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REVIEW

Applying the structural causal model framework for observational causal inference in ecology

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Abstract

Ecologists are often interested in answering causal questions from observational data but generally lack the training to appropriately infer causation. When applying statistical analysis (e.g., generalized linear model) on observational data, common statistical adjustments can often lead to biased estimates between variables of interest due to processes such as confounding, overcontrol, and collider bias. To overcome these limitations, we present an overview of structural causal modeling (SCM), an emerging causal inference framework that can be used to determine cause-and-effect relationships from observational data. The SCM framework uses directed acyclic graphs (DAGs) to visualize researchers' assumptions about the causal structure of a system or process under study. Following this, a DAG-based graphical rule known as the backdoor criterion can be applied to determine statistical adjustments (or lack thereof) required to determine causal relationships from observational data. In the presence of unobserved confounding variables, an additional rule called the frontdoor criterion can be employed to determine causal effects. Here, we use simulated ecological examples to review how the backdoor and frontdoor criteria can return accurate causal estimates between variables of interest, as well as how biases can arise when these criteria are not used. We further provide an overview of studies that have applied the SCM framework in ecology. SCM, along with its application of DAGs, has been widely used in other disciplines to make valid causal inferences from observational data. Their use in ecology holds tremendous potential for quantifying causal relationships and investigating a range of ecological questions without randomized experiments.

KEYWORDS

backdoor criterion, causal inference, directed acyclic graphs, frontdoor criterion, observational study, statistical ecology, structural causal model

INTRODUCTION

Observational studies in ecology rely on data that have not been experimentally manipulated and are commonly used to understand ecological patterns and processes seen in nature (Carmel et al., 2013). Observational approaches are increasing in relevance due to the emergence of large-scale ecological questions that are not easily manipulated or controlled, such as invasive species and the consequences of climate change. New advances

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in technology, such as remote sensing, environmental genetics, and animal-borne sensors, as well as increased availability of data online and from citizen scientists, have enhanced opportunities to answer previously intractable ecological questions using observational data (Sagarin & Pauchard, 2010).

Many observational studies in ecology are aimed at answering causal questions, such as the impact of marine protected areas on fishing communities (Mascia et al., 2010) or the effect of forest fragmentation on species richness (Sam et al., 2014). However, causal inference—the leveraging of theory and deep knowledge to estimate the impact of events, choices, or other factors on a given outcome of interest (Cunningham, 2021)—is rare. Yet without the consideration of causal relationships, statistical analysis can frequently lead to biased estimates (i.e., estimates that differ from the true parameter being estimated) that undermine ecological inferences by providing noncausal correlations among variables of interest (e.g., see Appendix S1). This is the basis of the often-repeated phrase “correlation does not imply causation” (F. A. D., 1900). We believe that increasing the use of causal inference methods in observational ecology will reduce bias throughout the discipline and lead to more accurate assessments across a range of ecological questions, especially when experimental approaches are unfeasible.

Structural causal modeling (SCM) (Pearl, 2009) is an emerging causal inference framework that unifies the strong features of structural equation modeling (SEM) (Shipley, 2016; Wright, 1921) and Rubin’s potential outcome (PO) framework (Rubin, 2005), among others, to create a powerful theory of causation and framework for causal inference. Importantly, this framework can be used to determine cause-and-effect relationships from observational data without needing to set up randomized control experiments (Pearl, 2009). SCM has been widely used across other disciplines, including econometrics (Imbens, 2020), epidemiology (Pearce & Lawlor, 2016), pediatrics (Williams et al., 2018), and psychology (Rohrer, 2018), as well as in a few ecological studies (Arif et al., 2022; Arif & MacNeil, 2022; Cronin & Schoolmaster Jr., 2018; Schoolmaster et al., 2020; Schoolmaster Jr. et al., 2022). It holds tremendous potential for increasing the use of causal inference across observational ecological studies.

Under the SCM framework, the derivation of causal effects rests on a set of causal assumptions about the data-generating process (e.g., X affects Y and not the other way around). These causal assumptions are visualized using directed acyclic graphs (DAGs), which represent researchers’ assumptions about the causal structure of a system or process under study (Morgan & Winship, 2014; Pearl, 2009). Given a DAG, a graphical rule known as the backdoor criterion determines the sufficient sets of variables for adjustment required to determine causal effects from observational data. When the backdoor criterion cannot be employed—due to the presence of an unobserved confounding variable—a second graphical rule called the frontdoor criterion can be employed. Using simulated ecological examples with specified (i.e., known) causal effects, we define these criteria and review how they can be employed to determine causal effects between variables of interest.

To date, the few ecological studies that have employed the SCM framework identified key causal relationships across study systems (Arif et al., 2022; Cronin & Schoolmaster Jr., 2018; Schoolmaster et al., 2020), outlined steps required for observational causal inference (Arif et al., 2022; Cronin & Schoolmaster Jr., 2018), clarified SCM theory (Schoolmaster Jr. et al., 2022), and highlighted the utility of SCM for experimental and quasi-experimental approaches (Arif & MacNeil, 2022; Schoolmaster et al., 2020; Schoolmaster Jr. et al., 2022). However, these studies can be niche topics and theoretically complex. Here, we provide an easily accessible overview of the SCM framework, highlighting two key tools—the backdoor and frontdoor criteria—that can be used for causal inference across observational ecological studies.

DIRECTED ACYCLIC GRAPHS (DAGs)

DAGs are used to represent causal relationships within a given system. A DAG consists of a set of nodes (variables) that are connected to each other by edges (arrows). These arrows represent causal relationships between variables, pointing from cause to effect, with causes preceding their effects. For example, the DAG in Figure 1 shows that X directly affects Y ($X \rightarrow Y$), Z directly affects both

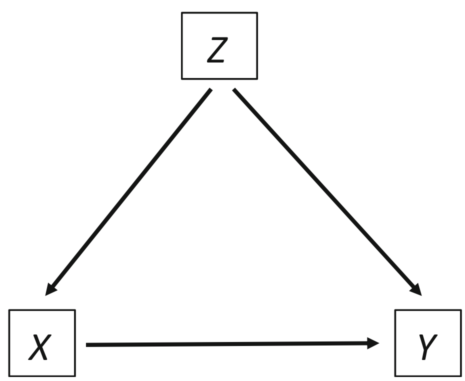

FIGURE 1 A directed acyclic graph (DAG) representing the causal structure between three variables, X, Y, and Z.

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X ($Z \rightarrow X$) and Y ($Z \rightarrow Y$), and Z indirectly affects Y through X ($Z \rightarrow X \rightarrow Y$). It is important to note that the arrows between nodes (variables) represent hypothesized causal relationships (i.e., a lack of causal relationship can be found following a SCM analysis). On the other hand, a lack of arrow between two nodes assumes no causal relationship between variables, representing strong a priori causal assumptions. Therefore, missing arrows encode causal assumptions, whereas arrows between nodes represent the possibility of an effect (Elwert, 2013).

A key characteristic of DAGs is that they must be *acyclic*, meaning that they cannot contain bidirectional relationships (i.e., arrows need to be unidirectional) or a feedback loop where a variable causes itself (Elwert, 2013; Glymour & Greenland, 2008). This limits the application of DAGs to ecological systems that do not contain bidirectionality and or feedback loops. However, one way to resolve this issue is to articulate the temporal sequence of events more finely (Greenland et al., 1999). For example, if temperature at time one (Temp_{t1}) effects ice cover, which then influences temperature at time two (Temp_{t2}), Temp_{t1} and Temp_{t2} can be represented as separate nodes within a DAG, without violating acyclic requirements. For interested readers, Schoolmaster et al. (2020) provide a published ecological DAG that incorporates the temporal sequence of events (see their Appendix S2).

Directed acyclic graphs are also nonparametric, meaning they make no assumptions about the stochastic nature of variables or their observation or the functional form of direct effects (e.g., linear, nonlinear, stepwise) and their effect size (Glymour & Greenland, 2008). In this sense, a DAG is qualitative: $X \rightarrow Y$ only communicates that X causally affects Y in some way, without specifying any other restrictions. This nonparametric nature of DAGs makes them compatible with a wide range of ecological systems.

