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RESEARCH ARTICLE

Weak reciprocal relationships between productivity and plant biodiversity in managed grasslands

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Abstract

1. Relationships between plant biodiversity and productivity are highly variable across studies in managed grasslands, partly because of the challenge of accounting for confounding's and reciprocal relationships between biodiversity and productivity in observational data collected at a single point in time. Identifying causal effects in the presence of these challenges requires new analytical approaches and repeated observations to determine the temporal ordering of effects.
2. Though rarely available, data collected at multiple time points within a growing season can help to disentangle the effects of biodiversity on productivity and vice versa. Here we advance this understanding using seasonal grassland surveys from 150 managed grassland sites repeated over 2 years, along with statistical methods that are relatively new in ecology, that aim to infer causal relationships from observational data. We compare our approach to common methods used in ecology, that is, mixed-effect models, and to analyses that use observations from only one point in time within the growing seasons.
3. We find that mixed models overestimated the effect of biodiversity on productivity by two standard errors as compared to our main models, which find no evidence for a strong positive effect. For the effect of productivity on biodiversity we found a negative effect using mixed models which was highly sensitive to the time at which the data was collected within the growing season. In contrast, our main models found no evidence for an effect. Conventional models overestimated the effects between biodiversity and productivity, likely due to confounding variables.

4. *Synthesis*. Understanding the biodiversity-productivity relationships is a focal topic in ecology, but unravelling their reciprocal nature remains challenging. We demonstrate that higher-resolution longitudinal data along with methods to control for a broader suite of confounding variables can be used to resolve reciprocal relationships. We highlight future data needs and methods that can help us to resolve biodiversity-productivity relationships, crucial for reconciling a long-running debate in ecology and ultimately, to understand how biodiversity and ecosystem functioning respond to global change.

KEYWORDS

biodiversity–productivity relationships, causal inference, managed grasslands, reciprocal relationships, temporal dynamics

1 | INTRODUCTION

Global biodiversity decline (WWF, 2022) has fuelled an ongoing research debate about the consequences of biodiversity loss for ecosystem functioning (Adler et al., 2011; Dee et al., 2022; van der Plas, 2019). A focal topic in this debate is the reciprocal nature of biodiversity-productivity relationships, in which biodiversity can affect productivity but productivity also drives biodiversity (Adler et al., 2011; Grace et al., 2016). In recent decades, numerous experimental studies concluded that random biodiversity loss reduces productivity (Cardinale et al., 2012; Tilman et al., 2001). However, in non-randomly assembled (semi-)natural ecosystems (e.g. managed grasslands), these relationships are less consistent (Adler et al., 2011; Dee et al., 2023; Grace et al., 2016), which challenges the generality of biodiversity effects on productivity (van der Plas, 2019). At the same time, the direction of the causal relationship between biodiversity and productivity has been debated for decades, with many earlier studies suggesting that biodiversity can also be driven by changes in productivity (Fraser et al., 2015; Grime, 1973; Gross & Cardinale, 2007). Yet despite recent evidence suggesting that both relationships of biodiversity on productivity and of productivity on biodiversity may co-occur (Grace et al., 2016), their causal effects remain elusive (Dee et al., 2023).

Teasing apart biodiversity-productivity relationships in natural and semi-natural ecosystems is challenging. First, confounding variables, such as land-use intensity can influence both biodiversity and productivity and modify their relationships (Grace et al., 2007; Socher et al., 2012). When unaccounted for, confounding variables can mask or mimic causal effects and lead to incorrect inferences (i.e. due to statistical bias, reviewed in Dee et al., 2023). Thus, the degree to which overall relationships in prior observational studies are positive or negative may be driven by variation in land-use intensity (Freitag et al., 2023; Grace et al., 2007; Socher et al., 2012) or how these studies control for confounding variables (Dee et al., 2023). Second, inconsistent biodiversity-productivity relationships could be caused by their reciprocal relationship (Figure 1a,

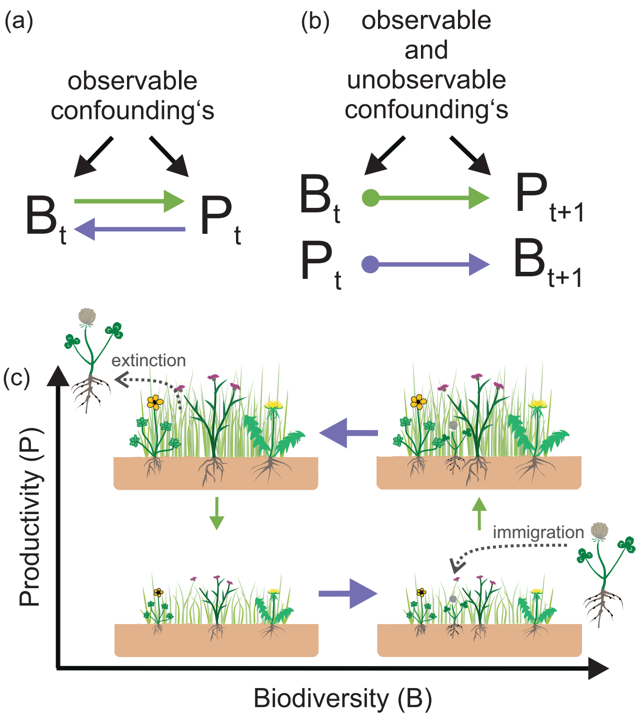

FIGURE 1 (a) Conceptual model showing the reciprocal relationship between plant biodiversity (B) and productivity (P) and additional observable confounding factors (i.e. environment and disturbance) hypothesized for (semi-)natural systems. (b) Statistical design using temporal sequences of biodiversity and productivity to unravel reciprocal relationships and to control for observable as well as unobservable confounding factors (e.g. soil fertility, climate and land use). (c) Expected changes in biodiversity and productivity in (semi-)natural systems (e.g. agriculturally managed grasslands). Size of the arrows indicates the expected relative importance of relationships suggested by previous findings from (agriculturally managed) grasslands (Grace et al., 2007; Socher et al., 2012). Note that depicted hypothesized changes in biodiversity and productivity are based on findings from classic biodiversity experiments and can differ under more 'real-world' settings (see Section 4).

Cardinale et al., 2009; Grace et al., 2007; Willig, 2011). In grasslands, high productivity can reduce plant biodiversity through increased light competition (Hautier et al., 2009) or changes in nutrient niche-dimensionality (Harpole et al., 2017). In contrast, studies focusing on effects of biodiversity on productivity often found positive relationships in artificial experimental systems (Cardinale et al., 2012; Loreau et al., 2001; Tilman et al., 2014), mainly due to increased complementarity (Barry et al., 2018), although more 'real-world' experiments (i.e. species loss experiments) have also found weaker relationships (Lisner et al., 2023; Sasaki et al., 2017; Smith & Knapp, 2003). These processes, however, are not mutually exclusive (Grace et al., 2016) and are hard to tease apart in observational data when they occur simultaneously (Dee et al., 2022). For instance, a negative effect of productivity on biodiversity could mask a positive effect of biodiversity on productivity (Schmid, 2002; van der Plas, 2019). Hence, to robustly estimate the effect of biodiversity on productivity and vice versa in (semi-)natural ecosystems, such as managed grasslands, isolating each direction of their reciprocal relationship from the other is crucial.

