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RESEARCH ARTICLE



Two-species occupancy modelling accounting for species misidentification and non-detection

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Abstract

- In occupancy studies, species misidentification can lead to false-positive detections, which can cause severe estimator biases. Currently, all models that account for false-positive errors only consider omnibus sources of false detections and are limited to single-species occupancy.
- 2. However, false detections for a given species often occur because of the misidentification with another, closely related species. To exploit this explicit source of false-positive detection error, we develop a two-species occupancy model that accounts for misidentifications between two species of interest. As with other false-positive models, identifiability is greatly improved by the availability of unambiguous detections at a subset of site x occasions. Here, we consider the case where some of the field observations can be confirmed using laboratory or other independent identification methods ("confirmatory data").
- 3. We performed three simulation studies to (1) assess the model's performance under various realistic scenarios, (2) investigate the influence of the proportion of confirmatory data on estimator accuracy and (3) compare the performance of this two-species model with that of the single-species false-positive model. The model shows good performance under all scenarios, even when only small proportions of detections are confirmed (e.g. 5%). It also clearly outperforms the single-species model.
- 4. We illustrate application of this model using a 4-year dataset on two sympatric species of lungless salamanders: the US federally endangered Shenandoah salamander *Plethodon shenandoah*, and its presumed competitor, the red-backed salamander *Plethodon cinereus*. Occupancy of red-backed salamanders appeared very stable across the 4 years of study, whereas the Shenandoah salamander displayed substantial turnover in occupancy of forest habitats among years.
- 5. Given the extent of species misidentification issues in occupancy studies, this modelling approach should help improve the reliability of estimates of species distribution, which is the goal of many studies and monitoring programmes. Further developments, to account for different forms of state uncertainty, can be readily undertaken under our general approach.

KEYWORDS

false positive, observation error, *Plethodon cinereus*, *Plethodon shenandoah*, site colonization, site extinction, species distribution modelling, species misidentification

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1 | INTRODUCTION

Estimation of species occurrence is central to many conservation efforts and scientific endeavours (Ferrier, 2002; Gaston, 2009; MacKenzie et al., 2006; Rushton, Ormerod, & Kerby, 2004). Indeed, interactions with sympatric species can be important drivers of a species' distribution dynamic (Wisz et al., 2013). For instance, competition between two species occupying similar niches might limit the range distribution, by limiting expansion or triggering range contraction, of one or both species (Sexton, McIntyre, Angert, & Rice, 2009). Reliable estimates of species occurrence and co-occurrence require accounting for observational errors, such as the imperfect detection of animals in the wild (MacKenzie et al., 2002; Tyre et al., 2003). When dealing with two species, accounting for detection is even more important because observation uncertainty exists for both species, which might introduce stronger biases on estimates of occurrence probabilities as well as on the species interaction parameter estimates (MacKenzie, Bailey, & Nichols, 2004). Occupancy models were explicitly developed to account for observation errors when estimating species occurrence. Generally, these estimators focus on only false absences, which occur when the species is present but not detected. Since the seminal paper of MacKenzie et al. (2002), occupancy methods have been extended to incorporate temporal dynamics (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003), species co-occurrence (MacKenzie et al., 2004), multistate variables (MacKenzie, Bailey, Hines, & Nichols, 2011; MacKenzie, Nichols, Seamans, & Gutiérrez, 2009) and community and regional patterns of occurrence (Dorazio, Royle, Söderström, & Glimskär, 2006; Miller & Grant, 2015).

While the set of tools available to account for false absences has been well developed, much less effort has gone into modelling falsepositive detections. False positives occur when a species is recorded as detected despite not being present at a site. The first attempt to deal with false positives within an occupancy framework was developed by Royle and Link (2006). They developed the basic estimator and provided a detailed outline of the challenges encountered when both false-negative and false-positive detection errors occur. Subsequent developments have focused on methods to increase identify ability of these two sources of observational heterogeneity. Examples include combining data with a second unambiguous source (Chambert, Miller, & Nichols, 2015; Miller et al., 2011, 2013), validating observations post hoc using a second method (e.g. DNA for scat samples), including multiseason dynamics in the model (Miller et al., 2013, 2015), spatial autocorrelation (Pacifici et al., 2017) and including information about the relative intensity of detections (Miller et al., 2011). In all these cases, including additional information improves the ability to generate accurate and unbiased estimates of species occurrence (Miller et al., 2015).

One unexplored source of information for identifying when false-positive errors are likely to occur comes from the process by which misidentifications usually occur. In most studies, a false-positive detection occurs because one species is misidentified as a second species. When these misidentification errors occur between only

two species, one can surmise that the probability of a false-positive detection for a species A is zero when a species B does not occur at the site and will be non-zero only when species B does occur. Thus, the distribution of the second species should help define where misidentification does and does not occur. In addition, as mentioned above, failing to account for confusion in the identity of co-occurring species can lead to bias in estimating single-species distributions as well as patterns of co-occurrence and species interaction. However, the distribution of species B is itself an unknown parameter and accounting for the second species requires simultaneously estimating occupancy of both species.