USING DAGS UNDER THE SCM FRAMEWORK

DAGs are central to the SCM framework because they are used to visualize and quantify causal relationships from observational data (Pearl, 2009). Figure 2 summarizes the SCM framework, which includes creating a DAG

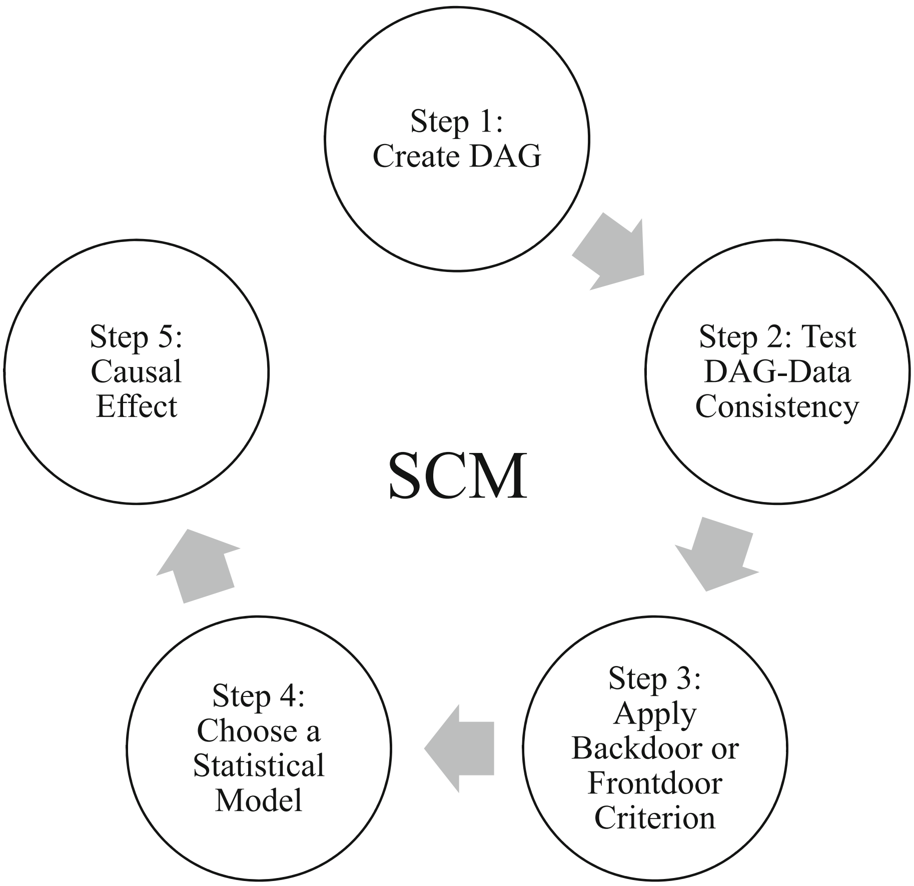

FIGURE 2 A workflow for going from directed acyclic graphs (DAGs) to causal inference under the structural causal model (SCM) framework.

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(Step 1), testing a DAG to ensure DAG–data consistency (Step 2), applying either the backdoor or frontdoor criterion (Step 3), choosing an appropriate statistical model (Step 4), and making an inference by quantifying a causal effect (Step 5). As we walk through our review, we will follow the workflow in Figure 2 using simulated ecological examples interspersed with relevant theory and background information.

Step 1: Creating a DAG

DAGs represent a researcher's causal assumptions about the data-generating process of a system or process under study (Morgan & Winship, 2014; Pearl, 2009). As such, researchers should ensure that their DAG represents the complete causal structure of the system or process, including all relevant measured and unmeasured variables, as well as all common causes of any pair of variables included in the DAG (Glymour & Greenland, 2008; Spirtes et al., 2001). DAGs should also be rigorously justified based on domain knowledge, theory, and research. A combination of background information, including experimental data, past literature, and domain knowledge, can be used to create DAGs of ecological systems. For example, Ethier and Nudds (2017) gathered information from the published literature and local stakeholder knowledge to create DAGs depicting factors affecting the population dynamics of the bobolink (*Dolichonyx oryzivorus*). In another study, Cronin and Schoolmaster Jr. (2018) synthesized past literature to create a DAG representing the causes of trait covariation. Expert opinion can also be elicited to generate DAGs. To ensure credibility and transparency, researchers should apply formal methods for surveying experts, which has been developed within the ecological literature (e.g., Choy et al., 2009; Drescher et al., 2013; Kuhnert et al., 2010; Martin et al., 2012), including for the development of causal diagrams (e.g., Marcot et al., 2006; McNay et al., 2006). For example, Marcot et al. (2006) showed how to use expert review to create their DAG on the probability of capture of northern flying squirrels.

As a general ecological example, Figure 3 presents a DAG adapted from Adams et al. (2015) showing how different factors are expected to influence forest species abundance across a hypothetical region (Step 1, Figure 2). Here, protected areas are shown to affect forest species abundance through three intermediate processes: fire, poaching, and logging (Adams et al., 2015). Other variables, including distance to roads and cities, slope, and elevation, affect both protected area placement (protected areas are often placed in high and distant places; Joppa & Pfaff, 2009) and forest species abundance through their effects on fire, poaching, or logging (Adams et al., 2015). We have created a simulated data set matching the causal structure of this DAG (Arif, 2022). We will use this DAG and simulated data set to work through the rest of the SCM workflow (Steps 2–5, Figure 2). Specifically, we will aim to answer how protected areas, fire, logging, and poaching each affect

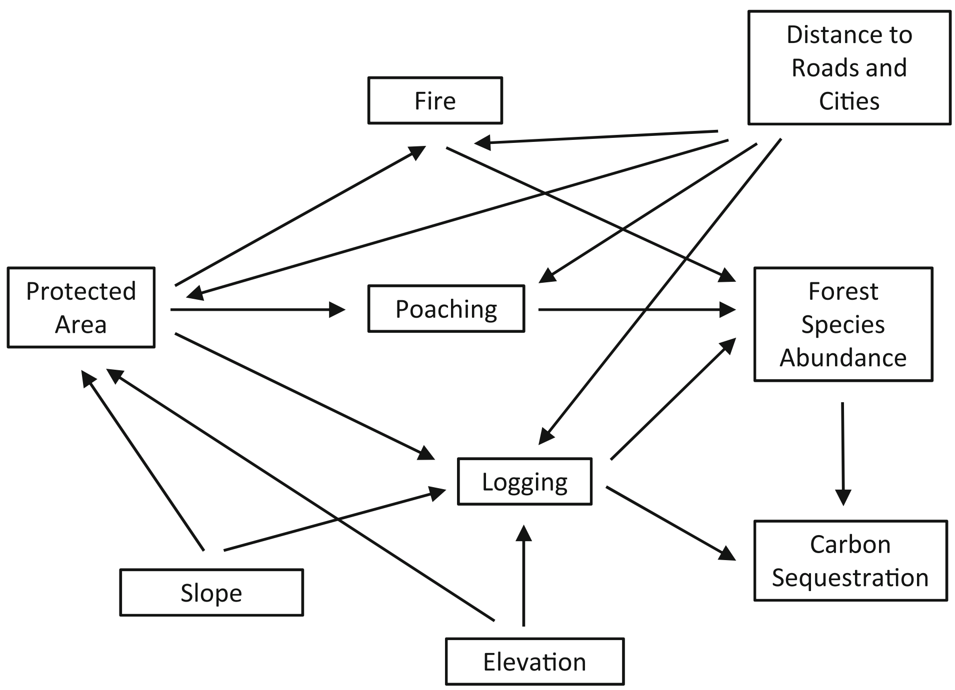

FIGURE 3 A directed acyclic graph (DAG) representing how different factors may influence forest species abundance.

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forest species abundance. Because our simulated data were created with specified (i.e., known) causal effects, we can use it to show how the SCM framework can return accurate causal estimates.

Step 2: Test DAG–data consistency

Once a DAG has been created, it can be tested against observational data to check for DAG–data consistency. Simply put, a DAG often asserts multiple independencies that should hold in the observational data, given that both the DAG and observational data are representative of the data-generating process. Given a DAG, a pair of variables can be independent of each other (e.g., X is independent of Y) if there are no paths (i.e., a sequence of nodes and arrows) connecting them. As well, a pair of variables can be conditionally independent. Conditional independencies emerge from d-separation (dependency separation; Pearl, 1988), a graphical rule for deciding whether a variable X is independent of another variable Y, given a set of variables, Z, in a path.