Despite the potential of reciprocal relationships between biodiversity and productivity to obscure attempts to isolate the effects of biodiversity on productivity from productivity on biodiversity and vice versa, few prior studies either attempt to account for it explicitly (*but see* Dee et al., 2023) or to study both directions in a single study (but see Chen et al., 2018; Grace et al., 2016; Paquette & Messier, 2011). For instance, of 31 studies reviewed in a comprehensive literature synthesis in van der Plas (2019) most do not address reverse causality (Dee et al., 2022). In a notable exception that examined effects in both directions of this bidirectional relationship, Grace et al. (2016) found a positive effect of biodiversity on productivity, and a negative effect of productivity on biodiversity in (semi-)natural grassland. However, this study used observations from single points in time, which creates challenges for determining the temporal ordering of causal effects. In particular, if productivity is inferred from plant biodiversity sampled at the same point in time (or vice versa), their effects will be hard to disentangle, causing simultaneity bias (Wooldridge, 2012)—even if they do not affect each other simultaneously. Furthermore, the effects of biodiversity on productivity (or vice versa) are likely not truly simultaneous and occur at different time scales (Costanza et al., 2007), for example, delayed effects which need a longer time to emerge (e.g. effects of biodiversity on productivity through plant–soil feedback effects). While some studies focused on long-term (across multiple years) effects between biodiversity and productivity (Isbell et al., 2018; Qiu & Cardinale, 2020), less is known about higher resolutions of temporal dynamics (e.g. within years—the scale at which productivity can reduce biodiversity through shading, for example) (Dullinger et al., 2013; Faust et al., 2012; Reich et al., 2012). However, using data from multiple time points within a year based on seasonal data allows us not only to estimate reciprocal relationships but also to explore different temporal dimensions of cause and effect (e.g. delayed causal effects from on season to another). Having repeated samples across the same sites over time (allowing analysis of within-site changes; longitudinal data hereafter) further enable statistical designs (i.e. two-way fixed-effect models; Wooldridge, 2012) that allow for control over a broader suite of observable and importantly, unobservable confounding variables without needing to know or measure them (Figure 1b,e.g. measurement error and micro-climate) (Dee et al., 2023; Larsen et al., 2019). Thus, to deal with the temporal precedence of effects and to tease out reverse causalities, longitudinal data, that is, surveys repeated both within years (across seasons) and across years, can be crucial if we aim to identify and estimate the causal effects between biodiversity and productivity (Dee et al., 2023; Larsen et al., 2019; Leszczensky & Wolbring, 2022).

Here, we compare the magnitude of the relationship of plant biodiversity on productivity with the reciprocal relationship of standing biomass (resulting from productivity) on biodiversity within managed grasslands that vary in land-use intensity. We use data collected over 2 years and two seasons per year on plant species richness, standing biomass and productivity across 150 managed grassland sites located across Germany. Previous studies observed negative correlations between biodiversity and productivity in these grasslands (Socher et al., 2012), even after controlling for multiple confounding variables (Le Provost et al., 2023). Here we build on these prior studies by using longitudinal data within a growing season, across years and so-called 'causal inference' methods (Figure 1b) to resolve and compare the relative magnitudes of reciprocal relationships between biodiversity and productivity. We show, for the first time, that higher-resolution longitudinal data (interannual, i.e. seasonal data, as opposed to single annual measurements used in previous studies) can be used to resolve reciprocal relationships. By using causal inference tools, we found that within managed grasslands, the estimated effects of biodiversity on productivity and vice versa are weak. When comparing inferences from our design that can control for more confounding variables to a typical statistical design in ecology (i.e. mixed-effect models), we find that our estimates differ both in signs and magnitudes, and that these effects are likely overestimated (by two standard errors) by conventional statistical designs. Ultimately, we conclude by highlighting future data needs and methods that can help us to resolve biodiversity-productivity relationships that can help to reconcile a long-running debate in ecology and ultimately, to understand how biodiversity and ecosystem functioning respond to global change.

2 | MATERIALS AND METHODS

2.1 | Study system

The grasslands are located within three German regions (north-east: Schorfheide-Chorin, central: Hainich-Dün, south-west: Swabian Alb) that are part of the Biodiversity Exploratories project (Fischer et al., 2010). All three regions differ in their climatic and edaphic conditions, with annual mean precipitation and elevation being highest in the South-west, and temperature and soil fertility (deep fertile organic soils, but also few sandy soils in the Schorfheide-Chorin) being highest in the North-east. All data was collected from permanently marked plots (1 × 1 m) within 50 grasslands per region (150 in total). These grasslands are managed, with plots selected to span a wide gradient of land-use intensity (see Table S10) typical of Central European grasslands (Blüthgen et al., 2012). Within Central European grasslands, fertilization, mowing and grazing are the most common land-use components, and all can be important drivers of plant biodiversity and productivity (Socher et al., 2012). Field work permits were issued by the responsible state environmental offices of Baden-Wurttemberg, Thüringen and Brandenburg (according to §72 BbgNatSchG).

2.2 | Data collection and processing

In both the spring (April–May) and summer growing season (July–August) of 2020 and 2021, we estimated standing biomass ($g\,m^{-2}$) and species-specific cover (in %) of vascular plant species in each of the 150 grassland plots. Standing biomass was non-destructively estimated using a rising plate meter, by taking vegetation density as a proxy for standing biomass (López-Díaz et al., 2011). Biomass estimations were calibrated using data of biomass measurements from two additional, adjacent (~2 m distance) 1 × 1 m grassland plots (100 plots per region, 300 in total) collected in spring 2021 (for more information see Andraczek, Weigelt, Hinderling, et al., 2023). In each grassland plot, we quantified biodiversity as vascular plant species richness, Evenness and Shannon Diversity (Jost, 2006). While previous studies predominantly used standing biomass as a proxy for productivity (which is challenging to measure in observational studies), we use both standing biomass (measured at one single point in time) and biomass production (as increments of standing biomass over time), which we refer to as productivity hereafter (measured as in Andraczek, Weigelt, Hinderling, et al., 2023, see Supplement). This distinction is done to disentangle reciprocal relationships between biodiversity and productivity, as negative feedback effects of productivity on biodiversity occur, at least in part, through changes in standing biomass (Grace et al., 2016). Although various productivity surrogates exist (e.g. soil fertility), we used aboveground standing biomass over time, as it is agriculturally most relevant and expected to respond more rapidly to changes in biodiversity.

