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REVIEW ARTICLE

Interactions in statistical models: Three things to know

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Abstract

1. In ecological studies, the magnitude and direction of interactions among two continuous explanatory variables x_1 and x_2 are commonly evaluated by fitting a statistical model of the form $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2$, where $x_1 x_2$ is an interaction term that measures departure from additivity of effects.
2. Here, we highlight three issues associated with evaluating interactions in statistical models of this form that appear underappreciated in the ecological literature, but which have important implications for how we fit models and correctly identify interactions.
3. First, the scale (additive or multiplicative) on which the outcome variable y is modelled matters. Transformations that change the scale of analysis alter the interpretation of interaction terms and can hide interactions of ecological importance. Second, spurious interactions can arise when explanatory variables are correlated and there are unmodeled nonlinear relationships, a situation likely to arise when fitting statistical models to non-experimental data. Third, interactions can be nonlinear such that the interaction term $x_1 x_2$ will not capture all interactions of ecological interest.
4. We illustrate how each of these issues can result in potentially misleading outcomes using examples linked to the impacts of multiple stressors on biodiversity. We provide recommendations aimed at correctly identifying interaction effects from statistical models.

KEYWORDS

antagonistic, dominance, ecological interactions, generalized additive model, multiple stressors, statistical interaction, stress, synergistic

1 | INTRODUCTION

Interactions among processes are central to understanding the dynamics of ecological systems and consequently there is a long history of studying interactions in ecology (Billick & Case, 1994; Brook et al., 2008; Darling & Côté, 2008; Didham et al., 2007; Morin et al., 1988; Sih et al., 1998; Wootton, 1994). This is particularly evident in studies grappling with the cumulative impacts of multiple stressors on ecosystems. In the face of increasing levels of habitat loss, invasive species, pollution, overexploitation and climate change, it is increasingly important to understand how stressors interact with each other to better identify and predict the cumulative impacts of multiple stressors on biodiversity (Brook et al., 2008; Côté et al., 2016; Orr et al., 2020). For example, identifying situations where stressors interact synergistically, meaning their combined effects are greater than expected so that impacts are amplified or magnified when they act together (Brook et al., 2008; Darling & Côté, 2008; Folt et al., 1999; Orr et al., 2020), could highlight systems at greater risk of collapse because relatively small increases in the stresses on the system could result in substantially larger impacts on biodiversity. Consequently, studies examining the cumulative impacts of multiple stressors routinely use study designs and analyses aimed at jointly estimating stressor effects and the strength and direction of interactions among stressors (Folt et al., 1999; Kath et al., 2018; Matthaei et al., 2010; Soluk & Collins, 1988).

In ecological studies, the strength and direction of interactions are commonly estimated using statistical models fitted to data. Given two continuous variables, x_1 and x_2, a standard way to model interactions is to include a multiplicative interaction term, x_1x_2, in a statistical model and estimate the associated coefficient and its uncertainty. The magnitude and direction of the coefficient associated with the interaction term is interpreted as measuring the degree to which the two variables interact, or their *interaction effect* (defined more precisely below). If the coefficient is sufficiently small or not statistically significantly different from zero, researchers typically conclude that variables x_1 and x_2 do not interact in an important way.

Our aim in this paper is to highlight three things that ecologists should know about modelling and interpreting statistical interactions that do not appear to be widely appreciated in the ecological literature. These three things are important because understanding their implications will likely influence how we choose to fit and interpret statistical models that include interaction terms. Their understanding also sheds light on what the coefficients associated with interaction terms tell us about the interactions we are interested in. The three things are as follows:

1. Whether a statistical interaction is inferred to be present or not can depend on the scale (additive or multiplicative) on which the outcome variable is modelled. Transformations that change the scale of analysis alter the interpretation of interaction terms and can hide ecological interactions we might be interested in.
2. Spurious interactions can arise when explanatory variables are correlated and there are unmodeled nonlinear relationships, a situation likely to be common when fitting statistical models to non-experimental data.
3. Interactions can be nonlinear such that the interaction term x_1x_2 may not capture an ecological interaction of interest.

We start by defining more precisely what we mean by an interaction effect. We then step through the three things we think ecologists should know, explaining why they are important and considering their implications for how we model and interpret interactions, particularly in the context of multiple stressor impacts on biodiversity.

2 | DEFINING AN INTERACTION EFFECT

An *interaction effect* involving two variables x_1 and x_2 occurs when (a) x_1 influences the value of an outcome variable y, and (b) the effect of x_1 on y depends on the value of x_2. To make this more precise, we can define the 'effect of x_1 on y' as the amount y changes for a unit change in x_1, which is the marginal effect of x_1 on y (Karaca-Mandic et al., 2012). Consider a situation where the outcome y is some measure of biodiversity (e.g. species richness) that is affected by two environmental variables x_1 and x_2 (e.g. mean temperature and annual precipitation) such that:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2. \tag{1}$$

In Equation 1, β_0 is the value of y when both environmental variables have the value 0, and β_1 and β_2 are the amounts by which y changes for every unit change in x_1 and x_2, respectively. In Equation 1, the marginal effect of x_1 on y is thus β_1, measuring the amount y changes for a unit change in x_1.

More specifically, β_1 in Equation 1 is the slope of the relationship between y and x_1. In this case, the relationship is a straight line, and the slope is constant. But more generally, for either straight or curved relationships, the slope of the relationship between y and x_1 is defined as the partial derivative of y with respect to x_1. We specify a partial derivative because y could be a function of multiple variables, as in this case, and we want to isolate the effect of x_1 on y while holding other variables constant. Solving this partial derivative for Equation 1:

$$\frac{\partial y}{\partial x_1} = \beta_1. \tag{2}$$

We can, therefore, define the marginal effect of x_1 on y more generally to be the partial derivative of y with respect to x_1, which will be a function specifying the slope of the relationship between y and x_1 (Gennings et al., 2005; Karaca-Mandic et al., 2012). In Equation 2, the partial derivative is a constant β_1. Because the slope of the relationship between x_1 and y, and hence the marginal effect of x_1 on y, does not depend on the value of x_2, there is no interaction effect (Gennings et al., 2005). The combined effect of x_1 and x_2 on y is just the sum of their individual effects, which is often termed an additive effect (Côté et al., 2016).

