

# Introducing recurrent event analyses to assess species interactions based on camera-trap data: A comparison with time-to-first-event approaches

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## Abstract

1. Camera-trap surveys are increasingly used to assess species interactions, with a growing focus on proximate co-occurrence, the conditional probability of one species occurring after another within a given time window. However, existing time-to-first-event models, commonly employed for this purpose, suffer from multiple limitations. For instance, they cannot fully quantify the interaction strength, that is how strongly one species affects the occurrence probability of another, nor the duration of this effect, nor identify the directionality of the interaction.
2. We propose reframing the question in terms of recurrent event analysis, which enables the use of a rich set of techniques to provide more information about the data-generating process. In particular, we use the piece-wise exponential additive mixed model (PAMM) to take into account all available information (including recurrent occurrences of species) and to estimate the non-linear temporal dynamics of the visitation rate of a species after the occurrence of another. As the estimation is performed within the framework of generalized additive models, it offers a rich, robust and established inferential toolbox.
3. We evaluated PAMM's performance in estimating species interactions through a simulation study involving two species under various scenarios of attraction or repulsion, with and without imperfect detection. Additionally, we compared the PAMM to six time-to-first-event methods commonly used in camera-trap studies and illustrated its application with real data.
4. PAMMs outperformed the other methods in terms of statistical power, output interpretability and ability to disentangle interactions. The robust performance of PAMMs underscores their potential as a valuable tool for studying species interactions based on camera-trap data. To facilitate its adoption, we present the new package *ctrecurrent* and provide a reproducible workflow from data preparation to model fitting.

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## KEYWORDS

attraction/repulsion, camera trap, community ecology, general additive model, recurrent events, spatio-temporal interactions, survival analysis, time-to-event model

## 1 | INTRODUCTION

Camera traps have become widely employed for assessing species interactions (Sollmann, 2018). Species interactions have often been studied based on the spatial (e.g. MacKenzie et al., 2004) and temporal overlap (e.g. Ridout & Linkie, 2009) between two species. Recently, though, there was a growing methodological interest in proximate co-occurrence, defined as the conditional probability of one species occurring after another within a specified time window (Schliep et al., 2018). Assessing proximate co-occurrence allows for considering space and time together, providing a more nuanced understanding of repulsion and attraction processes between species. Proximate co-occurrence is typically investigated using time-to-first-event methods, where the statistical unit is the time interval between consecutive observations of species A and B (AB or BA). Commonly used analytical methods to study time-to-first-event data include linear models (Harmsen et al., 2009; Niedballa et al., 2019), attraction-avoidance ratios (Parsons et al., 2016) and multi-response permutation procedures (Karanth et al., 2017; Murphy et al., 2021a).

However, these approaches exhibit various limitations. First, they only consider the first observation of species B after species A, whereas multiple observations of species B after species A are commonly observed, potentially neglecting important information about species interactions and reducing the statistical power (Claggett et al., 2018). Second, species interactions can be described with two components: strength and duration (Box 1). However, most time-to-first-event approaches conflate strength and duration and provide only summary values (e.g. the mean duration between the occurrences of A and B), thus not taking full advantage of the data and limiting the ecological interpretability of the results. Third, by drawing inferences based on comparing AB with BA, some of these methods cannot identify the directionality of the interaction (Box 1). For instance, in the case of predator-prey interactions, is the predator repelling the prey, the prey attracting the predator or do both processes occur? And in the case of interference competition, which species is repelling the other? Finally, many of these approaches require simulating random time-to-first-event distributions and comparing them with observed distributions, which are susceptible to type I or II errors (see Veech, 2013 and references therein). Simulations often rely on species' circadian activity to avoid over-simulating diurnal observations of nocturnal species, but do not consider variation in activity over longer periods. However, just like species activity at a camera trap is not uniform on a circadian scale, it is unlikely to be uniform on longer time scales due to the temporal dynamics of biotic and abiotic factors (e.g. weather conditions, resource availability, territory movement patterns). Moreover, randomly selecting sites for simulated observations overlooks

### BOX 1 Definitions of species interaction terms

*Strength*: the ratio between the odds of observing species B immediately after species A and the odds in the absence of species A, expressed in terms of odd ratio (OR). The closer the OR to 1, the lower the strength of the effect.

*Duration*: how long the effect persists, that is the times it takes to get OR back to 1.

*Direction*: in which direction is the effect, that is the effect of A on B (denoted hereafter as B|A) or the effect of B on A (denoted hereafter as A|B).

*Type*: repulsion (OR <1), attraction (OR >1) or neutral (OR=1).

*Primary species*: the species affecting the secondary species and being the focus of the model (mandatory).

*Secondary species*: the species being affected by the primary species (mandatory).

*Tertiary species*: all other species assumed to affect the secondary species, but not being the focus of the model, which serve to control for confounding effect from hetero-specifics (facultative).

*Censoring species pool*: all the primary and tertiary species that serve as censoring events during the survey constructions.

site-dependent imperfect detection issues, potentially leading to erroneous predictions (Bischof et al., 2014).

To overcome these limitations, we propose using techniques from the methodological toolbox of survival analysis (Clark et al., 2003). With this approach, we can model the distribution of occurrences of a species and visualize it in terms of event rates over time, which, as described later, allows a richer interpretation of the estimated repulsion or attraction effects. At the same time, we can view the data in terms of recurrent events, leveraging the information contained in successive observations of a species (see a review by Amorim & Cai, 2015). Bender et al. (2018) introduced a flexible, piece-wise exponential additive mixed model (PAMM) approach for time-to-event data, employing splines to model the hazard rate, or the rate of events. PAMMs allow for estimating complex relationships, including non-linear baseline hazard rates, time-varying and non-linear covariate effects, and cumulative effects of time-varying covariates (Bender & Scheipl, 2018). Building upon this, Ramjith et al. (2022) recently extended the PAMM approach to the recurrent events framework, thereby addressing many of the limitations

outlined previously: (i) the use of all available information, that is no event is discarded; (ii) the ability to identify the directionality of the interaction by fitting two separate models to study the effect of species A on B and the effect of species B on A (A|B and B|A); (iii) the ability to distinguish between the strength and the duration of the interaction; and (iv) the absence of a requirement for data randomization or simulation of a theoretical distribution. These advancements position PAMMs as a robust candidate for investigating species interactions using camera-trap data.

In this study, we investigated the effectiveness of PAMMs in evaluating proximate co-occurrence using camera-trap data. Through multiple simulations, we assessed the performance of PAMMs and compared them to the most common time-to-first-event approaches, typically employed in interspecific interaction studies. We further evaluated the impact of site- and species-specific imperfect detection on PAMM's performance and its ability to discern the direction of interaction. Finally, we present a case study utilizing real-world data to illustrate how PAMMs can be used to analyse camera-trap data using the new R package *ctrecurrent*.