Land-use-related information was derived from annual questionnaires of landowners (Vogt et al., 2019, 2023). Within each grassland, land-use intensity comprises the intensity of fertilization, mowing and grazing, which are used to generate an index of land-use intensity (LUI hereafter) as a composite variable of standardized measures of mowing (cuts $year^{-1}$), grazing (Livestock units × day $ha^{-1}\,year^{-1}$) and fertilization ($kg\,N\,ha^{-1}\,year^{-1}$) intensity (Blüthgen et al., 2012). To consider the effects of past LUI (from the previous year) on biodiversity and productivity, LUI was quantified for the years 2019 and 2020. To control for confounding variables, we obtained existing project data on edaphic conditions (i.e. soil P, soil N, soil pH, sand/clay content, slope and elevation; see Ostrowski et al., 2023; Schöning & Apostolakis, 2023; Schöning, Klötzing, Apostolakis, & Trumbore, 2023; Schöning, Klötzing, Apostolakis, Trumbore, & Schrumpf, 2023), climatic (i.e. mean temperature and precipitation in months before spring and summer, Hänsel et al., 2022) and hydrological variables (i.e. topographic wetness index, Manning, 2023). All confounding variables (LUI, soil P, soil N, soil pH and climatic variables) were collected before the biomass and biodiversity measurements to prevent collider bias in estimating causal effects. These variables were chosen because they are known to be important predictors of both biodiversity and productivity (Grace et al., 2016; Le Provost et al., 2023; Socher et al., 2012). Despite our comprehensive data, other important unmeasured confounding variables still exist, such as insect herbivory, soil micronutrients, historical land-use, plant pathogens or soil microbial composition, which motivated our use of statistical analyses from 'causal inference' that can account for unobservable confounding variables.

To control for different aboveground resource acquisition strategies (i.e. leaf economics) of plants that are known to influence biodiversity and productivity in managed grasslands (Allan et al., 2015), we additionally quantified community weighted means (CWM) of specific leaf area (SLA hereafter) for all plots, as the mean SLA of all species in a given plot weighted by relative cover of each species. SLA is a key indicator of 'fast' leaf economics (Reich, 2014), and previous studies have shown that the CWM of SLA is strongly correlated with productivity in our grasslands (Allan et al., 2015; Neyret et al., 2024). All trait data was obtained from the TRY database (Kattge et al., 2020). To quantify competition for light, we measured light availability as photosynthetically active radiation (in $\mu mol\,s^{-1}\,m^{-2}$) at ground level and 1.5 m.

2.3 | Statistical design and comparisons

We estimated the effect of biodiversity on productivity, and of productivity on biodiversity using longitudinal data including repeated samples of 150 plots from 58 sites across the growing season at two time points (i.e. spring and summer) and over 2 years, informed by directed acyclic graphs to visualize causal relationships (Figure S4; Arif & MacNeil, 2022, Laubach et al., 2021, Pearl, 2009). We applied both conventional statistical designs used in ecology (linear mixed-effects models directly controlling for confounding variables, Bates et al., 2015) and 'causal inference' techniques that aim to estimate causal relationships from temporal ('longitudinal' or 'panel') data by controlling for both observed and unobserved confounding variables (Dee et al., 2023; Larsen et al., 2019; Wooldridge, 2010). These methods are so far underutilized in ecology (but see e.g. Dee et al., 2023; Dudney et al., 2021; Ratcliffe et al., 2022). We compare inferences from more conventional (i.e. mixed effect models) with 'causal inference' statistical designs, including their associated ecological conclusions and assumptions.

Mixed-effect models statistically control for observable confounding variables by including them as covariates in the model, but unobservable confounding variables are relegated to the error term as the 'random effect'. In our application of these models, we control for several measured and known confounding variables: edaphic conditions, climate, management and hydrological variables (see Figure S4; Table S16). However, mixed models rely on strong assumptions (VanderWeele, 2012): to interpret an estimated effect as causal, the random effect should have no systematic correlation with any variable in the model. When violated, random effects are biased estimators (see Byrnes & Dee, 2024 for more details). Thus, these models assume that any omitted variable has no confounding effect, that is, has no relationship with both the response or effect, in this case richness and productivity.

Since our data is temporal (measured within the same plot at multiple points in time), we can use other methods that more flexibly control for observed and unobserved confounding variables (e.g. surrounding land-management), without the need to measure them (Dee et al., 2023; Wooldridge, 2010) (for more information on observable confounding variables which are deemed to be controlled for by the fixed effects in the two-way fixed effect models, see Figure S4). Specifically, two-way fixed effect estimators relax the strong assumption that no confounding variables are left out of the model and therefore are not controlled for. In contrast to the 'random effects' (Bolker et al., 2009), econometric 'fixed effects' are not constrained to any predefined distribution, and are fixed, estimable and not part of the random term. While this comes with a cost in statistical power, it requires fewer assumptions about confounding variables to be an unbiased estimator (Wooldridge, 2010). To account for both measured and unmeasured confounding variables (e.g. surrounding land management) influencing biodiversity-productivity relationships, we aggregated plots into management entities (sites hereafter) based on the respective land manager, reflecting similarities in characteristics that could be confounding (e.g. pollination or land-use history); this led to 26 sites in Swabian Alb, 22 sites in Hainich-Dün, and 10 sites in Schorfheide-Chorin, with on average 3 plots per site. Furthermore, we sub-grouped 5 sites depending on their proximity to each other to address that adjacent plot (managed by the same farmer) are more similar, with respect to sources of unobserved heterogeneity (e.g. natural herbivore densities), than more distant plots managed by the same farmer (on average 2 plots per sub-site).

However, mixed-effect models and two-way fixed effect models share one critical assumption: that there are no time-varying confounding effects on plot level that affected both biodiversity and productivity and are left out of the model (i.e. measured or unobserved). Yet, such confounding variables could exist (e.g. soil micronutrients, soil microbial composition, plant pathogens). In response, we assess the potential threat of unobserved time-varying confounding variables on plot-level for both mixed effect and two-way fixed effect models, testing if they could substantially change our results (see Section 2.3.5).

Our implicit assumption in our original models (i.e. both mixed-effect models and two-way fixed effect models) is that causal effects of biodiversity on productivity, and of productivity on biodiversity, are temporally dynamic (due to temporally delayed effects of, e.g. plant–soil feedbacks), here defined as delayed causal effects from one season to the next, or 1 year to the following year. However, it is also possible that these effects are not temporally dynamic, and that effects happen at the same time and are not delayed in time. Hence, to assess how the assumption of temporal dynamics affected the conclusions, we additionally modelled the effects between biodiversity and productivity using linear mixed-effect models and two-way fixed effect models but only using data measured in the same season (i.e. summer, similar to previous studies quantifying biodiversity and productivity at peak biomass).

We implemented all regression models in RStudio (v. 4.3.2) (R Core Team, 2021), used an ln-ln model specification and report z-transformed effect sizes to allow the comparison of the relative magnitude of the estimated causal effects. To achieve a more even distribution, LUI was square root transformed.