The discussion above suggests a more precise definition for an interaction effect: If the slope of the relationship between y and x_1 (given by the partial derivative of y with respect to x_1) is a function of x_2, then the marginal effect of x_1 on y depends on the value of x_2 and there is an interaction (Gennings et al., 2005). To illustrate, consider a standard way to model interactions statistically, which is to include an *interaction term* x_1x_2 such that the equation for y has the form:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2. \tag{3}$$

It is important to distinguish between an *interaction effect* and an *interaction term*. An interaction effect arises when two variables interact according to the definition above. An interaction term is a term included in an equation with the aim of specifying an interaction effect. In Equation 3, the coefficient β_3 measures the combined effect of x_1 and x_2 on y over and above the sum of their additive effects ($\beta_1 x_1 + \beta_2 x_2$). Hence, another way to define an interaction is an outcome that involves departure from additivity of effects (Berenbaum, 1985). For Equation 3, the partial derivative is

$$\frac{\partial y}{\partial x_1} = \beta_1 + \beta_3 x_2. \tag{4}$$

Equation 4, specifying the slope of the relationship between y and x_1, is a function of x_2. Hence, there is an interaction because the marginal effect of x_1 on y depends on the value of x_2. In this case, the coefficient of the *interaction term*, β_3, completely measures the *interaction effect* because this coefficient alone specifies how the slope of the relationship between y and x_1 depends on x_2. However, it is not always the case that the interaction term completely measures the interaction effect, as we will consider below. More generally, we can define the magnitude and direction of an interaction as the effect that a change in x_2 has on the slope of the relationship between y and x_1, which is given by the second partial derivative $\frac{\partial y^2}{\partial x_1 \partial x_2}$. For Equation 4 this is

$$\frac{\partial y^2}{\partial x_1 \partial x_2} = \beta_3. \tag{5}$$

Equation 5 confirms that the magnitude and direction of the interaction effect is completely described by the coefficient of the interaction term in Equation 3. Having defined an interaction effect, we next step through three things to know about statistically modelling interactions.

3 | CHANGING THE SCALE OF ANALYSIS CAN HIDE INTERACTION EFFECTS

In Equation 1, the outcome y is modelled on an *additive scale*: A unit change in x_1 causes y to change to $y + \beta_1$, and the combined effect of x_1 and x_2 on y is $\beta_1 x_1 + \beta_2 x_2$. In statistical analyses, however, it is common for transformations to change the scale on which the outcome variable y is modelled. This includes using log or logit link functions to analyse count or binomial data when fitting generalized linear models (McCullagh & Nelder, 2019), and log-transforming continuous outcome variables when fitting linear models with gaussian errors to better meet assumptions of normality and homogeneity of variances (Zuur et al., 2007). These transformations change the scale on which y is modelled from an additive to a *multiplicative scale*. If y in Equation 1 is log transformed (where log refers to the natural log scale), for example, a unit change in x_1 would cause $\log(y)$ to change to $\log(y) + \beta_1$, which equates to y changing to ye^{β_1}, and the combined effect of x_1 and x_2 is additive on the log scale but multiplicative on y.

Changing the scale on which y is modelled affects the interpretation of interaction terms. Interactions are often defined with reference to an additive baseline (Gennings et al., 2005; Rothman et al., 2008; Schäfer & Piggott, 2018; Sih et al., 1998) and involve departure from the additivity of effects *on the scale the outcome is modelled*. On an additive scale, interaction terms imply that outcomes differ from the *sum* of the individual effects. But when outcome variables are analysed on a multiplicative scale, interaction terms imply departure from additivity on that scale, which equates to outcomes that differ from the *product* of the individual effects (Knol et al., 2011).

When assessing whether variables interact or not, the scale on which the outcome variable is modelled matters because *if interactions are absent on one scale they will usually be present on the other scale* (Karaca-Mandic et al., 2012; Rothman et al., 2008). To illustrate this, consider a situation where the outcome variable is log transformed for statistical analysis, meaning the outcome is modelled on a multiplicative scale. We could test for an interaction on this scale by fitting a statistical model of the form:

$$\log(y) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2. \tag{6}$$

If the coefficient of the interaction term, β_3, was non-significant or sufficiently small, we would conclude that variables x_1 and x_2 do not interact in an important way. This is correct if we are interested in how x_1 affects y on a multiplicative scale but may not reflect how x_1 affects y on the additive scale. To see this, we can rewrite Equation 6 as:

$$y = e^{(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2)}. \tag{7}$$

Equations 6 and 7 are two ways of stating the same relationship, with y on an additive (Equation 7) or multiplicative scale (Equation 6). For Equation 7, the partial derivative of y with respect to x_1 is

$$\frac{\partial y}{\partial x_1} = \left(\beta_1 + \beta_3 x_2\right) e^{(\beta_0 + \beta_1 x_1 + \beta_2 x_2)}. \tag{8}$$

And the second partial derivative, specifying the magnitude and direction of the interaction effect is

$$\frac{\partial y^2}{\partial x_1 \partial x_2} = \left(\beta_1 \left(\beta_2 + \beta_3 x_2\right) + \beta_3 \left(\beta_2 x_1 + x_1 x_2 + 1\right)\right) e^{(\beta_0 + \beta_1 x_1 + \beta_2 x_2)}. \tag{9}$$