## 2 | METHODS

All simulations and analyses were performed using R 4.3.0 open-source software (R Core Team, 2023).

### 2.1 | The piece-wise exponential additive mixed model

To describe how the occurrence of one species affected the occurrence of a second species, that is proximate co-occurrence, we used the PAMM (Bender & Scheipl, 2018) to estimate the dynamics of the observation rate of the *secondary* species (B, Box 1) following the observation of the *primary* species (A). To do so, we estimate the hazard rate for occurrence of species B (following species A), that is the distribution of waiting times between occurrences of the species, potentially conditional on covariates  $x$  and a group  $l$  as

$$h(t|x, l) = \exp(\beta_0 + f_0(t) + f(x) + b_l)$$

Thus,  $h(t|x, l)$  is the hazard for observing species B at time  $t$  given previous occurrence of species A,  $\beta_0$  and  $f_0(t)$  are the constant and flexible components of the log-baseline hazard at time  $t$ , respectively, and  $f(x)$  are the potentially non-linear effects of a set of covariates  $x$ . The term  $b_l \sim N(0, \sigma_b)$ , represents a random effect for group  $l$  (in our context this could be the survey or the site at which camera traps were placed). Both,  $f_0(t)$  and  $f(x)$ , are estimated as smooth functions using penalized splines. For a more detailed mathematical description, see Ramjith et al., 2021.

Importantly, and similar to the Cox model (Cox, 1972), PAMMs make no assumption about the underlying distribution of waiting times. The effect of the smooth functions is best investigated visually as the potentially non-linear shape is what we are interested in.

Additionally, the effective degrees of freedom (*edf*), that is the effective degree of the spline needed to describe curvature (Wood, 2017), provides a compact indication of how far the estimated function deviates from a linear function (the further away from 1 the wigglier the estimate). Additionally, one can test for the difference of the estimated function from 0 ( $H_0: f(x) = 0$ ; see Wood, 2013).

### 2.2 | Simulation study

We conducted a simulation study to compare the performance of PAMMs with commonly used time-to-first-event methods, including linear models (Harmsen et al., 2009; Niedballa et al., 2019), attraction-avoidance ratios (Parsons et al., 2016) and multi-response permutation procedures (Karanth et al., 2017; Murphy et al., 2021a).

We simulated camera-trap observations of two species, A and B at 50 sites over 365 days. We used relative abundances for species A and B similar to those observed in large predator-prey dyads (1:100 ratio, Mech & Peterson, 2003) and considered bilateral effects, that is A had an effect on B and B had an effect on A (adapted from the unidirectional simulation by Niedballa et al., 2019). The interaction strength and type (Box 1) at time  $t$  were defined by the odds ratio (OR) between the odds of detecting species A in the absence of species B and the odds of detecting species A  $t$  hours after an observation of species B (and vice versa). The interaction strength was designed to diminish over time (as suggested in Kuijper et al., 2014; Wikenros et al., 2015), with the initial OR linearly recovering to 1 over a certain duration  $d$ .

In the first part of the simulation, designed to evaluate the statistical power of the PAMM, we generated species observations with a repulsion effect of A on B, with strength varying from OR=0.001 (strong repulsion) to OR=1 (no effect), and duration varying from  $d=0.5$  to  $d=30$  days. Observations of each species at each site were then randomly thinned to mimic species- and site-dependent imperfect detection. We also tested for the effect of the maximum survey duration considered by setting the maximum follow-up in datasets at either  $\tau_j=7$  or  $\tau_j=30$  days (see also recurrent events formatting section below). We replicated each simulation scenario 100 times, leading to a total of 5600 datasets. In the second part of the simulation, we addressed the issue of interaction directionality through five different scenarios: (i) mutual repulsion between the two species; (ii) A repulsing B only; (iii) A repulsing B and B attracting A; (iv) B attracting A only; and (v) mutual attraction between the two species. All effects were set to OR=10 (attraction) and OR=0.1 (repulsion) and to last for  $d=3$  days. For each scenario, we simulated 100 datasets, resulting in a total of 500 datasets (see Appendix 1 for a detailed description of the simulation process).

In the first simulation part, assessing the statistical power, we fit a PAMM only once for each dataset as we were testing for one direction only, B|A and coyote|white-tailed deer, respectively. However, in the second simulation part, assessing the interaction directionality, we fit a PAMM twice for each data set: one with the direction A|B and one with the direction B|A.

## 2.3 | Real-data example

To demonstrate how to use PAMMs with real data, we examined the interaction between white-tailed deer (*Odocoileus virginianus*) and coyotes (*Canis latrans*) in both direction: (i) the effect of white-tailed deer occurrence on coyotes' visitation rate dynamics over time and (ii) the effect of coyote occurrence on white-tailed deer visitation rate dynamics over time. We used camera-trap data from Murphy et al. (2021b) collected in public forests (Pennsylvania, United States) surrounded either by forest or agriculture/low-density housing, between 2016 and 2017. This requires the camera-trap data to be transformed to a specific format before model fitting (see Ramjith et al., 2022 on data transformation and mathematical details; for illustration see below and *ctrecurrent* package vignette, and <https://github.com/adibender/ctrecurrent>).

### 2.3.1 | Survey definition

In epidemiological studies, a survey begins when a patient enters the study, marking the initiation of a period during which specific recurrent event within the patient are monitored. In our case, a survey starts whenever the primary species, a white-tailed deer for the example was observed at a site, and continues for a pre-defined period of time or until censored (Figure 1a). Because some species other than white-tailed deer might also influence coyote observation rate, either through attraction or repulsion, we established a censoring species pool (Box 1). This censoring pool consisted of the primary species (in this case, white-tailed deer) and tertiary species, those other than the primary assumed to affect the secondary species through repulsion or attraction. In our example, tertiary species included white-tailed deer fawn, humans (*Homo sapiens*), black bears (*Ursus americanus*) and bobcats (*Lynx rufus*). When looking at the effect of coyotes on white-tailed deer visitation rate, the censoring pool encompassed coyotes (primary) as well as humans, black bears and bobcats (tertiary species). A survey thus ended when (i) a new observation of one of the censoring species occurred; (ii) upon removal of the camera trap (e.g. study ending); or (iii) when it reached the maximum survey duration, an arbitrarily defined time after which the interaction effect is assumed to have disappeared.

### 2.3.2 | Recurrent events formatting

For each survey, all observations of the secondary species (e.g. coyotes) were recorded and treated as recurrent events (Figure 1a). For each recurrent event, we recorded the time of the event since the start of the survey (*tstart*, the time since the last observation of a white-tailed deer), along with the time since the previous event (*tstop*, the time since the last observation of a coyote). The newly implemented *ctrecurrent* package (<https://github.com/adibender/ctrecurrent>) facilitates this transformation of raw camera-trap data into the recurrent events format (see Figure 1b, and the package vignette). This package allows for the

formatting of raw camera-trap data containing site, species and times-tamp information for each observation into distinct surveys containing recurrent events. Additionally, the function from the *reReg* package (Chiou et al., 2023), slightly adapted here for visual convenience, can be used to display the structure of the recurrent event data, providing an overview of the distribution of events among surveys and over time (Figure 3a,b).