2.3.1 | Estimating the effect of biodiversity on productivity

We first estimate the effect of richness in spring on productivity in summer using a two-way 'econometric fixed-effect' estimator ('fixed effects' hereafter, see, e.g. Halaby, 2004; implemented in *fixest* package v 0.11.0, Berge, 2018) as in the following equation (based on Figure 2a):

$$\begin{aligned}&\ln\left(\text{Productivity}_{\text{summer }[pt]}\right) \sim \beta \ln\left(\text{Richness}_{\text{spring }[pt]}\right) + \text{sqrt}\left(\text{LUI}_{[pt]}\right)\\&+\ln\left(\text{Standing biomass}_{\text{spring }[pt]}\right) + \delta_p + \mu_{st} + \epsilon_{pst},\end{aligned} \quad (1)$$

where *p* indicates plot and *s* site, *t* indexes the respective year and the respective season in which a variable is quantified indicated by *spring* or *summer*. This equation estimates individual plot effects on productivity by including *time-invariant* plot attributes (δ_p). Hence, δ_p controls for unobserved heterogeneity caused by confounding variables which operate at the plot scale but are constant across time (e.g. soil micronutrients, see Dee et al., 2022). Note that time-invariant site attributes (e.g. soil depth or elevation; see Figure S4) are not explicitly included in the equation because they are subsumed into the time-invariant plot attributes. However, as other confounding variables may vary over time and operate at larger spatial scales (e.g. precipitation and management), we additionally estimate *time-varying* site attributes (μ_{st}). In this case, we model a year-specific effect for each site on productivity. In particular, these *time-varying* site attributes control for confounding variables, whether they are measured or not, that vary across time and are site specific, such as weather. As land-use intensity (LUI) is an important driver of both biodiversity and productivity, we included LUI measured at plot level as a confounding variable to test for an interaction with richness and LUI (e.g. land-use intensity can change species composition/abundance, and hence, modifies effects of biodiversity on productivity). To investigate whether

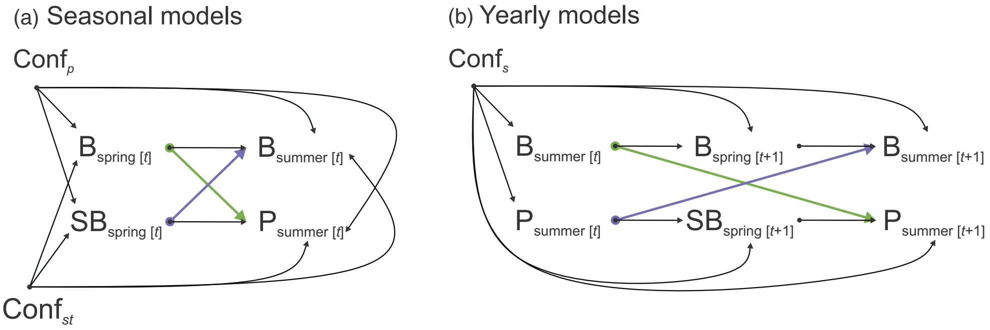

FIGURE 2 Simplified causal diagram reflecting the assumed relationships that inform our estimation strategy (a) for seasonal lag models and (b) yearly models estimating causal effects of biodiversity (B) on productivity (P) (green arrow) and standing biomass (SB) on biodiversity (purple arrow) used for the two-way fixed effect estimation design. Shown are time-invariant plot-level (Conf$_p$, δ_p) or site-level (Conf$_s$), and time-varying site-level (Conf$_{st}$, μ_{st}) confounding factors (both observable and unobservable). Time indexes respective years in which variables are quantified: $[t]=$year 1, $[t+1]=$year 2. Further, all confounding variables are measured a season or year *before* biodiversity and productivity was quantified preventing collider bias (see Section 2). For a more detailed directed acyclic graph representing the causal relationships between biodiversity and productivity and including additional confounding variables that are both observed and unobserved, see Figure S4.

changes in biodiversity or productivity in response to LUI are due to changes in community composition, we further run models including CWM of SLA instead of LUI (see Figure S4). All variation that is not explained by the main effects (see Equations 1 and 3), and the fixed effects (time-invariant or time-varying) will be captured by the error term ($\mathcal{E}_{pst}$). To control for static and dynamic effects we included past standing biomass as an additional covariate in all models.

2.3.2 | Robustness analyses of estimated effects of biodiversity on productivity

To assess the sensitivity of our estimated effect of biodiversity on productivity, we additionally tested for robustness of our results in several ways. First, while changes in species richness in spring may have relatively rapid effects on productivity in summer, it is likely that causal effects require longer to emerge (e.g. from previous to present year). Hence, we also tested alternative models, in which species richness in summer of the previous year $[t]$ affects productivity in summer of the present year $[t+1]$ using the following equation (based on Figure 2b):

$$\ln\left(\text{Productivity}_{\text{summer }[t+1]}\right) \sim \beta \ln\left(\text{Richness}_{\text{summer }[t]}\right) + \text{sqrt}\left(\text{LUI}_{[t]}\right) + \ln\left(\text{Standing biomass}_{\text{spring }[t]}\right) + \mu_s + \epsilon_{pst}, \quad (2)$$

In contrast to the models testing for seasonal dynamics between effects of biodiversity on productivity, in yearly models, we did not include δ_p as this model included a lagged independent variable of richness, and hence, including δ_p would bias estimated causal effects (Nickell, 1981). Second, for all model specifications described above, we assessed if estimated effects change when: (1) using Shannon Diversity instead of richness, (2) controlling for Evenness, (3) assuming non-linear effects of richness, and (4) clustering standard errors on plot or site level to account for serial correlation of error terms (e.g. due to temporal dependence, see Bertrand et al., 2004).

2.3.3 | Estimating the effect of productivity on biodiversity

We estimate the effect of standing biomass in spring (as proxy for productivity) on richness in summer (in the same year) as in the following equation (based on Figure 2a):

$$\ln\left(\text{Richness}_{\text{summer }[pt]}\right) \sim \beta \ln\left(\text{Standing biomass}_{\text{spring }[pt]}\right) + \text{sqrt}\left(\text{LUI}_{[pt]}\right) + \ln\left(\text{Richness}_{\text{spring }[pt]}\right) + \delta_p + \mu_{st} + \epsilon_{pst}, \quad (3)$$

where p indicates plot and s site, t indexes the respective year and the respective season in which variable is quantified indicated by *spring* or *summer*, while δ_p and μ_{st} are the same as above in Equation (1). As in Equation (1), this assumes no confounding variables at plot level that are plot specific and vary through time. To test if effects of LUI mask causal effects of productivity on biodiversity we included LUI, although we also tested whether changes in species abundance and/or community composition explains changes in biodiversity, by including CWM of SLA as a covariate (for more detailed information see Section 2.3.1). In addition, we tested for an interaction between standing biomass and LUI. To control for static and dynamic effects we included past richness as additional covariate in all models. Note that within models testing yearly dynamic effects, we use summer productivity, not standing biomass, as the latter might be biased due to mowing/grazing.

2.3.4 | Robustness analyses of estimated effect of productivity on biodiversity

To assess the robustness of the estimated effect of productivity on biodiversity, we first tested alternative models (see Section 2.3.2 for rational), in which productivity in summer of the previous year [t] affects richness in summer of the present year [$t+1$] using the following equation (based on Figure 2b):

$$\ln\left(\text{Richness}_{\text{summer }[t+1]}\right) \sim \beta \ln\left(\text{Productivity}_{\text{summer }[t]}\right) + \text{sqrt}\left(\text{LUI}_{[t]}\right) + \ln\left(\text{Richness}_{\text{spring }[t]}\right) + \mu_s + \epsilon_{pst}. \quad (4)$$

Second, for all model specifications described above, we assessed if estimated causal effects change when: (1) assuming non-linear effects of productivity/standing biomass and (2) clustering standard errors on plot or site level to account for serial correlation of error terms.

