

PERSPECTIVE

A Causal Inference Framework for Climate Change Attribution in Ecology

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ABSTRACT

As climate change increasingly affects biodiversity and ecosystem services, a key challenge in ecology is accurate attribution of these impacts. Though experimental studies have greatly advanced our understanding of climate change effects, experimental results are difficult to generalise to real-world scenarios. To better capture realised impacts, ecologists can use observational data. Disentangling cause and effect using observational data, however, requires careful research design. Here we describe advances in causal inference that can improve climate change attribution in observational settings. Our framework includes five steps: (1) describe the theoretical foundation, (2) choose appropriate observational datasets, (3) estimate the causal relationships of interest, (4) simulate a counterfactual scenario and (5) evaluate results and assumptions using robustness checks. We demonstrate this framework using a pinyon pine case study in North America, and we conclude with a discussion of frontiers in climate change attribution. Our aim is to provide an accessible foundation for applying observational causal inference to estimate climate change effects on ecological systems.

1 | Introduction

The increasing impacts of climate change on the world's ecosystems underscore the urgent need for accurate attribution in ecology (Lloyd and Shepherd 2020; Parmesan et al. 2011). Disentangling climate change impacts from other drivers of ecosystem change (e.g., land use, endemic disturbance regimes) is critical to understand how climate change is modifying ecosystems and to identify effective management strategies. If climate change impacts are misidentified, interventions can fail because management success depends on addressing the dominant drivers of change (Aplet and McKinley 2017; Dudney et al. 2018; Hobbs et al. 2009). Though climate change and associated

extremes threaten biodiversity and ecosystem services worldwide (Anderegg et al. 2020; Millar and Stephenson 2015), quantification and **attribution** (bolded terms are included in the glossary, Box 1) remain very challenging. Prior syntheses, for example, suggest that anthropogenic climate change attribution (hereafter **climate change attribution**) is often too difficult to pursue, given the complexity of impacts and the many study design and data limitations faced by ecologists (Parmesan et al. 2013). Thus, methodological advances are needed to accurately attribute shifts in ecosystems to climate change.

Climate change attribution requires isolating the causal effect(s) of relevant climate variables from other drivers of

Attribution: An estimate of the relative contributions of a causal driver(s) to a change in a biological variable or event. Attribution requires the detection of change in an observed variable (i.e., statistical confidence that change in the outcome variable of interest has occurred) (Parmesan et al. 2013).

Bias: Nonrandom, systematic error in the estimation of a treatment effect (e.g., an explanatory variable of interest) (Holmberg and Andersen 2022).

Climate Change Attribution: Quantifies how much of an observed ecological change can be directly linked to anthropogenic climate change. Anthropogenic climate change can include shifts in shorter-term and longer-term annual means, climate variability, extreme events, and other climate forcings (e.g., Pacific Decadal Oscillation [PDO] and El Niño Southern Oscillation [ENSO]). The cause of these climatic changes is assumed to be anthropogenic emissions (Parmesan et al. 2013).

Collider bias: when the explanatory (i.e., treatment) and the outcome variables (or other variables causing these variables) each influence a third variable—that is controlled for in the research design or analysis (which contrasts to **confounding variables**, which are *not* controlled for). Collider bias can be introduced by inadvertently controlling for a variable that occurs after the treatment or intervention, and it threatens the internal validity of a study.

Confounding variable: A confounder is a variable that affects both the dependent and independent variables. Because the confounding variable impacts both the dependent and independent variables, its presence can distort or mask the effects of the explanatory variable of interest, leading to inaccurate estimates of the causal relationship (e.g., climate effects).

Counterfactual prediction: When data with the full set of potential outcomes is not available, a counterfactual scenario can be used to estimate the potential outcomes given different treatment variables. For climate change attribution, the counterfactual is the predicted impact of climate forcing that does not include warming trends attributed to greenhouse gas emissions. This can be somewhat comparable to a predicted ‘control treatment’ that is compared to the actual (observed) climate change impacts (Hsiang 2016; Mendelsohn et al. 1994). Note: counterfactual scenarios are not observed and therefore cannot be verified.

Fixed effects panel model: A regression model that includes individual intercepts (i.e., fixed effects) for each unit of observation and time period in the data. Fixed effects control for unobserved confounding differences between groups (e.g., sites or organisms) that are time-invariant, while temporal fixed effects (e.g., years) control for temporal variation that is common to all units. Importantly, fixed effects in this context have a distinct meaning from fixed effects defined by biostatisticians (i.e., non-random variables) (Bolker et al. 2009; Larsen et al. 2019).

Internal validity: Whether or not a study accurately identifies a causal relationship within the context of the study—i.e., whether changes in the dependent variable are caused by changes in the independent variable or whether this relationship is confounded.

External validity: Whether the results of a study can be generalised to other settings, populations, times and conditions beyond the scope of the study (i.e., whether or not the study's results can be extrapolated).

Omitted variables bias: Occurs when a confounding variable is excluded from a statistical model, leading the model to compensate for the missing information by misattributing its effects to the included variables, resulting in biased estimated effects of the explanatory variables.

Mediator variables: Variables that explain the mechanism through which an explanatory variable influences an outcome variable, clarifying *why* or *how* this relationship occurs. They usually do not need to be included in regression models.

Moderator variables: Variables that influence the strength or direction of the relationship between an explanatory variable and an outcome variable. In statistical models, moderation effects are typically assessed through interaction terms.

Parallel trends: The assumption that the difference between the treatment and control group would have been constant over time had there been no treatment—i.e., in the absence of the treatment, both treatment and control groups would have had parallel trends through time.

Stable Unit Treatment Assumption: Causal inference analysis assumes that the treatment of one unit does not affect the outcomes of other units (an example of interference or spillover effects).

ecosystem change. To identify causal effects of climate change, ecologists use a variety of techniques, including lab-, field- and computer-based experiments. For instance, tank experiments have quantified the effects of warming on coral species (Dove et al. 2013; McLachlan et al. 2020), and the Jasper Ridge Global Change Experiment has found variable responses of above- and below-ground grassland communities to warming (Gutknecht et al. 2012; Liang and Balser 2012; Zhu et al. 2016). Complementary empirical studies and process-based models

have provided further evidence of causal links between warming and ecological shifts, including changes in butterfly emergence (Kearney et al. 2010), tree mortality (Adams et al. 2013; Choat et al. 2018), and species' range shifts (Fitt et al. 2019). Comparative analyses of experimental and observational studies, however, suggest that experimental results often underestimate climate change impacts (Lenoir 2020; Smith et al. 2024). These important discrepancies may be due to methodological limitations—e.g., treatments might not match realised climate

change effects because they do not capture the variability of conditions or the appropriate timescales) (Catford et al. 2022; Cottingham et al. 2005). Given these limitations, adopting analytical approaches that enable the identification of causal effects in observational settings is an important frontier in ecology (Larsen et al. 2019; Parmesan et al. 2013).

Though observational studies can provide insight into realised climate impacts in natural (i.e., non-experimental) systems, estimating causal relationships between climate and observed changes is very challenging (Gonzalez et al. 2023). Obstacles to observational causal attribution include ecological complexity, data limitations that can undermine statistical power, and most critically, the challenge of isolating climate from other drivers of change (including **confounding variables**). Standard statistical approaches in ecology, such as information-theoretic approaches that optimise for a model's explanatory performance (Arif and MacNeil 2022a; O'Connor et al. 2015; Parmesan et al. 2011), are limited in their ability to disentangle climate effects from other correlated drivers. Thus, in ecology, we need to move beyond predictive models to accurately isolate climate change from other drivers in observational settings. Fortunately, there are a suite of tools that have been developed in other disciplines that are increasingly applied to ecological analyses—some of these concepts and tools are also useful in the context of climate change attribution in ecology (see list of papers in Table S1).

Here we outline a causal inference framework for robustly quantifying the realised effects of climate change on ecosystems using observational data. To illustrate this approach, we use longitudinal tree-ring data to estimate climate change effects on two-needle pinyon pine (*Pinus edulis*) growth. Subsequently, we discuss important strategies and limitations associated with this framework and highlight new research directions at the frontier of climate change attribution. Our goal is to provide an accessible foundation for applying causal inference to climate change attribution studies in ecology, thereby extending our ability to quantify impacts and manage the accelerating threat to natural systems.