Importantly, the *interaction effect* in Equation 9 does not equal the coefficient of the *interaction term* β_3 in Equation 6. Hence, the magnitude, and potentially the direction, of the interaction effect changes when we change the scale on which the outcome variable is modelled. Furthermore, if we set β_3 to zero in Equation 6, so there is no interaction on the multiplicative scale, Equation 9 simplifies to

$$\frac{\partial y^2}{\partial x_1 \partial x_2} = \beta_1 \beta_2 e^{(\beta_0 + \beta_1 x_1 + \beta_2 x_2)}, \tag{10}$$

revealing there is an interaction on the additive scale if neither β_1 nor β_2 are zero. Hence, when an interaction is absent on the multiplicative scale, there will usually be an interaction on the additive scale (Rothman et al., 2008; Figure 1a,c). The converse also holds: when an interaction is absent on the additive scale, there will usually be an interaction on the multiplicative scale (Rothman et al., 2008). To see this, we can transform Equation 1 to a multiplicative scale:

$$\log(y) = \log\left(\beta_0 + \beta_1 x_1 + \beta_2 x_2\right). \tag{11}$$

Equations 1 and 11 describe the same relationship, with Equation 1 modelling the outcome on an additive scale and Equation 11 on a multiplicative scale. The partial derivative of x_1 with respect to y in Equation 11 is

$$\frac{\partial y}{\partial x_1} = \frac{\beta_1}{\beta_0 + \beta_1 x_1 + \beta_2 x_2}. \tag{12}$$

Equation 12 is a function of x_2, meaning there is an interaction on the multiplicative scale despite no interaction on the additive scale if neither β_1 nor β_2 are zero (Figure 1b,d). Karaca-Mandic et al. (2012) show that any non-linear transformation of an equation will produce a similar outcome.

Although our discussion has focused on continuous explanatory variables, the outcomes also apply to variables with discrete levels.

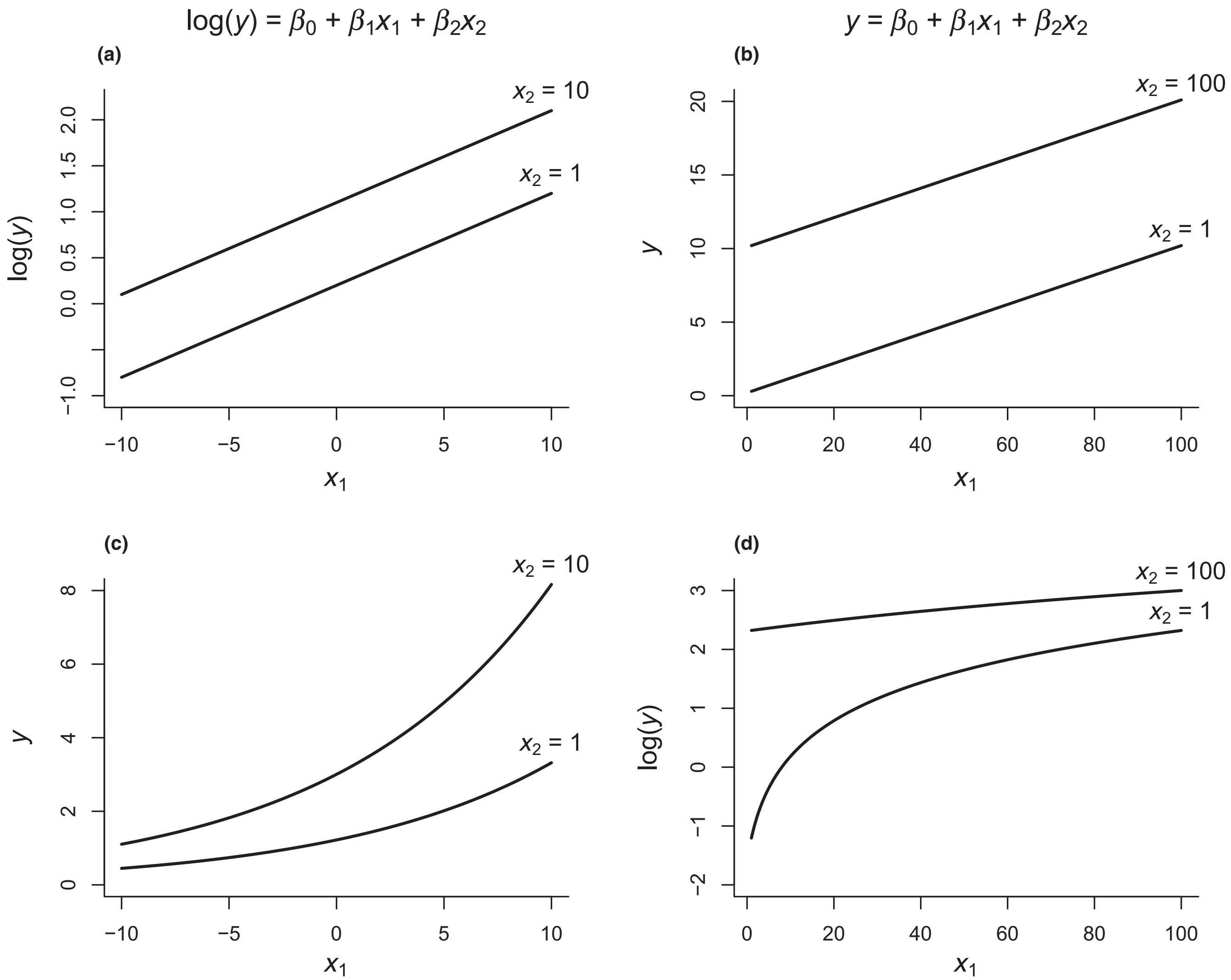

FIGURE 1 Plot of relationships between y and x_1 for different values of x_2 showing that when interactions are absent on one scale (additive or multiplicative) they are present on the other scale. The two data generating models are shown above each pair of plots. For both models: $\beta_0 = \beta_1 = \beta_2 = 0.1$. In panel (a), x_1 and x_2 do not interact when y is analysed on the log (multiplicative) scale (the data generating model), but panel (c) shows there is an interaction when y is analysed on the additive scale. In panel (b), x_1 and x_2 do not interact when y is analysed on the additive scale (the data generating model), but panel (d) shows there is an interaction when y is analysed on the log (multiplicative) scale