1. In d-separation (Pearl, 1988), a set of variables, Z, is said to block (or d-separate) a path from one variable to another if either (i) the path contains at least one arrow-emitting variable that is in Z or (ii) the path contains at least one collider variable (variable with two incoming arrows) that is outside Z and does not cause any variables in Z.
2. If all paths between X and Y are blocked (or d-separated) by Z, then X and Y are independent given Z, written $X \perp Y | Z$. For a more detailed discussion of d-separation, readers can reference Shipley (2000) and Shipley (2016), which discuss d-separation within an ecological context.

DAG–data consistency requires that all implied independencies for a given DAG (including conditional independencies based on d-separation rules) are consistent with the observational data set. For example, in a simplified DAG, $X \rightarrow Z \rightarrow Y$, X is independent of Y, given Z (an arrow-emitting variable that d-separates the path from X to Y). Therefore, the associated observational data should show that X is independent of Y when Z is adjusted for. Often a DAG will hold many independencies, and these independencies can be tested against a data set to ensure DAG–data consistency. If all implied independencies within a DAG coincide with the data set, then this supports DAG accuracy. However, if at least one implied independency is refuted (i.e., does not match the data), then the DAG is not consistent with the data and would need to be adjusted.

For our DAG (Figure 3), there are 28 independencies that can be tested against our simulated data to ensure DAG–data consistency (Appendix S2: Section S1). In an observational study, we would test these independencies against observational data. Here, we proceed by testing DAG–data consistency using our simulated data set, to walk readers through the process. Specifically, we use the dagitty R package, which provides a user-friendly way to evaluate whether a DAG is consistent with a data set, even when DAGs become increasingly complex and include many variables (Textor et al., 2016). Dagitty uses a formal test of zero correlation to test whether each identified independency of a specified DAG is consistent with a given data set; see Textor et al. (2016) for details. Using dagitty, we tested DAG–data consistency and found that all 28 independencies were consistent with our simulated data set (Step 2, Figure 2; see Arif [2022] for R code). This is expected as our simulated data was created to match the causal structure of our DAG.

In real-world applications, a DAG may require a series of adjustments until DAG–data consistency is achieved. As an ecological example, Schoolmaster et al. (2020) provided a real-world example of a DAG used to understand the relationship between tree species composition and canopy cover. Their initial DAG failed DAG–data consistency and was subsequently updated using a combination of domain knowledge and results from failed independence tests (Schoolmaster et al., 2020). Ankan et al. (2021) provided general examples and guidelines on updating DAGs based on DAG–data consistency, using the dagitty R package. Importantly, they noted that this process should be handled with care and always supported by domain knowledge. Failed independence tests are not necessarily proof that a DAG is incorrect; they can also indicate problems with the data (e.g., if the collected data do not represent the data-generating process). Ultimately, there should be a firm theoretical basis for creating and revising DAGs.

Once a DAG has been sufficiently justified and tested and updated based on DAG–data consistency, the backdoor (or frontdoor) criterion can be employed (Step 3, Figure 2). Before moving on to the application of the backdoor and frontdoor criteria, we briefly review why they can be applied to DAGs to determine causal effects from observational data.

DAGs for causal effects

Causal effects describe the extent to which a predictor variable X (i.e., the cause) influences a response variable Y (i.e., an effect). The SCM framework uses counterfactual

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reasoning to determine the causal effect of X on Y (Pearl, 2009). A counterfactual represents the potential outcome that would be realized if a predictor variable X was set to a different value, i.e., $X = x$. Specifically, a counterfactual for response variable Y is noted as $Y_x(u)$, which represents the value of (outcome) Y, had (predictor) X been x in unit (or situation) $U = u$ (Morgan & Winship, 2014; Rubin, 2005). This counterfactual $Y_x(u)$ is represented by the following equation:

$$Y_x(u) \triangleq Y_{M_x}(u). \tag{1}$$

In the SCM framework, a DAG represents a structural model, M. In Equation (1), M_x stands for a modified version of a model M, where X is intervened upon (i.e., "if X had been x," $X = x$). Graphically M_x is represented by a modified DAG, where the arrows pointing to X are eliminated. Equation (1) states that the counterfactual $Y_x(u)$ is the solution for Y in the modified model M_x (see Galles & Pearl, 1998 for axiom of Equation 1).

This definition of counterfactuals can be used to predict the effect of interventions from observational data alone. In the SCM framework, interventions are denoted by what's known as the do-operator, written do() (Pearl, 1995, 2009). For example, the query $Q = P(y|\mathrm{do}(x))$ asks what the distribution of Y would be if X were set to a particular value of x (i.e., the causal effect of X on Y). In relation to Equation (1), this can be defined as

$$P(y|\mathrm{do}(x)) \triangleq \mathrm{P}_{M_x}(y), \tag{2}$$

showing that the distribution of outcome Y (if X is set to a particular value of x) is equal to the distribution of Y in the modified model M_x (Pearl, 1995, 2009).

Given that we do not have postinterventional data (following the distribution of M_x), the question becomes whether the query $Q = P(y|\mathrm{do}(x))$ can be estimable from observational data (following the distribution of M) and the set of causal assumptions represented by its associated DAG. When a query includes a do-expression, an algebraic procedure known as do-calculus (Pearl, 1995) can be used to *equate* postinterventional distributions (those represented in M_x) to preinterventional (or observational) distributions (those represented in M). To identify an interventional query, for example, $Q = P(y|\mathrm{do}(x))$, the inference rules of do-calculus (outlined in Pearl, 1995) need to be repeatedly applied until an expression is obtained that no longer contains a do-operator. If this can be done, then the postinterventional query is estimable from observational data. Although the application of do-calculus makes for challenging reading, based on its derived inference rules, Pearl created the "backdoor criterion" and the "frontdoor criterion," which are two DAG-based graphical rules that can be applied to estimate interventional queries from observational data (i.e., the causal effect of X on Y), without the need for do-calculus operations.

Step 3 (Option 1): Apply backdoor criterion

The backdoor criterion (Pearl, 1993, 2009) is used to identify a set of variables, Z, that, when adjusted for, allows the postinterventional query $Q = P(y|\mathrm{do}(x))$ to be accurately estimated from observational data. The backdoor criterion states that a set of variables, Z, is sufficient for estimating the causal effect of X on Y under two conditions:

1. The variables in Z block all *backdoor paths* from X to Y. A *path* within a DAG is any sequence of arrows and nodes connecting two variables of interest, X and Y, regardless of direction. A *backdoor path* is a path between X and Y with an arrow pointing into X. Backdoor paths create bias by providing one or more indirect, noncausal pathways through which information can leak from one variable through another, leading to a spurious correlation. To block a backdoor path from X to Y, the backdoor path from X to Y must be d-separated. Again, the rules for d-separation are as follows: In d-separation (Pearl, 1988), a set of variables, Z, is said to block (or d-separate) a path from one variable to another if either (i) the path contains at least one arrow-emitting variable that is in Z or (ii) the path contains at least one collider variable (variable with two incoming arrows) that is outside Z and does not cause any variables in Z.
2. No element of Z is a descendant of (i.e., caused by) X.

When applied, the backdoor criterion blocks all noncausal pathways between a predictor and response variable of interest, while leaving all causal paths open. As such, the application of backdoor criterion eliminates common statistical biases that can otherwise plague observational studies, including confounding, overcontrol, and collider bias. Appendix S1 defines each of these biases and shows how the backdoor criterion removes each of them. The main takeaway is that given a DAG, the application of the backdoor criterion will avoid all three biases, allowing for causal estimates to be made.

Given our DAG (Figure 3), we can use the backdoor criterion to determine the sufficient set for adjustment required to answer our causal questions (Step 3, Figure 2). For example, if we want to quantify the causal effect of protected area on forest species abundance, there are nine backdoor paths that need to be blocked (i.e., d-separated):

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1. Forest Species Abundance → Carbon Sequestration ← Logging ← Elevation → Protected Area
2. Forest Species Abundance → Carbon Sequestration ← Logging ← Slope → Protected Area
3. Forest Species Abundance ← Fire ← Distance to Roads and Cities → Logging ← Elevation → Protected Area
4. Forest Species Abundance ← Fire ← Distance to Roads and Cities → Logging ← Slope → Protected Area
5. Forest Species Abundance ← Logging ← Elevation → Protected Area.
6. Forest Species Abundance ← Logging ← Slope → Protected Area
7. Forest Species Abundance ← Poaching ← Distance to Roads and Cities → Protected Area
8. Forest Species Abundance ← Logging ← Distance to Roads and Cities → Protected Area
9. Forest Species Abundance ← Fire ← Distance to Roads and Cities → Protected Area

The first four backdoor paths are already blocked because we have not adjusted for a collider variable (i.e., a variable with two incoming arrows: $\rightarrow X \leftarrow$) in each of these four paths. Specifically, carbon sequestration acts as a collider variable in Backdoor Paths 1 and 2, and logging acts as a collider in Backdoor Paths 3 and 4. The remaining backdoor paths do not contain collider variables and must be blocked by adjusting for an arrow-emitting variable that is not a descendant of (i.e., caused by) a protected area, our predictor variable. As such, Path 5 can be blocked by adjusting for elevation, Path 6 can be blocked by adjusting for slope, and Paths 7–9 can all be blocked by adjusting for distance to roads and cities. Collectively, the causal effect of protected area on forest species richness, given this DAG can be quantified by adjusting for slope, elevation, and distance to roads and cities.