2.3.5 | Sensitivity test

We conducted a sensitivity analysis (using the *sensemakr* package, Cinelli & Hazlett, 2020) exploring the robustness of our estimated effects to potential unobserved confounding variables which are systematically correlated with biodiversity and productivity following methods developed by Altonji et al. (2005) and Oster (2019). These sensitivity test assesses the extent to which the results (estimates) would substantially change due to the presence of such a confounder, and to what degree depending on the potential importance of the confounder (see also Dee et al. (2023) for another ecological application and example). Specifically, the sensitivity test probes the assumption that the observable confounding variables that drive both the dependent variable (e.g. biodiversity) and the independent variable (e.g. productivity) are adequately controlled for in our models. If this assumption is valid, we can assess under which conditions and unobserved confounding variable could change the estimated effects in our models (see Tables S16–S19). Using this sensitivity analysis, we can mimic the effect of failing to include a powerful potential confounding variable in our statistical designs for both the mixed effect models and the two-way fixed effects models, while the strength of the potential confounder is relative to the variation not explained by the covariates included in the respective models (unexplained variance in the mixed-effect models: 30%–50%, two-way fixed effect models: 10%–20%). However, since *sensemakr* does not support mixed effect models in the current version (due to the complexity of mixed effects, e.g. the variability within and between groups), we tested the sensitivity based on linear models. While not fully comprehensive, this can still provide some insights into the robustness of the fixed effect in our models to unmeasured confounding variables, because mixed-effect models and linear models are both making the assumption that the variables that are confounding are being included in the model. Nevertheless, in the sensitivity analysis of the linear models the strength of the unobserved confounding variable was relative to the unexplained variance in the mixed effect models, to address that the random effects would partly explain some of the unobserved confounding variables if included. For more detailed information, see supplement.

3 | RESULTS

3.1 | Relationships between biodiversity and productivity using random effect estimator

Using linear mixed-effect models, while controlling for multiple environmental and management covariates (see Table S1), we observed that a high species richness in spring was positively associated with a high summer productivity (effect size: 0.20; 95% CI: 0.04, 0.36, $p=0.02$, Figure 3a). For the reverse relationship, a high-standing biomass in spring was associated with a low species richness in summer (effect size: −0.16; 95% CI: −0.28, −0.04, $p=0.01$, Figure 3b). Effects of species richness on productivity were robust when controlling for species Evenness, although relationships between Shannon diversity and productivity were overall weaker (see Tables S11 and S12).

3.1.1 | Relationships between biodiversity and productivity using two-way fixed effect estimators

Using two-way fixed effect models, seasonal dynamic models (assuming temporal dynamic effects between biodiversity and productivity mediated from spring to summer) showed that a high species richness in spring decreased (albeit non-significantly) productivity on average (effect size: −0.10; 95% CI: −0.43, 0.24). Yearly dynamic models (assuming temporal dynamic effects between biodiversity and productivity mediated from the previous year to the next year) showed that a high species richness in summer tended to be associated (albeit non-significantly) with a high productivity of the following year (effect size: 0.08; 95% CI: −0.14, 0.29, Figure 4a). Thus, using two-way fixed-effect estimators, we observed that estimated effect of biodiversity on productivity, and productivity on biodiversity were weak, with 95% confidence intervals of effects always overlapping with 0, but that the strength and direction of these effects slightly differed depending on whether seasonal or yearly dynamics of causal relationships were assessed (Figure 4; Tables S2–S5). This was despite observed relatively large changes in biodiversity and productivity (Figure 5).

For the reverse relationship, the effect of productivity on richness, standing biomass in spring had virtually no effect on species richness in summer (effect size: −0.01; 95% CI: −0.14, 0.11), which was also found when examining the yearly dynamic effects of productivity in summer on species richness in spring (effect size: 0.08; 95% CI: −0.04, 0.19, Figure 4b). The direction and strength of the estimated effects remained comparable even when controlling for non-linear relationships, Evenness or when using Shannon Diversity instead of richness (see Supplement S6–S9).

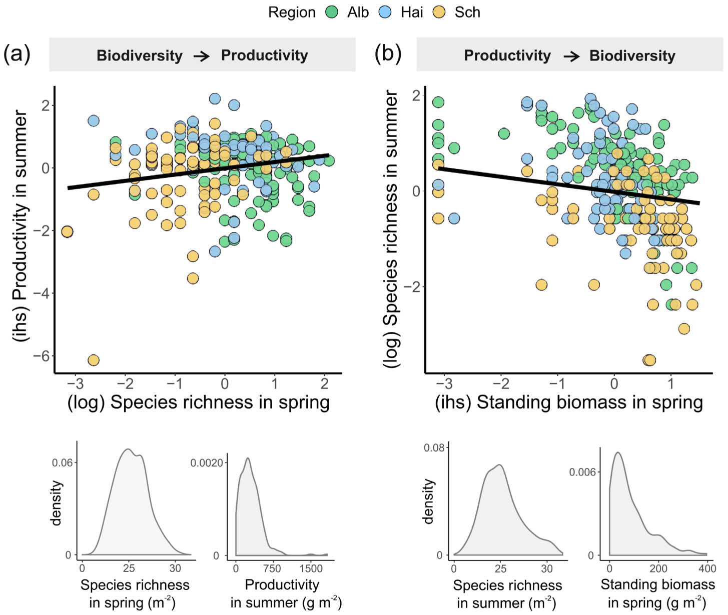

FIGURE 3 Relationship based on linear mixed effect models (which we call the 'conventional approach') between (a) species richness in spring and productivity in summer, and between (b) standing biomass in spring and species richness in summer, colour coded by region (Alb: Swabian Alb, Hai: Hainich-Dün, Sch: Schorfheide-Chorin) (for further information see Table S1). Note that variables are on logarithmic (log) or inverse hyperbolic sinus (ihs) scale and z-transformed. Frequency plots represent gradients of species richness (in spring and summer), standing biomass in spring and productivity covered by overall data.