A robust set of estimators has been developed for estimating patterns of occurrence and co-occurrence using two-species models (MacKenzie et al., 2004; Richmond, Hines, & Beissinger, 2010; Waddle et al., 2010). These methods have been extended to incorporate multiseason dynamics (Yackulic et al., 2014) and both habitat dynamics and species interactions (Davis et al., 2017; Miller, Brehme, Hines, Nichols, & Fisher, 2012). However, these methods all assume that the two species are not misidentified, hence ignoring the potential for false-positive detections.

In this paper, we develop a general approach for modelling false-positive errors when error rate for one species is dependent on the presence of another species. We provide a general parameterization for dealing with misidentification errors and explore if and how the model reduces bias and improves accuracy using both simulated and real-world datasets.

2 | MODEL DESCRIPTION

This model estimates site occupancy probability for two species, from detection/non-detection data, when misidentification between the two species of interest can occur. First, we consider the case of a single season occupancy study, and then describe the multiseason extension, which models colonization and extinction dynamics, for each species, between consecutive seasons (MacKenzie et al., 2003).

2.1 | Single season occupancy model

The sampling frame for data collection is as follows. In a single season, a selected number of sites $i = \{1,, I\}$ is surveyed, repeatedly, J_i times. Individual surveys (i.e. sampling occasions) are denoted $j = \{1, ..., J_i\}$. For the sake of simplicity, in what follows, we will consider an equal number of sampling occasions for all sites, such that $J_i = J$ for any site i. At each site x occasion $\{i, j\}$, field observers record whether they detected either of the two species of interest, which we will refer to as species A and species B. Field observation (y_{ij}) can thus take four values (hereafter, "observation states"): "O" if neither of the species was detected; "A" if only species A was detected; "B" if only species B was detected; "AB" if both species were detected. Similarly, we model the true, unknown occupancy status (z_i) of any site i as a multistate process

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combining the presence/absence of both species, which leads to four possible values (hereafter, "occupancy states"): "0" if neither of the species is present; "A" if only species A is present; "B" if only species B is present; "AB" if both species are present. As with most occupancy models, we assume closure, which means that the occupancy state of a site remains constant across all sampling occasions.

We consider two different model formulations for the species' probabilities of occupancy and co-occurrence. The first model formulation, which follows MacKenzie et al. (2004), considers a general interaction between the two species. The probability of occupancy of each species is defined unconditionally on the other species' presence or absence, and the probability of co-occurrence is modelled through a common interaction term (γ). Under this formulation (hereafter, the general interaction), we define ψ_i^A and ψ_i^B as the unconditional probabilities of occupancy of species A and B, respectively, at site i. The probability of co-occurrence is defined as $\psi_i^{AB} = \psi_i^A \times \psi_i^B \times \gamma$, where γ is the interaction term, sometimes referred to as the species interaction factor (SIF; MacKenzie et al., 2004). When γ = 1, the two species occur totally independently of each other. On the other hand, γ < 1 indicates that the two species tend to avoid each other (e.g. competition), while $\gamma > 1$ indicates that they favour co-occurrence (e.g. similar habitat preferences). Under this general interaction model formulation, the vector of probabilities (Φ) describing the four mutually exclusive occupancy states (0, A, B and AB respectively) is:

$$\Phi = \begin{bmatrix} 1 - \psi^A - \psi^B + \psi^{AB} & \psi^A - \psi^{AB} & \psi^B - \psi^{AB} & \psi^{AB} \end{bmatrix}.$$

Note that we removed the site subscripts (i) here for ease of reading, but this vector of probabilities could be made site-specific (Φ_i).

The second model formulation, which follows Richmond et al. (2010), considers that one species is dominant over the other. Under this formulation (hereafter referred to as the dominance interaction), occupancy of species A (the dominant species) is independent of the presence or absence of species B (the subordinate species). The unconditional probability of site occupancy of species A is defined as ψ_i^A . Occupancy of species B is conditional on whether or not species A is present at the site of interest. We define $\psi_i^{B|a}$ as the probability of occupancy of species B at sites where species A is not present, and $\psi_i^{B|A}$ as the probability of occupancy of species B at sites where species A is present. To be consistent with the notation used in the general interaction model, we redefine $\psi^{B|A}\!=\!\psi^{B|a}\!*\!\gamma,$ where γ can be interpreted has the effect of presence of species A on the probability of site occupancy of species B. Here, γ = 1 indicates no effect, γ < 1 indicates a negative effect, such that species B is less likely to be present when species A occupies the site (e.g. one-way competitive effect), while $\gamma > 1$ indicates a positive effect of species A on the probability of occurrence of species B. Under this dominance interaction formulation, the multistate occupancy probability vector Φ is (here again, not including site-specific subscripts i):

$$\Phi = \left[(1 - \psi^A)(1 - \psi^{B|a}) \quad \psi^A(1 - \psi^{B|A}) \quad (1 - \psi^A)\psi^{B|a} \quad \psi^A\psi^{B|A} \right].$$

For both formulations, the two-species occupancy state process is then modelled as a multinomial process:

$z_i \sim Multinomial(\Phi)$.