Given that application of the backdoor criterion can rapidly become difficult to keep track of for increasingly complex DAGs, researchers are encouraged to draw out their DAG at www.daggity.net (instructions within site), which will apply the backdoor criterion and generate the minimal sufficient adjustment set(s) required to determine causal effects, given a specified DAG and causal question. As an example, readers can visit dagitty.net/m18S_bV to work with our protected area DAG. Using this website (see Appendix S2: Section S2 for quick steps), to determine the causal effect of fire on forest species abundance, we can adjust for either (distance to roads and cities and protected area) or (logging and poaching). To determine the causal effect of poaching on forest species abundance, we can adjust for either (distance to roads and cities and protected area) or (fire and logging). Finally, to determine the causal effect of logging on forest species richness, we can adjust for either (distance to roads and cities and protected area) or (fire and poaching). When there are multiple options for a sufficient adjustment set based on the backdoor criterion, researchers can choose a set based on data availability and measurement error. If known, it is best to select the set where variables are measured most accurately.

We note that, given our DAG and linear simulated data, causal effects between variables of interest could also be determined using alternative methods, such as SEM. However, a strength of the backdoor criterion is that it can allow causal estimation without requiring the availability of all variables in a DAG (Pearl, 2009). For example, the effect of a protected area on forest species abundance requires observational data on only variables for protected area, forest species abundance, slope, elevation, and distance to roads and cities. By only including variables necessary for answering specific causal queries, this can further enhance estimation accuracy by reducing researchers' reliance on noisy and irrelevant data (MacDonald, 2004). In addition, the application of the backdoor criterion does not require lengthy algebraic manipulations, is not computationally taxing, and is compatible across linear and nonparametric statistical approaches (Pearl, 2009). Ultimately, it provides ecologists with a widely applicable method for covariate selection across observational studies.

Step 4: Choose a statistical model

Once the backdoor criterion is used to determine the sufficient set(s) for adjustment, researchers must decide on an appropriate statistical model to carry out their causal analysis. Since our simulated data were created with a linear causal structure, we chose linear regression models for analysis (Step 4, Figure 2). However, it is up to researchers to decide what form of analysis will best suit their data. Because DAGs are nonparametric, they make no assumptions about the distribution of variables (e.g., normal) or the functional form of effects (e.g., linear, nonlinear, stepwise), making them compatible with a wide range of statistical methods. DAGs are also compatible with both frequentist and Bayesian statistical approaches since they are used to determine the sufficient set(s) for adjustment and not the analysis itself. Statistical models developed under the SCM framework are still subject to the same issues of sample size and measurement error in terms of the precision of resulting estimates; however, they are based on causal reasoning.

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Step 5: Causal effect

Figure 4 shows that when the backdoor criterion was used to determine the sufficient set for adjustment, our linear regression models were able to correctly estimate the causal effect between selected predictor variables and forest species abundance, our response of interest (Step 5, Figure 2; see Arif [2022] for R code). This is achieved because the backdoor criterion blocks all noncausal pathways (i.e., backdoor paths) between our predictor and response variable of interest while leaving all causal paths open. By adjusting for specific variables (if necessary) to answer specific causal

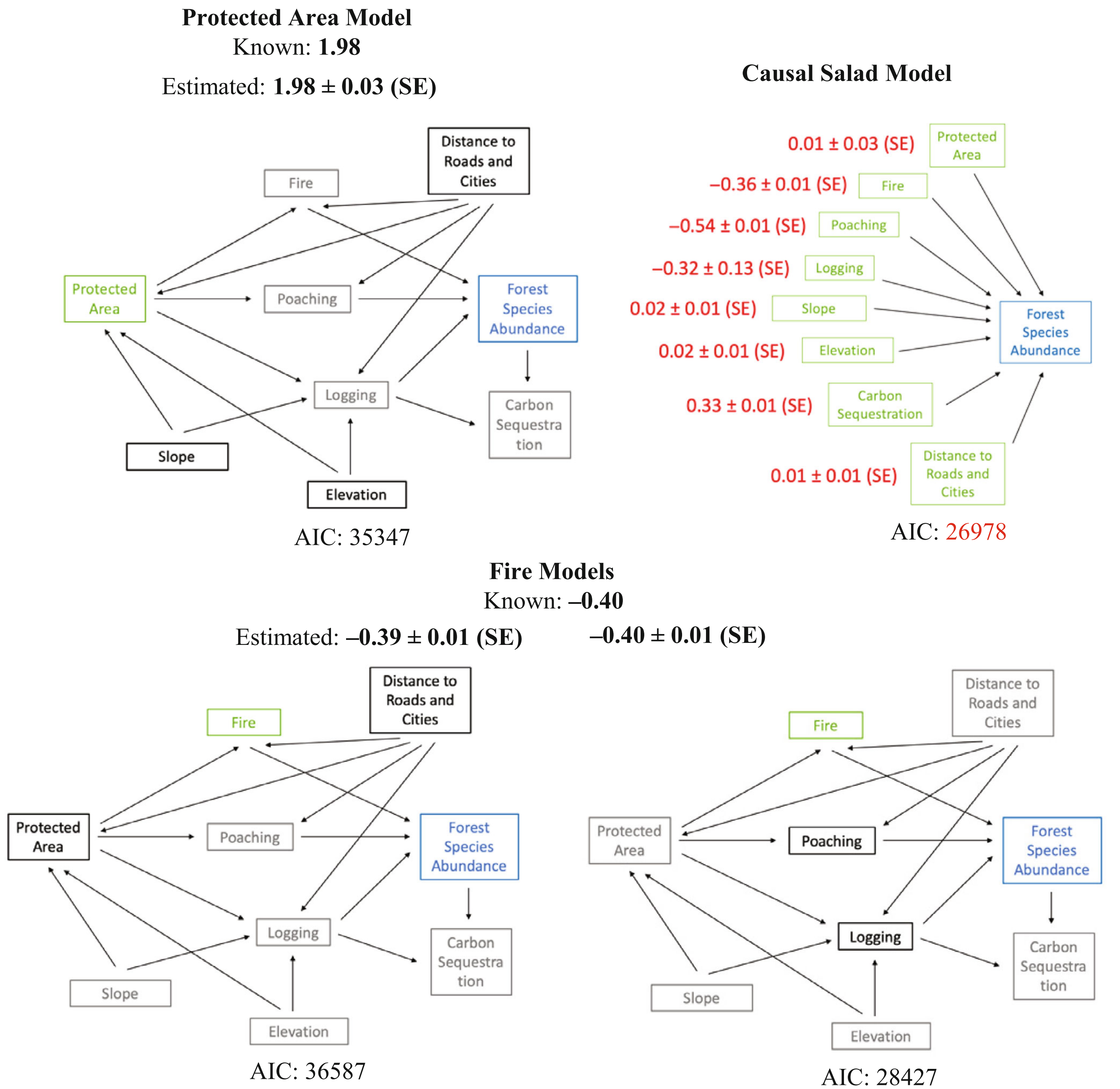

FIGURE 4 Results from linear regression models that employed the backdoor criterion to determine the causal effect of different predictor variables on forest species abundance using our simulated data set with specified (i.e., known) causal effects. Predictor, response, and control variables are highlighted in green, blue, and black, respectively; omitted variables are shaded in gray. We chose generalized linear regression as our statistical models; for example, the protected area model is represented by the following linear regression equation: Forest Species Abundance$_i$ = $\alpha + \beta_1$Protected Area$_i$ + β_2Slope$_i$ + β_3Elevation$_i$ + β_4Distance to Roads and Cities$_i$ + ε_i. The known and estimated causal effects, along with Akaike information criterion (AIC) values, are noted for each model. Lastly, the results from a causal salad model (where all variables are placed under one model) are shown as a contrast, with estimated effects for each included variable noted in red.