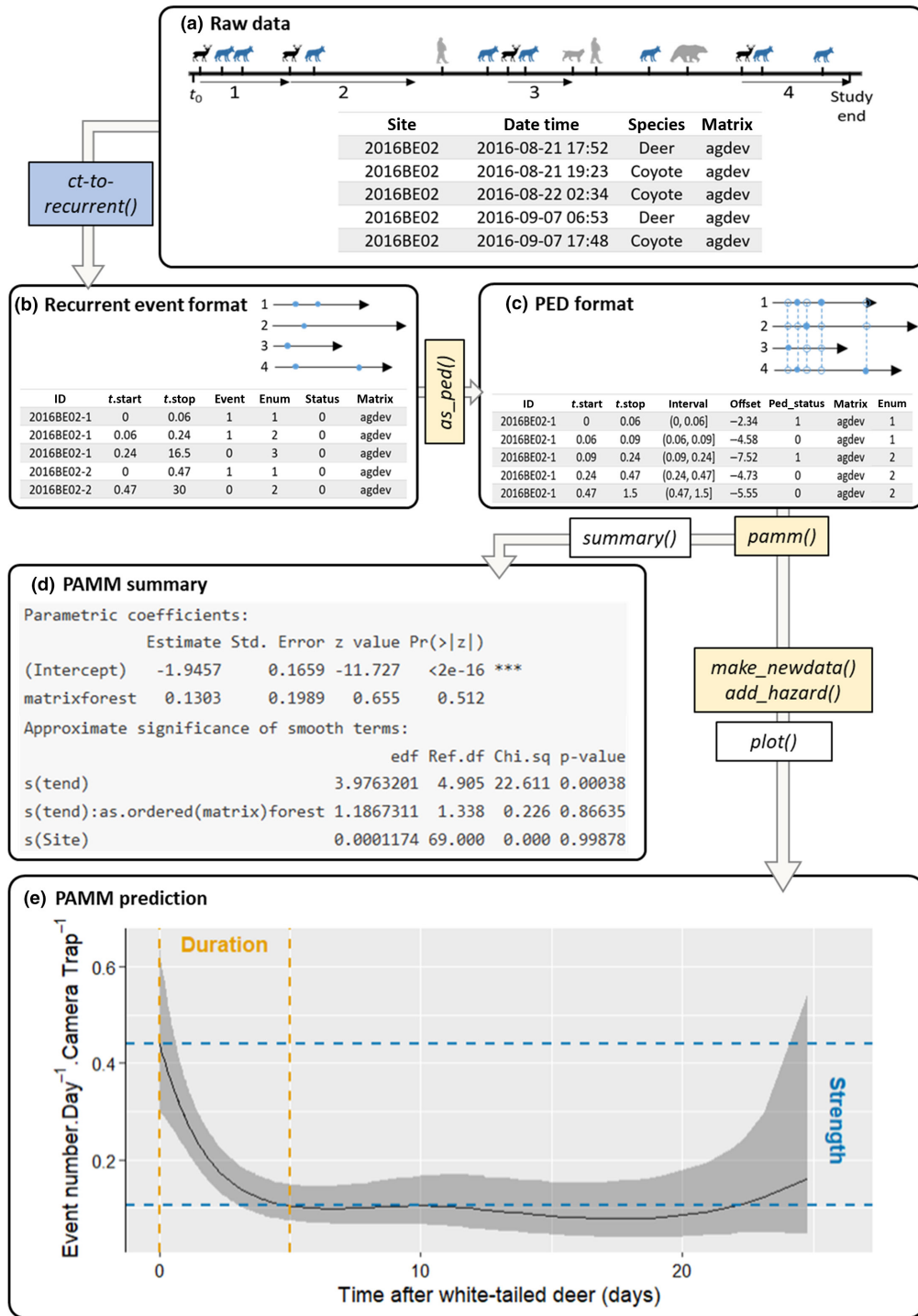
### 2.3.3 | Piece-wise exponential data (PED) transformation

PAMM requires the dataset to be discretized into  $J$  intervals with cutpoints  $0 = \tau_0 < \tau_1 < \dots < \tau_J$ , where the  $j$ th interval is defined as  $(\tau_{j-1}, \tau_j]$  and  $\tau_j$  is the maximum time, either set arbitrarily or because of censoring (see above). Here, we considered a maximum duration of  $\tau_j = 30$  days. Pseudo-observations are then created for each interval (Figure 1c, Bender et al., 2018; Ramjith et al., 2021; see the *ctrecurrent* vignette for an example).

### 2.3.4 | PAMM fitting and interpretation

Using the piece-wise exponential data, we can then fit PAMMs (Figure 1d). In the simulation section, where no covariate was generated, the model simply entailed the effect of time on the event rate, represented by a single smooth function on the variable *tend* (Table 1—Model 1). However, in the real-data example, and following Murphy et al. (2021a), we incorporated a covariate (*matrix*) to evaluate the impact of the landscape matrix, specifically distinguishing between 'agricultural/developed' areas and 'forest' areas, on interspecific interactions. We fit PAMM twice, one for each interaction direction: (i) the effect of white-tailed deer on coyote visitation rate and (ii) the effect of coyotes on white-tailed deer visitation rate. For each direction we might have considered two different models. First, we might have assumed proportional hazards between the two categories 'forest' and 'agricultural/developed', maintaining a consistent difference between the two environments over time, and included landscape matrix as a linear covariate (Table 1—Model 2). Alternatively, PAMM allows for estimating a stratified model with separate temporal dynamics of observation rates for each level of the landscape matrix covariate (Table 1—Model 3). We used the latter model. In addition, all models incorporated a (log-)normal survey random effect to account for dependency between events of the same survey, represented by the argument  $s(ld, bs = 're')$ .

Finally, we interpreted the model results based on the edf, test significance and the visual inspection of the smoothing function (i.e. evolution of the coyote observation rate over time) facilitated by the *make\_newdata()* and *add\_hazard()* functions from the *pammtools* package. These functions allow to create new data and predict event rates over time, based on PAMM estimates, which can then be visualized using generic plotting functions (e.g. *ggplot()* from the *ggplot2* package, Wickham, 2016).