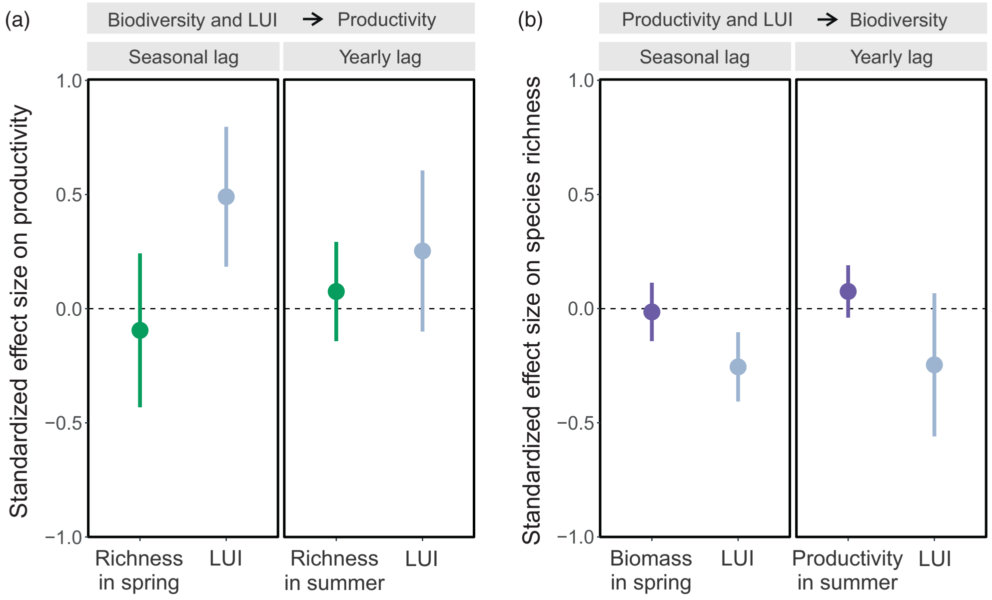

FIGURE 4 Relationships based on two-way fixed effect models. (a) Standardized effects of species richness (green) and land-use intensity (LUI, light blue) on productivity and (b) productivity (purple) and LUI (light blue) on species richness for models testing different temporal dynamics (seasonal vs. yearly lag). All estimated mean effects are on a log (richness) or log-inverse-hyperbolic-sine (productivity) scale, *z*-transformed and shown with 95% confidence intervals. For more detailed information see Tables S3–S6.

3.2 | Effect of land-use intensity on biodiversity and productivity through time

Using two-way fixed effect models, we found strong associations of LUI on both species richness and productivity, although the strength of estimated effects of LUI differed when considering seasonal or yearly dynamics of causal relationships (Figure 4; Tables S2–S5). Overall, a high LUI was associated with high productivity when considering seasonal (effect size: 0.49; 95% CI: 0.18, 0.80) or yearly dynamics (effect size: 0.25; 95% CI: −0.10, 0.61) of effects (Figure 4a). However, within-seasonal effects of LUI on productivity were larger compared to yearly models.

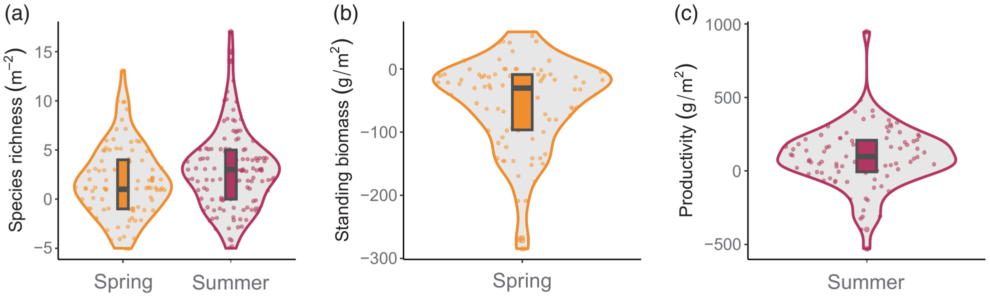

FIGURE 5 Seasonal variation in (a) species richness (in m^{-2}) across 2020 and 2021 (number of species in spring: Species gained = 3.67, lost = 2.23; in summer: Gained = 4.54, lost = 2.07), and year-to-year variation in (b) standing biomass (as proxy for productivity in spring, in g/m^2) (standing biomass gained in g/m^2 in spring: gained = 35.0, lost = 70.9) and (c) productivity (increment between spring and summer standing biomass, in g/m^2) (productivity gained in g/m^2 in spring: gained = 180.0, lost = 148.0).

In contrast, in both seasonal (effect size: −0.25; 95% CI: −0.41, −0.10) and yearly models (effect size: −0.25; 95% CI: −0.56, 0.07) a high LUI was associated with a low species richness in summer (Figure 4b). Furthermore, in the yearly dynamic models, we found a significant negative interaction between productivity in summer and land-use intensity on species richness in summer (effect size: −0.20, 95% CI: −0.35, −0.05, Table S5).

3.3 | Effect of functional composition on biodiversity and productivity through time

Comparing two-way fixed effect models with SLA instead of LUI as a covariate revealed that the strength of inferred causal effects of biodiversity on productivity was partly explained by shifts in community composition (Tables S2–S5). Originally negative estimated causal seasonal dynamic effects of biodiversity on productivity became approximately neutral (effect size: 0.05; 95% CI: −0.40, 0.49) when including SLA instead of LUI. Overall, we observed that a high SLA was associated (albeit non-significantly) with a high productivity when both considering seasonal (effect size: 0.23; 95% CI: −0.10, 0.56) and yearly (effect size: 0.10; 95% CI: −0.27, 0.47) dynamic effects. In contrast, a low SLA was associated with a high species richness in both seasonal (effect size: −0.07; 95% CI: −0.35, 0.20) and yearly (effect size: −0.26; 95% CI: −0.37, −0.14) models.

3.4 | Sensitivity analysis

The sensitivity analysis revealed that estimated effects of biodiversity on productivity (Figure S5a), and of productivity on biodiversity (Figure S5b), were not robust against bias from unobserved time-varying confounding variables in linear models (see Figure S5a,b), suggesting that linear mixed-effect models are more susceptible to bias from unobserved confounding variables (which is also more likely due to the unexplained variance in the mixed effect models estimating the effect of biodiversity on productivity: ~50%; and of productivity on biodiversity: ~30%). Specifically, for the linear models, the estimated upper bound shifted towards positive for the estimated effect of productivity on biodiversity, and towards negative for the estimated effect of biodiversity on productivity (Figure S5a,b), crossing the threshold at which originally significant effects would become insignificant (as unobserved confounding effects explain away effects of biodiversity on productivity, or vice versa). In contrast, for the two-way fixed effect models, the estimated upper bounds were still neutral for effects of productivity on biodiversity, and vice versa (Figure S5c,d). Hence, we conclude from the analysis that the neutral effect of productivity on biodiversity, and vice versa, is robust to a potential unobserved confounder.

4 | DISCUSSION

Causal effects between biodiversity and productivity are likely obscured by their reciprocal relationships, potentially explaining the high variability of relationships observed in (semi-)natural ecosystems. Despite few attempts to account for their reciprocal nature, disentangling cause from effect between biodiversity and productivity remains challenging. Here, we demonstrate a 'novel' approach to resolve reciprocal relationships between biodiversity and productivity using higher- resolution longitudinal data (i.e. surveys repeated across seasons, as well as across years, within the same sites), which also allows us to control for a broader suite of confounding variables than possible in commonly-used approaches (i.e. mixed-effect models). We show that within managed central European grasslands, effects of biodiversity on productivity, and productivity on biodiversity are weak. We also demonstrate that estimates from conventional statistical designs are less robust to bias from unobserved confounding variables (see Figure S5), and thus likely fail to isolate the effects of biodiversity on productivity, and vice versa. In contrast, our two-way fixed effects models can also control for unmeasured and unobserved confounding variables (see Figure S5), contributing to their robustness. Indeed, the estimated effect of biodiversity on productivity using standard approaches was more than two standard errors from our estimated effects from a design that can control for a broader suite of confounding variables (Figure S3), and the conclusion drawn would be qualitatively different. Further, tests assessing the sensitivity of estimated effects against bias from unobserved confounding variables reveal that mixed-effect models are susceptible to bias, while two-way fixed effects are robust.