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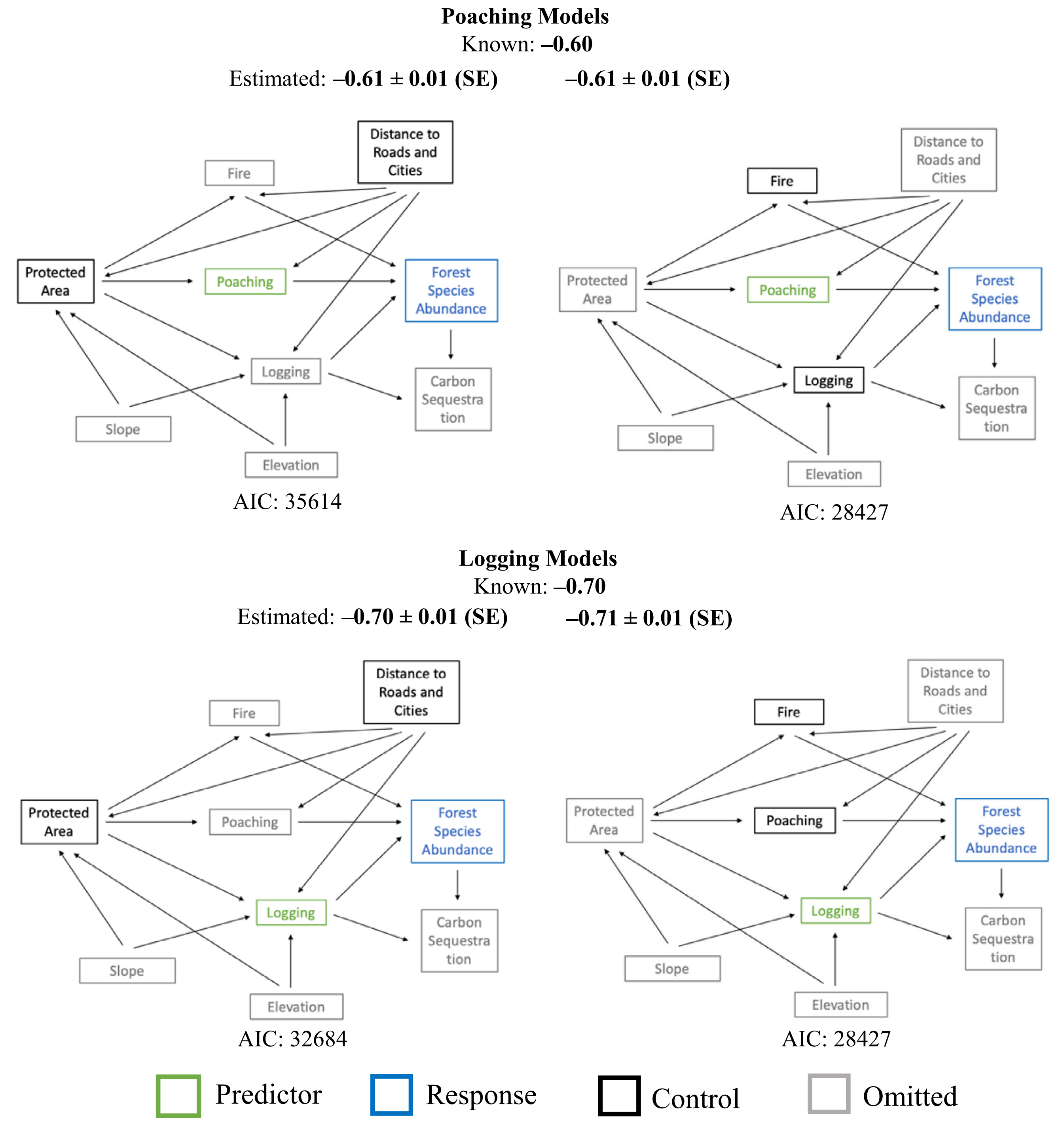

FIGURE 4 (Continued)

questions, the backdoor criterion can guide causal inference in observational settings.

Importantly, in performing a causal analysis, we are not trying to find a "best model" of the data according to criteria of model fit, such as AIC, which seek to find the model with the greatest predictive support, regardless of potential biases present in estimated effect sizes (Burnham & Anderson, 2002; Grace & Irvine, 2019). For example, in Figure 5 we include a "causal salad" model (McElreath, 2020) typical of ecological observational studies (including our own past work), whereby all available variables thought to affect a response are thrown into one statistical model and subsequently interpreted, without directly addressing the causal structure of the system. In our simulated example, the causal salad model (Figure 4) is strongly favored over all other models by AIC, yet it provides an entirely inaccurate picture of the causal structure in the system. Under this

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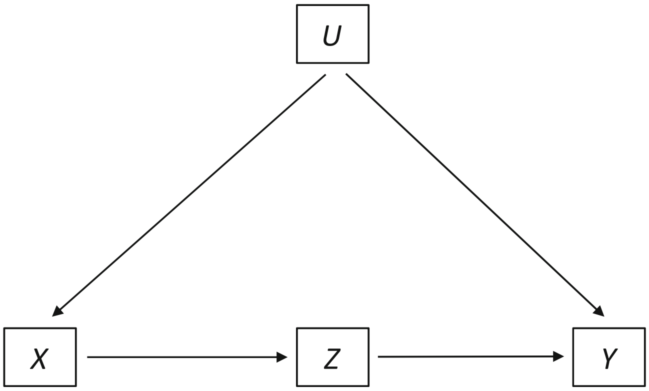

FIGURE 5 A directed acyclic graph (DAG) where the effect of X on Y cannot be estimated (due to an unobserved confounding variable U) without the use of the frontdoor criterion.

approach, we obtain inaccurate estimates of our predictor variables of interest (Figure 4). For example, the estimated effect of protected area on forest species abundance is negligible due to overcontrol bias (Appendix S1) occurring from the inclusion of fire, poaching, and logging, which are intermediate variables between the predictor and response variable of interest. Effect sizes for fire, poaching, and logging are also biased due to the inappropriate inclusion of carbon sequestration, which is not a predictor variable but is instead influenced by our response variable of interest. Collectively, these results demonstrate the general principle that the models used for causal inference must be carefully built to consider relevant causal relationships within a system prior to analysis. It also directly undermines "variance explained" as a modeling objective or arbiter of truth—without causal thinking to support modeling decisions, it is easy to add variables that seem to represent a better model according to a range of widely used statistical criteria. In this, the backdoor criterion can play a critical role in model development in a way that sets it apart from typical model-selection methods by determining the sufficient set(s) for adjustment required for causal inference.

THE FRONTDOOR CRITERION

The DAG-based approach to causal models up to this point has assumed we have observational data on all variables needed to satisfy the backdoor criterion. However, in some circumstances, there may be a known but unobserved variable that confounds our results, preventing application of the backdoor criterion for determining causal effects. For example, if we want to determine the causal effect of X on Y for the DAG in Figure 5, the backdoor criterion instructs us to adjust for U. However, U is unobserved and therefore cannot be used as a covariate in our final model. In such cases, an approach called the frontdoor criterion can be employed for causal inference (Pearl, 1995, 2009). To quantify the effect of X on Y in the presence of unobserved confounders, a variable Z satisfies the frontdoor criterion if

1. Z blocks all directed paths from X to Y.
2. There are no unblocked paths from X to Z.
3. X blocks all backdoor paths from Z to Y.

Once a Z variable is identified, the causal effect of X on Y can be determined by first employing the backdoor criterion to separately determine the effect of X on Z and Z on Y (Figure 5). The product of these two causal effects (i.e., point estimates) then becomes the effect of X on Y (Pearl, 1995, 2009). In what follows, we show how to apply the frontdoor criterion to determine the effect of sharks on rays based on a hypothetical ecological example.

Step 1: Create a DAG

The DAG in Figure 6a asserts that sharks affect rays, which in turn affect bivalves, through a top-down trophic cascade that was previously supported (Baum & Worm, 2009; Myers et al., 2007) and refuted (Grubbs et al., 2016) in the literature. In our hypothetical scenario, we also assert that fishing pressure affects both sharks and bivalves, but not rays. Here, observational data on fishing pressure is not available, making it an unobserved variable. Like our prior example, we created a simulated data set (with known causal effects) matching our DAG (see Arif [2022] for R code) to demonstrate the use of the frontdoor criterion. Specifically, we will show how to employ the frontdoor criterion to return the causal effect of sharks on bivalves, which we set to 0.02.

