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Asymmetric Biotic Interactions Cannot Be Inferred Without Accounting for Priority Effects

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ABSTRACT

Understanding biotic interactions is a crucial goal in community ecology and species distribution modelling, and large strides have been made towards improving multivariate computational methods with the aim of quantifying biotic interactions and improving predictions of species occurrence. Yet, while considerable attention has been given to computational approaches and the interpretation of these quantitative tools, the importance of sampling design to reveal these biotic interactions has received little consideration. This study explores the influential role of priority effects, that is, the order of habitat colonisation, in shaping our ability to detect biotic interactions. Using a simple set of simulations, we demonstrate that commonly used cross-sectional co-occurrence data alone cannot be used to make reliable inferences on asymmetric biotic interactions, even if they perform well in predicting the occurrence of species. We then show how sampling designs that consider priority effects can recover the asymmetric effects that are lost when priority effects are ignored. Based on these findings, we urge for caution when drawing inferences on biotic interactions from cross-sectional binary co-occurrence data, and provide guidance on sampling designs that may provide the necessary data to tackle this longstanding challenge.

1 | Introduction

No organism is independent of others, and therefore understanding biotic interactions is a crucial goal in ecological studies of free-living and symbiotic species (Hellard et al. 2015; Morales-Castilla et al. 2015). Ecologists have long recognised that habitat colonisation order, known as priority effects, can profoundly shape the structures of communities (Connell and Slatyer 1977). Yet, despite considerable recent computational advances, priority effects have rarely been considered in interpreting species co-occurrence patterns. One reason for this is that ecologists often attempt to draw inferences about biotic interactions using binary cross-sectional data (Peres-Neto, Olden, and Jackson 2001; Kissling et al. 2012), which

capture the established structure of a community at the timepoints in which these data were collected. Common statistical approaches to infer biotic interactions are, therefore, based on correlative approaches that draw inferences based on these cross-sectional co-occurrence frequencies. However, these data, and models used to analyse them, inherently lack information on colonisation order. This is problematic because the order of colonisation, or priority effect, affects both the environmental niches and biotic interactions between species, and therefore, failing to account for these effects can lead to largely erroneous interpretations.

Priority effects are a very common and broadly recognised phenomenon that have been demonstrated in many different

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ecological contexts (Fukami 2015; Debray et al. 2022; Stroud et al. 2024). One way that these priority effects can affect community structure is through modified environmental niches. This can occur in at least two different ways. First, niche pre-emption occurs when the arrival the first species results in the reduction of resources available to other species that require these same resources for reproduction and survival (Fukami 2015), as shown in Figure 1a. Due to resource depletion, the priority effect in this situation is always inhibitory (Fukami 2015). An example of this type of interaction between free-living species has been demonstrated between tadpoles of the southern leopard frog and the southern toad, whereby the development rate and survival of the toad are reduced by overwintering of the frog, due to algal depletion in ponds (Hernandez and Chalcraft 2012). Similar priority effects can occur in within-host parasitic species, such as with different strains of *Borrelia burgdorferi* infecting the same host tissue (Devevey et al. 2015), or helminth and malaria parasites competing for resources within red blood cells of the host (Graham 2008).

The second way in which priority effects can affect environmental niches is through niche modification, whereby the early-arriving species alters the underlying environment as an ‘ecosystem engineer’ and determines the environmental conditions encountered by the late-arriving species (Fukami 2015), as illustrated in Figure 1b. Unlike niche pre-emption, niche modification can have either inhibitory or facilitative effects. An example of inhibitory

effects through niche modifications has been demonstrated by the increased disturbance caused by burrowing and foraging activities of mole rats which have been shown to decrease the species richness of plant species (Hagenah and Bennett 2013). Conversely, a microbiome study demonstrated that a greater number of within-host ecosystem engineers can reduce competitive exclusion and promote colonisation and community diversity of pathogens (Yeakel et al. 2020). Within-host immune modulation caused by early arrival of parasites that have also been demonstrated to promote co-infection is another example of facilitative niche modifications (Halliday et al. 2020), although the opposite effect has also been described among co-infecting symbionts (Halliday et al. 2017). When considering more complex community assembly with larger numbers of interactions between species, niche modification can concurrently exhibit both inhibitory and facilitative effects. For instance, the early arrival of some fire-resistant plant species with combustion properties can boost the severity of fire, promoting the incursion of subsequent fire-resistant species and simultaneously decreasing the suitability of the environment for fire-sensitive species (Odion, Moritz, and DellaSala 2010; Fukami 2015). These studies collectively underscore the importance of priority effects in shaping species communities through environmental modifications that determine the identity of subsequent colonising species.

In addition to influencing community assembly through environmental pre-emption or modification, priority effects can also