The observation process that links latent occupancy states (z_i) to the multistate data (y_{it}) consists of two types of processes: (1) the detection of a species (A and/or B) given that it is truly present at a site and (2) the false detection of a species (A or B) given that is not present at a site, which, here, can only result from the misidentification of some specimen from the other species. It is this latter constraint on the process of misidentification that distinguishes this new class of models from existing false-positive models (Chambert et al., 2015; Miller et al., 2011, 2013). To model the observation state process, we define the following sets of parameters: (1) $p^{A}[p^{B}]$ is the probability of correctly detecting species A [B] at a site where only species A [B] is present; (2) $r^{A}[r^{B}]$ is the probability of correctly detecting species A [B] at a site where both species are present; (3) ω^A and ω^a [ω^B and ω^b] are the probabilities of erroneously detecting species B [A] at a site where only the other species, A [B], is present (i.e. some specimens of species A [B] are misidentified as species B [A]). We refer to these (ω) parameters as probabilities of species misidentification, and the distinction between ω^A and ω^a [ω^B and ω^b] is defined as follows. Uppercased parameter ω^A [ω^B] represents the probability that some specimens of species A [B] are misidentified as being species B [A] when species A [B] has also been correctly detected at that site x occasion. Lowercased parameter ω^a [ω^b] is the probability that some specimens of species A [B] are misidentified as being species B [A] when species A [B] has not been correctly detected at that site x occasion. This distinction allows us to account for the non-independence that might exist between true detection and misidentification. For instance, when several animals are caught and held next to each other, if some are easily identified as belonging to, let's say, species A, this might influence the identification of the remaining specimens, for which identity might be less clear-cut. In the analyses presented in this paper, we consider two cases: (1) the case where misidentification and correct detection are independent (i.e. $\omega^a = \omega^A$ and $\omega^b = \omega^B$) and (2) the case where the probability of misidentification is influenced, positively or negatively, by the occurrence of correct detections ($\omega^a \neq \omega^A$ and $\omega^{b} \neq \omega^{B}$).

The probabilities of field observation states ($y_{ij} = \{0, A, B, AB\}$), conditional on the true occupancy state z_i of a site, are defined by the probability matrix Π shown in Table 1. Field data are thus modelled as:

$$y_{it}|z_i \sim Multinomial(\Pi_{z_i}),$$

where Π_{z_i} is the probability vector corresponding to a specific occupancy state z_i (i.e. a row of matrix Π ; Table 1)

As one can see from matrix Π (Table 1), the three non-null states $(z_i = \{A, B, AB\})$ cannot be strictly disentangled from field observations only, such that none of the states can be unambiguously determined. Indeed, whenever we observe A, B or AB, any of these three states is possible. Without any additional assumption, this creates issues of

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TABLE 1 Probability matrix (Π) for the field data observation state process (columns), conditional on true occupancy state (rows)

	Field data (y_{ij}) : observation state				
True state	0	Α	В	AB	
$z_i = 0$	1	0	0	0	
$z_i = A$	$(1 - p^{A})(1 - \omega^{a})$	$p^A(1-\omega^A)$	$(1-p^A) \omega^a$	$p^A_{\omega}^A$	
$z_i = B$	$(1 - p^{B})(1 - \omega^{b})$	$(1 - p^B)\omega^b$	$p^{B}(1-\omega^{B})$	$p^B\omega^B$	
$z_i = AB$	$(1-r^A)(1-r^B)$	$r^{A}\left(1-r^{B}\right)$	$(1-r^A)r^B$	$r^{A}r^{B}$	

Each row corresponds to the probability vector Π_z that defines the probabilities of each observation state conditionally on a site's occupancy state z_r . See the main text for a description of the parameters shown in Table.

 p^{A} [p^{B}] is the probability of correctly detecting species A [B] at a site where only species A [B] is present; $r^A[r]^B$ is the probability of correctly detecting species A [B] at a site where both species are present; ω^A and $\omega^{a} [\omega^{B}]$ and ω^{b} are the probabilities of erroneously detecting species B [A] at a site where only the other species, A [B], is present (i.e. some specimens of species A [B] are misidentified as species B [A]).

parameter identifiability, so additional data will usually be required. Typically, in the presence of misidentification, one will try to confirm species identity for at least a subset of animals that were captured. For instance, species identity could be confirmed through post hoc analyses of genetic material collected in the field or from detailed morphological investigation (e.g. under the microscope) of collected specimens. We will refer to these confirmed species-identity data as confirmatory data, wii, which will be assigned a value for all site x occasions ($I \times J$). Confirmation of species identity can only occur if we detected (captured) some animals, so, by definition, for any site x occasion where $y_{ii} = 0$, we cannot confirm identity. In these cases, we define $w_{ii} = 0$, which means that no identity was confirmed. Similarly, for any site x occasion where $y_{ii} \neq 0$, but for which no confirmation was done, we will assign $w_{ii} = 0$. Species identity confirmation will typically only be performed on a subset of specimens and thus only for a fraction of site x occasions. The reason is that the confirmation process (e.g. genetic analyses) has a cost, and it is often prohibitive or undesirable to confirm 100% of our detections. In fact, if we did, we would not need to use a misidentification model and could simply use the existing co-occurrence models (MacKenzie et al., 2004; Richmond et al., 2010). For site x occasions where animals were detected and species identity confirmed for at least some of them (e.g. we detected five animals and ran genetic analyses on three), data w;; can take one of three possible values: "A" if only species A was confirmed, "B" if only species B was confirmed, "AB" if both species A and B were confirmed. This additional information reduces uncertainty in occupancy state for any site i where confirmatory data are available. Indeed, if $w_{ii} = A [w_{ii} = B]$, the only possible states are now z_i = A or AB [z_i = B or AB], and if w_{ii} = AB, we now know with certainty that z_i = AB. We emphasize that, here, confirmation of species A only [B only] does not negate the possibility of the presence of the other species, B [A], for two reasons. First, we might have failed to catch species B [A] in the field, so no specimen of that species was available for the confirmation process. Second, we might have caught some