2 | Observational Causal Inference Is Well-Suited for Climate Change Attribution

Climate change attribution in ecology seeks to draw causal conclusions about the magnitude of climate change effects on biological systems (Rosenzweig et al. 2008). Increasingly, ecologists are pursuing causal questions using observational data by applying causal inference methods (Butsic et al. 2017; Dee et al. 2023; Dudley et al. 2021; Larsen et al. 2019; Suskiewicz et al. 2024). Causal inference seeks to isolate and quantify the effect of some change (e.g., temperature) on an outcome of interest (e.g., net primary productivity) using a combination of theory and robust statistical tools. By isolating causal effects using observational data, these techniques provide an important complement to traditional climate change attribution approaches (e.g., experiments and process-based models) that can sometimes oversimplify complex systems (Stecher and Baumgärtner 2024).

Importantly, causal inference techniques are distinct from many statistical approaches that ecologists have traditionally applied to observational data (Gonzalez et al. 2023). For example, ecologists

often prioritise prediction and generalisability, as evidenced by the common practice of selecting models based on their parsimony or predictive skill (Hernán et al. 2019). However, predictive skill does not necessarily imply causation (Arif and MacNeil 2022a; Ferraro et al. 2019) nor clarify the assumptions needed for causal interpretation of estimated climate change effects. To answer the important question at the heart of climate change attribution (e.g., what is the causal effect of climate change?), ecologists can benefit from statistical approaches that use observational data. These approaches can produce estimates of climate change impacts that are more accurate and transparent, which is particularly relevant for implementing effective policy and climate change mitigation strategies (Kolstad and Moore 2020).

An important distinction and strength of causal inference tools is that they focus on reducing bias to isolate the causal relationship of interest (Larsen et al. 2019; Pearl 2009; Rubin 2005; Siegel and Dee 2025). For example, temperature and plant productivity may both be affected by increases in CO₂. If CO₂ is omitted from the model, it can confound the causal relationship between temperature and productivity. This example of **omitted variable bias** is one of many forms of statistical bias that leads to misidentification of the true causal relationships of interest (reviewed in Byrnes and Dee 2024 for ecologists). A key challenge for observational causal inference is to rule out biases through: (1) a priori knowledge about the influences on the response variable of interest, and (2) careful research design and statistical control of potential sources of bias. When implemented correctly, causal inference is well-suited to climate change attribution because it can isolate the impact of climate change drivers from the complex array of potentially confounding variables (Hsiang and Kopp 2018).

3 | A Causal Inference Framework for Climate Change Attribution

Our framework for climate change attribution using observational causal inference (Figure 1) is focused on attributing historical climate change to observed changes in outcome variables of interest. Below, we explain the five steps of the framework: (1) describe the theoretical foundation and develop testable hypotheses, (2) choose appropriate observational data that enable accurate tests of the hypotheses, (3) estimate the causal relationships of interest, (4) simulate a counterfactual scenario and (5) evaluate results and assumptions using robustness checks.

3.1 | Step 1. Describe the Theoretical Foundation

The first step of a causal analysis is to clearly define the research question and associated hypotheses. To develop a defensible causal analysis, a hypothesis should be strongly grounded in logic, theory, and prior knowledge. Once the question and hypothesis have been defined, a common approach that can help researchers identify and evaluate causal relationships is Directed Acyclic Graphs (DAGs) (Arif and MacNeil 2022b; Huntington-Klein 2021; Pearl 2009). DAGs are a graphical representation of causal, directional effects (Figure 1, Step 1). They identify not only the primary causal path(s) of interest (e.g., temperature effects on forest productivity) but also the potential confounding variables and other sources of bias (e.g.,

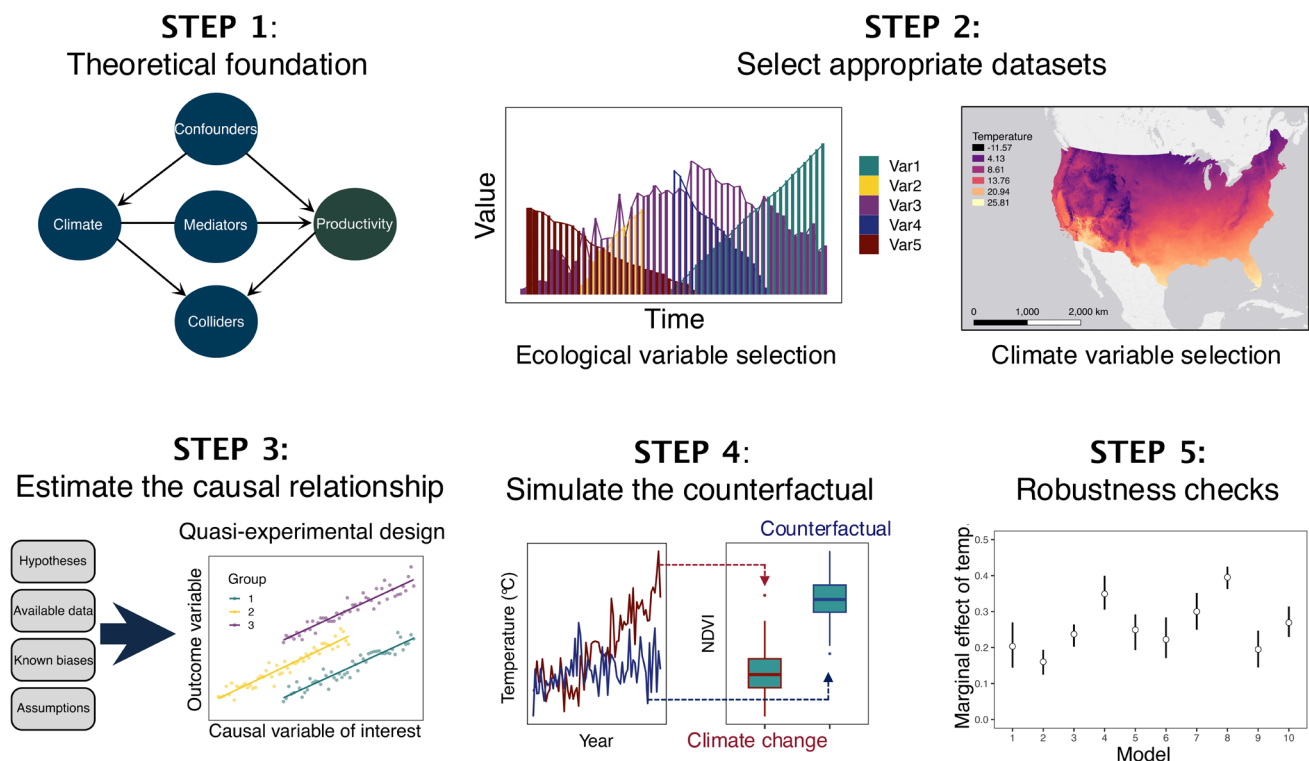


FIGURE 1 | A causal inference framework for climate change attribution in ecology. Step 1: Describe the theoretical foundation, including the causal relationships of interest and confounding variables. Arrows and circles illustrate a simplified directed acyclic graph (DAG) showing different classes of variables that can be included in a DAG (e.g., **mediators** and confounders). Step 2: Choose appropriate observational datasets of the treatment, response, and confounding variables. The left figure shows simulated data, and the map displays variation in mean annual temperature (°C) across the US (Daly et al. 2008). Step 3: Estimate the causal relationships of interest. The figure shows four important steps when developing a causal inference research design and a hypothesised causal relationship of interest. Step 4: Simulate a counterfactual scenario using the causal relationships estimated in Step 3 and compare the predicted outcome of the counterfactual scenario to the ‘actual’ climate change scenario (NDVI=Normalised Difference Vegetation Index). Step 5: Evaluate results and assumptions using robustness checks to build certainty and validity, which can be displayed in a specification chart.

colliders) (Huntington-Klein 2021). A robust DAG includes all arrows from confounding variables (that need to be controlled for) to establish a defensible foundation for the causal research design (see case study). Huntington-Klein (2021) and Arif and MacNeil (2022b) offer accessible introductions to DAGs with descriptions of the terminology and underlying assumptions that must be evaluated in the formation of a DAG.