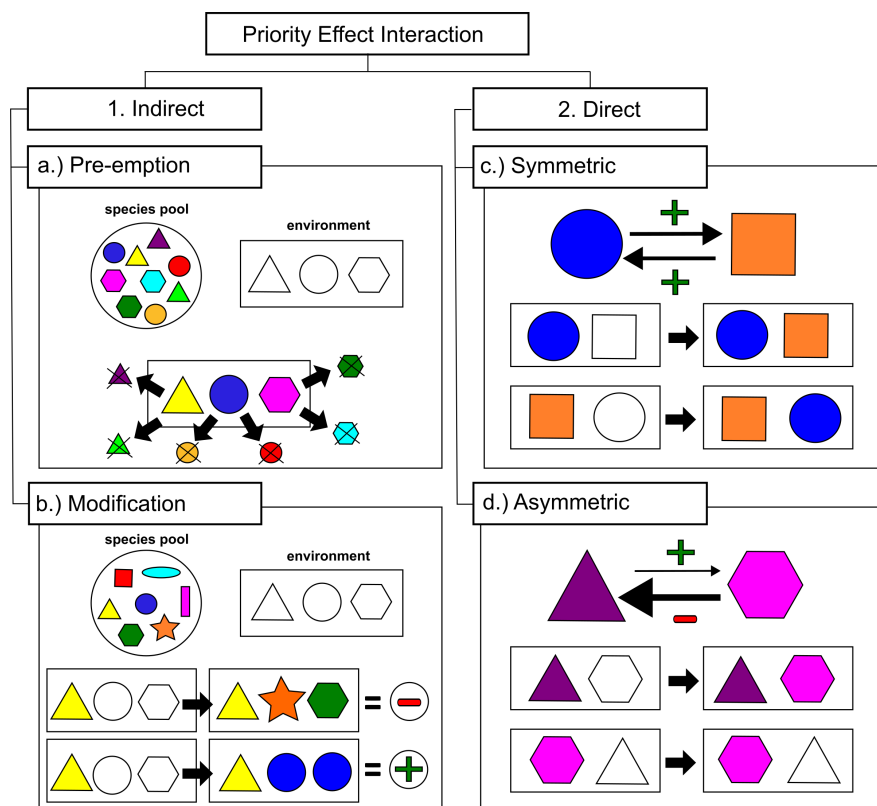


FIGURE 1 | Diagram illustrating the (1) indirect and (2) direct ways that priority effects can shape species co-occurrence patterns. Indirect effects include (a) pre-emption, whereby the first colonising species inhibits subsequent colonisation through resource depletion; and (b) modification, whereby the early coloniser modifies the characteristics of an environment to either facilitate or inhibit subsequent colonisation of another species. Direct priority effects refer to the effect of colonisation order that favours the direction of a biotic interaction. These interactions may be (c) symmetric, in which case the biotic interaction of one species on another is equal in both directions and therefore prior colonisation will not affect community assembly; or (d) asymmetric, where the effect of one species on another is unequal in each direction, and therefore, prior colonisation of a species will affect community assembly. This diagram is an extension of the figures illustrating niche pre-emption and niche modification by Fukami (2015).

affect the structure of a community through direct biotic interactions, as illustrated in Figure 1c,d. Considering the two-sidedness of the direction and magnitude of interactions is crucial because interactions in nature are often asymmetrical (Bascompte, Jordano, and Olesen 2006). This asymmetry can be manifested in different ways, such as with varying strengths in the same direction, as demonstrated by studies on asymmetric competition with parasitic fungi (Natsopoulou et al. 2015) and tickborne pathogens (Rynkiewicz et al. 2017), where one parasite demonstrates stronger inhibitory effects than the other. Similarly, not all interactions are necessarily reciprocal. For instance, a 3-year field experiment revealed interspecific competitive effect of leaf-eating ungulates on the leaf beetle *Timarcha lugens*, while no reciprocal effect was detected, revealing asymmetrical interactions more closely reflecting amensalism rather than competition (Gómez and González-Megías 2002). Furthermore, interactions can also occur in opposing directions. For example, another experimental study investigating the impacts of priority effects on co-infection outcomes revealed that prior infection with the protozoan *Chilomastix mesnili* enhanced the fitness of both itself and yeasts of the genus *Metschnikowia*, while reversing the order of colonisation led to a decline in the fitness of both species (Lohr, Yin, and Wolinska 2010). Considering the different ways that asymmetric interactions naturally occur, failing to account for priority effects when drawing inferences from binary cross-sectional data means that we assume that colonisation order had no effect on the observed community or interactions, biasing interpretations of interactions towards symmetric interactions (Blanchet, Cazelles, and Gravel 2020).

Given the interest in inferring biotic interactions, particularly with the widespread acknowledgement of their impact in driving species co-occurrence and community assembly, a growing body of literature has emerged to caution against inferences of these types of interactions with binary co-occurrence data (Sander, Wootton, and Allesina 2017; Dormann et al. 2018; Blanchet, Cazelles, and Gravel 2020). Yet, while considerable attention has been given to methodological approaches and the interpretation of these methods, the importance of sampling design to reveal these biotic interactions has so far received little consideration. In this paper, we explore the influential role of priority effects in shaping our ability to detect direct biotic interactions. Using a simple set of simulations combined with a parsimonious statistical model, we demonstrate that commonly used cross-sectional binary data without information on colonisation history simply cannot be used to make reliable inferences when the direction and/or strength of the effect of one species on another is likely to differ. This is the case even if the chosen model performs well in predicting the occurrence of species. We then show how sampling designs that account for colonisation order can recover the asymmetric effects that are lost when priority effects are ignored. We urge for caution when drawing inferences from cross-sectional binary co-occurrence data, and we conclude with guidance on the types of sampling designs that may provide ecologists with the necessary data to tackle this longstanding challenge.