Previous evidence suggests that the effect of biodiversity on productivity in managed grasslands are negative (Grace et al., 2007; Le Provost et al., 2023; Socher et al., 2012), which has been implied to result from strong negative effects of productivity on biodiversity (and by our naïve model in Figure 3). However, we do not find evidence for a strong negative effect of productivity on biodiversity in any of our main models. One reason that our results differ from prior studies is that they rely on observations from single points in time, making it challenging to account for potential bias due to reciprocal relationships (Wooldridge, 2012). Similarly, using mixed-effect models based on higher-resolution longitudinal data, enabling to resolve the reciprocal relationships between biodiversity and productivity, we would conclude that plant biodiversity increased productivity, while increases of standing biomass caused plant biodiversity to decline. However, when applying approaches that can control for a broader suite of confounding variables (Dee et al., 2023; Halaby, 2004; Wooldridge, 2010), the observed strong negative effect of productivity on biodiversity disappears. The weak effects of productivity on biodiversity observed in our study contrast the strong negative effects found in earlier studies (Grace et al., 2007, 2016; Socher et al., 2012), which are suggested to arise from negative effects of light competition (Hautier et al., 2009). However, frequent biomass removal (by mowing and grazing) in our studied grasslands likely compensated for some of these negative effects by alleviating light competition (Andraczek, Weigelt, Hinderling, et al., 2023; Eskelinen et al., 2022; Lamb, 2008). These results indicate that the effects of productivity on biodiversity strongly depend on management intensity and likely differ in less intensively managed grasslands.

In contrast to many prior experimental studies, we find no evidence for a positive effect of biodiversity on productivity. Classic grassland experiments often show that the positive relationship of biodiversity on productivity flattens at a relatively low number of species (~10 species) (Tilman et al., 2014), suggesting a saturation of resource use (although observed relationships are often weaker in more 'real-world' experiments, see Lisner et al., 2023; Sasaki et al., 2017; Smith & Knapp, 2003). By exceeding the number of species in many grassland experiments, previous studies suggested that the relevant functional niche space in managed grasslands is largely saturated (Freitag et al., 2023; Ladouceur et al., 2020). However, we also found that the effects of biodiversity on productivity tended to be negative (albeit non-significant), likely due to shifts in the plant community composition associated with increases in land-use intensity (Figure S2) (Allan et al., 2015; Boeddinghaus et al., 2019). Specifically, communities with a high biodiversity were dominated by species with low SLA and these were typically slow-growing and small species (Hautier et al., 2009; Vojtech et al., 2007), so that negative effects of biodiversity on productivity weakened when the CWM of SLA (i.e. mechanisms of the effect of biodiversity on productivity) was accounted for—corroborating our reasoning.

By using higher-resolution seasonal data, we were able to explore different temporal dynamics between biodiversity and productivity. We found that estimated effects between biodiversity and productivity tended to differ (albeit weakly) when considering seasonal (within a growing season) or yearly (between years) dynamics effects. Moreover, the typical approach (i.e. mixed-effect models) is highly sensitive to temporal dynamic effects (see Figure S3), and the results for the effect on productivity on biodiversity change in sign, from negative to positive (−0.16 to 0.07), when only using data from one point in time and ignoring the temporal dependence of effects. Specifically, this flip in sign of the effect of productivity on biodiversity indicates that conventional models are likely statistically biased due to unobserved time-varying confounding variables (e.g. unmeasured weather shocks). Previous studies suggest that relationships between biodiversity can be temporally dynamic across years, but less is known for higher resolutions (i.e. within years) of temporal dynamics (Dullinger et al., 2013; Faust et al., 2012; Reich et al., 2012). Higher resolution longitudinal data could allow crucial insights into the mechanistic understanding of relationships between biodiversity and productivity, such as delayed effects of plant–soil feedbacks (Thakur et al., 2021), or temporal partitioning of resources (Barry et al., 2018) on productivity. However, the relatively limited time series in our study likely prevented to observe stronger temporal dynamics between biodiversity and productivity, explaining the general weak observed differences between seasonal and yearly dynamics. Nevertheless, our findings emphasize the importance of data collected at multiple points in time (e.g. in different seasons and years) to understand the temporal ordering when attempting to estimate causal effects.

Our results indicate a strong correlation of land-use intensity (LUI) and both biodiversity and productivity, with LUI being positively associated with productivity, and negatively with biodiversity. These findings highlight the importance of LUI as one of the main drivers of biodiversity and productivity in managed grasslands (Grace et al., 2007; Socher et al., 2012), likely strongly modifying the relationships between biodiversity and productivity (Andraczek, Weigelt, Cristóbal, et al., 2023). Thus, we did observe a significant negative interactive effect of LUI and productivity on biodiversity when considering yearly dynamic effects (Table S5), potentially due to increased fertilization at higher LUI which amplifies the negative effects of productivity on biodiversity (Band et al., 2022). Overall, the correlation of LUI with biodiversity and productivity was strongest with the seasonal dynamic effects between biodiversity and productivity, likely because of yearly variability in LUI within the same field. Interestingly, we found that the negative correlation of LUI and biodiversity exceeded the effects of productivity on biodiversity, suggesting a weaker importance of aboveground productivity-mediated effects (e.g. due to light competition) of LUI on biodiversity, hinting towards alternative pathways (e.g. changes in belowground competition or species pool size; Harpole et al., 2016, Smith et al., 2000).

The use of directed acyclic graphs (Arif & MacNeil, 2022) and two-way fixed effect designs, coupled with sensitivity tests (see Section 2), enable more robust and transparent causal inference compared to conventional statistical designs by controlling for unobserved confounding variables and increasing transparency in assumptions required for a causal interpretation of estimates. However, we acknowledge that there are still uncertainties and assumptions being made for causal inference. In addition, while two-way fixed effects designs help to eliminate different sources of bias from confounding factors, one drawback is that they also require a larger sample size to obtain precise estimated effects (as seen when comparing the size of standard errors in the mixed versus fixed effects models in Figure S3). Estimating the effects of biodiversity on productivity, and vice versa, from these methods also relies on changes in biodiversity and productivity over time—for example, due to changes in land-use intensity, herbivory pressure, or other natural or human-mediated processes—as the variation used to estimate effects. Although the observed short-term changes in biodiversity and productivity in our grasslands were relatively large (Figure 5), longer time series would be beneficial to improve the statistical power while capturing a broader range of changes in biodiversity, productivity and their drivers (e.g. climatic extremes). Nevertheless, our study highlights that more fine-scale time series can be crucial to unravel the cause from effect between biodiversity and productivity. Furthermore, changes in species richness could also have been attributed to phenological changes, which would not represent productivity changes in response to species gains of new species or species loss. Although we cannot fully tease apart changes due to phenology and other drivers (e.g. changes in land-use intensity), we observed that between 2020 and 2021, different species were gained or lost (Figure S1), and hence, we assume that species changes between seasons and years were not predominantly attributed to seasonal patterns of species phenology.