When developing causal models, evaluating tradeoffs between simplicity and complexity is important. Researchers might gravitate toward simple models because they are often easier to interpret, reduce concerns of overfitting, and can lead to greater statistical power (e.g., by trimming explanatory variables) (Aho et al. 2014). Favouring simplicity, however, is not always beneficial for causal inference (Coelho et al. 2019). An imprecise but unbiased estimate (i.e., the expected value of the estimate is equal to the true value of the relationship being estimated (Dee et al. 2023; Simler-Williamson and Germino 2022)) is often preferred to a precise yet potentially biased estimate from a simple model. Though simplicity is not the focus, an initially complex system of causal relationships can ultimately result in a simple statistical model (see Step 3 below). A causal relationship of interest that is embedded in a complex system, for instance, can be estimated with just a few variables if there are no confounding variables. Ultimately, the goal is to carefully identify the causal

effect and control for known and potentially unknown confounding variables, regardless of complexity.

3.2 | Step 2. Choose Appropriate Observational Datasets

After articulating the relationship(s) of interest (Step 1), the next step is to identify appropriate data to test the hypothesised causal relationships (Figure 1, Step 2). There are at least three types of variables to consider: (1) the outcome variable(s) of interest (e.g., biomass, mortality, fecundity), (2) the explanatory variable(s) (e.g., precipitation, temperature, soil moisture) and (3) variable(s) that may confound the relationship of interest (e.g., population density or land-use change). For each variable, researchers can weigh trade-offs across multiple desired attributes, including a dataset’s theoretical consistency, accuracy and spatio-temporal extent and resolution.

Researchers ideally address several key aspects of their datasets to minimise bias and ensure reliable causal estimates. First, they can evaluate how well the available data aligns with the theoretical model of interest. Existing datasets, for instance, may describe an imperfect proxy (e.g., remotely sensed vegetation indices) to approximate the true variable of interest (e.g., carbon

stored in aboveground biomass). Second, assessing the accuracy of data is crucial, as measurement error can result in bias and reduce the accuracy or precision of coefficient estimates (Bound et al. 2001; Regan et al. 2002). Classical measurement error, when the mean of the error is zero (i.e., the error is random), can result in more conservative coefficient estimates due to attenuation bias—the coefficient estimate is biased toward zero due to increased noise (Sengewald et al. 2019; Wooldridge 2010). In contrast, non-classical measurement error, where the error is not random, can lead to a bias with an unsigned direction (Lundquist et al. 2010). For example, a study that uses data from one weather station may suffer from non-classical measurement error if the location of the weather station is uncharacteristically warm. As the number of weather stations increases, however, the likelihood of systematic measurement error decreases.

Additionally, datasets must provide adequate spatio-temporal coverage and resolution. Many causal inference research designs (Step 3) require panel data that track the same units (e.g., individuals, plots, pixels) over multiple points in time (Siegel and Dee 2025; Wooldridge 2010). These research designs typically identify causal relationships by contrasting changes in outcomes across units that experience different changes in the treatment variable (e.g., uncorrelated changes in precipitation across space) (Auffhammer et al. 2013). As a result, researchers may want to confirm that their chosen data and study sites include spatial, as well as within-unit, temporal variation in the treatment. If all units experience highly correlated shocks (e.g., changes in precipitation are relatively uniform across space), researchers may need to expand their study region, choose different datasets with higher resolution weather information, or acknowledge that their study is limited in its ability to identify a causal effect.

Finally, researchers can test for spatial and temporal autocorrelation in climate data, which can affect standard error estimates and subsequent statistical inference (Dell et al. 2014). Autocorrelation is only a problem if found in the residuals of a fitted model, as predictors can remove it if they vary with the same temporal or spatial pattern (Hawkins 2012). Further, if autocorrelation is not a problem in the model, correcting for it can improperly inflate standard errors. To control for problematic autocorrelation, either robust standard errors or incorporation of autocorrelation into the error structure of a model may be sufficient. To ensure a transparent causal interpretation, discussions of limitations, potential sources of bias and model specification decisions are critical to include in every analysis.

3.3 | Step 3: Estimate the Causal Relationships of Interest

The key challenge underpinning any climate change attribution study is the estimation of a causal relationship of interest. Observational causal inference can be a powerful tool to estimate these relationships in real-world settings. For example, a researcher might seek to estimate changes in coral mortality caused by a one-unit decline in ocean pH. Leveraging quasi-random, inter-annual variation in ocean pH, the researcher can use carefully selected research designs to isolate how these changes in acidity cause changes in mortality. These approaches seek to approximate the logic of a controlled experiment, while

taking advantage of natural variation in treatment. Rather than prioritising specific estimation procedures, causal inference emphasises the use of rigorous research designs with carefully articulated assumptions.

Researchers have developed a variety of quasi-experimental research designs to enable causal inference in a wide variety of study contexts (Table S1; Butsic et al. 2017; Byrnes and Dee 2024; Cunningham 2021; Larsen et al. 2019; Siegel and Dee 2025). For example, instrumental variables (IV) (Imbens 2020) and regression discontinuity (Cattaneo and Titiunik 2022; Imbens and Lemieux 2008) help control for both observed and unobserved confounding variables when their assumptions are met (Figure 1, Step 3). Butsic et al. (2017) and Larsen et al. (2019) provide tables explaining the applications and underlying assumptions of different causal inference methods, while Siegel and Dee (2025) provide a decision tree for choosing a causal inference study design based on the available data and underlying assumptions. Fixed effect panel models have emerged as a common method to estimate continuous treatment effects (e.g., climate change) on economically relevant outcomes (Carleton 2017; Hsiang 2016; Mérel and Gammans 2021). Within each research design, a variety of regression techniques are available for estimation (e.g., OLS, Bayesian and structural equation models). A useful heuristic that can help researchers select between research designs is to carefully consider which design most closely approximates random assignment of the treatment. Ultimately, the design and choice of statistical models should be selected based on the contemporary understanding of the system, hypotheses (Step 1), available data (Step 2) and known sources of bias.

All causal inference research designs include underlying assumptions that need to be considered and interrogated. These assumptions are additional to statistical assumptions commonly evaluated in ecological analyses (e.g., linearity, heteroskedasticity, clustering of residuals or non-Gaussian error distributions) (Zuur et al. 2009). Examples of important causal assumptions include **parallel trends**, no confounding from observed and unobserved variables, and the absence of spillovers across units with different treatment exposures (part of the **Stable Unit Treatment Value Assumption [SUTVA]**). To develop a defensible causal analysis, it is critical to evaluate the assumptions made in the research design and transparently describe how the research design controls for theoretically relevant sources of bias.

3.4 | Step 4. Simulate a Counterfactual Scenario

Statements about climate change impacts implicitly compare two states of the world—a world with observed changes to climate and a counterfactual world without climate change (Figure 1, Step 4). Making such counterfactual comparisons explicit can help disentangle how much climate change has contributed to the observed changes, yielding stronger evidence of climate change impacts (Swain et al. 2020). Examples of counterfactual comparisons include Lobell et al.'s (2011) analysis of climate change's impacts on crop yields and Dudley et al.'s (2021) analysis of tree disease range shifts. The researchers first estimated the causal effect of climate on the outcome of interest (Step 3). Then they used historical, observed weather data to predict the

outcome under observed climate change (the ‘actual’ scenario) and compared it to the counterfactual scenario, which was predicted using weather distributions reflecting the absence of climate change. By comparing the actual and counterfactual scenarios, the authors provided robust estimates of ‘how much’ climate change shifted outcomes.

Though estimating counterfactual scenarios is an essential step for climate change attribution, it presents significant methodological challenges. Past studies have used a variety of approaches, including historical climate data taken from the period predating climate change (Dudney et al. 2021), detrended data (e.g., data that removes the increasing temperature trend) (Lobell et al. 2011), or publicly available counterfactual climate datasets (Mengel et al. 2021) (Figure 2). Each method has limitations. Trend removal, for example, can be sensitive to the chosen spline function and selected time period, whereas model-based approaches can inherit uncertainties from climate models. The choice of counterfactual can significantly influence attribution results (Hannart et al. 2016), underscoring the need for careful justification and consideration of multiple approaches to ensure robust conclusions. Though counterfactual analysis is imperfect, this step is critical to help readers interpret the magnitude of causal relationships and improve our understanding of the impacts of climate change.

3.5 | Step 5. Evaluate Results and Assumptions

Finally, researchers should conduct additional analyses to build confidence that their results reveal true causal relationships (**internal validity**) and the extent to which these results can be generalised to other systems and conditions (**external validity**). An important concern that could undermine both internal and external validity is a researcher’s degrees of freedom: researchers can make decisions about data selection, processing and statistical analyses that may consciously or subconsciously accentuate desired statistical results (Head et al. 2015). One way to address this concern is

to pre-register each of these decisions through a pre-analysis plan (Nosek et al. 2018). Given that preregistration can be impractical (Olken 2015), a more accessible solution is developing a specification chart (Figure 1, Step 5) that clearly illustrates the effect that these decisions have on the final result (Simonsohn et al. 2020). The chart can comprise different weather windows and variables, alternate model structure (e.g., nonlinear terms) and possible variations among statistical packages or estimation methods to probe the robustness of the researcher’s design. If the results are consistent across many different model specifications, this increases the overall confidence that the analysis has captured a true effect (Dee et al. 2023).

