of two binary traits. However, a recent extension of Pagel's method provides a highly flexible Bayesian implementation of tests for causal coevolution for multiple traits of any distribution [78]. Thinking more broadly, applying these methods to matched genetic and behavioural data may help to understand how genes and culture interact, i.e., a causal understanding of gene-culture coevolution [10,79]. For example, linking ecotype-specific foraging strategies of killer whale (*Orcinus orca*) behaviour with genomic and phylogenetic data would allow one to test whether genetic changes were a leader or follower in the diversification of behaviour (see [80]).

5. Concluding remarks

Our goal in this manuscript was to establish that explaining ecological and evolutionary phenomena in the face of reciprocal causation is challenging but possible, and a worthy target for empiricists. We encourage researchers to consider both the theoretical and quantitative consequences of potential feedback in their study systems, and apply methods including those described here when isolating directional causal effects is necessary. Our review can be synthesized in the following three key points:

1. Bidirectional relationships are common in nature.
2. Common statistical methods (e.g., regression and generalized linear models) can lead to bias in the presence of bidirectionality.
3. Methods exist that can identify bidirectional effects from both longitudinal and cross-sectional datasets.

Empiricists in ecology and evolution face a tension between the importance of feedbacks for theory and practical applications, and the complexity that such analyses entail. Of course, this complexity mirrors the true complexity of ecological and evolutionary systems. Confronting and quantifying this complexity (e.g., incorporating an increasing number of causal effects, confounds, etc.) should be done cautiously, as larger causal diagrams entail more causal assumptions [55], and thus may be more prone to error. Generally, we suggest that the methods presented here be applied where there is underlying theory that suggests that reciprocal causation may be occurring or is important to the biological question.We believe that a better understanding of how to manage and infer bidirectional causation from observational datasets will enhance the understanding of ecological and evolutionary systems. From an applied perspective, moving beyond a correlational approach to one in which potentially bidirectional causes are explicitly quantified is important for successful intervention [81]. Our aim was not to produce an exhaustive list of methods, but instead to present the most widely applicable theory-driven approaches towards quantifying bidirectional causes in observational data. This article is intended to serve as a primer to assist researchers in identifying feedback processes to test, and as data collection allows, to identify the appropriate branch of methods for quantifying such feedbacks.

Table 2 - Summary of methods for causal inference in the presence of feedbacks.

Method	**Description**	**Data requirements**	**Main assumptions**	**Challenges**
Cross-lagged effects	Variables are represented in a temporally explicit directed acyclic diagram (DAG) so that both auto-regressive and cross-lagged (reciprocal) effects can be estimated.	Co-inciding longitudinal (i.e., time series) data of variables of interest.	The simplest implementations assume that effects are constant over time. However, time-varying effects can also be estimated. Time gaps between repeated measurements fit the expected timescale for the study system in question [38].	May be difficult to collect adequate data, particularly for decades-long ecological or evolutionary processes. DAGs may become quite complex when confounds or other causal pathologies are present.
Continuous time models	Fit a system of differential equations that incorporate reciprocal causation to data.	Co-inciding longitudinal (i.e., time series) data of variables of interest.	Various – assumptions will depend on the continuous time equation in question. For example, simple predator-prey cycle models may assume that predators do not switch to other prey species when abundances are low.	Estimating parameters (i.e., fitting ODEs to data) can be difficult and sensitive to choice starting parameters.
Instrumental variables	One or more "instrumental variables" are used to isolate a direct causal relationship between two variables that are the result of reciprocal causal effects.	Cross-sectional data is suitable (i.e., no time series needed). One instrumental variable for each causal direction of interest.	An instrument to recover the causal effect of X on Y must: 1. Cause X. 2. Only cause Y through X (some exceptions, see below).	Can be difficult to find variables that satisfy all conditions, especially independence from secondary variable of interest, though the use of "conditional instruments", i.e., instruments that satisfy the criteria if

		Instruments must have strong causal effects for accurate inference.	3. Be causally unrelated to any unobserved confounds of X and Y. Note that assumption 2 can be relaxed if additional pathways from I to Y can be blocked (e.g., if I causes W which causes Y, conditioning on W will allow for I to be used as an instrument).	an additional covariate is controlled for, can help.

Data accessibility

No data were used in this article. All code, including simulations and models used to generate figures, have been archived on the Open Science Framework, and are also available on a Github repository accompanying this article.

OSF: https://osf.io/zw84x

Github: https://github.com/swalmsley/Causal-Feedbacks-EEB

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