2 | Case Study: Simulated Scenarios

To demonstrate the impact of including or excluding priority effects on the ability to retrieve biotic interactions under varying

degrees of asymmetry, we simulated six different interaction types: positive and negative symmetric biotic interactions (Pos-Sym, Neg-Sym), positive and negative asymmetric interactions (Pos-Asym, Pos-Neg) of same directions, as well as small and large opposing asymmetric interactions (Sml-Opp-Asym, Lge-Opp-Asym). While the specific simulated effect values are arbitrary, these six different interaction-type scenarios are intended to be generalisable to similar ecological contexts with similar patterns of strength and direction. For each interaction type, we generated 1000 two-by-two interaction matrices between two species (i and j) by drawing random numbers from a uniform distribution within a specified range. These matrices represented pairwise biotic interactions between the two species in 1000 different communities. Using these interaction matrices, we generated co-occurrence data, from which we could attempt to retrieve these ‘true’ interaction values in statistical models with and without the inclusion of priority effects. The steps used to generate these co-occurrence datasets are illustrated in Figure 2, and the process is described in more detail below. For simplicity, we kept these interaction effects constant over time, while we anticipate that in real-world situations the strength of biotic interactions might change over time if, for example, an increase in density of a colonising species over time alters the strength of interactions.

To generate co-occurrence data that resembles the kind of cross-sectional data commonly used for analysing biotic interactions, we simulated two arbitrary covariates with varying effects on the probability of species occurrence to capture the possible effects that other (abiotic/environmental) factors besides the biotic interactions may have on co-occurrence. Covariate values (‘EnvCov’) were drawn from standard Normal distributions (Figure 2a). The effect of each covariate (on the logit scale) was simulated by drawing random effect sizes separately for each species–covariate relationship: a mean of 0.3 and standard deviation of 0.1 to simulate a positive effect for the first covariate (β_1), and a mean of -0.3 and standard deviation of 0.1 to simulate a negative effect for the second covariate (β_2). Mean occurrence probabilities (α), again on the logit scale, were drawn from a normal distribution with a mean of -0.5 and a standard deviation of 0.5 for each species. We then simulated two successive events of ‘colonisation’ for 1000 independent ‘sites’. In the first, the probability of colonisation (‘Pr(colonisation)’) at each site was calculated for each species (i and j):

$$\begin{aligned} \text{Pr}(\text{colonisation})_i &= \text{inv} \cdot \text{logit}(\alpha_i + \beta_{1,i} \times \text{EnvCov1} + \beta_{2,i} \times \text{EnvCov2}) \\ \text{Pr}(\text{colonisation})_j &= \text{inv} \cdot \text{logit}(\alpha_j + \beta_{1,j} \times \text{EnvCov1} + \beta_{2,j} \times \text{EnvCov2}) \end{aligned} \quad (1)$$

as shown in Figure 2b. At each site, the probability of no colonisation was also calculated based on the probabilities of colonisation by the two species, species i and j :

$$\text{Pr}(\text{no colonisation}) = (1 - \text{Pr}(\text{colonisation})_i) \times (1 - \text{Pr}(\text{colonisation})_j) \quad (2)$$

as shown in Figure 2c. We assumed that only one species (or neither species) could initially colonise the empty site. Specifically, a multinomial draw based on these probabilities was used to initialise the colonisation state matrix, resulting in a vector of occupancy states for each site where the possible states were: ‘Species i present’, ‘Species j present’ or ‘Unoccupied’.