**FIGURE 1** Workflow of the PAMM analysis of camera-trap data to assess the effect of white-tailed deer on coyotes' visitation rate dynamics over time. (a) Raw camera-trap data consist of observations of white-tailed deer (primary species, in black), coyotes (secondary species, in blue) and humans, bears and bobcats (tertiary species, in grey). (b) The raw data are re-structured into a recurrent event format, based on surveys starting with the occurrence of the primary species and ending when another primary (survey 1) or tertiary (survey 3) species occurs, the survey reaches the duration threshold (survey 2), or the camera trap is inactive (e.g. study end, survey 4). (c) Recurrent event data are transformed into piece-wise exponential Data (PED) format, by creating pseudo-observations (blue circles). Finally, the PAMM is fitted to the prepared data, and (d) the `summary()` function is used on the PAMM object to display model estimates (e.g. *edf*, see model section for details). (e) Finally, model predictions can be obtained and visualized using plots of the partial effects of the smoothing function, for instance with the temporal dynamics of coyote visitation rate following the presence of a white-tailed deer as predicted by the PAMM (without covariate effect for visual convenience). An attraction effect is visible, with the highest probability of observing coyotes immediately after the occurrence of white-tailed deer at the site, followed by a gradual decrease over time. The duration of the attraction, delineated by orange vertical lines, was estimated at approx. 5 days, after which the coyote visitation hazard rate reached a plateau. Blue horizontal dashed lines delineate the strength of the effect. Here, the probability of observing a coyote at  $t=0$  is four times higher than at  $t \geq 5$  days. Functions highlighted in the blue, yellow and white rectangles represent functions from the `ctrecurrent`, `pammtools` or base R packages, respectively.

Model type	Model formulation
Model 1: baseline hazard and site effect	$h(t l) = \exp(\beta_0 + f_0(t) + b_l)$
Model 2: linear effect of $x$ (landscape matrix; reference coded) (Proportional Hazard assumption)	$h(t x, l) = \exp(\beta_0 + f_0(t) + \beta_1 x + b_l)$
Model 3: stratified baseline hazards w.r.t. $x$ (landscape matrix)	$h(t x, l) = \exp(\beta_0 + f_0(t) + \beta_1 x + f_x(t)x + b_l)$

Note: Model 1 was used for the simulation part; Model 2 is a fictitious example and Model 3 was used for the real-data example. As before,  $\beta_0 + f_0(t)$  is the log-baseline hazard,  $b_l \sim N(0, \sigma_b)$  a random effect for each site. Here  $x$  is a reference coded two-categorical variable (agriculturally developed (reference) vs. forest). Model 3 is a stratified hazards model, where  $f_x(t)x$  indicates the deviation of the baseline hazard for forest sites compared to the log-baseline hazard  $f_0(t)$  (agriculturally developed sites).

We refer to *ctrecurrent* (<https://adibender.github.io/ctrecurrent/>) and *pamtools* (<https://adibender.github.io/pamtools/>) vignettes for the most current workflow examples and detailed explanations.

## 2.4 | Model comparisons

In order to evaluate the efficiency and usefulness of the PAMM approach, we compared results from the PAMMs to results from six commonly used time-to-first-event approaches (Table 2). To compare robustness against imperfect detection and to avoid the problem of different methods returning different metrics, which makes direct comparison of the outputs cumbersome, a power analysis was performed based on method-specific metrics, briefly described in Table 2. When possible, the statistical power of each method was calculated as the percentage of significant tests (at  $\alpha=0.05$ ) from the 100 replicated datasets for each simulation scenario. A method was considered reliable if the power was  $>0.8$  (Niedballa et al., 2019). For output interpretability comparison and precision of the models, we fit all models to (i) the real dataset for testing the effect of white-tailed deer on coyotes and (2) the simulation example with a repulsive effect of A on B and an attraction effect of B.

## 3 | RESULTS

### 3.1 | Simulation—Statistical power

PAMM exhibited an overall similar or higher statistical power than the other approaches tested, particularly for short surveys ( $\tau_j=7$  days) with weak ( $OR=0.5$ ) and short-term ( $d=2$  days) repulsive effects under perfect detection conditions (see Appendix 4). Similar results were observed with MRPP-2 on AB interval. However, in the MRPP analysis, the outcomes varied significantly depending on which species the permutations were done (Appendices 3 and 5). Notably, a substantial decrease in statistical power was observed when permuting the species of lower abundance (in this case, species A, Appendix 5). These contrasting results based on the permuted species underscore the importance of carefully selecting species for

TABLE 1 Examples of PAMMs model formulation.

permutation with these methods. LM-2 exhibited a pattern similar to PAMM but with slightly lower power for weak effects ( $OR=0.5$ ,  $d=2$  days). Conversely, MRPP-1 and both AARs demonstrated low statistical power, as they consistently failed to efficiently detect weak ( $OR=0.5$ ) repulsive effects. LM-1 suffered from a high type II error across all scenarios and failed to detect interaction effects efficiently. Furthermore, imperfect detection decreased statistical power across all models, with similar effects observed across different approaches (Appendix 4).

### 3.2 | Simulation—Interaction directionality

As a single PAMM tests for a specific interaction direction, the approach had no issue with the directionality issue, efficiently detecting the effect of species A on species B regardless of whether species B influenced species A through repulsion, attraction or had no effect (Figure 2 PAMM-B|A). Additionally, PAMMs performed well in assessing the effect of species B on species A, despite the smaller number of surveys and detections of species A overall (Figure 2 PAMM-A|B). When AAR-1 or LM-2 was used, distinguishing between A repulsing B or B attracting A was impossible (Figure 2 AAR-1 & LM-2). Although the AAR-2 BAB/BB approach, focusing on the effect of species A on species B, effectively distinguished between situations of no effect or repulsion of species A on species B, it was not entirely independent of the effect of species B on species A, as noted by Parsons et al. (2016). Specifically, the ratio differed depending on whether species B repelled, had no effect or attracted species A (Figure 2 AAR-2—BAB/BB). The ratio ABA/AA, examining the effect of species B on species A, yielded inconclusive results, as the median calculated for each site was based on only a few ratios, lacking robustness (Figure 2 AAR-2—ABA/AA). LM-1 faced similar challenges (Figure 2 LM-1; see Appendix 3). MRPP-1 and MRPP-2 distinguished the different situations well, with the exception of opposite effects (i.e. B attracting A and A repulsing B). In this situation, MRPP-1 did not differentiate between intervals AB and BA (Figure 2 MRPP-1 and 2). However, when permuting on A, all three MRPP versions experienced a significant decrease in statistical power, raising further questions regarding the choice of species for permutation (Appendix 5).