To illustrate, consider a situation where the underlying relationship between an outcome variably y and two explanatory variables, x_1 and x_2, is given by Equation 13:

$$y \sim \mathcal{N}\left(e^{(3+0.1x_1+0.1x_2)}, 50\right), \tag{13}$$

where $\mathcal{N}(a, b)$ specifies a normal distribution with mean a and standard deviation b. Now consider a full factorial experiment designed to measure the combined effects of x_1 and x_2 on y by specifying two treatment levels (low and high) for each explanatory variable, with values for low = 10 and high = 20, with 5 replicates for each combination of low and high values. Figure 2 shows one set of simulated data from this scenario, illustrating how changing the scale on which the outcome variable is modelled changes the nature of the interaction. If we log transform y and fit a model to the data using Equation 6 (with x_1 and x_2 taking dummy values 0 for the low and 1 for the high treatment levels) and specifying gaussian errors, the interaction term is close to zero and not statistically significant (Figure 2a, $\beta_3 = -0.02$, standard error = 0.15, p-value = 0.91). This is expected because log transforming the mean expression for y in Equation 13, which was used to generate the data, results in an additive model on the multiplicative scale with no interaction. Equation 10, however, indicates there will be an interaction in the combined effects of x_1 and x_2 on untransformed values of y. The interaction term in this model was highly significant (Figure 2b, $\beta_3 = 424$, standard error = 46, p-value < 0.0001) and including the interaction term in the model increased the explained variance by about 9%, suggesting the interaction is important. Hence in this example, changing the scale on which the outcome variable was modelled by log transforming y hid a strong interaction on the additive scale.

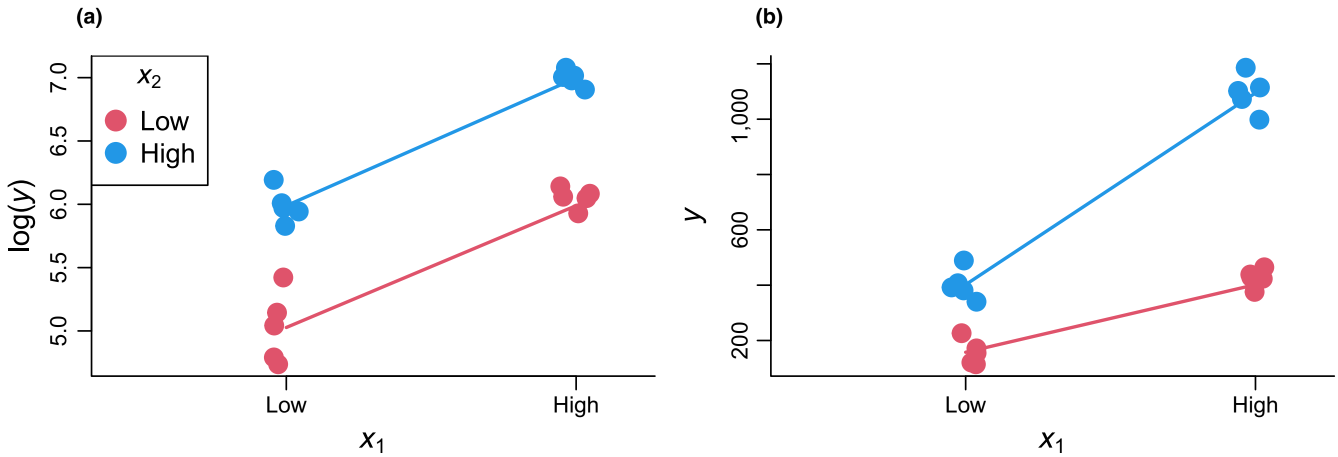

FIGURE 2 Data from a simulated factorial experiment with two levels (low = 10, high = 20) for each of two treatment variables (x_1 and x_2) with five replicates for each treatment combination. The data-generating model is Equation 13. The same data are shown in both panels, with the outcome variable y plotted on a multiplicative (natural log) scale in panel (a), and on an additive scale in panel (b). The lines connect mean values for treatment combinations

4 | UNMODELED NONLINEAR RELATIONSHIPS CAN GENERATE SPURIOUS INTERACTION TERMS

The second thing to be aware of is that spurious interaction terms can arise when fitting statistical models if (a) explanatory variables are correlated with each other and (b) there are unmodelled nonlinear relationships between the outcome and explanatory variables. To illustrate this problem, we simulated data comprising 2,000 values for two correlated explanatory variables, x_1 and x_2:

$$\begin{aligned} x_1 &\sim \mathcal{N}(0, 0.5), \\ x_2 &\sim 0.5x_1 + \mathcal{N}(0, 0.5). \end{aligned} \tag{14}$$

For the set of simulated data we analysed, the linear correlation between x_1 and x_2 was $r = 0.44$. We then generated three outcome variables (y_1, y_2, y_3) using different data generating equations in which each y was causally related to both x_1 and x_2 (Figure S1):

$$y_1 \sim \mathcal{N}(x_1 + 0.5x_2, 1), \tag{15}$$

$$y_2 \sim \mathcal{N}(x_1 + 0.5x_2 + 0.5x_1x_2, 1), \tag{16}$$

$$y_3 \sim \mathcal{N}(x_1 + 0.5x_2 + 0.5x_1x_1, 1). \tag{17}$$

We fitted a regression model to each of the three outcome variables (y_1, y_2, y_3) of the form: $y = \beta_0 + \beta_1x_1 + \beta_2x_2 + \beta_3x_1x_2$ specifying gaussian errors. For Equation 15, which specified linear relationships and no interaction, analysis of the simulated data correctly identified no statistically significant interaction term (Table 1). For Equation 16, which specified linear relationships and an interaction, the analysis correctly identified a statistically significant interaction term (Table 1). For Equation 17, however, which specified a nonlinear (quadratic) relationship between y_1 and x_1 and no interaction, the analysis incorrectly identified a statistically significant interaction term (Table 1). Residual plots (Figure S2) and other model diagnostics revealed nothing untoward about the fit of all three models to the data.

Why did the regression analysis detect an interaction in the data generated by Equation 17 when no interaction was present? The answer lies in the similarity of Equations 16 and 17 when x_1 and x_2 are correlated. In this situation, the quadratic term x_1x_1 in Equation 17 will be correlated with the interaction term x_1x_2 in Equation 16. Consequently, the interaction term in the fitted regression model will absorb some of the variation arising from the nonlinear term in Equation 17, leading to a statistically significant but spurious interaction term (Cortina, 1993; Ganzach, 1997).