In contrast, external validity can be probed by reflecting on whether the causal climate relationships hold true across different populations, settings, time periods (Spake et al. 2023) and variations in climate change treatment (Wolkovich et al. 2012). Researchers can also add counterfactual no-climate change scenarios and conduct a cross-validation or subgroup analysis (e.g., subsetting the data randomly or with natural groupings in the data, including specific regions or plots; also referred to as heterogeneity analysis (Burke et al. 2015)). However, often observational data do not capture the full range of climate effects across space and time—particularly under future conditions not yet observed—leading to greater internal than external validity.

4 | The Utility and Limitations of Two-Way Fixed Effects Panel Models for Attribution

A common research design used in climate change attribution studies is the **two-way fixed effects panel model** (TWFE model) (Carleton 2017; Dudney et al. 2021; Kolstad and Moore 2020). TWFE models use panel datasets, which consist of repeated measurements of the same units of observation—e.g., site, plot, or organism—over time. TWFE models are frequently adopted because they can control for some

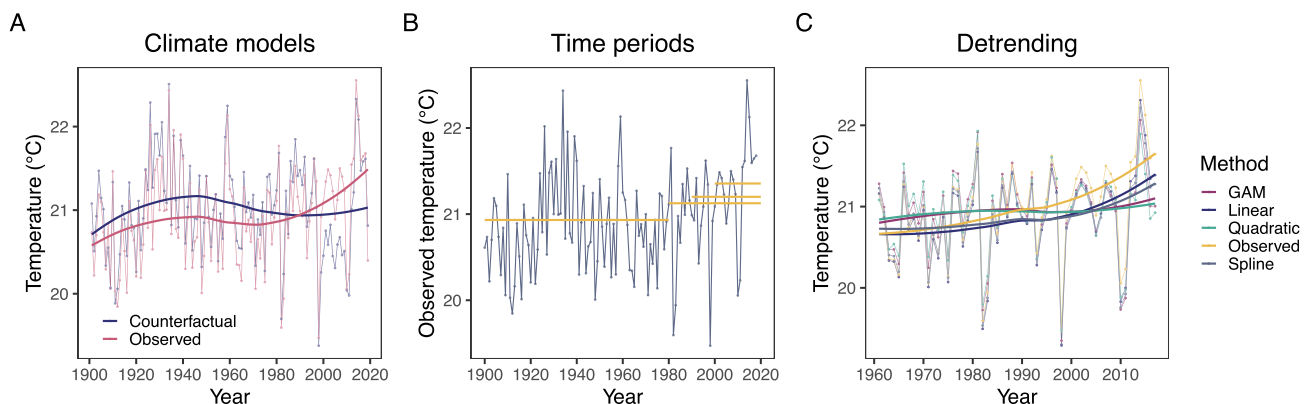


FIGURE 2 | Various approaches that can be used to estimate counterfactual climate scenarios. (A) The comparison between the observed temperature trend from randomly selected plots across California using PRISM data (Daly et al. 2008) and an estimated counterfactual temperature estimate (i.e., the absence of anthropogenic emissions) using a published counterfactual climate dataset (Mengel et al. 2021). (B) A counterfactual temperature scenario that compares a historical mean temperature (longest yellow line) to the mean of a more recent weather window (shorter yellow lines); length of the counterfactual period will vary depending on the system and available data. (C) A continuous counterfactual temperature is estimated by detrending the PRISM dataset using four different approaches Generalised Additive Model (‘GAM’), a linear model (‘Linear’), a quadratic term (‘Quadratic’), the PRISM values (‘Observed’) and a cubic spline (‘Spline’).

unobserved sources of confounding. In this research design, variables can be classified as time-varying (i.e., the values change through time) and time-invariant (i.e., values remain constant throughout the study period). By estimating distinct intercepts, also called fixed effects, for each unit of observation and each time period, TWFE models estimate causal relationships using deviations from unit-level means. In this way, TWFE models can control for both local, time-invariant sources of confounding—e.g., soil and topography—as well as confounding variables that are time-varying, but uniform across units—e.g., regional droughts or nitrogen deposition (Byrnes and Dee 2025; Siegel and Dee 2025). When applied to spatially and temporally extensive datasets, these models can provide causal estimates of climate effects, provided key assumptions are met (Dee et al. 2023; Dudney et al. 2021; Larsen et al. 2019).

Unlike hierarchical mixed-effects models, panel models explicitly control for time-invariant factors without assuming that they are uncorrelated with explanatory variables (Byrnes and Dee 2025). Mixed effects models commonly used in ecology, for example, assume that random effects are uncorrelated with explanatory variables. As a result, correlated explanatory variables are often included (e.g., topography is often correlated with site random effects), which can lead to variance inflation, especially when the correlation is strong (Byrnes and Dee 2025). TWFE panel models, in contrast, use within-unit comparisons over time (i.e., deviations from the mean) to eliminate the influence of time-invariant confounders (e.g., persistent site characteristics). Thus, TWFE panel models can provide stronger evidence for causal relationships between climate change and ecological outcomes (Dee et al. 2023; Dudney et al. 2021).

Though TWFE models are widely used to estimate causal effects (Burke et al. 2015; Hsiang 2016; Nordhaus 1992), they have important limitations. A key concern is that TWFE models often capture short-term weather effects, which may differ from long-term climate responses (Box 2; see Frontiers section on adaptation) (Dell et al. 2014; Wooldridge 2010). For instance, the impact of a 1.2°C temperature increase in a single year may not reflect the cumulative effects of sustained warming on an ecosystem over multiple years or decades (Deschênes and Greenstone 2011). Additionally, trade-offs exist between controlling for confounding variables and estimating long-run climate effects, which are typically removed in TWFE panel models (Dell et al. 2014; Deschênes and Greenstone 2011).

TWFE panel models also rely on several assumptions that can be easily violated, including (1) treatment and control units would have experienced **parallel trends** in the outcome of interest had neither group received exposure to the treatment, (2) uniform timing of treatment across units, (3) no interference among units and (4) no feedbacks through time (Callaway and Sant'Anna 2021; Ferraro et al. 2019; Sun and Abraham 2021). Researchers can conduct robustness tests to build confidence that these assumptions hold in their study setting. If such tests fail, researchers may need to reconsider their research design to ensure that they are isolating the causal parameters of interest. Further, emerging solutions that allow researchers to relax

some of these assumptions, including difference-in-differences analyses that are robust to staggered treatments and continuous treatment variables, are being developed with new estimator packages now available in R (Callaway et al. 2024; Roth et al. 2023). Finally, TWFE models require sufficiently uncorrelated changes in weather across sites to ensure that weather variation is not fully absorbed by the site and unit fixed effects. As a result, TWFE models are best suited for studies with spatially distributed sites that experience uncorrelated weather shocks.

5 | Estimating Climate Change Impacts on Pinyon Pine Growth

We provide an accessible, simplified application of our climate change attribution framework to isolate climate change's impacts on pinyon pine (*P. edulis*) growth (Figure 3B). Pinyon pine grows slowly, has two needles per fascicle, and is a widely distributed species in the western United States (Barger and Woodhouse 2015). Since 1980, temperatures throughout its range have experienced a statistically significant increasing trend (Figure 3E).

5.1 | Case Study Step 1: Describe the Theoretical Foundation

We hypothesise that climate change—specifically increases in temperature—has recently led to decreases in growth based on the well-documented negative relationship between growth and temperature in water-limited systems (Dudney et al. 2023; Hartl-Meier et al. 2014; Williams et al. 2013). Collating all hypothesised causal and confounding variables, we developed a DAG (Huntington-Klein 2021) that was then simplified using logic and prior knowledge (Figure 4A). We classified the variables into time-varying or time-invariant. Because shifts in precipitation are difficult to link to anthropogenic emissions (Lehner et al. 2020; Pierce et al. 2018), we focused our analysis on the causal effects of temperature and conducted robustness checks to validate this approach (see Case study step 5). Our DAG makes the important assumption that every omitted variable and arrow (relationship) has a nominal effect—that is, there are no unobserved, confounding variables that are influencing both tree growth and temperature. We note that, for the sake of simple exposition, we have ignored other theoretical sources of confounding, such as disturbance or nitrogen deposition. In addition, we ensure that the DAG does not include **collider** variables that would bias the temperature effect if included in the model (Huntington-Klein 2021).