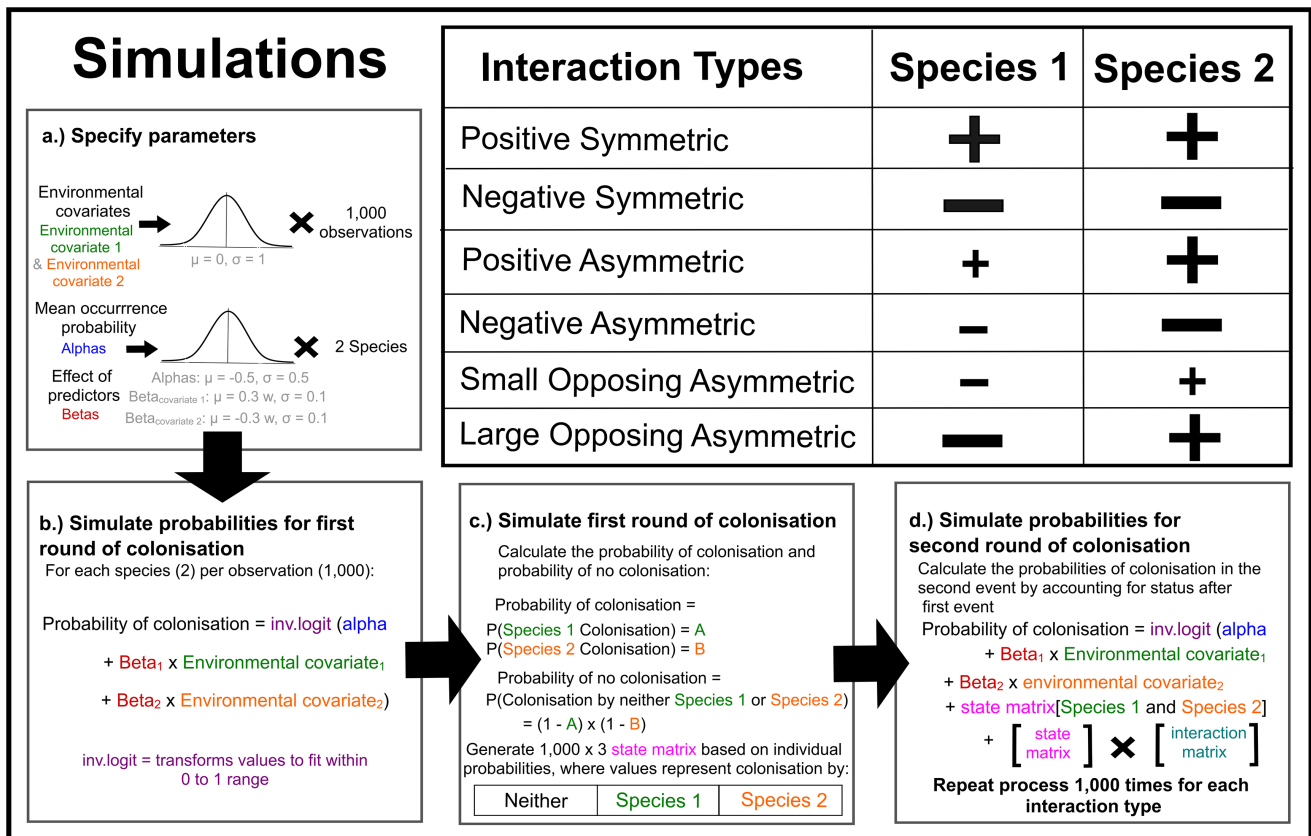


FIGURE 2 | Diagram illustrating the data simulation process for six interaction types: positive and negative symmetric, positive and negative asymmetric, small opposing and large opposing asymmetric. (a) Specifying parameters for a simulated dataset with 1000 records for the presence of two species: two environmental covariates were simulated by drawing 1000 random numbers from a normal distribution with a mean of 0 and standard deviation of 1. The alpha values for each species, representing the average prevalence of each species on the logit scale, were drawn from a normal distribution with a mean of -0.5 and standard deviation of 0.5 . The beta coefficients for each of the environmental predictors were drawn from two separate normal distributions with standard deviations of 0.1 , the first with a mean of 0.3 and the second with a mean of -0.3 . (b) The subsequent step in simulating the data was to simulate the probabilities of species colonisation in an empty environment. This was done for each species for the entire dataset of 1000 observations, where the probability of colonisation is equal to the inverse logit of the species' average prevalence (alpha value) and the environmental predictors multiplied by their respective coefficients. (c) Once probabilities for the first colonisation event were obtained, we simulated a 'first colonisation event', whereby either species could colonise during this time based on their respective probabilities, or the possibility of no colonisation. This was done 1000 times so that each observation recorded colonisation by either species, species i or species j , which were subsequently recorded in a state matrix. (d) Once the first event was recorded, the probabilities of colonisation were adjusted based on the colonisation state in event one, and the interaction coefficient corresponding with the order of colonisation. Using these updated probabilities, we simulated the second colonisation event accounting for the colonisation status in event 2. The resulting dataset, therefore, contained 1000 observations of the presence-absence of species i and j generated in two colonisation events, the colonisation status after event 1, and the environmental covariate values. This process was repeated 1000 times to generate 1000 datasets for each of the six interaction types.

We then simulated a second event of colonisation, here termed site filling ('Pr(filling)'), that allowed the occurrence probabilities for each species to be adjusted, conditional on the colonisation state resulting from the first event:

$$\begin{aligned} \text{Pr}(\text{filling})_j &= \text{inv} \cdot \text{logit}(\alpha_j + \beta_{1,j} \times \text{EnvCov1} + \beta_{2,j} \times \text{EnvCov2} + \gamma_{ij} \times I_i) \\ \text{Pr}(\text{filling})_i &= \text{inv} \cdot \text{logit}(\alpha_i + \beta_{1,i} \times \text{EnvCov1} + \beta_{2,i} \times \text{EnvCov2} + \gamma_{ji} \times I_j) \end{aligned} \quad (3)$$

where I_i and I_j are indicator functions of whether or not species i or species j were present at each site after the first colonisation event, respectively, and γ_{ij} and γ_{ji} are the priority effects of species i on species j and of species j on species i , respectively, during the site-filling event, as illustrated in Figure 2d. For example, if species i colonised a site after the first event of

colonisation, its occurrence probability was fixed at 1 (it occupied the site, regardless of what happened in the second event, therefore $\text{Pr}(\text{filling})_i = 1$) and its interaction effect would have an influence on the ability of species j to colonise in the second event. If no species colonised a site during the first event, the colonisation probabilities for each species in the second event were determined only by their respective mean occurrence probabilities and environmental covariate effects. We randomly drew binary occurrence/co-occurrence data from these final occurrence probabilities.

The resulting dataset included information typically found in cross-sectional co-occurrence data, that is, presence-absence values for each species and the environmental covariates. However, it also contained a state variable indicating whether

species i , species j or neither species colonised a site after the first colonisation event. We show below how this extra information, which requires longitudinal rather than cross-sectional sampling (in our simulations, two subsequent colonisation events), can be used to gain more accurate insights into asymmetric interaction effects from binary data.

To quantify ‘interaction effects’ (γ_{ij} and γ_{ji}) from co-occurrence data with and without accounting for colonisation history, we used univariate generalised linear models (GLMs). Specifically, we constructed two individual GLMs for each species (i and j) that aimed to estimate both the environmental responses and biotic interaction effects. The first model represented what researchers might typically do with cross-sectional data to estimate the occurrence of one species, using the binary vector of the co-occurrence of the second species as a covariate (Biotic _{j} or Biotic _{i}). The second model took advantage of the additional information from the recorded colonisation history, instead using the presence of the second species *after the first colonisation event* as Biotic _{j} or Biotic _{i} . In other words, this second model could estimate a different probability of occurrence for one species depending on whether or not the other species had *priority* at the site (i.e., had previously occupied the site). In comparison, the first model could only estimate a different probability of occurrence for a given species depending on whether a site was jointly *occupied* by the other species, which we show below makes it impossible to estimate asymmetric interaction effects. Both models also included effects of the two environmental variables (EnvCov^T):

$$\begin{aligned} \text{Presence}_i &\sim \text{Bernoulli}(p_i) \\ \text{logit}(p_i) &= \alpha_i + \beta_i \times \text{EnvCov}^T + \gamma_{ij} \times \text{Biotic}_j \\ \text{Presence}_j &\sim \text{Bernoulli}(p_j) \\ \text{logit}(p_j) &= \alpha_j + \beta_j \times \text{EnvCov}^T + \gamma_{ji} \times \text{Biotic}_i \end{aligned} \quad (4)$$