Step 2: Test DAG–data consistency

Given the DAG in Figure 6a, two independencies can be tested based on d-separation rules: (1) fishing pressure is independent of rays, given sharks, and (2) sharks are independent of bivalves, given fishing pressure and rays. However, testing either independency requires observational data on fishing pressure (our unobserved variable). Therefore, owing to our unobserved confounding variable, DAG–data consistency cannot be tested based on d-separation rules in this case. However, we can still apply the frontdoor criterion for causal estimates with our asserted DAG (unchecked for DAG–data consistency).

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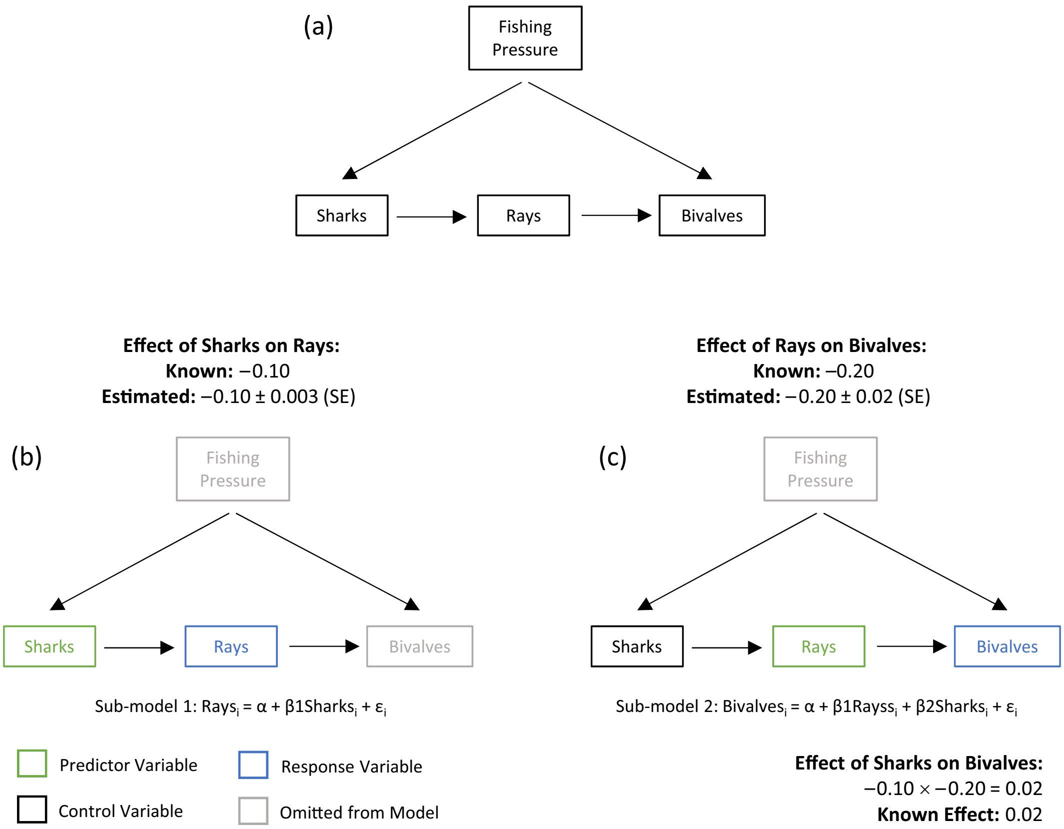

FIGURE 6 Employing the frontdoor criterion. (a) A directed acyclic graph (DAG) representing the causal structure between sharks and bivalves. Here, fishing pressure is an unobserved variable, and the frontdoor criterion needs to be employed to determine the effect of sharks on bivalves. (b, c) Employing the frontdoor criterion to determine the effect of sharks on bivalves from our simulated shark-bivalve data set. Linear regression models were used to first determine the effect of sharks on rays and the effect of rays on bivalves using the backdoor criterion to determine the sufficient set for adjustment. The product of these two effects gives us the effect of sharks on bivalves. Known causal effects (from our simulated data) between variables of are noted for comparison.

Step 3 (Option 2): Apply frontdoor criterion

The frontdoor criterion can be employed to find the effect of sharks on bivalves. Rays satisfy the frontdoor criterion since (1) they block all directed paths from sharks to bivalves, (2) there are no unblocked backdoor paths from sharks to rays, and (3) all backdoor paths from rays to bivalves are blocked by sharks (see rules for frontdoor criterion given previously). To determine the effect of sharks on bivalves, we first need to apply the backdoor criterion to determine the effect of sharks on rays (which can be estimated without any adjustments) and the effect of rays on bivalves (which can be estimated by adjusting for sharks). Both submodels can employ the backdoor criterion without needing to adjust for fishing pressure (our unobserved variable). The causal effect of sharks on bivalves can then be estimated by multiplying the effect of sharks on rays by the effect of rays on bivalves.

Step 4: Choose a statistical model

We use linear regression models because our simulated data were created using linear relationships.

Step 5: Causal effect

Figure 6 shows that when the frontdoor criterion was employed, we were able to accurately determine the causal effect of sharks on bivalves (see Arif [2022] for R code). Specifically, the product of the effect of sharks on rays (Figure 6b) and the effect of rays on bivalves (Figure 6c) gave us an accurate causal estimate of sharks on bivalves (0.02) without having to adjust for fishing pressure, our unobserved confounding variable. In contrast, a model with just rays regressed on sharks gives a misleading estimate of 0.99. Here, the correlation between sharks and rays is spurious due to the confounding effect of our unobserved fishing pressure variable.

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The frontdoor criterion is not as widely applicable to ecological data as the backdoor criterion, because it requires a specific causal structure, specified by its three rules (see earlier discussion). However, in cases where these rules are met, the frontdoor criterion can provide causal estimates, regardless of the strength of unobserved confounding. As well, it can be employed in the presence of multiple unobserved confounding variables.

EXAMPLES OF SCM IN ECOLOGY

Although currently underutilized, the SCM framework, along with its application of DAGs, has been used to understand the causal structure of ecological systems. Here we provide an overview of three recent applications of Pearl's SCM framework in ecology.

What causes climate-induced coral reef regime shifts?

Climate-induced bleaching events can sometimes lead to coral reef regime shifts, whereby the benthic composition of a coral reef ecosystem abruptly transitions from one dominated by coral to one dominated by macroalgae (Bellwood et al., 2004). However, not all coral reef regimes shift following a bleaching event, and it is expected that certain factors may influence the likelihood of climate-induced regime shifts. Although past correlative studies found correlations between key predictor variables (e.g., depth, structural complexity; Graham et al., 2015) and regime shift trajectory, these studies were not grounded in causal inference. For example, a literature review of observational coral reef regime shift studies showed that no studies to date have used causal inference methods, though they often used causal language to communicate their results (e.g., "the effect of"; Arif et al., 2022). Instead, these studies either used a causal salad approach or included no covariate adjustment, without communicating the overall causal structure of the system under study (Arif et al., 2022).

To overcome these limitations, Arif et al. (2022) applied the SCM framework to understand how different factors influenced regime shift trajectory following the 1998 bleaching event across Seychelles coral reefs. They created a DAG depicting the causal structure of how factors are expected to influence regime shift trajectory in Seychelles, based on expert opinion and scientific literature (Figure 7). Given their DAG, they applied the backdoor criterion to determine whether, and to what extent, different factors influenced regime shift trajectory in this region. As expected, they found that reduced depth and structural complexity and high nutrient levels increased the likelihood of regime shifting. Importantly, Arif et al. (2022) found additional factors that were not evident from a past correlative study using the same data set and a causal salad approach (e.g., Graham et al., 2015).