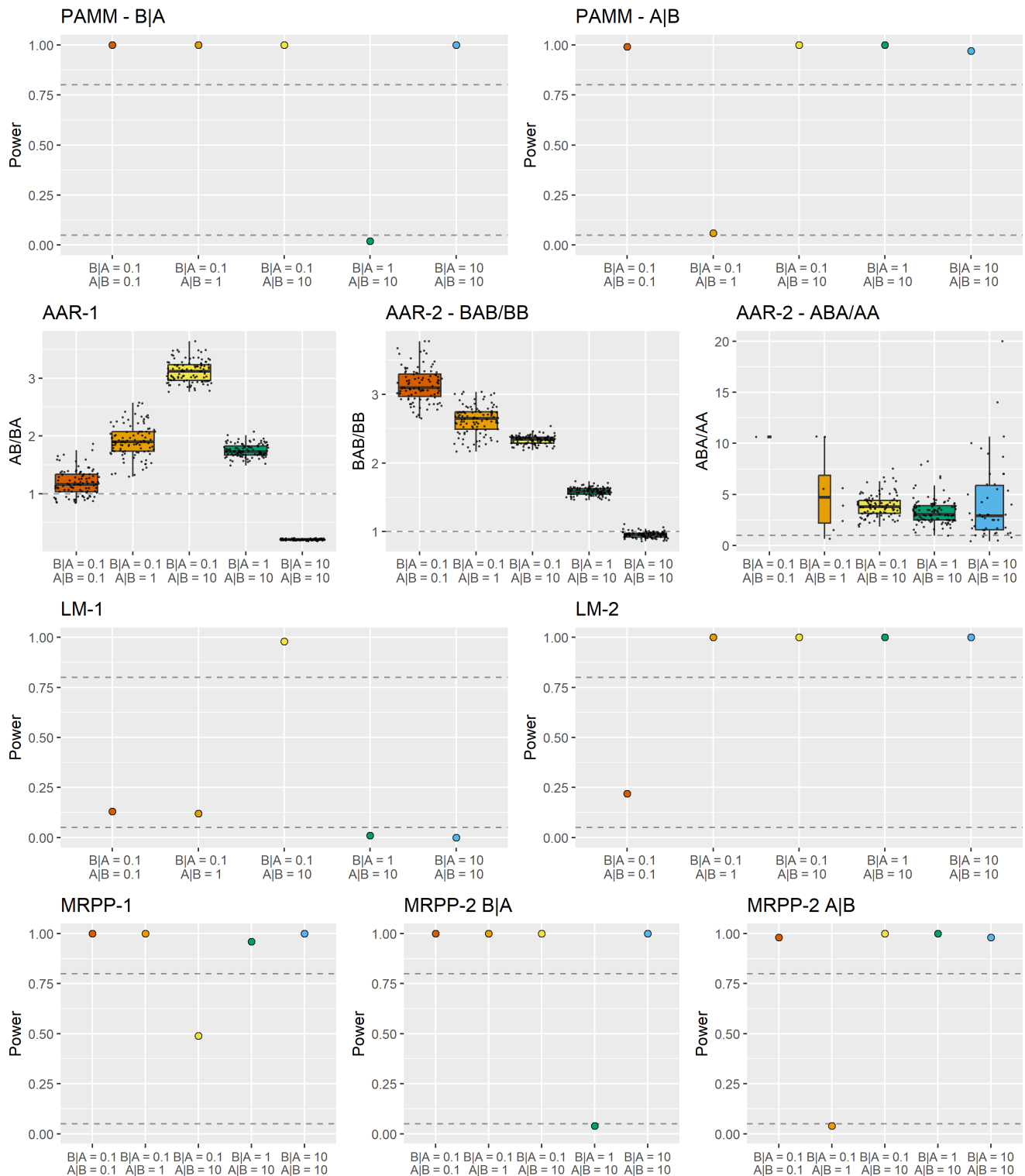
**TABLE 2** Description of the six approaches compared to PAMM and of the metric used for comparison. Detailed descriptions of the different metrics calculations are provided in [Appendix 3](#).

Method	Study	Description	Metric
<i>Recurrent event model</i>			
PAMM	Ramjith et al. (2021)	Described in the main text (Method–PAMM–Model section)	<i>p</i> -value of the smoothing term of time (log-baseline hazard)
<i>Linear model</i>			
LM-1	Harmsen et al. (2009)	Linear model with the log <sub>10</sub> -transformed time interval as the response variable. The identity of the species observed first and second are used as explanatory variables. A significant interaction effect between the species is an indication of a longer (or shorter) interval between AB and BA captures than between AA and BB captures	<i>p</i> -value of the interaction effect
LM-2	Niedballa et al. (2019)	Direct comparison between AB and BA, with the log <sub>10</sub> -transformed time interval as response variable and the type of interval as covariate ('BA' as reference vs. 'AB')	<i>p</i> -value of the interval type covariate
<i>Attraction–avoidance ratio</i>			
AAR-1	Parsons et al. (2016)	Calculation of the ratio BA/AB, averaged by camera-trap site	Median ratio BA/AB
AAR-2	Parsons et al. (2016)	Calculation of the ratio BAB/BB (or AA/ABA), the time intervals between two successive observations of the secondary species B without and with the passage of the primary species A (vice versa for AA/ABA), averaged by camera-trap site	Median ratio BAB/BB (or ABA/AA)
<i>Multi-response permutation procedure</i>			
MRPP-1	Karant et al. (2017) described in Mielke et al. (1976)	Calculation of the median time interval (AB and BA intervals undifferentiated), followed by a constrained randomization of the observations and calculation of the rank of the observed median among the random medians. This rank is converted into the probability that the observed median is shorter than under a random process (see <a href="#">Appendix 2</a> for a more detailed explanation of the approach)	Rank of the observed median
MRPP-2	Murphy et al. (2021a)	Extension of the MRPP-1 with a directional approach by distinguishing AB from BA	Rank of the two observed medians (AB and BA)