5.2 | Case Study Step 2: Choose Appropriate Observational Datasets

We use ring width index (RWI) to capture tree growth, our outcome variable of interest (van Mantgem et al. 2023; Millar et al. 2012). Pinyon pine RWI data were downloaded from the International Tree Ring Data Bank (ITRDB) (Grissino-Mayer and Fritts 1997), which included 1980 trees from 108 sites in the U.S. (Figure 4B). We selected maximum temperature and total

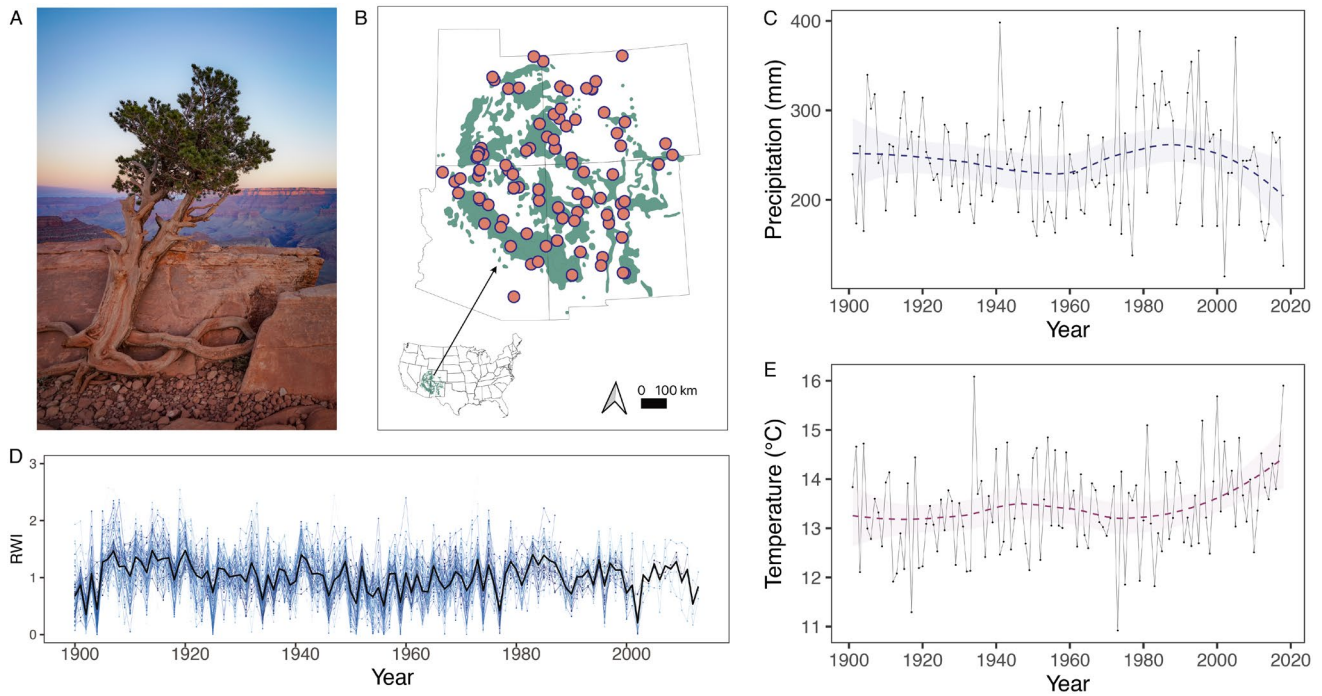


FIGURE 3 | The pinyon pine study system. (A) A tenacious pinyon pine (*P. edulis*) growing in the Grand Canyon, Arizona (photo by J. Dudney). (B) The spatial distribution of plots in the ITRDB. Green shading highlights the *P. edulis* range; plots are pink. (C) Variation in water-year precipitation (mm; first summed across months and then averaged across all plots for each year); showing a loess smoothed trend line and the 95% CI in grey. (D) Mean annual ring-width length (RWI, black line) and mean plot-level RWI (blue lines) across the timeseries. (E) Average temperature across the timeseries; showing a loess smoothed trend line and the 95% CI in grey.

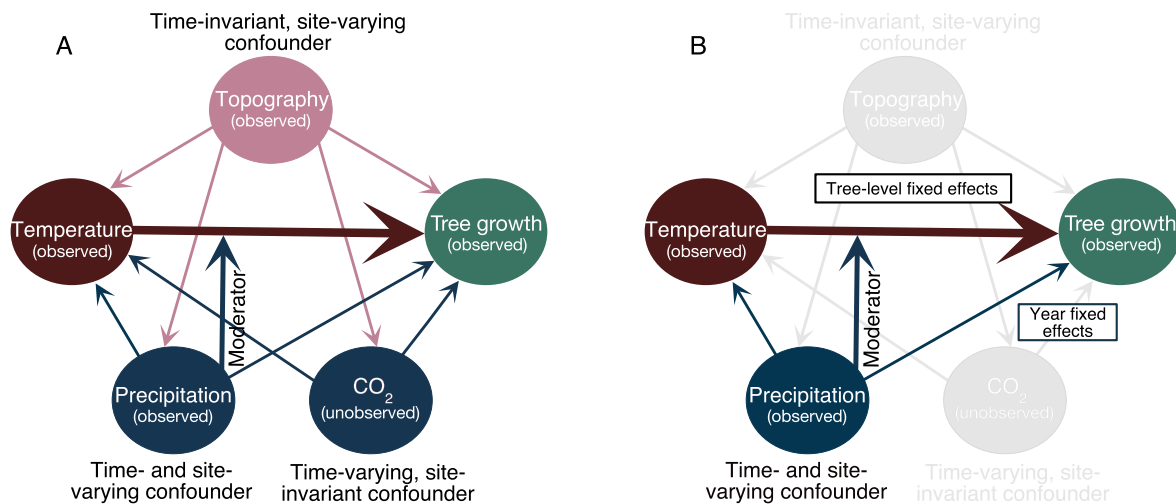


FIGURE 4 | Simplified causal diagrams used to frame the climate change attribution analysis. (A) Directed acyclic graph (DAG) of pinyon pine growth. Thick darkred arrow shows the causal relationship of interest (temperature; darkred circle) on the outcome variable of interest (tree growth; green circle). Pink arrows show confounding, time-invariant and site-varying variable effects. Dark bark blue arrows show confounding, time-varying effects (blue circles), including site-varying precipitation and site-invariant changes in atmospheric CO₂. Precipitation is also a moderator of temperature (thicker dark blue line). (B) Explanations of how confounding paths are broken (grey arrows and grey circles) in the DAG through model specification and statistical design. Text boxes explain the reasoning behind the solved arrow(s) underneath (refer to main text for more details); the moderator arrow highlights that precipitation is interacted with temperature in the regression.

precipitation (between October–June) as the key weather variables for our model. Various studies suggest that other weather windows, including weather lags, are also important for pinyon pine growth (Barger and Woodhouse 2015; Meko et al. 1993;

Williams et al. 2013); thus we conduct robustness checks to determine the sensitivity of pinyon pine growth to alternate weather specifications. We extracted climate data from the PRISM dataset, which has a spatial resolution of 4 km (Daly et al. 2008). Our DAG

included ambient CO₂ and topography as potential confounders that should be addressed in our model (Figure 4A). We do not have local data detailing ambient CO₂; thus, we need to carefully select a research design that can control for this unobserved variable (Step 3). Although local data on topography is available, the panel research design we select in Step 3 eliminates the need to explicitly include topographic data.