The similarity between Equations 16 and 17 is due to the similarity between the quadratic (x_1x_1) and interaction (x_1x_2) terms, and it might seem that other types of nonlinear relationship (such as higher order polynomials, exponential or power functions) could be less problematic because the nonlinear terms will be less closely matched to the interaction term. However, some variation in almost any nonlinear relationship will be captured with a quadratic term, meaning an interaction term will invariably absorb some variation arising from nonlinearity. Hence, when two explanatory variables are correlated, and when there are unmodelled nonlinear relationships in the data, there is the potential to have significant interaction terms despite no real interaction effect (Belzak & Bauer, 2019; Matuschek & Kliegl, 2018).

To further examine this, we used Equation 17 to simulate 1,000 datasets, each with 2,000 observations, that differed in the strength of the correlation between x_1 and x_2. We then analysed each dataset by fitting a regression model as above. The magnitude and statistical significance of the estimated interaction term depended strongly on the strength of the correlation between x_1 and x_2: the stronger the correlation (either positive or negative) the larger the interaction term and the more likely it was deemed statistically significant

TABLE 1 Results from fitting two regression models to data generated by the equations shown in the first column (see Equations 14–17 in the main text). The table shows the estimate, standard error and *p*-value for each coefficient (the βs) for the two fitted models. The smoothed terms in the generalized additive model ($s(x_1)$ and $s(x_2)$) do not have point estimates and standard errors (see Pedersen et al., 2019). All models were fitted using maximum likelihood

		Fitted regression model					
		$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2$			$y = \beta_0 + s(x_1) + s(x_2) + \beta_3 x_1 x_2$		
Data generating model		**Estimate**	***SE***	***p***	**Estimate**	***SE***	***p***
Equations 15–17							
$y_1 = x_1 + 0.5x_2$	β_1	0.963	0.050	<0.001			
	β_2	0.529	0.045	<0.001			
	β_3	0.018	0.073	0.805	0.018	0.073	0.805
$y_2 = x_1 + 0.5x_2 + 0.5x_1x_2$	β_1	0.998	0.050	<0.001			
	β_2	0.500	0.045	<0.001			
	β_3	0.511	0.073	<0.001	0.509	0.073	<0.001
$y_3 = x_1 + 0.5x_2 + 0.5x_1x_1$	β_1	0.976	0.051	<0.001			
	β_2	0.608	0.046	<0.001			
	β_3	0.318	0.075	<0.001	−0.008	0.091	0.927

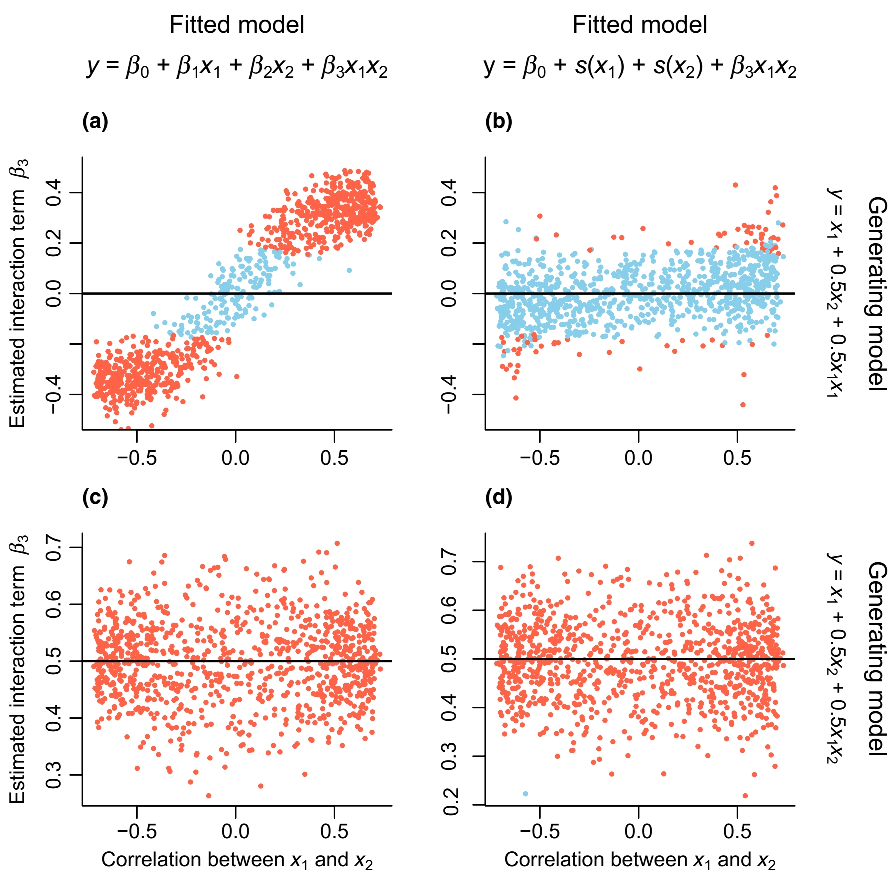

FIGURE 3 Panels (a)–(d) show results obtained from analysing 1,000 simulated datasets, each generated by the model shown at the right of each row and analysed by fitting the model shown above each column. Each dataset comprised 2,000 values of x_1 and x_2 generated using Equations 16 and 17, but with the coefficient for x_1 in Equation 16 taking values at random between −1 and 1, which resulted in the correlation between x_1 and x_2 varying between datasets. Each point plots the coefficient of the interaction term from the fitted model (β_3 in the models above each column) against the correlation between x_1 and x_2 for each dataset. Red points are interaction coefficients that differed significantly ($p \le 0.05$) from zero, blue points are interaction coefficients that were not significantly different from zero ($p > 0.05$). The true interaction effect is shown as a horizontal line in each panel. The fitted model above panels (b) and (d) is a generalized additive model specifying smoothed terms ($s(x_1)$ and $s(x_2)$) for the relationships between outcome and explanatory variables. Both fitted models specified gaussian error distributions

($p < 0.05$, Figure 3a). In these datasets, statistically significant but spurious interactions occurred when x_1 and x_2 were only weakly dependent (above a correlation of about 0.2 or below −0.2). Hence, in relatively large datasets like this (2,000 observations), spurious interactions can arise when explanatory variables are only weakly correlated and there are only slight nonlinearities (Belzak & Bauer, 2019; Matuschek & Kliegl, 2018).