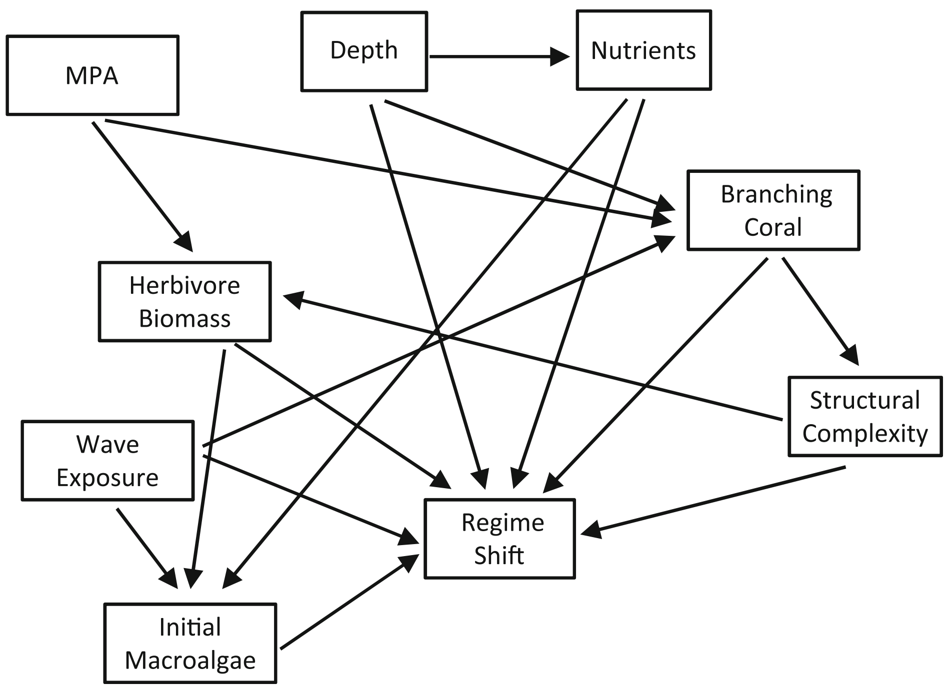

FIGURE 7 A directed acyclic graph (DAG) representing how different factors may influence coral reef regime shifts following a climate-induced bleaching event across Seychelles, from Arif et al. (2022).

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Additional insights included the positive effect of predisturbance macroalgae cover, branching coral, and wave exposure of regime shift occurrence (Arif et al., 2022). These results highlight that when dealing with observational data, different statistical adjustments can lead to different conclusions about a study system. Given this, Arif et al. (2022) recommend applying DAGs and the backdoor criterion for model selection across observational coral reef studies.

What causes species-level trait covariation?

Ecological theory suggests that there may be several causes of species-level trait covariation, including size, pace of life, evolutionary history, and ecological condition (Cronin & Schoolmaster Jr., 2018). Although numerous studies have attempted to quantify the causal effect of these factors on trait covariation, these studies did not consider the causal structure driving trait variation, which in turn can lead to inappropriate statistical adjustments and biased estimates.

To resolve this, Cronin and Schoolmaster Jr. (2018) the synthesized relevant literature and domain knowledge to create a DAG representing the causes of species-level trait covariation that can be applied to across multiple kingdoms. As their Figure 8 DAG suggests, size and pace of life may be two direct causes of trait covariation, and their influence on traits is confounded by evolutionary history and ecological conditions. To determine how size and pace of life affect trait covariation, they first had to accurately quantify their causal effect on each trait, since this information was subsequently used to determine their influence on trait covariation. One way to do this is to employ the backdoor criterion. For example, to determine the effect of size on a trait (e.g., Trait 1 in Figure 8), the backdoor criterion instructs us to adjust for either pace of life or evolutionary constraints and ecological condition to remove the confound of evolutionary history and ecological condition. In contrast, previous studies have estimated the effect of either size or pace of life on traits without first controlling for these confounding variables (e.g., Brown et al., 2004; Johnson et al., 2012). Another widely accepted approach has been to first account for evolutionary constraints and then analyze the residuals (e.g., Bielby et al., 2007; Huang et al., 2013). However, Cronin and Schoolmaster Jr. (2018) show that these approaches lead to erroneous estimates about the causes of trait covariation. They also showed that methods including principal component analysis (PCA) and exploratory factor analysis (EFA) are not able to partition trait covariance when the direct causes (size and pace of life) are correlated due to shared drivers (evolutionary history and ecological conditions). This is concerning as several high-profile studies have used these techniques to reach their conclusions (e.g., Wright et al. [2004] concluded from a PCA that size is the only causes of lead trait covariance). Taken together, a well-considered DAG guides ecologists on the sufficient set(s) for adjustment required to quantify the causes of trait covariation and further highlights the utility of Pearl's SCM framework for observational causal inference.

Is biodiversity a cause of ecosystem functioning?

A central goal of ecology is to understand the causes of ecosystem functioning (Mittelbach, 2012); however, correctly identifying these causes has been difficult because numerous hypothesized drivers are often interrelated. A widespread belief among ecologists is that biodiversity is a prominent cause of ecosystem functioning (Tilman

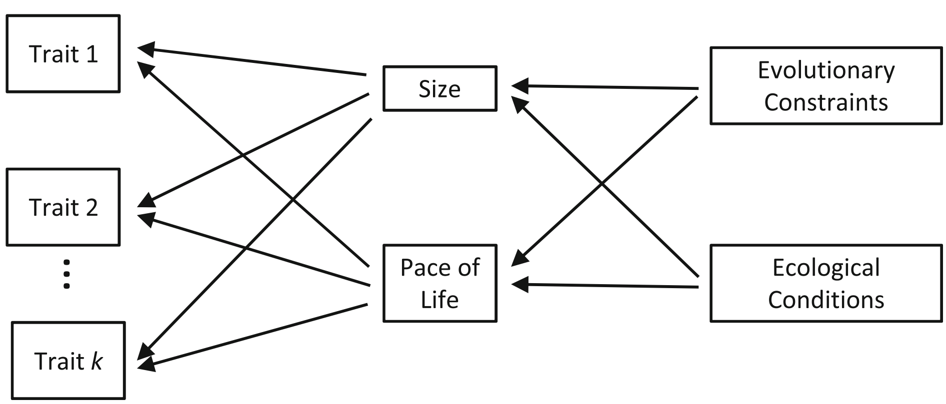

FIGURE 8 A directed acyclic graph (DAG) representing how different factors influence species-level trait covariation, from Cronin and Schoolmaster Jr. (2018).

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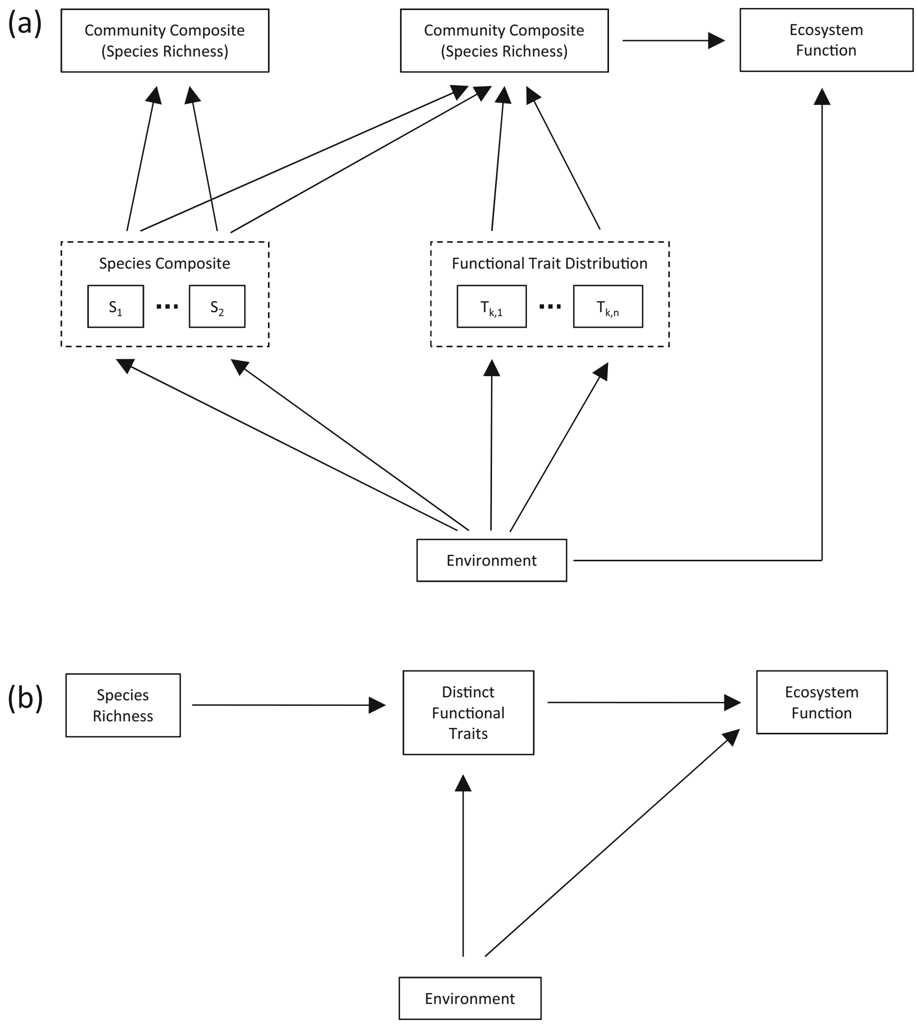

FIGURE 9 Two directed acyclic graphs (DAGs) representing the causal relationship between biodiversity and ecosystem function. The DAG in (a) is from Schoolmaster et al. (2020), whereas that in (b) is from Grace et al. (2022).

et al., 2014). Hundreds of papers have published biodiversity–ecosystem function (BEF) correlations across various ecological systems, with conflicting theories and conclusions (Schoolmaster et al., 2020). To better understand whether biodiversity causally affects ecosystem functioning, Schoolmaster et al. (2020) created a DAG by synthesizing the BEF literature and logic (Figure 9a). Their DAG deviates from the standard model whereby species richness is assumed to affect ecosystem functioning through functional trait diversity (Loreau et al., 2001) and instead posits that species composition affects both species richness and functional trait diversity, with functional trait diversity driving ecosystem functioning (Figure 9a).