From these models, we extracted the coefficient estimates for the interaction terms (γ_{ij} and γ_{ji}) that accounted for either colonisation history/priority effects (γ_{priority}) or co-occurrence (γ_{occ}) to compare the ability of the models in recovering the true interaction effects between species in each scenario.

3 | Inference on Asymmetric Interactions in Statistical Models

Models that included priority effects provided accurate estimates of interaction effects (γ_{priority}) across all interaction types (Figure 3). In contrast, estimates from co-occurrence models (γ_{occ}) were largely variable, with more accurate estimates obtained when interactions were symmetric. These findings are consistent with existing evidence that occurrence data can be potentially useful for inferring species interactions from nontrophic interactions (Freilich et al. 2018). However, for the two scenarios with opposing interactions, the interaction estimates for γ_{occ} tended towards zero with large uncertainty. This indicates that the models that exclude priority effects may lead researchers to conclude that there is no statistical support for interaction effects, even when the true effects could be strong in opposing directions. These findings are consistent with previous

suggestions that occurrence data do not allow for inferences on species interactions, unless strong signals of mostly nontrophic positive interactions are discernible from noise and environmental forcing (Freilich et al. 2018).

A finding that may be surprising to many users of co-occurrence models, which we feel underpins the need for this paper, is that the co-occurrence estimates were never able to detect asymmetry in interaction effects. Figure 4, which shows the absolute difference between the true interaction effects among the species pairs and those estimated by the models (i.e., the absolute difference between the true effect of species i on species j and species j on species i , and the corresponding absolute difference between the estimated effects), highlights that the inclusion of priority effects accurately captured asymmetric interactions, particularly in cases with opposing interactions (Figure 4a). In contrast, co-occurrence models that did not consider colonisation history always inferred that any possible interactions were symmetric. This means that, regardless of how asymmetric interactions are, interpretations of detected associations from cross-sectional binary data will never capture such asymmetric effects. Instead, these models were prone to suggesting spurious symmetric interactions (Figure 4b), highlighting that there is simply not enough information content in cross-sectional binary data to detect these effects. Combined with the findings relating to the true interaction estimates, highly asymmetric opposing interactions will never ever be detected if priority effects are not included within the model.

4 | Predicting the Probability of Species Occurrences

A secondary aim of our study was to understand whether inclusion of colonisation history impacted predictive accuracy of models. We compared the predicted species occurrence probabilities to the true (simulated) occurrence probabilities, and quantified the accuracy of these predictions as Brier scores:

$$\text{Brier Score} = \frac{1}{N} \sum_{s=1}^N (\text{predicted} - \text{observed})^2 \quad (5)$$

where the Brier score value can range from 0 to 1, with 0 representing perfect accuracy and 1 representing perfect inaccuracy. Figure 5 compares the mean Brier scores of models that excluded priority effects versus models that included priority effects. Models that included priority effects consistently showed better performance. This improvement in predictive performance, particularly for asymmetric interactions, may be dependent on the relative importance of these interactions as predictors of species occurrence, as suggested in parasitic interactions (Natsopoulos et al. 2015). But despite this, both models tended to show good predictive performance, as indicated by relatively low mean Brier scores (i.e., under 0.12). In other words, variation in species occurrence/co-occurrence appears to be almost equally well captured in variables that account for the true interactions (including priority effects) or the joint occurrence and any additional covariates. This is particularly relevant when considering the usefulness of co-occurrence models for predictive performance, given that cross-sectional co-occurrence data