specimens of species B [A] in the field, but none of these was selected as part for the confirmation process. In this case, it means that, by chance, we only selected specimens from species A; hence, only species A could be confirmed. For a given analysis, the more confirmatory data that are available, the more accurate estimators will be (Ruiz-Gutierrez, Hooten, & Grant, 2016). To capture this notion, we define the "proportion of confirmatory data" (PCD) as the proportion of site x occasions with some confirmed detections ($w_{ii} \neq 0$) among all site x occasions with some field detections ($y_{ii} \neq 0$):

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$$PCD = \sum_{i}^{I} \sum_{j}^{J} \{i,j\}_{w_{ij} \neq 0} / \sum_{i}^{I} \sum_{j}^{J} \{i,j\}_{y_{ij} \neq 0}$$

Overall, the confirmatory data w_{ii} can take the same four values as field data y_{ii} , that is, {0, A, B, AB}. To distinguish sites-occasions {i, j} where no observation was confirmed (w_{ii} = 0 with probability 1) from sites-occasions where some observations were confirmed ($w_{ii} \neq 0$), we define the binary variable g_{ii} , with $g_{ii} = 1$ indicating confirmation and g_{ii} = 0 the absence of confirmation. The matrix Ω (Table 2) provides the probability statements of each possible value of confirmatory data w_{ii} conditional on (i) the occupancy state of site i and (ii) the value of g_{ii} . Any time that no observation was confirmed ($g_{ii} = 0$), the only possible state for w_{ij} is 0. On the other hand, when $g_{ij} = 1$, the probability that $w_{ii} = 0$ is null, as something was necessarily confirmed. If the site is truly occupied by species A [B] only, then the only possible value for w_{ii} is A [B], as it is impossible to confirm a species that is not present at a site. In Table 2, parameters $\eta^{\text{A}}[\eta^{\text{B}}]$ represent the probability that only species A [B] is confirmed at a site that was actually occupied by both species (e.g. only specimens of species A [B] were collected and sent for genetic analyses). By complementarity, the probability that both species A and B were confirmed is defined as $\eta^{AB} = 1 - \eta^A - \eta^B$. It is important to note that, here, we do not model the misidentification process at the level of individual observations, but only at the site level. This approach is equivalent to the Site Confirmation design described by Chambert et al. (2015).

From the probability vector Φ and the probability matrices Π and Ω , we can write the probability statement of any site's encounter history $h_i = \{y_i, y_i\}$. For instance, consider a site with three surveys and the following data $h_i = \{y_i = A \ 0 \ A; \ W_i = 0 \ 0 \ A\}$: Species A was detected two times in the field and confirmed once. Species B was never detected in the field nor confirmed. This site is surely occupied by species A, but it could also be occupied by species B, if we failed to detect it. As we only confirmed observation(s) from occasion 3, we define $g_{i1} = g_{i2} = 0$ and $g_{i3} = 1$. Under the general interaction model, the probability statement for this encounter history is:

$$\begin{split} & \text{Pr}\left(h_{i} = \left\{y_{i.} = A \, \text{OA}; w_{i.} = 0 \, \text{OA}\right\}\right) \\ & = \left(\psi^{\text{A}} - \psi^{\text{AB}}\right) \times \left[p^{\text{A}} \, \left(1 - \omega^{\text{A}}\right) \left(1 - g_{j1}\right) \times \left(1 - p^{\text{A}}\right) \left(1 - \omega^{\text{a}}\right) \left(1 - g_{i2}\right) \times p^{\text{A}} \, \left(1 - \omega^{\text{A}}\right) \, g_{i3}\right] \\ & + \, \psi^{\text{AB}} \times \left[r^{\text{A}} \, \left(1 - r^{\text{B}}\right) \left(1 - g_{j_1}\right) \times \left(1 - r^{\text{A}}\right) \left(1 - r^{\text{B}}\right) \left(1 - g_{j_2}\right) \times r^{\text{A}} \, \left(1 - r^{\text{B}}\right) \, g_{i3}\right] \end{split}$$

The first part of the equation (left hand side of the "+" sign) corresponds to the case where $z_i = A$, while the second part (right hand side of the "+" sign) corresponds to the case where z_i = AB. If we replace g_{ii} with its known values, we have $(1 - g_{i1}) = (1 - g_{i2}) = 1$ and g_{i3} = 1, and therefore, the statement reduces to:

TABLE 2 Probability matrix (Ω) for the confirmatory data observation state process (columns), conditional on true occupancy state (rows) and on whether $(g_{ij}=1)$ or not $(g_{ij}=0)$ any observation was confirmed at the site x occasion $\{i,j\}$ of interest

	Confirmatory data (w _{ij}): observation state							
True state	0	Α	В	АВ				
$z_i = 0$	1	0	0	0				
$z_i = A$	1 – g _{ij}	g_{ij}	0	0				
$z_i = B$	1 - g _{ij}	0	g_{ij}	0				
$z_i = AB$	1 - g _{ij}	$g_{ij} \times \eta^{A}$	$g_{ij} \times \eta^B$	$g_{ij} \times \left(1 - \left(\eta^A + \eta^B\right)\right)$				