Spurious interactions due to unmodelled nonlinear relationships should not be a problem if the explanatory variables x_1 and x_2 are statistically independent and hence should not be an issue in experimental studies where explanatory variables are manipulated independently. Spurious interactions are much more likely in non-experimental studies where explanatory variables are frequently correlated and nonlinear relationships may be common but not modelled. One solution to minimize the chances of finding spurious interactions is to allow for nonlinear relationships between outcome and explanatory variables (Belzak & Bauer, 2019; Cortina, 1993; Ganzach, 1997; Matuschek & Kliegl, 2018). This could be achieved by fitting models that include quadratic terms for explanatory variables (Cortina, 1993) or by fitting nonparametric models that allow for smooth nonlinear relationships, such as generalized additive models (GAMs; Kath et al., 2018; Matuschek & Kliegl, 2018; Pedersen et al., 2019).

To illustrate how modelling nonlinear relationships can deal with spurious interactions, we fitted a GAM to each dataset depicted in Figure 3a, specifying smoothed terms to allow for nonlinear relationships between the outcome and explanatory variables and including the interaction term x_1x_2 (see Figure 3 caption for details). Relative to the model specifying linear relationships that was fitted to the data in Figure 3a, specifying nonlinear relationships substantially reduced the propensity of models to overestimate the magnitude of the interaction term and uncover statistically significant but spurious interactions (Figure 3b), although the proportion of significant interactions in Figure 3b (0.085) was slightly higher than the number of false positives we expect given a significance threshold of 0.05. Hence, as previous studies have highlighted, fitting models that specify nonlinear relationships between explanatory and outcome variables substantially reduces the chance of detecting spurious interactions (Cortina, 1993; Matuschek & Kliegl, 2018).

Nevertheless, allowing for nonlinear relationships could have the undesired effect of reducing the chance of detecting interactions when they do occur. That is, nonlinear terms could inadvertently absorb some or all the variation associated with a real interaction effect (Ganzach, 1997). To examine this, we generated data with linear relationships between outcome and explanatory variables and an interaction effect, and then assessed whether regression models specifying linear and nonlinear relationships could correctly recover the interaction. For 1,000 simulated datasets, both the linear and nonlinear relationship models did an equally good job of identifying the true interaction effect (Figure 3c,d). Hence, the results in Figure 3 illustrate that fitting models specifying nonlinear relationships between explanatory and outcome variables can reduce the chance of finding spurious interactions when explanatory variables are correlated without overly decreasing the chance of detecting interactions when they are present (see also Belzak & Bauer, 2019; Cortina, 1993; Ganzach, 1997; Matuschek & Kliegl, 2018).

5 | LINEAR INTERACTION TERMS MAY NOT ALWAYS DETECT INTERACTIONS OF INTEREST

It is standard to test for interactions in statistical models by including an interaction term of the form x_1x_2. Nevertheless, there is no reason that interactions will necessarily take this form. For example, if x_1 and x_2 interact such that outcome values y are disproportionately greater at high values of x_2 but intermediate values of x_1, this might suggest a nonlinear interaction of the form $x_1^2x_2$. Specifying a linear interaction term (x_1x_2) is useful because, if an interaction is present, we anticipate that a linear interaction term might capture some of the variation, and hence identify that an interaction is present, even if the interaction is not precisely of that form.

But this need not be the case. To illustrate, we analysed one dataset from a recent meta-analysis quantifying the strength and direction of interactions among stressor variables in freshwater ecosystems (case 167 in Birk et al., 2020). We chose this dataset because it illustrates several of the points we have raised. The data for case 167 came from a study of river basins in the United Kingdom and comprised measurements at 1,704 sample sites in rivers where the outcome variable (y) was the Benthic Diatom Assessment Index (BDAI), an index linked to river health (see Kelly et al., 2008). The BDAI was related to two stressor variables measured at each sample site: standardized mean annual soluble reactive phosphorus concentration (x_1) and fine sediment deposition risk (x_2). We followed the approach in Birk et al. (2020) and tested for an interaction by fitting a model of the form $y = \beta_0 + \beta_1x_1 + \beta_2x_2 + \beta_3x_1x_2$ specifying gaussian errors, where y, x_1 and x_2 were log transformed and then scaled to mean zero and standard deviation one. The log transformation puts the outcome variable y on a multiplicative scale.

The results of fitting this first model to the data (Table 2; Figure 4a) agreed with the results reported in Birk et al. (2020): there were significant negative relationships between both stressors and the outcome variable, and a significant positive interaction term. Birk et al. (2020) classified this interaction as antagonistic because the direction of the interaction (positive) opposed that of the main effects (negative), meaning that at high stressor values, the combined effect of the stressors on the outcome was less than expected from their additive effects (Figure 4a).

For these BDAI data, the two stressors were moderately correlated ($r = 0.47$), suggesting potential for a spurious interaction if unmodelled nonlinear relationships were present. To examine this, we fitted a second model: a GAM of the form: $y = \beta_0 + s(x_1) + s(x_2) + \beta_3x_1x_2$ where $s(x_1)$ and $s(x_2)$ specified smooth terms for the relationships between the two stressors and the outcome variable, and $\beta_3x_1x_2$ was a linear interaction term. This

TABLE 2 Results of fitting three regression models (shown in the first column) to the data for case 167 in Birk et al. (2020). ΔAIC is the difference in AIC between the best-fitting model, which has ΔAIC = 0, and the other models. Larger positive values of ΔAIC indicate poorer fitting models relative to the best-fitting model of the three. Also shown is the proportion of variation explained (R^2), and estimates, standard errors and p-values of the fitted coefficients for each model. The smoothed terms in the generalized additive models ($s(x_1)$, $s(x_2)$ and the smoothed interaction $ti(x_1, x_2)$) do not have point estimates and standard errors (see Pedersen et al., 2019). All models were fitted using maximum likelihood