5.3 | Case Study Step 3: Estimate the Causal Relationships of Interest

Step 3 requires the careful selection of a statistical design that allows for causal interpretation. Given our hypothesis, DAG, and available data, a two-way fixed-effect (TWFE) panel regression is well suited because it can help control for multiple forms of **omitted variable bias** (Gantois 2022). Specifically, our TWFE model is defined as:

$$RWI_{i,t} = \beta_1 \text{Temp}_{i,t} + \beta_2 \text{Precip}_{i,t} + \beta_3 \text{Temp}_{i,t} \times \text{Precip}_{i,t} + \gamma_i + \eta_t + \epsilon_{i,t}$$

where γ_i represent tree-level fixed effects and η_t represent year fixed effects. Thus, our TWFE panel model estimates how year-to-year changes in temperature for each tree (conditional on precipitation) affects year-to-year changes in that tree's RWI. The causal relationship of interest is thus defined by the combination of parameters β_1 and β_3 . The tree-level fixed effects (γ_i) control for confounding from all variables that vary by tree but not over time (e.g., soil type). In the context of our DAG (Figure 4), these fixed effects address the concern that topography could confound our causal estimates. In contrast, year fixed effects (η_t) control for time-varying shocks that are common to all sites (e.g., El Niño cycles, federal policy). Temporal fixed effects can

therefore flexibly control for increases in ambient CO₂, which primarily varies regionally rather than locally. Importantly, these fixed effects are unable to control for sources of confounding that vary across both sites and over time. To control for the confounding effects of precipitation (which can shift solar radiation) (Gantois 2022), and to evaluate the moderating effect of precipitation (Dudney et al. 2023), we include an interaction between temperature and precipitation in our model (Figure 5). Once we have carefully specified our model, we estimate it using the fixest R package (Berge 2020) (Table S2). We assume that trees would have experienced **parallel trends** in growth if all trees had experienced the same interannual fluctuations in temperatures.

In addition to controlling for bias from potentially confounding variables, it is important to evaluate the precision of our estimates (e.g., Type 1 error—a false positive). For example, if autocorrelation is not accounted for in a model, the coefficient is not necessarily biased; but the model likely overestimates the precision of the effect estimate. Here we use Moran's I test to test for spatial autocorrelation, which is not significant (Table S3). We use cluster-robust standard errors to control for heteroskedasticity, temporal autocorrelation, unobserved tree-level effects within plots, and other causes of non-independence of observations (Abadie 2005).

5.4 | Case Study Step 4: Simulate a Counterfactual Scenario

To quantify the realised effect of climate change (i.e., how much anthropogenic climate change has shifted tree growth), we predicted tree growth under two scenarios: an 'actual

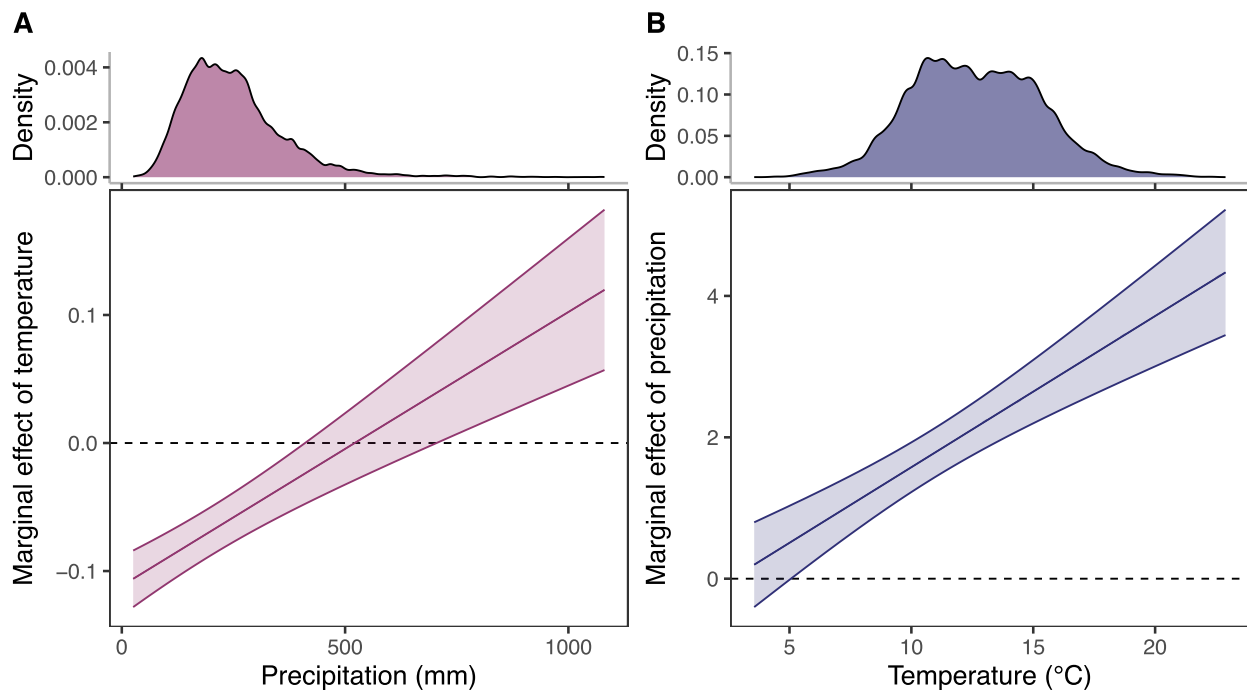


FIGURE 5 | Marginal effects of climate variables on tree growth. (A) Marginal effect of temperature on tree growth (RWI) across the precipitation gradient, with the precipitation density distribution shown in the top panel. (B) Marginal effect of precipitation on tree growth across the temperature gradient, with the temperature density distribution shown in the top panel. Marginal effects plots display the 95% CI around the mean estimated marginal effect. Coefficients derived from models estimated using the fixest package (Berge 2020).

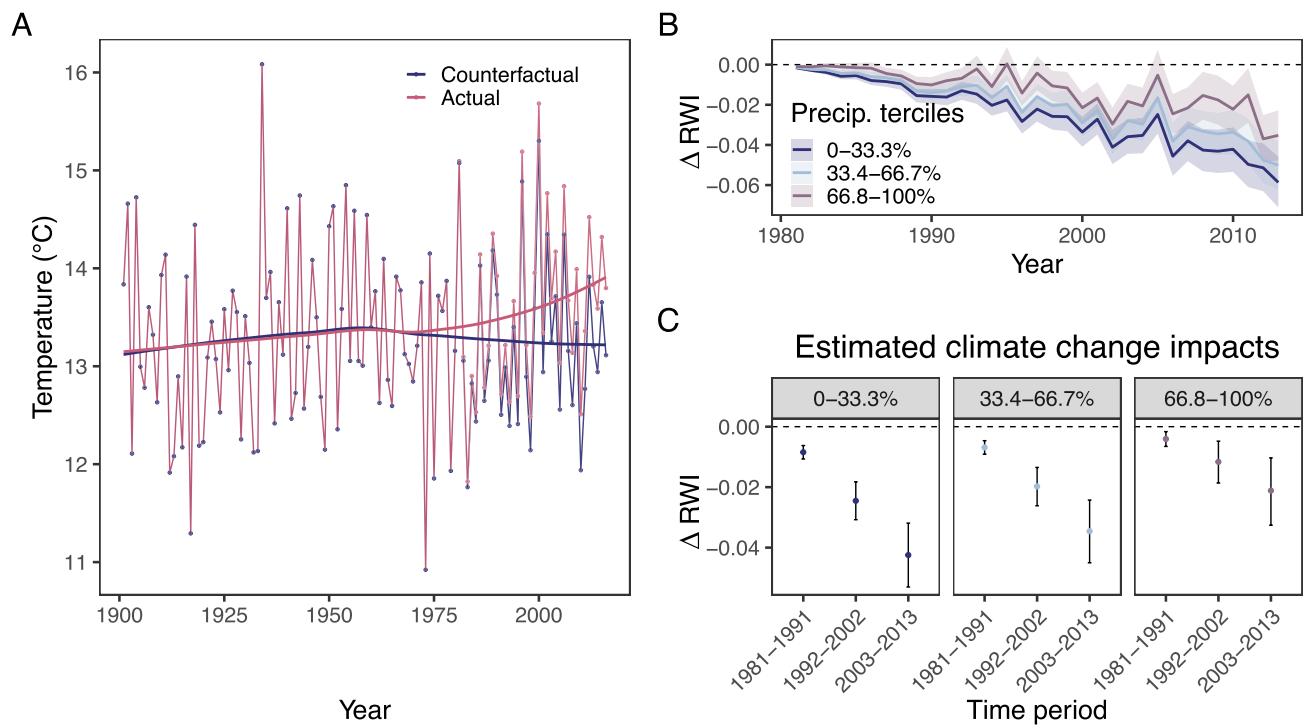


FIGURE 6 | Estimated climate change impacts on tree growth. (A) The actual temperature (i.e., the observed values; pink) and estimated counterfactual temperature (i.e., the estimated detrended values of the ‘no climate change’ scenario; blue) across the study period. (B) M.C. simulation results estimating the difference between the actual and counterfactual predicted growth scenarios—conditional on historical, site-level precipitation terciles—between 1981 and 2013. Showing the mean line and 95% CI estimated from 1000 simulations. (C) Mean change in growth attributed to climate change across precipitation terciles for three time periods. Coloured points show the mean difference and error bars represent the 95% CI.