We note that g_{ij} are known values, not parameters to be estimated. See the main text for a description of the parameters shown in table. $\eta^A[\eta^B]$ is the probability that only species A [B] is confirmed at a site that was actually occupied by both species.

$$Pr(h_i = \{y_i = A \ 0 \ A; w_i = 0 \ 0 \ A\})$$

$$= (\psi^A - \psi^{AB}) \times [p^A (1 - \omega^A) \times (1 - p^A)(1 - \omega^A) \times p^A (1 - \omega^A)]$$

$$+ \psi^{AB} \times [r^A (1 - p^B) \times (1 - r^A)(1 - r^B) \times r^A (1 - r^B)\eta^A].$$

Under the *dominance interaction* model, the probability statement would almost be the same; we would simply replace ($\psi^A - \psi^{AB}$) with ψ^A (1 – $\psi^{B|A}$) and ψ^{AB} with $\psi^A\psi^{B|A}$. It is also useful to note that, without the confirmation data at occasion 3 (i.e. if w_{i3} = 0), the probability statement would include an additional piece corresponding to the case where z_i = B:

$$\begin{split} & \Pr(h_{i} = \{y_{i} = A \ OA; \mathbf{w}_{i} = \mathbf{0} \ \mathbf{0} \ \mathbf{0} \}) \\ & = (\psi^{A} - \psi^{AB}) \times [p^{A}(1 - \omega^{A}) \times (1 - p^{A})(1 - \omega^{a}) \times p^{A}(1 - \omega^{A})] \\ & + \psi^{AB} \times [r^{A} \ (1 - r^{B}) \times (1 - r^{A})(1 - r^{B}) \times r^{A}(1 - r^{B}) \eta^{A}] \\ & + (\psi^{B} - \psi^{AB}) \times [(1 - p^{B})\omega^{b} \times (1 - p^{B})(1 - \omega^{b}) \times (1 - p^{B})\omega^{b}] \end{split}$$

We note that in the first example, where $w_{i3} = A$, the statement corresponding to $z_i = B$ (last line here) equals zero because $\Pr\left(w_{i3} = A|z_i = B\right) = 0$. In the second example, the whole statement for $\Pr(w_{i3} = A \mid z_i = B) = 0$ is maintained because $\Pr\left(w_{i3} = 0 \mid z_i = B\right) = 1 - g_{i3} = 1$, given that $g_{i3} = 0$. This approach to writing probabilistic statements is generalizable to any encounter history and can be succinctly expressed as:

$$\Pr\left(h_{i}|g_{i},\boldsymbol{\theta}\right) = \Phi * \left[\prod_{j=1}^{J_{i}} \left(\Pi_{y_{ij}} \times \Omega_{\mathbf{w}_{ij}}\right)\right]$$

where $\boldsymbol{\theta}$ represents all of the model's parameters, $g_{i.}$ is the ensemble of g_{ij} values of site i across all sampling occasions j, and $\Pi_{y_{ij}}$ and $\Omega_{w_{ij}}$ are probability vectors corresponding to the columns of matrices Π and Ω for observation states y_{ij} and w_{ij} , respectively (Tables 1, 2). The symbol * denotes a matrix multiplication, while X denotes a scalar product among the corresponding cell probabilities (i.e. same "occupancy state X observation state" cell of matrices Π and Ω). The overall model likelihood is obtained by multiplying all sites' encounter history probabilities:

$$L(\boldsymbol{\theta}|\boldsymbol{h}, \boldsymbol{g}) = \prod_{i=1}^{l} Pr(\boldsymbol{h}_{i}|\boldsymbol{g}_{i}, \boldsymbol{\theta})$$

where g is the ensemble of g_i values across all sites.

This model can be extended to >1 seasons. The multiseason extension is presented in Appendix A1.

3 | ANALYSES

3.1 | Simulated data

We performed three simulation studies to evaluate the properties of the single-season model described (see Appendix A2 for full details). First, we assessed the performance of different model formulations (species interaction: general vs. dominance; misidentification: dependent vs. non-independent). All model formulations performed well (Figure 1). There was no or very little bias, precision and accuracy (RMSE) were high, and the 95% CI coverage was close to 0.95 for all parameters (see also Appendix A2).

Next, we investigated the influence of increasing proportions of confirmatory data (PCD) on estimation accuracy: PCD = {5%, 10%, 20% and 30%}. As expected, estimation accuracy (especially precision) increased with more confirmatory data (Figure 2), but we note that the model performed really well even at low PCD values (e.g. 5%).

Finally, we compared the performance of this two-species model with the single-species false-positive model developed by Miller et al. (2011). The two-species model always provided more accurate estimates (lower bias, more precise) than the single-species model (Table 3; for more details, see also Appendix A2).

3.2 | Real data

We applied the modelling approach to real data on two closely related species of Plethodontid salamanders which historic literature suggests are in strong competition (Jaeger, 1971): the widespread red-backed salamander *Plethodon cinereus* (coded as "C" below, e.g. ψ^{C}) and the Federally Endangered Shenandoah salamander *Plethodon shenandoah* (coded as "S", e.g. ψ^{S}). A full description of the methods used for data collection and confirmation of species identity is available in Appendix A3.