### 3.3 | Real-data example—PAMM interpretation

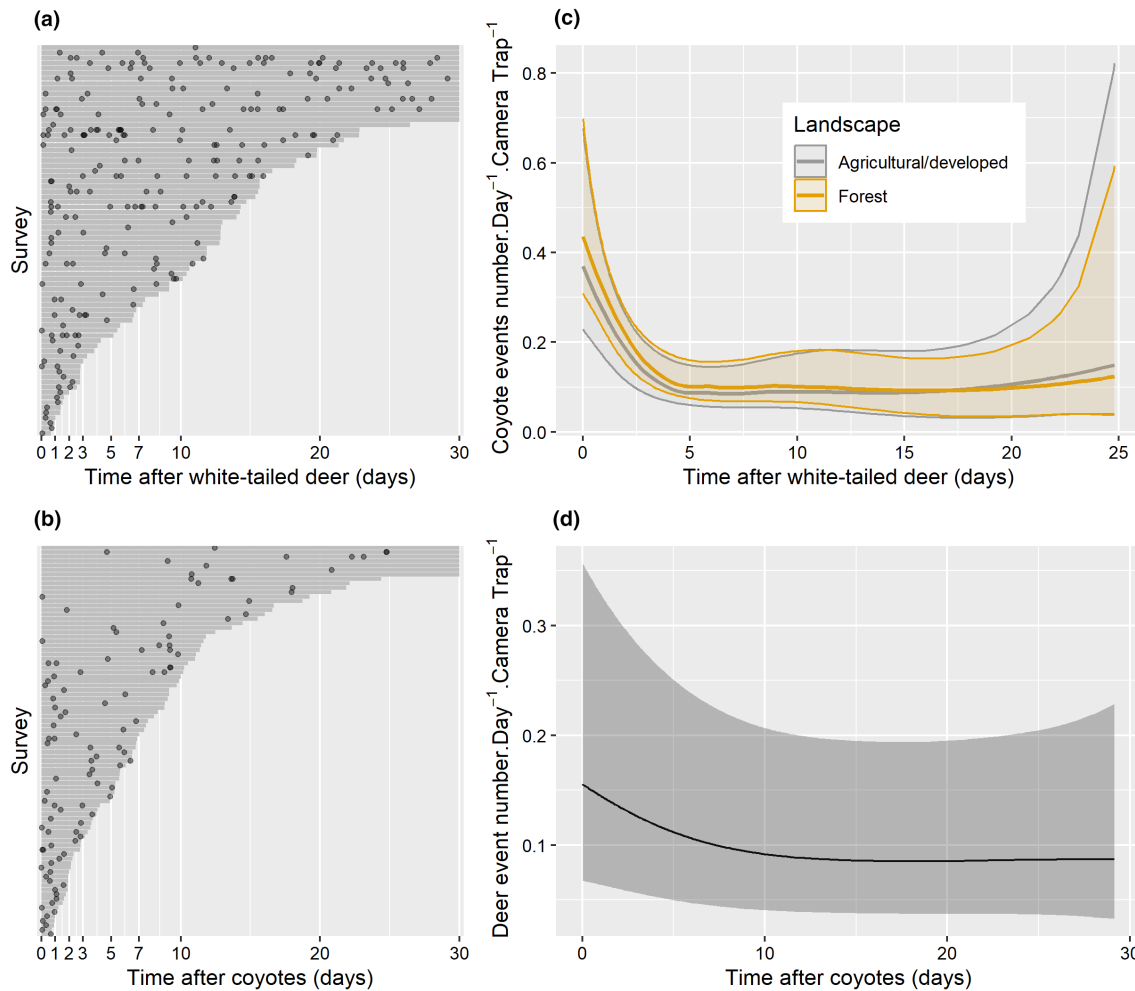
The output from PAMM contains two main parts ([Figure 1d](#)): (i) the parametric coefficients showing the estimation of the linear effect of covariates, and (ii) the approximate significance of smooth terms. In our analysis, a significant non-linear effect of time on (i) coyote event rates was observed following the occurrence of

white-tailed deer (edf=3.98, ref.df=4.9,  $\chi^2=22.61$ ,  $p<0.001$ , [Figure 1d](#)) and on (ii) white-tailed deer visitation rate following the occurrence of coyote (edf=2.12, ref.df=2.65,  $\chi^2=10.56$ ,  $p=0.02$ ) both in the agricultural/developed areas. Visual inspection revealed that the observation rate of coyotes was highest immediately after a white-tailed deer observation, gradually decreasing over time until a plateau four times lower (indicating the



**FIGURE 2** Assessment of the interaction direction determined by the different approaches for the following situations: (i) mutual species repulsions ( $OR(B|A)=OR(A|B)=1/10$ , in red), (ii) A repulsing B ( $OR(B|A)=1/10$ , in orange) only, (iii) A repulsing B ( $OR(B|A)=1/10$ ) and B attracting A ( $OR(A|B)=10$ , in yellow), (iv) B attracting A ( $OR(A|B)=10$ , in green) only and (v) mutual species attraction ( $OR(B|A)=OR(A|B)=10$ , in blue). All effects were configured to last 3 days. Horizontal dashed lines for PAMM-B|A, PAMM-A|B, LM-1, LM-2, MRPP-1, MRPP-2 B|A and MRPP-2 A|B denote the 0.8 power threshold and the 0.05 threshold for the upper and lower lines, respectively. Models were deemed efficient in a situation when they exceeded the 0.8 threshold. Additionally, horizontal dashed line for all AARs indicates a ratio equal to 1, signifying no effect. AARs were deemed efficient when they did not overlap this line.