scenario’ using historically observed temperatures in each site, and a ‘counterfactual scenario’ that reflects historical temperatures in the absence of anthropogenic forcing. To estimate temperatures under this counterfactual scenario, we use a simple, nonlinear detrending approach (Figure 6A). Then, we use the estimated model from Step 3 to predict tree growth under both the actual and counterfactual temperature scenarios. To incorporate model uncertainty in our predictions, we use a Monte Carlo simulation (Dudney et al. 2021). To estimate the effect of climate change on tree growth (thereby answering the ‘how much has climate change affected growth’ question), we subtract the actual scenario from the counterfactual scenario (Figure 6B,C). We also calculate this change in growth within individual time periods to test whether the impact of climate change has been increasing over time (Figure 6B,C). Our results indicated that between 2003 and 2013, climate change on average reduced growth by 0.03 RWI (with a 95% confidence interval [CI] of 0.02–0.4 RWI) relative to the counterfactual temperature scenario (equivalent to a 3.4% decrease in growth). This effect was strongest in the driest plots (Figure 6B,C).

5.5 | Case Study Step 5: Evaluate Results and Assumptions

To determine the robustness of our results to research design and model specification choices, we conduct multiple analytical checks and present them in a specification chart (Figure 7).

This specification chart can help readers form a more nuanced understanding of the sensitivity of results to a variety of modeling decisions (Dudney and Heilmayr 2025; Ortega et al. 1997). Here, the specification chart illustrates five key points. First, our decision to cluster standard errors at the plot yields more conservative confidence intervals compared to a model with simple heteroscedasticity robust standard errors (Figure 7: model A vs. C) and yields similar confidence intervals to a model with Conley standard errors (Figure 7: model A vs. B). Second, our results are generally robust to alternate models that do not include an interaction term (Figure 7E), include quadratic functional forms for precipitation and temperature (Figure 7D), or include controls for lagged temperature and precipitation (Figure 7F). Third, our results are relatively consistent with alternate weather windows (Figure 7G,H). Fourth, our results are robust to alternate statistical designs (e.g., linear mixed models, models J and K, and the removal of year fixed effects, model L). Finally, dropping individual sites that exhibit the smallest (Figure 7M) or largest (Figure 7N) effect size yields relatively similar results, addressing concerns that our results may be driven by individual plots that are outliers. The results of this specification table (Figure 7) build confidence that the main model of interest (Figure 7: model A) provides an accurate estimate of temperature effects.

In addition, we conducted a comparison of different counterfactual temperature scenarios. Our results suggested that our estimates of the effect of climate change were robust to different detrending methods (Figure S1). Further, we validated our

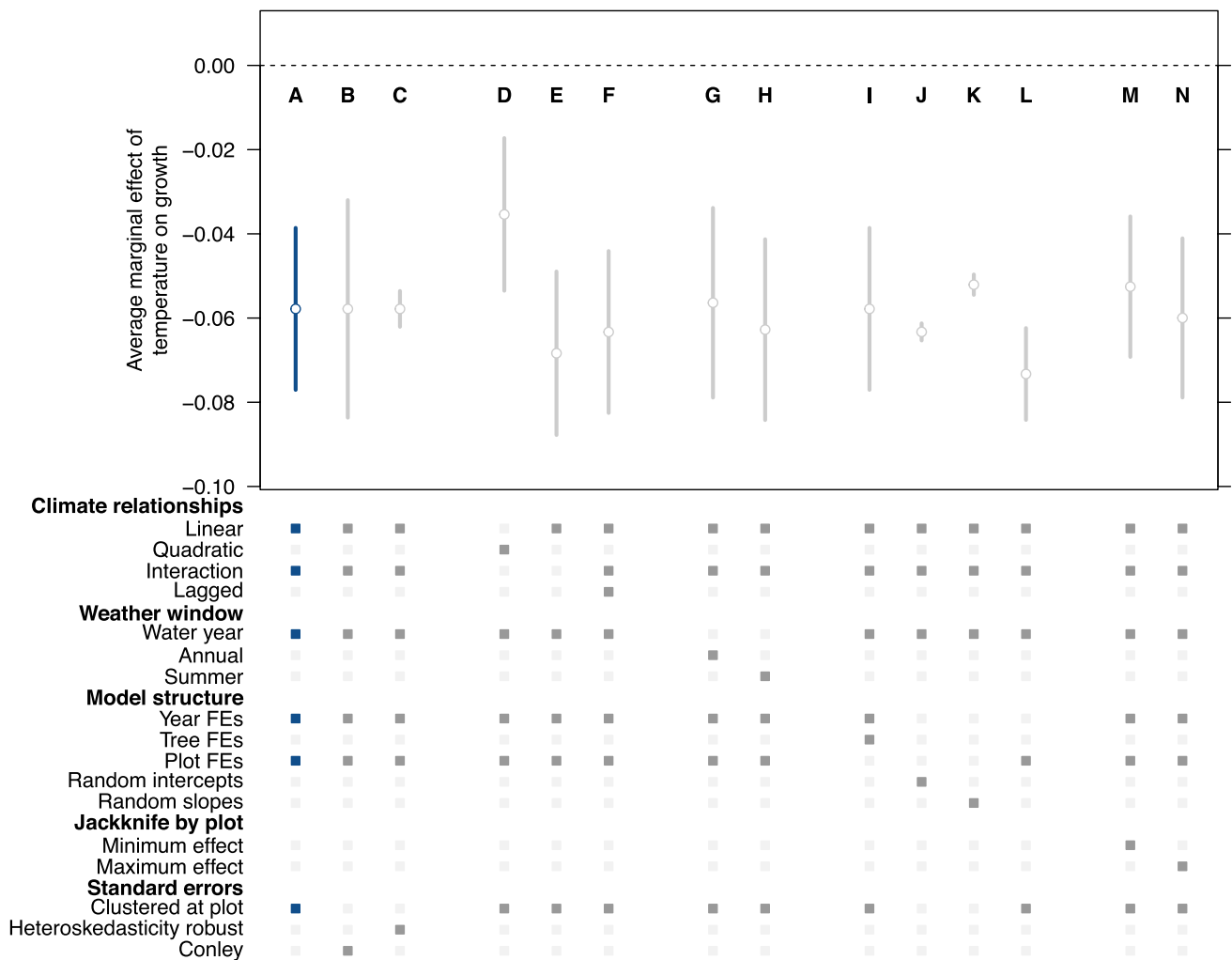


FIGURE 7 | Specification chart of temperature effects. Top panel: comparison of the average marginal effect of temperature across different model structures and specifications (A–N). Vertical grey lines display the 95% confidence interval of the direct effect of temperature (open points are the coefficient estimates); dark blue highlights this paper's baseline result. Bottom panel: visualisation of each model's specification across a variety of different modelling choices. Bolded grey squares indicate that the specification described by the text on the left is included in the coefficient displayed directly above in the top panel.

choice of counterfactual scenario by demonstrating that our results are consistent with a counterfactual scenario that incorporated detrended precipitation data (Figure S2). Though beyond the scope of this worked example, other robustness tests can be conducted, including placebo tests, permutation tests (e.g., randomising data to establish significance), and ‘leave one out’ (e.g., where each site is sequentially excluded to test prediction accuracy against observed data) (Efron and Tibshirani 1994; Eggers et al. 2024).

Finally, we consider challenges to the external validity of our study. External validity could be a concern if we predicted growth responses to temperatures outside of the range of the observed temperatures that we used to estimate our TWFE model (Step 3). Temperatures in our counterfactual climate scenarios, however, fall within the range of historically observed temperatures; thus, both of our estimated scenarios are likely valid (Step 4). We do caution, however, that biases in the selection of ITRDB sites may affect the external validity of our

conclusions. Specifically, ITRDB sites are frequently selected to maximise weather sensitivity. Although our conclusions are valid for ITRDB sites, our analysis likely overstates the impacts of climate change if extrapolated to the rest of the species' range.