We used the multiseason model to account for potential changes in site occupancy states between consecutive years. We started the analysis using the *general independent* model which consisted of 15 model parameters (see Table 4). This model ran well, but for four of the parameters (γ^C , ε^C , r^C and η^C), which were either close to a boundary (0,1) or informed by very little data, estimation of standard errors was unreliable (Table 4). We solved this issue by a slight simplification of the model's parameterization (going from 15–13 parameters), assuming $r^C = p^C$ and $r^S = p^S$. This assumption simply states that the detection of each species is independent of whether or not the other species is present at the same site, which seems appropriate given the ecology of these salamanders. This model ran well and standard errors were identifiable for all parameters (Table 4), although still poorly estimated for parameters on the boundary, which is a common issue. All other model parameters were estimated precisely, and

(c) dominance, independent

Bias = 0.045 RMSE = 0.247 Cl cov. = 0.972

120

8

9

8

200

150

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20

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150

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8

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100

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8

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10

γ

(a) general, independent

8

80

8

40

8

150

100

20

50

유

8

8

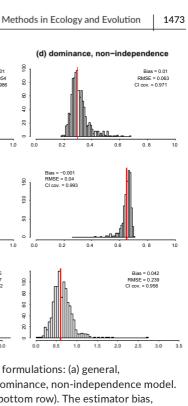


FIGURE 1 Summarized results of the first simulation study, which focused on four different model formulations: (a) general, independence model; (b) general, non-independence model; (c) dominance, independence model; (d) dominance, non-independence model. Estimation accuracy of the three occupancy parameters is shown: ψ^A (top row), ψ^B (middle row) and γ (bottom row). The estimator bias, root-mean-squared error (rmse) and the coverage of 95% Cl's (Cl cov.) is shown on each individual plot. The proportion of site x occasion for which some detections were confirmed was 30%. The red line represents the true parameter value used to generate the data

Bias = 0.032 RMSE = 0.182 Cl cov. = 0.898

(b) general, non-independence

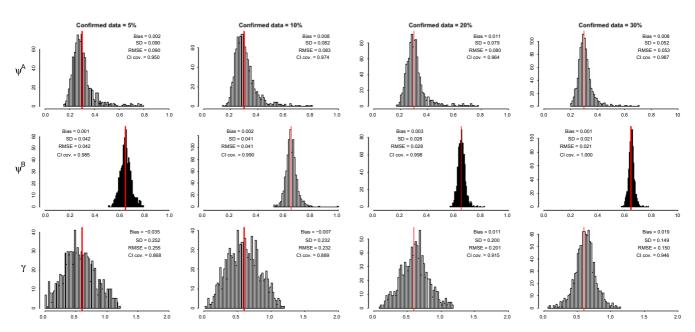


FIGURE 2 Results of the second simulation study. Model performance was assessed for the following proportions of confirmatory data: 5%, 10%, 20% and 30% (left to right columns on the graph). Data were simulated and analysed using the "general interaction, independence misidentification" model. Estimation accuracy of the three occupancy parameters is shown: ψ^{B} (top row), ψ^{B} (middle row) and γ (bottom row). The estimator bias, standard deviation (SD), root-mean-squared error (rmse) and the coverage of 95% Cl's (Cl cov.) is shown on each individual plot. The red line represents the true parameter value used to generate the data

they were virtually identical to those of the model with 15 parameters (Table 4), which reinforces our confidence that the issue with this latter model only concerned standard errors (and not point estimates of the parameters). As expected, the probability of occupancy of red-backed salamanders was much higher (almost threefold) than

that of the Shenandoah salamander ($\hat{\psi}^C = 0.41 [0.30 - 0.53], \hat{\psi}^S = 0.15$ [0.08-0.27], Table 4). The species interaction factor for 2011 was very close to 1.0 ($\hat{\gamma}$ =0.98 [0.50-1.95]) suggesting that both species occurred independently of each other. We interpret this latter result with caution because sampled sites cover an area much larger than

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the known range of Shenandoah salamanders, which may obscure any interaction that could be observed if the sampling was confined to just the areas where both species could be interacting (such as on the range boundary of the Shenandoah salamander). As expected, we also found occupancy of red-backed salamanders to be very stable over the survey period $(\hat{\delta}^{C} = 0.00 [0.00 - 1.00], \hat{\epsilon}^{C} = 0.00 [0.00 -$ 1.00]), while for Shenandoah salamanders, the turnover was clearly non-null ($\hat{\delta}^S$ = 0.19 [0.06-0.47], $\hat{\epsilon}^S$ = 0.10 [0.02-0.37]). This pattern of colonization-extinction can be explained by true differences in each species' turnover dynamics but, also in part, by the fact that the sampling covered the entire range (and beyond) of Shenandoah salamanders, but only a small part of the red-backed salamander's range.