Given their DAG (Figure 9a), the backdoor criterion states that functional trait distribution and the environment need to be adjusted to determine the causal effect (or lack thereof) of biodiversity on ecosystem functioning. Using simulated and empirical data, Schoolmaster et al. (2020) show that when this is done, there is no causal relationship found between biodiversity and ecosystem functioning. Instead, they argue that previous observational studies that found an association between biodiversity and ecosystem functioning were based on model misspecification (i.e., having an incomplete or incorrect set of predictors). For example, given their DAG, confounding bias from failing to condition on environmental factors can lead to spurious (i.e., noncausal) associations between biodiversity and ecosystem functioning. Given their DAG, Schoolmaster et al. (2020) concluded that BEF correlations were noncausal associations. Instead, their model suggests that it is species composition and not biodiversity that drives ecosystem functioning.

Recently, a comment on Schoolmaster et al. (2020) was published by Grace et al. (2022), criticizing the former's DAG and conclusions, asserting that biodiversity causally affects ecosystem functioning. They provide an alternative DAG that maintains that biodiversity can causally effect ecosystem functioning indirectly through

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its effect on trait diversity (i.e., "distinct functional trait"; Figure 9b). This aligns with the standard model (Loreau et al., 2001) based on BEF correlations being causal. Schoolmaster Jr. et al. (2022) responded with a comprehensive reply, addressing critiques of their DAG, clarifying the SCM framework, and showing that the standard model and past interpretations of BEF experiments are not supported by causal analyses. Interestingly, Schoolmaster Jr. et al. (2022) note that the simulations provided by Grace et al. (2022) do not represent the standard model DAG they defend but instead map onto the DAG presented by Schoolmaster et al. (2020).

Although the issue of BEF correlation versus causation has yet to be resolved, there now exist two contradictory DAGs that can be used to focus critical debate and deepen our understanding of this potential process. As noted by Grace et al. (2022), DAGs allow researchers to state their causal assumptions explicitly and transparently. Ultimately, this allows other researchers to examine those causal assumptions and subsequent interpretations critically, as was done by Grace et al. (2022) and Schoolmaster Jr. et al. (2022). Ultimately, communicating and critiquing researchers' causal assumptions through DAGs may lead to a deeper understanding of BEF correlations, as well as other ecological phenomena.

ADDITIONAL CONSIDERATIONS

Inaccurate or unknown causal structure

One of the potential limitations of DAGs is that they may not accurately represent the true causal nature of an ecological system. Simply put, inaccurate DAGs will lead to inaccurate causal inference. This can arise when using incorrect theory and background information or by creating DAGs based on available data, rather than incorporating all relevant variables (such as omitted or unobserved variables). However, as a researcher's causal assumptions are explicitly stated through graphical representation, DAGs allow reviewers to explicitly critique and correct potential problems with far more transparency than is typical (Pearl, 2009). Further, the ability to test DAG–data consistency via d-separation rules facilitates more reliable conclusions (Textor et al., 2016).

We believe that SCM should be used whenever researchers have causal objectives and sufficient background knowledge to create and justify the assertions made in their DAGs. If, however, the causal structure between the predictor and response variables of interest are not fully known, but there exists enough background knowledge and support to create several plausible DAGs (each of which supports DAG–data consistency), it may be advantageous to present all DAGs as plausible alternatives, reflecting this epistemic uncertainty. This should provide more accurate estimates, especially when predictor variables have the same covariate adjustments across a range of plausible DAGs. We emphasize that since several DAGs can pass DAG–data consistency, it is always imperative to first justify a DAG (or set of DAGs) based on theory, instead of relying solely on DAG–data consistency.

Application within quasi-experimental and experimental approaches

In recent years, ecologists have promoted the use of quasi-experimental methods for causal inference, including propensity score matching, before-after control-impact (BACI) studies, regression discontinuity design, and instrumental variables (Butsic et al., 2017; Larsen et al., 2019). Here, DAGs and the principles of the SCM framework (e.g., the backdoor criterion) can be used to create more robust study designs and explicitly communicate assumptions required for quasi-experimental approaches (Arif & MacNeil, 2022). For example, propensity score matching is used to remove confounding bias associated with ecological observational studies (e.g., Ramsey et al., 2019). However, although past ecological studies assumed confounding variables that entered a propensity score analysis, it is unclear how these variables related to one another and within the broader causal structure of a study system. Without this knowledge, it is unclear whether there are unmeasured variables that need to be included in the propensity score (leading to confounding bias) or whether the inclusion of selected variables may lead to other forms of bias (e.g., overcontrol and collider bias; Mansournia et al., 2013, Shrier, 2009; Sjölander, 2009). As noted by Pearl, for a propensity score analysis to be valid, the selected variables that enter a propensity score must satisfy the backdoor criterion to remove bias (Pearl, 2009). In other words, the variables that enter a propensity score should be the sufficient set for adjustment based on the backdoor criterion. For an overview of how the SCM framework can guide quasi-experimental study designs (including propensity score and other matching methods, BACI studies, regression discontinuity designs, and instrumental variables), we refer readers to Arif and MacNeil (2022). By utilizing DAGs and the principles of the SCM framework, ecologists can design more robust quasi-experimental approaches while explicitly communicating their causal assumptions to their audience.

DAGs and the SCM framework can also guide causal inference in experimental studies. Like observational studies, experimental studies rely on causal assumptions that must be ensured by the researcher (Kimmel et al.,

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2021). Here, DAGs can be used to understand whether data collected from an experimental setup (e.g., natural experiment or randomized control trail [RCT]) can be used for causal inference or if there are sources of bias that need to be accounted for (e.g., Schoolmaster et al., 2020; Schoolmaster Jr. et al., 2022; Williams et al., 2018). For example, Williams et al. (2018) presented an overview of a RCT investigating the effect of an intervention promoting breastfeeding on cognitive development during childhood. A DAG of this study clarified that only using data from individuals who attended a follow-up session could lead to collider bias because both the intervention and outcome could affect the likelihood of individuals following up; therefore, follow-up data should not be distinctly analyzed (Williams et al., 2018). As an ecological example, Schoolmaster et al. (2020) used their BEF DAG to argue that BEF experiments do not directly manipulate biodiversity but rather manipulate community structure, failing to isolate for the biodiversity effect.

CONCLUSIONS

Ecology has relied on observational data from its inception (Elton, 1927), yet the use of causal logic has typically been limited to controlled randomized experiments. Our ongoing reliance on observational data to understand fundamental questions in ecology requires the increased use of valid causal inference methodologies. Here we introduced Pearl's SCM framework, which allows causal inference to be made in a wide range of observational contexts. The SCM framework uses DAGs to visualize the hypothesized causal structure of a system or process under study, allowing researchers to explicitly communicate their causal assumptions. Once a DAG has been built that is sufficient to characterize a system or process under study, the backdoor or frontdoor criterion can be used to guide appropriate statistical adjustments required for causal inference. Doing so can improve conclusions made from observation-based research and will ultimately increase the depth and pace of ecological research.

AUTHOR CONTRIBUTIONS

Suchinta Arif and M. Aaron MacNeil conceived the idea of this study. Suchinta Arif led the writing of the manuscript. Both authors contributed to drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Code for simulations and statistical analysis (Arif, 2022) is available on Figshare at https://doi.org/10.6084/m9.figshare.19541059.v1.

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