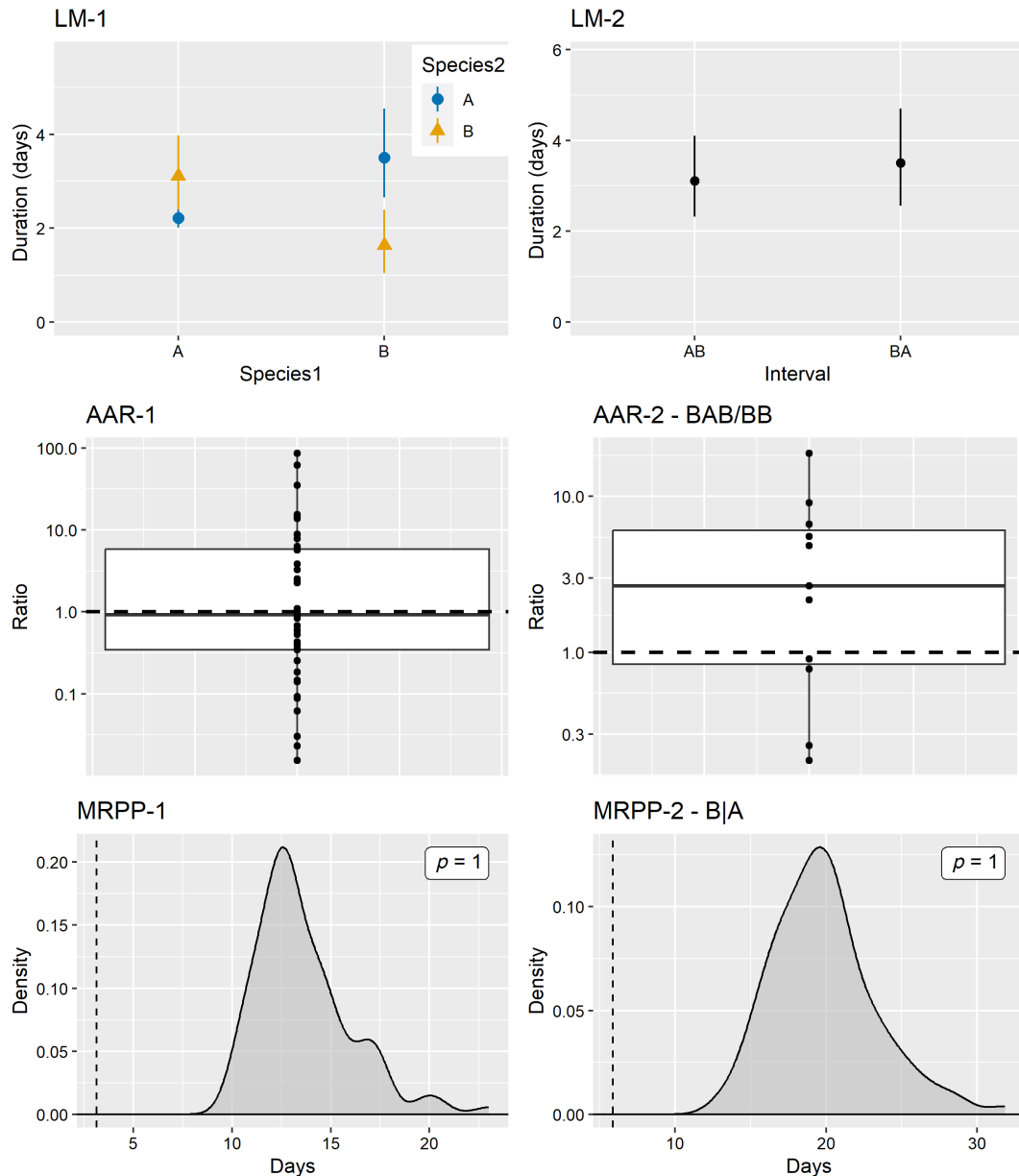


**FIGURE 3** Recurrent event surveys, that is distribution of coyote observations following the occurrence of a white-tailed deer (a) and of white-tailed deer observations following occurrence of a coyote (b). Black dots represent recurrent events, and grey lines represent surveys generated using the `plotEvent()` function (Chiou et al., 2023). (c) PAMM predictions of the dynamics of coyote visitation rate over time after white-tailed deer presence and (d) of white-tailed deer visitation rate over time after coyote presence. An attraction pattern was observed for both (Figure 1e for more details). No discernible difference was observed between forest and agricultural/developed areas, indicating no time-varying effect of the landscape matrix for any of the directions of the interaction.

interaction strength, Figures 1e and 3c), 5 days later (representing the interaction *duration*). This attraction pattern was also observed for white-tailed deer after coyote occurrence, but less pronounced (strength ca. 1.5–2 and duration ca. 10 days) and with higher variability. In this data, there did not appear to be a need for stratification w.r.t. the environment. Specifically, the temporal dynamics of (i) coyote event rates following the observation of a white-tailed deer (edf = 1.19, ref.df = 1.34,  $\chi^2 = 0.23$ ,  $p = 0.87$ , Figures 1d and 3c) and of (ii) white-tailed deer after coyote presence (edf = 1, ref.df = 1,  $\chi^2 = 2.05$ ,  $p = 0.15$ ) were not different between agricultural/developed and forest areas. The random effect for the site had a variance close to zero for both model, indicating that there were no site-specific differences for (i) the occurrence of coyotes given the occurrence of white-tailed deer (edf = 0, ref.df = 69,  $\chi^2 = 0$ ,  $p = 1$ ) and (ii) the occurrence of white-tailed deer given the occurrence of coyotes (edf = 0.23, ref.df = 43,  $\chi^2 = 0.12$ ,  $p = 0.93$ ).

### 3.4 | Real-data example—Model comparison

Both MRPP approaches also highlighted an attraction of the deer on coyotes ( $p = 1$ , Figure 4). Interpreting LM-1, despite detecting a significant effect of the interaction, was challenging as it is unclear which interval estimations to compare. LM-2 and AAR-1 failed to detect any significant effect. This suggests that deer are also more likely to appear shortly after the occurrence of coyotes, a finding corroborated by both PAMM and MRPP (1 and 2) methods (Figure 3d). Conversely, AAR-2 did not identify any attraction process; instead, it seemed to indicate a repulsion of coyotes towards deer (ratio > 1). This discrepancy was also observed in the simulation case, where AAR-2 indicated repulsion despite an attraction effect (see Appendix 6). Ultimately, all these methods faced challenges in terms of interpretability. While the PAMM precisely depicts the response of the secondary species by estimating its visitation rate



**FIGURE 4** Plots of the different approaches' output for the coyote-white-tailed deer interaction study. LM-1 estimates the mean duration ( $\pm$ SE) of four intervals: AA, AB, BA and BB. LM-2 compares the duration of AB with BA intervals (mean  $\pm$  SE). Both AAR methods provide a ratio of intervals (AB/BA for AAR-1 and BAB/BB for AAR-2) for each site. The horizontal dashed line indicates no difference between intervals and thus no interaction. For AAR-2 BAB/BB, values above 1 indicate repulsion, while values below the line ( $<1$ ) indicate attraction. Finally, both MRPP methods (undirected for MRPP-1 and directed for MRPP-2—B|A) compare the rank of the observed median interval duration (indicated by the vertical dashed lines) with the distribution of theoretical median interval durations.

dynamics over time, other approaches summarized this temporal dynamics into a single value (e.g. interval duration or a ratio). However, such summary values cannot disentangle the strength from the duration of the interaction.

## 4 | DISCUSSION

In this study, we explored the effectiveness of recurrent event analysis, particularly PAMMs, to study species interactions using

camera-trap data, comparing it with other commonly employed time-to-first-event models. Overall, PAMM demonstrated better performance than the time-to-first-event methods, we considered and provided the following advantages.

First, its statistical power either matched or surpassed that of the alternative methods, in both perfect and imperfect detection scenarios. Despite an overall loss of statistical power, none of the approaches considered exhibited bias due to imperfect detection at either the species or site level. However, it is important to note that the simulated imperfect detection process was generated

randomly and was not linked to environmental covariates (e.g. habitat openness) or species characteristics. While this approach offers simplicity, it does not fully capture the complexities of real-world processes that could lead to erroneous predictions, as highlighted by Bischof et al. (2014) and Dorman et al. (2018, see below). Future simulation studies incorporating covariate-based imperfect detection processes could provide valuable insights into this matter. By incorporating environmental variables that influence detection probabilities, such simulations could better mimic the intricacies of ecological systems and help elucidate any potential biases introduced by imperfect detection in species interaction studies.

Second, PAMMs (and linear models) also present the advantage of allowing for the incorporation of any (a)biotic information when evaluating interaction patterns. Dormann et al. (2018) emphasized the importance of considering underlying processes and potential (a)biotic confounding factors in species interaction studies to prevent misinterpreting statistical interactions as ecological interactions. While our simulations did not specifically address confounding effects of environmental covariates, our real-data example showed how PAMMs can integrate environmental covariates, such as vegetation openness levels or human disturbance. Although researchers should exercise caution in making ecological interpretations, incorporating environmental information in PAMMs may help disentangle true ecological interactions from confounding effects.

Third, PAMMs were less sensitive to the relative abundance of the species than other methods. In our simulations, species B exhibited relative abundance approximately 100 times higher than species A, and this asymmetry in abundance posed challenges when calculating intervals for all time-to-first-event methods (except for LM-1; see Appendix 3). We initially intended to focus our PAMM analysis on estimating the repulsion effect of species A on species B, given the greater abundance of species B and the corresponding higher number of observations of B, and thus richer information per survey. However, despite the sparse data, we successfully estimated both the duration and strength of the attraction effect of species B on species A. Therefore, it appears feasible to employ the PAMM approach even in scenarios involving species dyads with similar, relatively low abundances (e.g. between two apex predator species).