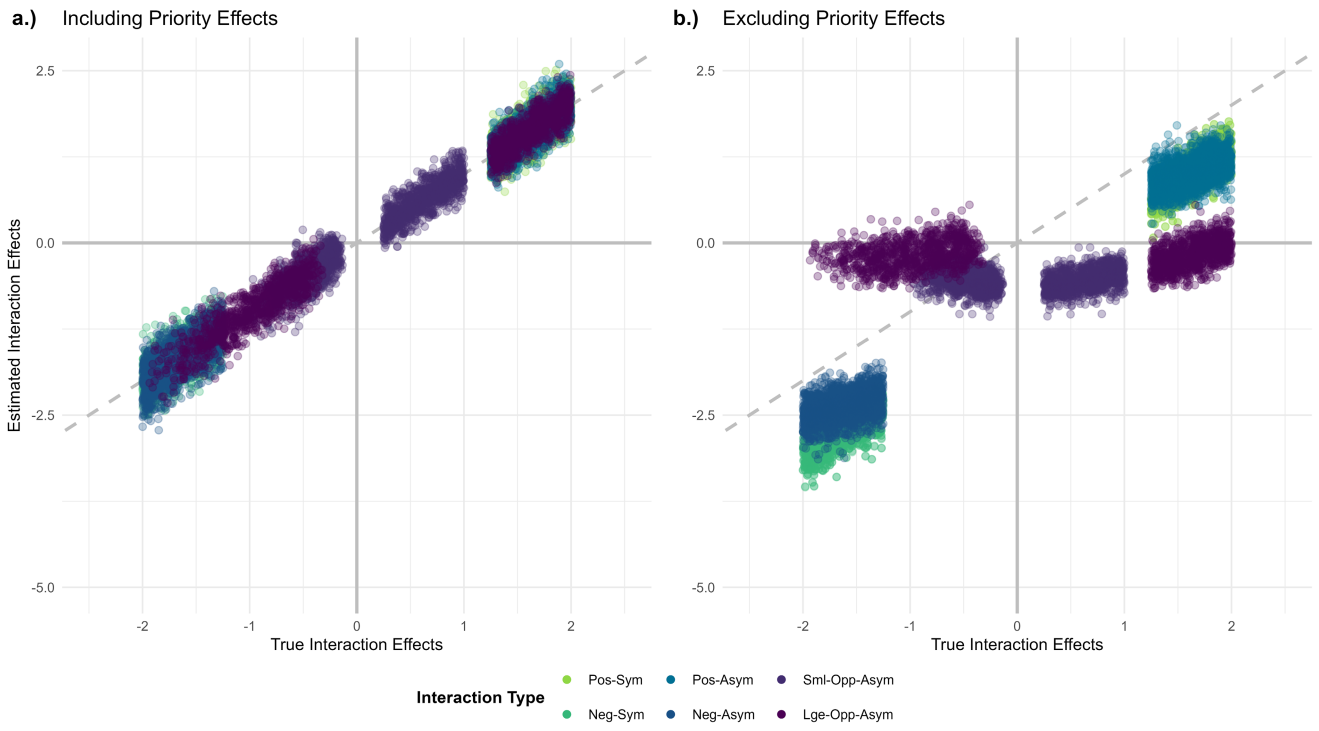


FIGURE 3 | Scatterplot showing the true interaction effects on the *x*-axis and the estimated interaction effects on the *y*-axis based on generalised linear model β coefficient estimates that (a) included priority effects and (b) excluded priority effects. Six interaction types are represented in the plot: positive and negative symmetrical interactions (green), positive and negative asymmetrical interactions (blue) and small opposing and large opposing asymmetrical interactions (purple). The 1:1 ratio line is indicated by the grey dashed line.

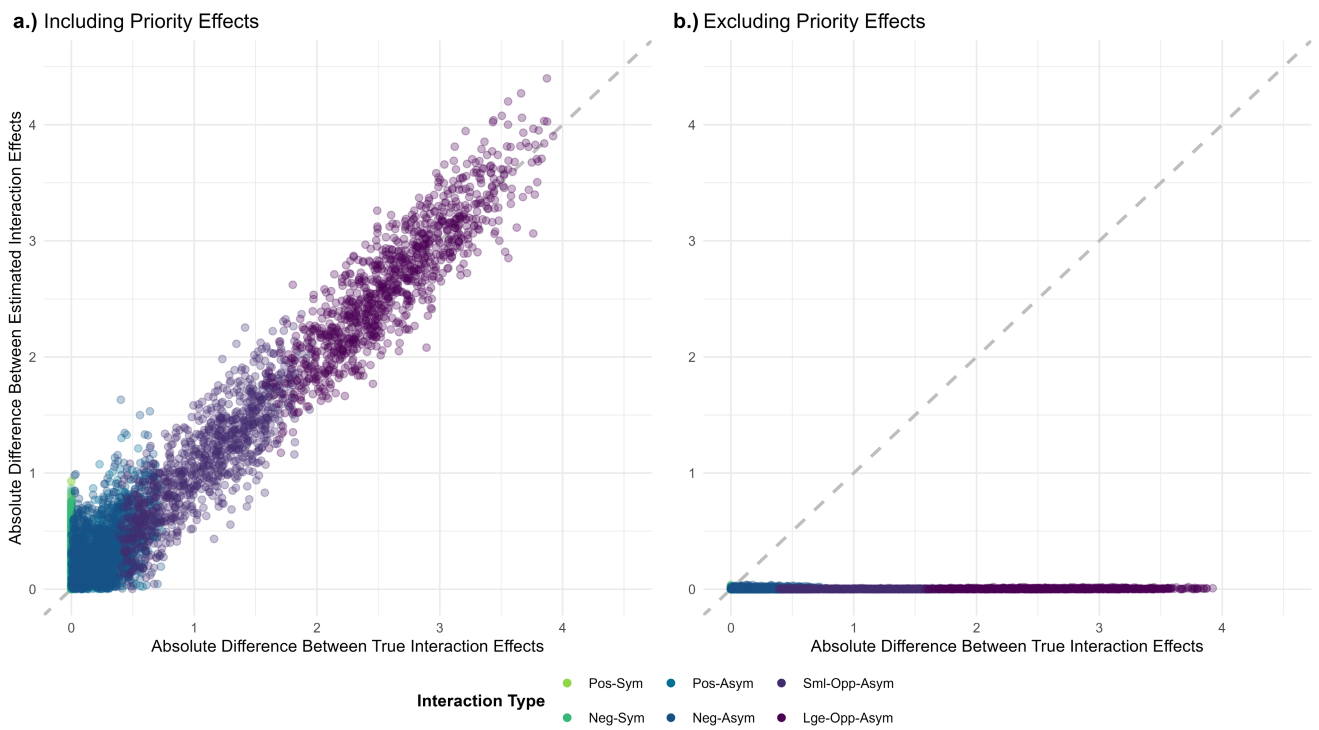


FIGURE 4 | Scatterplot showing the true absolute difference between the interaction effects of species *i* and species *j* on the *x*-axis and the absolute difference between the interaction effect estimates of species *i* and species *j* on the *y*-axis based on generalised linear model estimates that (a) included priority effects, and (b) excluded priority effects. Six interaction types are represented in the plot: positive and negative symmetrical interactions (green), positive and negative asymmetrical interactions (blue) and small opposing and large opposing asymmetrical interactions (purple). The 1:1 ratio line is indicated by the grey dashed line.