5 | CONCLUSIONS

Understanding the biodiversity-productivity relationships is a major challenge in ecology. By using higher-resolution longitudinal data allowing to resolve reciprocal relationships, we found that within managed grasslands, the relationships between biodiversity and productivity are weak although showing a tendency to be temporally dynamic. Hence, higher-resolution longitudinal data is a promising tool to resolve reciprocal relationships (Dee et al., 2023), also allowing to explore the temporal dynamics of biodiversity-productivity relationships (Lepš, 2014; van Ruijven & Berendse, 2005). As we highlight, additional future work using higher-resolution longitudinal data (higher number of observations per year) could further enable crucial insights into the temporal precedence of the effects of biodiversity on productivity, or vice versa. Furthermore, future studies should also identify the underlying mechanisms explaining their temporal dynamics. Thus, experiments manipulating both biodiversity and productivity under more 'real world' conditions and at larger temporal and spatial scales (see, e.g. Freitag et al., 2023; Pichon et al., 2023), could help to elucidate our mechanistic understanding about the temporal ordering of cause and effect between biodiversity and productivity.

When done rigorously, by carefully assessing the core assumptions that allow for inferring causality from experimental data (see Kimmel et al., 2021); these studies can also help assess the validity of our causal assumptions. Ultimately, our results show that the choice of analytical methods can strongly determine the observed relationships between diversity and productivity, casting doubt over the true nature of these relationships in a range of environments. Meanwhile, they also point a way forward by showing that advancing our understanding of the temporal dependency of causal relationships between biodiversity and productivity is necessary for us to resolve the long-running debate about the nature of biodiversity-productivity relationships.

AUTHOR CONTRIBUTIONS

Fons van der Plas, Alexandra Weigelt, Laura E. Dee and Karl Andraczek conceived the ideas and designed the study together with Christian Wirth, Peter Manning, Gaëtane Le Provost and Daniel Prati; Judith Hinderling, Fons van der Plas, Alexandra Weigelt and Karl Andraczek collected the data; Karl Andraczek analysed the data, with input and code from Laura E. Dee, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and the R code used in this study are available on the Zenodo repository: https://doi.org/10.5281/zenodo.12686128 (Andraczek, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: (a) Species loss and (b) species gains in 2020 and 2021, averaged over all plots and all three regions.

Figure S2: Pearson correlation between Species richness, community weighted mean of specific leaf area (CWM SLA), and lagged LUI for spring and summer averaged across 2020 and 2021 and for each region (Swabian Alb, Schorfheide-Chorin, Hainich-Dün).

Figure S3: Comparison of estimated effects using mixed effect models and two-way fixed effect models with different assumptions of temporal delays between cause and effect: either assuming temporal dynamic effects (for comparability, here only estimates from seasonal lag models shown) or no temporal dynamic effects (using data collected in the same season i.e., summer) for models estimating the effect of (a) species richness on productivity and (b) productivity on species richness.

Figure S4: Directed acyclic graph (DAG) showing the hypothesized causal relationships between biodiversity and productivity, and confounding variables.

Figure S5: Sensitivity analysis.

Table S1: Linear mixed effect model showing the effect of species richness in spring on productivity and standing biomass in spring on species richness in summer, including all three regions (Swabian Alb, Schorfheide-Chorin, Hainich-Dün) and both years 2020 and 2021.

Table S2: Effects of (1) species richness in spring on productivity with seasonal lag and LUI as additional covariate, (2) with SLA in spring instead of LUI, and (3) including an interaction between LUI and species richness in spring, using two-way fixed effect estimation.

Table S3: Effects of (1) standing biomass in spring on species richness in summer with seasonal lag and LUI as additional covariate, (2) with SLA in spring instead of LUI, and (3) including an interaction between LUI and standing biomass in spring, using two-way fixed effect estimation.

Table S4: Effects of (1) species richness in summer of 2021 on productivity of 2021 with yearly lag and LUI of 2020 as additional covariate, (2) with SLA in summer of 2020 instead of LUI in 2020, and (3) including an interaction between LUI in 2020 and species richness in summer 2020, using two-way fixed effect estimation.

Table S5: Effects of (1) productivity of 2020 on species richness in summer of 2021 with yearly lag and LUI of 2020 as additional covariate, (2) with SLA in summer of 2020 instead of LUI of 2020, and (3) including an interaction between LUI in 2020 and productivity in summer 2020, using two-way fixed effect estimation.

Table S6: Column (1) shows the results of the main models estimating causal effects of species richness in spring on productivity in summer with seasonal lag.

Table S7: Column (1) shows the results of the main models estimating causal effects of standing biomass in spring on species richness in summer with seasonal lag.

Table S8: Column (1) shows the results of the main models estimating causal effects of species richness in summer of 2020 on productivity of 2021 with yearly lag. Shown are robustness tests, when (2) controlling for evenness, (3) using effective Shannon Diversity instead of species richness, (4) clustering standard errors on site level, (5) clustering standard errors on plot level, and (6) assuming non-linear (quadratic) richness effects.

Table S9: Column (1) shows the results of the main models estimating causal effects of productivity of 2020 on species richness in summer of 2021 with yearly lag. Shown are robustness tests, when (2) clustering standard errors on plot level, and (3) assuming non-linear (quadratic) biomass effects.

Table S10: Descriptive information about the averages and ranges (in brackets) of species richness in spring and summer, productivity in summer and land-use components (fertilization, mowing and grazing) collected in each region (Swabian Alb, Schorfheide-Chorin, Hainich-Dün) for both 2020 and 2021.

Table S11: Linear mixed effect model showing the effect of Shannon diversity in spring on productivity and standing biomass in spring on Shannon Diversity in summer, including all three regions (Swabian Alb, Schorfheide-Chorin, Hainich-Dün) and both years 2020 and 2021.

Table S12: Linear mixed effect model showing the effect of species richness in spring on productivity when controlling for Evenness, including all three regions (Swabian Alb, Schorfheide-Chorin, Hainich-Dün) and both years 2020 and 2021.

Table S13: Linear mixed effect model showing the effect of species richness in summer on productivity in summer and standing biomass in summer on species richness in summer, including all three regions (Swabian Alb, Schorfheide-Chorin, Hainich-Dün) and both years 2020 and 2021.

Table S14: Effects of species richness in summer on productivity in summer (omitting temporal dynamic effects) and LUI as additional covariate using two-way fixed effect estimation.

Table S15: Effects of productivity in summer on species richness in summer (omitting temporal dynamic effects) and LUI as additional covariate using two-way fixed effect estimation.

Table S16: Information about confounding variables which are controlled for in the linear mixed effect models to test the effects of biodiversity on productivity, or productivity on biodiversity.

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