Finally, the use of PAMMs effectively circumvented the issue of interaction directionality, offering a way to discriminate between intricate scenarios of interactions between two species. Only MRPP-2 had the same ability to discriminate between the different situations but solely provided a measure of the median duration between successive detections of two species as a measure of the interaction effect. The problem with this approach is that the same median duration can correspond to vastly different scenarios (e.g. a strong but short effect versus a weak, long-lasting one, Appendix 4—Figure 6). On the opposite, PAMMs yielded outputs that were easier to interpret and more comprehensive, describing

the complete interaction effect over time along with its associated strength and duration.

However, certain limitations remain. As far as we know, no comprehensive data exists regarding the distribution of the strength and duration of repulsion and attraction processes between species *in natura*. Consequently, categorizing any effect as 'weak' or 'short' presents a challenge. However, our findings shed light on this issue. In our simulations, which mirrored predator–prey dynamics, it became evident that if the interaction effect was negligible (i.e. lasting less than 1 day), none of the tested approaches was able to detect it efficiently. Furthermore, it is important to note that our simulations were devoid of environmental noise, unlike real-world data, which are usually influenced by myriads of biotic and abiotic factors. Introducing noise into the interaction signal will likely exacerbate the challenge of detecting weak and/or short-term effects. Therefore, we advise exercising caution when interpreting the absence of an effect of one species on another.

Nonetheless, PAMMs are a promising tool to study species interactions, and the fact that they allow for non-linear temporal dynamics also offers new opportunities in ecological research. When employing a time-to-first-event model, it is assumed that the first observation of the secondary species reflects the expected response (repulsion or attraction), which implies that the individual observed is already aware of the previous presence of the primary species. However, this assumption may not always hold. Kuijper et al. (2014) observed that red deer (*Cervus elaphus*) exhibited behavioural responses to wolf (*Canis lupus*) scats only within 2 m of the scat. In a camera-trap setting, this could mean that some individuals of the secondary species may be detected at a site (i.e. in the field of view of the camera) before they become aware of the previous presence of the primary species. For instance, when the secondary species does not follow the same path as the primary species to arrive at the camera-trap site, it is probably unaware of the proximity to the primary species before arriving at the site, as no detectable cues were available. In such a situation, the first observation of a secondary species is likely to be 'naïve' regarding the proximity to the primary, and a time-to-first-event-based approach may fail to capture the attraction or repulsion response at all. In contrast, the recurrent event approach should be able to identify this change in an animal's behaviour after the first detection. For instance, we might expect a higher variability of the visitation rate estimation at the very beginning of the survey, as this period would represent a mixture of 'naïve' and 'aware' individuals. Future simulation work could focus on this process of information gathering on heterospecific presence and the subsequent reaction of the animals encountered at a camera trap, for example by simulating camera-trap data where all first events are naïve and the probability of occurrence shifts after the first visit (i.e. after information about the presence of the other species was gathered).

PAMM has demonstrated its capacity to handle two-species systems with complex species interaction structures. However, in natural ecosystems, species seldom interact without interference

from other species. To avoid the potential confounding effects of other interacting species, most methods rely on data censoring. For example, Parsons et al. (2016) considered only BAB intervals without any other tertiary species between two B events when applying AAR-2. Similarly, Swinkels et al. (2023) interrupted intervals whenever another non-target species appeared while assessing AB and BA intervals. We also implemented this approach when formatting the camera trap before applying PAMM. However, being able to incorporate information on the occurrence of tertiary species during the survey would be beneficial when estimating species interactions in a multi-species system for several reasons. It is, for instance, essential to note that the relative abundance of the different species can strongly influence the ability to use time-to-first-event or recurrent event-type models in the first place, as it can significantly impact the number of available intervals for time-to-first-event models or the number of events within surveys for recurrent event models. For example, when assessing the effect of a rare species (e.g. large carnivore) on another (e.g., prey), placing camera traps on hiking trails could reduce the number of useable surveys to zero if many humans are observed daily. Similarly, testing a repulsive effect between two large predators (e.g. leopard and tiger) might be challenging if preys occur at high abundances and frequently appear within leopard–tiger intervals. Nevertheless, we believe that with PAMM, it is possible to incorporate the effect of rare species on others by no longer including the rare species as the primary but, for instance, as a time-dependent covariate. For instance, by modelling the effects of tiger on leopard, we could control the effect of prey on leopard by including the time since the prey was observed as a time-dependent covariate. Further, we always considered the occurrence of a secondary species based on primary species and considered tertiary species as censoring events. In the future, one might try to model more complex relationships with different interactions between different species. Such work could further take into account different spatio-temporal dependencies (e.g. based on coordinates of the camera-trap sites and seasonality).

## 5 | CONCLUSIONS

Our simulations and real-data study revealed that PAMMs, as part of the recurrent event analysis framework, generally outperform time-to-first-event approaches in detecting species interactions. By disentangling the duration and strength of the interaction, PAMMs provide intuitive and interpretable outputs. Moreover, they can distinguish between complex situations that include mixed processes of repulsion and attraction between species. They also do not require permutations or comparisons with a theoretical model, often relying on strong and usually unverified assumptions. Overall, our study showed that reframing the question in terms of time-to-event analysis on the one hand and estimation in terms of GAMs on the other hand using PAMMs provides a

large, established toolbox of methods allowing all modelling strategies available for GAMs that can now be applied in the context of camera trap to answer a large set of ecological questions about species interactions.

## AUTHOR CONTRIBUTIONS

Nicolas Ferry, Pierre Dupont and Marco Heurich conceived the ideas; Nicolas Ferry designed the methodology; Nicolas Ferry simulated and analysed the data; Nicolas Ferry and Andreas Bender implemented the package; and Nicolas Ferry 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 conflicts of interest.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14338>.

## DATA AVAILABILITY STATEMENT

All data and R scripts are available via the Zenodo Digital Repository <https://doi.org/10.5281/zenodo.11085006> (Ferry et al., 2024).

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## SUPPORTING INFORMATION

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

**Appendix 1.** Complete description of (A) the simulation workflow and (B) the random thinning of observation mimicking imperfect detection.

**Appendix 2.** Detailed description of Karant et al. (2017) Multi Response Permutation Procedure approach applied to camera trap data.

**Appendix 3.** Visual description of the interval calculations for all the tested approaches and of the associated issues due to relative abundance (e.g., predator-prey dyad).

**Appendix 4.** Results of the part "Simulation - Statistical Power" for all tested approaches in case of perfect and imperfect detection.

**Appendix 5.** Details on the relative abundance issue and on the consequences of the species on which permutations are done for the Karanth et al. (2017) approach.

**Appendix 6.** Simulation example comparing the interpretability of the results between the different approaches.

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