DISCUSSION

We presented a modelling approach aimed at estimating site occupancy for two species in the presence of misidentification errors. We provided both single- and multiseason versions of this model, the latter allowing estimation of colonization and extinction dynamics. More than a simple extension of previous false-positive occupancy models to >1 species, this model provides a clear improvement in estimation accuracy, because it accounts explicitly for the source of false detections. Indeed, false detections are often due to the misidentification with another species (Miller, Weir, et al., 2012), as illustrated by our real data example on two closely related species of terrestrial salamanders. Existing false-positive models (Chambert et al., 2015; Miller et al., 2011, 2013; Royle & Link, 2006) do not explicitly recognize this feature and, instead, define an omnibus (or ubiquitous) source of false detections, assumed to be homogeneous across all sites. Our twospecies model provides a very natural approach to modelling the misidentification process more explicitly, which ultimately leads to higher estimation accuracy, as shown in our third simulation study. Indeed, the data available for one species' occupancy are also informing the chance of erroneously detecting the other species at a given site. Of course, the lower performance observed for the single-species model cannot be extrapolated beyond cases where false detections are directly due to the misidentification of specimens from a sympatric species. When false detections are primarily due to other factors (e.g. wind disturbance in automated acoustic surveys), the single-species approach remains the most appropriate model.

Our two-species model performed very well under the various scenarios and assumptions assessed (see simulation 1). With the realistic sample sizes used in our simulations (100 sites, 6 visits per site), we found good estimator accuracy even with small proportions of confirmatory data (simulation 2). For instance, in our simulation scenario considering 5% of confirmatory data, some detections (not necessarily all of them) were confirmed at only 15 sites of 296 sites with detections. This represents a fairly small and entirely realistic effort. Doubling this effort to 30 sites would lead to even higher estimation accuracy (see Figure 2; PCD = 10%).

Estimates from the real data analyses displayed levels of standard errors that were acceptable, except for the few parameters

Results of the third simulation study. Root-mean-square error (RMSE) of each species' occupancy estimators က TABLE

				Two-species model	model		Single-species model	s model	
Associated figure	Interaction model	Misidentification model	Occupancy model	Species A	Species B	Summed RMSE	Species A	Species B	Summed RMSE
3A	General	s = 0.5	ψ ^A < ψ ^B	0.058	0.020	0.078	0.049	0.045	0.094
3B	General	0,5 < 00,5	$\psi^A < \psi^B$	0.065	0.023	0.088	0.144	0.052	0.196
3C	Dominance	$0.0^{\circ} = 0.0^{\circ}$	$\psi^A < \psi^B$	0.056	0.024	0.080	0.057	0.047	0.104
3D	Dominance	0,5 < 0,5	$\psi^A < \psi^B$	0.068	0.028	960.0	0.192	0.064	0.256
4A	General	0° > 00 S	$\psi^A < \psi^B$	0.065	0.024	0.089	0.166	0.071	0.237
4B	Dominance	0, > 0, S	ψ ^A < ψ ^B	0.068	0.028	960:0	0.204	0.080	0.284
5A	General	s < 00 < 00	ψ ^A > ψ ^B	0.046	0.043	0.089	0.099	0.089	0.188
5B	Dominance	0° > 0° S	$\psi^A > \psi^B$	0.037	0.031	0.068	0.063	0.108	0.171

The summed RMSE is the sum of the RMSE for the two species' occupancy estimator, under a given model (single- or two-species model)

estimated close to zero. The results provided very relevant levels of occupancy for both species, with the red-backed salamander occupying about three times as many sites as the Shenandoah salamander, as we expected based on the differences in the coverage of our sampling across the species' ranges. Results did not reveal any apparent competition between the two species (SIF close to 1), but they clearly indicated that the Shenandoah salamander had much higher turnover dynamics than the red-backed salamander. Both these results concur with the fact that the sampling covered the entire range of the Shenandoah salamander, but only a small part of the red-backed salamanders. Regarding the observation process, the probability of detection for both species was fairly high $(p^{C} = 0.84 [0.74-0.91], p^{S} = 0.65 [0.50-0.77])$, and the probability of site's status misclassification (as a result of species misidentification) was higher than expected, especially for the rare species $(\omega^S = 0.12 [0.05-0.26])$. In the field, specimens were preferentially collected and sent for genetic confirmation at sites where species overlap was strongly suspected, and when there clearly was a doubt about the specimen in hand. This non-random selection process for the confirmatory detection might have inflated the estimate of misidentification. Also, given the low proportion of confirmatory detections available (PCD = 3.8%), some caution is warranted when interpreting these results. Some issues of parameter identifiability were also observed in the real dataset analysis, likely due to the small sample sizes (substantially lower than those used in the simulations) and the fact that the model included additional parameters for the multiseason colonization-extinction dynamics. Here, our sample size provided us with about 11 [resp. 13] data

points per parameter for the model with 15 [resp. 13] parameters. In contrast, in our simulation study, we had about 60 data points per model parameter. We suspect that this model can become data hungry as more parameter complexity is introduced (multiseason dynamics, covariate and random effects, etc.), and advise caution in the presence of small sample sizes. Ideally, one should target sample sizes of ≥30 data points per parameter, but it seems that even with sample sizes around 15 data points per parameter, the model should perform adequately. Further investigation of this and other false-positive models is warranted to better understand how they behave at small sample sizes (Clement, 2016).