Fitted regression model	ΔAIC	R^2	Coefficient	Estimate	*SE*	*p*-value
$y = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2$	139.5	0.43	β_1	−0.461	0.021	<0.001
			β_2	−0.306	0.021	<0.001
			β_3	0.134	0.021	<0.001
$y = s(x_1) + s(x_2) + \beta_3 x_1 x_2$	13.1	0.47	$s(x_1)$			<0.001
			$s(x_2)$			<0.001
			β_3	0.002	0.026	0.944
$y = s(x_1) + s(x_2) + ti(x_1, x_2)$	0	0.48	$s(x_1)$			<0.001
			$s(x_2)$			<0.001
			$ti(x_1, x_2)$			0.012

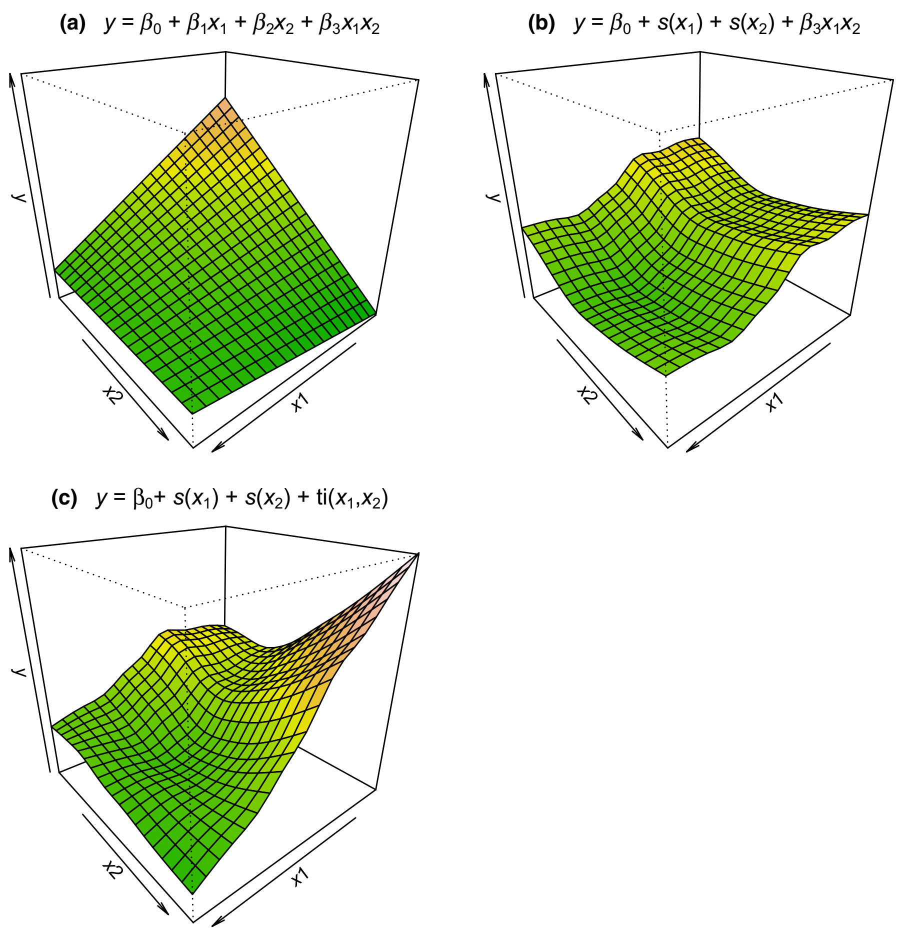

FIGURE 4 Surfaces derived from three regression models (panels a–c) fitted to the data from case 167 in Birk et al. (2020). The response variable y was the Benthic Diatom Assessment Index, variable x_1 was standardized mean annual soluble reactive phosphorus concentration (a measure of nutrient stress), and variable x_2 was fine sediment deposition risk. All variables were log transformed and scaled to mean zero and standard deviation one prior to analysis. The equations for the fitted regression models are shown above each panel. See Table 2 for differences in AIC values and estimated coefficients of the fitted models

allowed us to compare a model that allowed for non-linear relationships with the first model that specified only linear effects, with both models allowing for a linear interaction term. The second model fitted the BDAI data substantially better than the first model as measured by Akaike's information criterion (AIC; Table 2, the AIC value for the second model was 126.4 less than the AIC value for the first model, with lower AIC indicating a better-fitting model). This result indicates that associations between the stressor and outcome variables were much better described by nonlinear than linear relationships in these data (Figure 4b). Moreover, having accounted for the nonlinear relationships, the interaction term in the second model was no longer statistically significant (Table 2), suggesting the significant interaction term identified in the first model was spurious.

Finally, we fitted a third model of the form: $y = \beta_0 + s(x_1) + s(x_2) + ti(x_1, x_2)$ to the BDAI data, where the term $ti(x_1, x_2)$ allowed for a smooth nonlinear interaction in the GAM. This third model fitted the data better than the second model (difference in AIC of 13.1) and included a statistically significant interaction term (Table 2). Rather than an interaction whereby the combined effect of the stressors was less than expected from their additive effects (Figure 4a), the third model indicated that increasing fine sediment deposition (x_2) had a positive effect on the BDAI at low nutrient stress (x_1) but a negative effect at high nutrient stress (Figure 4c). Hence, although the first and third models both identified significant stressor interactions, the nature of the interaction differed substantially between these models (compare Figure 4a,c), with the third model providing a much better description of the data.

6 | DISCUSSION

The three issues we have identified associated with fitting and interpreting interactions in statistical models are not new but appear under-appreciated in the ecological literature. As previous studies have identified, and our examples show, all three issues have important implications for correctly identifying interactions (Cortina, 1993; Griffen et al., 2016; Karaca-Mandic et al., 2012; Knol & VanderWeele, 2012; Rothman et al., 2008).