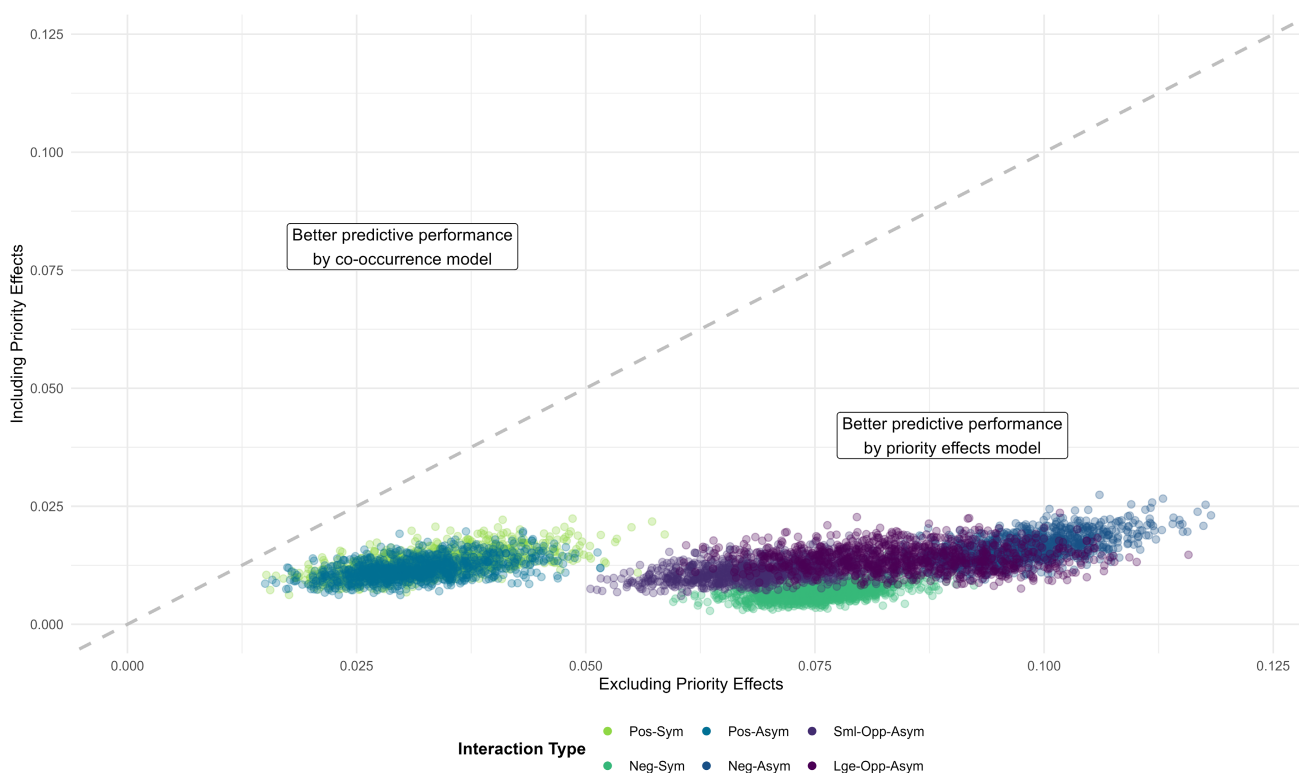


FIGURE 5 | Scatterplot comparing the mean Brier scores calculated from the probability predictions from generalised linear models, with the scores for models that excluded priority effects on the x-axis and scores for models that included priority effects shown on the y-axis. Six interaction types are represented in the plot: positive and negative symmetrical interactions (green), positive and negative asymmetrical interactions (blue) and small opposing and large opposing asymmetrical interactions (purple). The 1:1 ratio line is indicated by the grey dashed line, where values above the line indicate better predictive performance by the co-occurrence model, and values below the line indicate better predictive performance by the priority effects model.

are much more readily available than the type of additional data required for analysing priority and biotic interaction effects. This also emphasises that a model's predictive performance does not necessarily allow insights into whether covariates represent the true underlying mechanisms at work, an argument that is consistent with the much debated challenge on separating biotic interactions from environmental forces in biotic interaction modelling (Godsoe, Franklin, and Blanchet 2017).