The model presented in this paper belongs to the class of multistate occupancy models (MacKenzie et al., 2009; Miller, Brehme et al., 2012; Yackulic et al., 2014), but with an added layer of parameters to account for state uncertainty. An important feature of our approach is that it relies on a subset of confirmatory data to reduce the uncertainty of some sites' status (Chambert et al., 2015). Without this additional information, model parameters can still be identifiable, given that adequate sample sizes are available, but estimation accuracy is greatly improved by the addition of such information, as shown for other false-positive models (Miller et al., 2011; Ruiz-Gutierrez et al., 2016). We strongly encourage investigators to collect, when possible, any additional information when they suspect species misidentification to be an issue. Confirmatory data must correspond to unambiguous (or less ambiguous) detections, and they can be provided through different means, as shown elsewhere (e.g. Chambert et al., 2015; Miller et al., 2013; Pillay, Miller, Hines, Joshi, & Madhusudan, 2014). They might correspond to a different

TABLE 4 Estimates of model parameters from the salamander data analysis. Results from both analyses (i.e. models with 15 and 13 parameters) are shown

	Model with 15 parameters				Model with 13 parameters			
Parameter	Estimate	SE	LCL	UCL	Estimate	SE	LCL	UCL
ψ^{C}	0.42	0.056	0.32	0.53	0.41	0.058	0.30	0.53
ψ^{S}	0.13	0.039	0.07	0.23	0.15	0.049	0.08	0.27
γ	0.90	0.360	0.42	1.91	0.98	0.343	0.50	1.95
δ^{C}	0.00	NA	NA	NA	0.00	0.003	0.00	1.00
ϵ^{C}	0.00	NA	NA	NA	0.00	0.007	0.00	1.00
δ^{S}	0.16	0.078	0.06	0.37	0.19	0.105	0.06	0.47
ε ^S	0.13	0.071	0.04	0.34	0.10	0.075	0.02	0.37
p ^C	0.78	0.041	0.69	0.85	0.84	0.043	0.74	0.91
p ^S	0.68	0.068	0.54	0.80	0.65	0.070	0.50	0.77
r ^C	1.00	NA	NA	NA	-	-	-	-
r ^S	0.76	0.089	0.55	0.89	-	-	-	-
ω^{C}	0.06	0.023	0.03	0.13	0.03	0.026	0.01	0.14
ω^{S}	0.11	0.038	0.05	0.21	0.12	0.050	0.05	0.26
η^{C}	0.66	0.284	0.14	0.96	0.67	0.276	0.15	0.96
η^{S}	0.00	NA	NA	NA	0.00	0.060	0.00	1.00

Species C corresponds to the red-backed salamander P. cinereus and species S to the Shenandoah salamander P. shenandoah.

The SE as well as the lower (LCL) and upper (UCL) limits of the 95% confidence intervals are also provided. The model with 15 parameters considers $r^C \neq p^C$ and $r^S \neq p^S$, while the model with 13 parameters considers $r^{C} = p^{C}$ and $r^{S} = p^{S}$.

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type of observation collected during the same or different surveys as the ambiguous observations. For instance, a large volume of ambiguous data might be provided through auditory detections, while infrequent visual observations provide fewer, but unambiguous detections (Miller et al., 2011). Similarly, in large predator surveys (Molinari-Jobin et al., 2012), it is common to collect any clue available, some of which are highly uncertain (pug marks, scats) while others are totally unambiguous (reports of a dead animal found, visual observation of the animal by an expert). On the other hand, they can be provided by the a posteriori validation of ambiguous detections, for instance, through the analysis of genetic material of captured animals, as in our salamander example. Other examples include the validation, under the microscope, of specimens collected in the field (insects, larvae), validation by an expert of a subset of acoustic detections provided by an automated call-recognition programme (Chambert et al., 2017, in press) and post hoc analysis of specimen photographs (Conn et al., 2013; McClintock et al., 2015).

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Occupancy approaches have become a method of choice for many wildlife studies and monitoring programmes (Bailey, MacKenzie, & Nichols, 2014). Many of the assumptions and limitations of the seminal occupancy models (MacKenzie et al., 2002, 2006) have already been relaxed (Bailey et al., 2014). Species misidentification can be a major impairment to the success of such studies, because it is likely to cause large biases (McClintock, Bailey, Pollock, & Simons, 2010; Miller et al., 2011, 2015). The model described here, along with falsepositive models previously developed (Chambert et al., 2015; Miller et al., 2011, 2013; Ruiz-Gutierrez et al., 2016), provide an important step to making occupancy approaches even more useful and reliable. Although such an approach can be data hungry and might require substantial field effort, it should still involve much less effort than what is typically required for individual-based monitoring, such as mark-recapture methods. Finally, it is important to note that this approach, which falls under a Hidden Markov Model framework, can easily be generalized to deal with any kind of state uncertainty, such as breeding or species residency states (Pradel, 2005). This model will likely be extended to further expand the occupancy toolkit available to wildlife ecologists.

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AUTHORS' CONTRIBUTIONS

T.C., D.M. and J.N. conceived and developed the methodology; E.G. conceived the field sampling protocols and collected the data; K.M. and A.B. generated and analysed the genetic data; T.C. analysed the

final data; T.C., E.G., J.N. and D.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data used in this paper: detection/non-detection data, for the two salamander species: *Plethodon cinereus* and *Plethodon shenandoah*. These data are available in a Dryad Digital Repository https://doi.org/10.5061/dryad.88ks4g5 (Chambert et al., 2018).

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SUPPORTING INFORMATION

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