Previous ecological studies have highlighted that changing the scale on which the outcome variable is modelled from additive to multiplicative or vice versa can affect whether interactions are detected in statistical models or not (Dey & Koops, 2021; Folt et al., 1999; Griffen et al., 2016; Schäfer & Piggott, 2018; Sih et al., 1998). Here, we explain why this occurs and identify that, when interactions are absent on one scale, they will usually be present on the other scale (Karaca-Mandic et al., 2012; Rothman et al., 2008). Nevertheless, while changing scale can generate or hide interactions, the importance of this will depend on the magnitude of the interaction effect and the variability in the data. Changing scale may be of little consequence if interaction effects are of small magnitude, or the effects are uncertain due to highly variable data.

As others have identified (Griffen et al., 2016), we suspect that most ecologists make decisions about transforming outcome variables on statistical grounds (e.g. to better meet the assumptions of an analysis) without considering how these decisions affect the interpretation of interaction effects. This could lead to problems assessing the frequency of interactions in meta-analyses (e.g. Crain et al., 2008; Jackson et al., 2016) because studies in which analyses are conducted on different scales will not be directly comparable. For example, in a synthesis of 171 studies of multiple stressor effects in marine systems (Crain et al., 2008), about one-third of studies used log transformed outcome variables without explicitly acknowledging that interactions estimated on a multiplicative scale are not directly comparable to interactions estimated on an additive scale (Griffen et al., 2016).

Moreover, it may not be obvious which, if any, scale is most appropriate for analysis (Tekin et al., 2020). Consider an outcome such as species richness. On the one hand, we might be interested in *how many* species we expect to gain or lose per unit change in a stressor variable (i.e. the effect on an additive scale). On the other hand, we might be interested in the *proportion* of species gained or lost per unit change in a stressor variable (i.e. the effect on a multiplicative scale). Either may be a valid outcome depending on the research question. The issue that the magnitude and direction of interactions can change, and that interactions can be present on one scale but absent on the other, has been widely discussed in the epidemiology literature (Rothman et al., 2008; Weinberg, 2012) with no clear resolution, leading some researchers to advocate presenting and interpreting results on both scales if there is no reason to favour one scale over another (Knol & VanderWeele, 2012). At the very least, researchers should be clear about the scale they use to define interactions and should ideally choose a scale best suited to their research questions (Sih et al., 1998).

In addition, with regard to multiple stressors, several authors have advocated shifting focus away from fitting statistical models with interaction terms to developing mechanistic models of stressor effects and their interactions, and testing predictions that arise from those mechanistic models (Dey & Koops, 2021; Griffen et al., 2016; Laender, 2018; Schäfer & Piggott, 2018; Thompson et al., 2018; see also Wootton, 1994). We agree that modelling underlying mechanisms has the potential to provide biological insights. Nevertheless, the inclusion of nonlinear relationships and nonlinear interaction terms in statistical models, where data permit (see above and also Kath et al., 2018), would allow for a wider range of outcomes than captured by the linear relationships and linear interaction terms usually included in statistical models that test for stressor interactions (e.g. Birk et al., 2020). Hence, although they may not have a mechanistic basis, nonlinear terms in statistical models could better describe relationships in data (e.g. Figure 4c), with better descriptions of relationships pointing to potential underlying mechanisms.

The problem that spurious interactions can arise in statistical models when explanatory variables are correlated and there are unmodelled nonlinearities does not appear to have been identified in the ecological literature, although the issue has been identified elsewhere (Belzak & Bauer, 2019; Cortina, 1993; Ganzach, 1997; Matuschek & Kliegl, 2018). Although this issue should not be a problem in experimental studies if explanatory variables are manipulated independently, it could be common in non-experimental studies. Indeed, surveys examining the impact of multiple stressors on biodiversity at large spatial scales are likely to have both correlated explanatory variables, because stressor impacts often covary across the landscape (Allan, 2004), and nonlinear relationships between stressor and outcome variables due, for example, to thresholds in the value outcome variables can take (Hewitt et al., 2016). Our reanalysis of the benthic diatom survey from Birk et al. (2020) revealed that the antagonistic interaction reported in that study was spurious. It remains to be seen how often such spurious interactions arise in non-experimental studies and whether, as in the Birk et al. (2020) case study, other nonlinear interactions are present but undetected.

Fitting statistical models is the main method ecologists use to uncover ecological interactions in data. Identifying these interactions is becoming increasingly important as ecologists seek to understand and mitigate the cumulative impacts of an increasing number of stressors on ecosystems globally (Brook et al., 2008; Mantyka-Pringle et al., 2012). Given the issues we have raised, we make the following recommendations regarding the use of statistical models to test for interactions:

1. Explicitly state the measurement scale (additive or multiplicative) on which outcome variables are analysed. Ideally, the choice of scale should be tailored to the research question being addressed, although transformation for statistical reasons will also be a consideration. Where an appropriate scale is not obvious, an option is to report interactions on both additive and multiplicative scales.
2. Meta-analyses combining results from multiple studies should recognize that scale is important and that interactions identified on one scale may be absent, or of a different magnitude and/or direction, on the other. Meta-analyses focused on interactions should compare studies with outcome variables modelled on the same scale and/or report statistics on the prevalence of interactions on both multiplicative and additive scales.
3. To minimize the potential for spurious interactions, studies could either a) conduct experiments where interacting variables are manipulated independently or b) where it is not feasible, or desirable, to conduct experiments, check and account for correlations between explanatory variables and nonlinear relationships between explanatory and outcome variables using appropriate statistical models.
4. Consider, and test for the possibility of, nonlinear interactions.

This paper has focused on interactions between two explanatory variables, but the same issues will arise when dealing with higher-order interactions among three or more explanatory variables. Moreover, as the example in Figure 2 illustrates, the issues we raise need not be confined to analyses involving continuous explanatory variables but can arise in settings with discrete values or treatment levels (see also Kreyling et al., 2018). Hence, the issues we raise, and the solutions we have identified, are likely to apply to most studies that estimate interaction effects using statistical models.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

Both authors conceived the idea; R.P.D. did the analyses and wrote the first draft and both authors revised the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

R code to reproduce the simulations and analyses in this paper are publicly available in a Zenodo repository (Duncan & Kefford, 2021). The data for the case study from Birk et al. (2020) are available at https://github.com/sebastian-birk/MultiStressorImpacts.

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