5 | Future Directions: Considering Sampling Design

In this study, we chose a straightforward approach that allowed us to simulate interactions between two species to highlight a very simple point: that without consideration of priority effects, we cannot infer asymmetric interactions from binary cross-sectional data. This does not mean that priority effects will always be present or strong enough to influence asymmetric interactions; rather, if they are, they cannot be detected with cross-sectional data. While we have used GLMs to highlight this, similar findings have been demonstrated with other models. For example, a recent study that simulated co-occurrences with various interaction types including mutualistic, competitive, amensalism, commensalism and predator-prey interactions to evaluate the efficacy of joint species distribution models (JSDMs) in discerning interactions found that while mutualistic

interactions could be accurately identified, these models were unable to detect predator-prey interactions with opposing interaction direction (Zurell, Pollock, and Thuiller 2018). Similarly, correlation-based approaches have also been shown to be highly unreliable in experimental studies, which often resulted in estimated interaction effects that were in the opposite direction to true underlying interactions (Fenton et al. 2014). While other studies have noted some variability in terms of the reliability of JSDMs to infer interactions, with some models indicating superior performance over others, the potential utility of these is limited to symmetric interactions (Harris 2016; Sander, Wootton, and Allesina 2017; Barner et al. 2018), and therefore, do not extend to asymmetric opposing interactions. While we do not believe our simple models will be enough to detect these interactions from real data, our example builds on these findings by demonstrating that cross-sectional data will fail to detect asymmetric interactions if colonisation order is not considered.

One of the main reasons that researchers might be driven to use cross-sectional co-occurrence data is the ease at which it can be collected compared to longitudinal data, which requires more forward planning and consideration of design. However, depending on these data for inferring biotic interactions can be very misleading and should, therefore, be avoided, even if some models might offer good predictions of species distributions. If asymmetric effects are to be captured, we suggest that attention should be paid equally to building more sophisticated models

and to considerations of sampling designs specifically suited for inference. For disease ecologists seeking to understand interactions between pathogens, experimental study designs would be best suited for obtaining information on colonisation history, as also suggested by others (Stroud et al. 2024), as this allows for the order of colonisation to be easily controlled. Indeed, this approach has been previously adopted (Hoverman, Hoyer, and Johnson 2013; Doublet et al. 2015; Natsopoulos et al. 2015; Wuerthner, Hua, and Hoverman 2017). For example, one study experimentally examined how the sequence of host exposure to two trematode parasites influenced interactions within hosts, finding no evidence for interactions when colonisation occurred simultaneously, and asymmetric competition when introduced sequentially (Hoverman, Hoyer, and Johnson 2013). Similar approaches might also be feasible for ecologists seeking to understand interactions between plants (Ploughe, Carlyle, and Fraser 2020) and for smaller species, including insects and amphibians (Hernandez and Chalcraft 2012; Rasmussen, van Allen, and Rudolf 2014). However, designing sampling strategies where experimental approaches are not feasible is more challenging. Longitudinal sampling strategies with several sampling events may be a suitable approach (Fenton et al. 2014), provided that they are able to differentiate between the order of arrival for each species of interest. Before–after control design studies that use comparative sampling over time across similar locations may improve the ability of longitudinal designs to obtain information on colonisation history (Krushelnycky and Gillespie 2010). However, unless both species are introduced sequentially, asymmetric effects will not be able to be recovered. Alternatively, existing data from previously published studies, or ongoing long-term ecological programmes such as the National Ecological Observatory Network (2024), or the Biodiversity Exploratories (2024), as well as large-scale citizen science projects such as eBird (2024), might offer ecologists the opportunity to use retrospective data on estimate the probability that one species was present in a site before another species attempted to colonise. This strategy may be particularly suited to modelling invasion pathways or recolonisation events after major disturbances.

Although we argue the importance of colonisation history in sampling design and demonstrate the strong capability of detecting interactions through the inclusion of priority effects in our simulated example, this does not necessarily mean that interactions will always be detectable. While we have focused specifically on how priority effects shape direct biotic interactions, priority effects can also shape community assembly patterns of co-occurrence through environmental pre-emption and modification (Fukami 2015), making the detection of direct biotic interactions more challenging. The relative importance of these effects may be reflected, for instance, in the timing of prior colonisation, which may influence the strength of the detected biotic interactions. For example, in mice, the competitive effects between distinct clones of malaria parasites were found to be stronger when there was a greater time difference between inoculation events (de Roode et al. 2005). Similarly, the relative timing of arrival, or size-mediated priority effects, was found to alter the nature of intraguild interactions between nymphs of two dragonfly species, where earlier arrival resulted in greater exclusion of the late arrival (Rasmussen, van Allen, and Rudolf 2014). Moreover, the

timing of species interactions and potential priority effects in the context of the dynamical processes of site colonisation and establishment could also lead to transient dynamics and variable long-term outcomes (Hastings et al. 2018; Tao et al. 2021), which, to our knowledge, remain largely unexplored. Furthermore, other important factors that could influence the ability to detect these interactions should also be considered, such as the scales at which inferences are made as interactions may be dynamic at both the spatial scale (König et al. 2021) and at the population scale (Clay et al. 2019).

6 | Conclusions

Through simple simulations and models, this study demonstrates why biotic interactions cannot be inferred from binary cross-sectional occurrence data. Doing so can lead to particularly misleading conclusions if the underlying interactions have asymmetric effects. The way forward requires appropriate sampling design, where, at the very least, colonisation order is recorded so that priority effects can be taken into account.

Author Contributions

FPR played a critical role in the coding and design of the study, created figures and led the writing of the manuscript. KW co-conceived the ideas for this study, contributed significantly to the study design, code for simulations and analysis, provided valuable input during analysis and contributed to the manuscript writing. NJC co-conceived the ideas for this study, initially scripted the code for simulations and contributed critically to the development of the code in later versions, contributed to the study design, provided valuable analysis input and contributed to the writing of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All corresponding data and code required to replicate this analysis have been made available in the Zenodo repository: <https://doi.org/10.5281/zenodo.13363723>. Detailed citation information is provided in the reference list (Powell-Romero, Wells, and Clark 2024).

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14509>.

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