6 | Frontiers of Climate Change Attribution in Ecology

At the forefront of climate change attribution is the need to integrate dynamic biological responses into our understanding and estimation of climate change impacts. While the framework detailed above provides a general approach for attributing specific and relatively simplistic ecological shifts to climate change, natural systems are inherently complex and dynamic, offering multiple opportunities for further methodological development. Here we reflect on several important dynamic responses to climate change and highlight novel tools and opportunities for future research.

6.1 | Acclimation and Adaptation

Organisms and ecosystems can dynamically buffer climate impacts over short (i.e., acclimation) and long (i.e., adaptation) time scales. Acclimation allows individual organisms to respond to short-term weather shocks or more gradual changes over the course of their lifespan (Henn et al. 2018), while longer-term adaptations can enable a species to persist in the face of climate change (Gantois 2022; Nadeau et al. 2017). These processes are important to consider in most climate change attribution studies because they can modify species and ecosystem-level responses to rising temperatures at different timescales. Thus, a critical frontier in climate change attribution is to test for—or at minimum evaluate—the possibility of these dynamic mechanisms shifting outcomes. For instance, models that capture only immediate effects of ocean temperature on kelp growth (Krumhansl et al. 2016) risk misrepresenting the true sensitivity of the ecosystem, as selective pressures over time may shift populations toward more resilient genotypes (Mérel and Gammans 2021; Vranken et al. 2021).

Researchers are developing innovative econometric approaches that enable more accurate estimates of acclimation and adaptation. These include subsetting data by time or region (Hsiang 2016; Kalkuhl and Wenz 2020; Schlenker and Roberts 2009), incorporating time-period-by-climate interactions (Dudney et al. 2021), and adding interaction terms or nonlinear weather variables (Dell et al. 2014; Gantois 2022; Kolstad and Moore 2020). Complementary to these statistical methods are direct eco-evolutionary experiments—such as common garden and reciprocal transplant experiments—that provide mechanistic insights into acclimation and adaptation processes (Bisschop et al. 2022; Henn et al. 2018; Merilä and Hendry 2014; Nadeau et al. 2017). Together, these approaches push the frontier by leveraging empirical measurements and advanced statistical techniques to capture dynamic biological responses to climate change.

6.2 | Extreme Events

Extreme events—including hurricanes, floods, and heatwaves—are an emerging frontier in climate change attribution. Due to their nonlinear and disproportionately large impacts, extreme event attribution challenges traditional estimation approaches (Diffenbaugh et al. 2015; Hagmann et al. 2021; Williams et al. 2023). As a result, researchers are exploring methods that explicitly model nonlinear relationships, including employing quadratic or cubic terms and non-parametric binned analyses (Deschênes and Greenstone 2011; Gantois 2022; Schlenker and Roberts 2009). Given the low probability and high variability of these events (Auffhammer 2018), researchers are also refining techniques to evaluate the duration and spatial extent of impacts, as well as the relative contributions of anthropogenic and natural forcing (Swain et al. 2020; Trenberth et al. 2015). Such methodological advances are crucial for improving the accuracy of attribution studies and for informing policy decisions in the face of an increasingly variable climate. Finally, for extreme events that have clear spatial (e.g., area burned in a fire) or temporal boundaries (e.g., flooding), researchers may find opportunities to take advantage of an expanded set of causal research designs, including spatial

regression discontinuity designs, difference in differences, or synthetic control (Butsic et al. 2017).

6.3 | Lagged Effects

Lagged effects, or legacy effects, are temporally dynamic effects that can influence climate change effects on organisms and ecosystems (Dudney et al. 2017; Suttle et al. 2007). Kelp abundance in New England, for example, is not only influenced by warmer spring temperatures, but also by the previous summer's temperature effects on kelp mortality (Suskiewicz et al. 2024). Researchers are advancing our understanding of lagged effects by integrating time-lagged explanatory variables into their models or applying novel statistical approaches that can better capture their dynamic effects. For example, researchers can include lagged explanatory variables at the hypothesised temporal scale of influence in their model (Dudney et al. 2017) or apply nonlinear approaches, including distributed lag nonlinear models (DLNMs), that can precisely estimate lagged effects (Gasparrini et al. 2021; Moore et al. 2019). More novel methods include PCMC (Peter and Clark momentary conditional independence) and CCM (Convergent Cross Mapping). PCMC is designed for high-dimensional time series data and can detect indirect links among lagged variables (Docquier et al. 2024; Runge et al. 2019), while CCM can detect time-lagged causal relationships in complex ecological systems using time series data (Gao et al. 2023; Sugihara et al. 2012).

6.4 | Spatial Spillovers

Spatial spillovers are phenomena where changes in one geographic area influence outcomes in neighbouring or spatially disconnected areas. In climate change attribution studies, spatial spillovers represent an important—yet understudied—frontier (Pecl et al. 2017; Potter et al. 2003). For example, climate change is associated with hotter droughts, which can have spatially variable impacts on tree physiology and bark beetle populations. As bark beetle populations grow exponentially in drought-stressed regions, they can attack and kill trees in nearby regions due to their high numbers, even if the trees in that location are experiencing less drought stress (Raffa et al. 2008). Thus, the effect of climate change on tree mortality in one region has an effect on tree mortality in another region. To test for spatial spillovers, researchers are developing new methods that can provide greater insight into spatially explicit effects of climate change (Ogburn and VanderWeele 2014; Reich et al. 2021; Vanderweele and Tchetgen Tchetgen 2011). For example, researchers can include spatial lags of the treatment as additional predictors in a regression to explicitly estimate spillover effects (Andam et al. 2008).

6.5 | Interaction Effects

Interaction effects are an important frontier because they help identify context-dependent effects between two or more variables that can deepen our understanding of the consequences of climate change. To determine whether interaction effects are critical to estimate, extensions to DAGs, including interaction DAGs (Nilsson et al. 2021), allow researchers to determine which variables are

likely to interact (see our case study above). Additionally, random forests can identify subgroups for further analysis of heterogeneous effects (Athey and Imbens 2016; Miller 2020). Epidemiologists have also developed empirical tests for causal interactions, which could be used in ecology (VanderWeele et al. 2012; VanderWeele and Robins 2007). By employing these methods, researchers can enhance the validity and comprehensiveness of attribution studies, leading to a more accurate and nuanced understanding of complex ecological responses to climate change.

7 | Conclusion

The escalating threat of climate change to biodiversity and ecosystem services necessitates a robust and accurate approach to climate change impact evaluation. To date, observational analyses that do not necessarily establish causation have limited our ability to quantify the impacts of climate change in ecology (Parmesan et al. 2013). Here we demonstrate how observational causal inference approaches, which have been used to quantify climate change impacts in social systems (Auffhammer et al. 2013; Burke et al. 2024; Carleton et al. 2022), and more recently natural systems (Dudney et al. 2021), are well suited for climate change attribution in ecology. If certain conditions are met, our framework helps researchers build analytical certainty and increases the accuracy of estimated climate change effects. Though our approach is not comprehensive of all causal research designs and does not guarantee causal interpretation of effects (Imbens 2020), it does provide a useful framework for evaluating ecological research designs and statistical approaches used to identify climate change effects. Additionally, global initiatives, including the Intergovernmental Panel on Climate Change (IPCC) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), underscore the urgency for empirical evidence of climate change impacts (Druckemiller 2022). By adopting our framework, ecologists can enhance the accuracy and reliability of climate change impact assessments, thereby providing policymakers and managers with the robust, empirical evidence needed to develop effective climate change mitigation and adaptation strategies.

Author Contributions

Joan Dudney, Laura E. Dee, Robert Heilmayr, Jarrett Byrnes, Katherine Siegel: conceptualization. **Joan Dudney:** data curation. **Joan Dudney, Robert Heilmayr:** formal analysis. **Joan Dudney:** project leadership. **Joan Dudney:** visualisation. **Joan Dudney, Laura E. Dee, Robert Heilmayr, Jarrett Byrnes, Katherine Siegel:** writing – original draft. **Joan Dudney, Laura E. Dee, Robert Heilmayr, Jarrett Byrnes, Katherine Siegel:** writing – review and editing.

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Data Availability Statement

All of the analyses were performed using R. Data for the case study analysis can be found in two places: (1) Zenodo: <https://doi.org/10.5281/zenodo.15611164> or <https://zenodo.org/records/15611164> and (2) GitHub: <https://github.com/Landscapes-of-Change-Lab/CausalClimateChangeAttribution>

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70192-sup-0001-supinfo.docx.