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1 A spatial Markovian framework for estimating regional 2 and local dynamics of annual plants with dormancy

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7 Abstract

Many species have a dormant stage in their life cycle, including seeds for plants. The dormancy stage influences the species dynamics but is often undetectable. One way to include dormancy is to model it as a hidden dynamical state within a Markovian framework. Models within this framework have already been proposed but with different limitations: only presence/absence observations are modelled, the dormancy stage is limited to one year, or colonisation from neighbouring patches is not taken into account. We propose a hidden Markov model that describes the local and regional dynamics of a species that can undergo dormancy with a potentially infinite dormancy time. Populations are modelled with abundance classes. Our model considers the colonisation process as the indistinguishable influence of neighbour non-dormant population states on a dormant population state in a patch. It would be expected that parameter estimation, hidden state estimation and prediction of the next non-dormant populations would have an exponential computational time in terms of the number of patches. However, we demonstrate that estimation, hidden state estimation and prediction are all achievable in a linear computational time. Numerical experiments on simulated data show that the state of dormant populations can easily be retrieved, as well as the state of future non-dormant populations. Our framework provides a simple and efficient tool that could be further used to analyse and compare annual plants dynamics like weed species survival strategies in crop fields.

8 *Keywords:* Metapopulation, Seed bank, Hidden life stage, Colonisation,
9 Prediction, Expectation-Maximisation algorithm

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1. Introduction

A species's distribution depends on its local and regional dynamics (Hanski, 1998; Bullock et al., 2006). The metapopulation model, developed by Levins et al. (1969), uses colonisation and extinction parameters to describe a species dynamics across multiple patches. Levins' model considered colonisation to be dependent on the fraction of occupied patches. Multiple studies have used the metapopulation concept on different types of species (Hanski, 1994; Dornier et al., 2011). However, for many organisms (plants or animals) that can survive rough environmental conditions by stopping their development through a process called dormancy, the use of the original metapopulation model has been questioned due to the fact that the dormancy stage is not modelled (Freckleton and Watkinson, 2002; Bullock et al., 2006). Fréville et al. (2013) have shown that such models tend to overestimate colonisation and extinction parameters for annual plants with seed banks. Understanding and modelling dormancy in a species dynamics is important in order to better conserve and control the species.

Multiple models have been developed to represent the dynamics of species that can undergo dormancy using information on the dormant and non-dormant populations of the species (Cohen, 1966; Levin et al., 1984; Jarry et al., 1995; Amarasekare and Possingham, 2001; Mistro et al., 2005; Soubeyrand et al., 2009; Han et al., 2014). However, in practice, data is often only collected on the species' non-dormant population since the dormant population is hard to observe. This implies that the models mentioned above, which require full knowledge about local dormant populations, would not be adapted to estimating a species' local and regional dynamics from partial data alone. A model with incomplete information where the dormancy stage is modelled as a hidden variable and the non-dormant stage is the observable data is more appropriate to estimate the dynamics of a species that can undergo dormancy.

The local dynamics of species with dormancy stages has already been studied using models with incomplete information (David et al., 2010; Quintana-Ascencio et al., 2011; Lamy et al., 2013; Fréville et al., 2013; Borgy et al., 2015; Manna et al., 2017). The models in Lamy et al. (2013), Fréville et al. (2013), Borgy et al. (2015), and Manna et al. (2017) use a Markovian framework where the current state of the population only depends on the state of the population in the previous time step. A classical extension of the Markov model to deal with incomplete observation is the Hidden Markov

Model (HMM). In a HMM, a hidden Markov chain emits information at each time step and the emitted information does not influence the states of hidden chain. By considering the species non-dormant population as observable and the species dormant population as hidden, it would be tempting to use HMM to study such species. However, the HMM does not include the influence of a species' non-dormant populations on its dormant populations. Therefore, Borgy et al. (2015) and Pluntz et al. (2018) extended the HMM to include the influence of emitted observations on the hidden variables. The model was used to analyse the dynamics of weed species in crop fields from real data on weed abundance and weed occurrence. We will refer to this model as a HMM with Data Feedback (HMM-DF).

The main limitation of the models developed by Pluntz et al. (2018), Borgy et al. (2015), Fréville et al. (2013), Lamy et al. (2013), Quintana-Ascencio et al. (2011), and David et al. (2010) is the absence of an explicit contribution of neighbouring patches in the colonisation process. Colonisation, when modelled, is through seed rain, as the propagule rain effect described in Gotelli (1991). As a result, these authors consider patches to be independent. To take colonisation between patches into account, the model should include interactions between patches. Factorial HMM (Ghahramani and Jordan, 1997) or Coupled HMM (Brand et al., 1997; Wainwright and Jordan, 2008) are models that extend HMM to include interactions between patches (see Appendix A for a graphical representation). However, Factorial HMMs consider that the observation at time n depends on the state of the hidden variables of all chains at time n and, more importantly, that this observation does not influence the hidden states at $n+1$. Thus, the colonisation process, from non-dormant populations to dormant ones, cannot be modelled with a FHMM. In a Coupled HMM the hidden state of a patch at time n influences the hidden states of other patches at time $n+1$. This implies that the colonisation process occurs between dormant populations. This assumption is often wrong since dormant populations usually cannot move. In addition to having a dependency structure unsuited to model colonisation, the Expectation Maximisation (EM) algorithm (Dempster et al., 1977), which is often used for parameter estimation based on incomplete information, has a time complexity exponential in terms of the number of patches, for both frameworks (Ghahramani and Jordan, 1997; Brand et al., 1997). The model proposed in Manna et al. (2017), which extends the model of Fréville et al. (2013), considered patches to be organised on a circle with colonisation coming from the closest neighbouring patches. Their model makes it possible to

compare the relative impact of seed dormancy and limited dispersal on the species dynamics. However, they conserved the limiting assumptions of the model of Fréville et al. (2013), such as: dormant and non-dormant populations modelled by presence/absence; seed bank survival limited to one year; and the automatic presence of seeds in the seed bank when plants were found in the same patch at the previous time step.

In order to avoid these assumptions, we propose a Multidimensional HMM with Data Feedback (MHMM-DF) that includes local (within patch) and regional (between patches) dynamics to describe the dynamics of species that undergo dormancy. The model considers that dormant and non-dormant populations depend stochastically on each other and the species non-dormant and dormant populations are modelled with abundance classes. The state of a dormant population in a given patch at time n is described as the result of four processes : (i) dormancy, i.e., survival of a population in the dormant stage between successive time steps where this survival is not limited in time; (ii) locally newly produced dormant individuals; (iii) colonisation from neighbouring patches; and (iv) exogenous colonisation. Processes (ii) and (iii) induce a dependency of the observed data on the hidden state.

A MHMM-DF model is fully defined by the framework describing the interactions between populations. Since data on non-dormant populations are rarely collected over a long period of time, we propose a parametric version of the MHMM-DF. This version relies on simple probability distributions and functional forms for the sake of parsimony. The resulting parametric MHMM-DF has seven parameters and can characterise the dynamics of annual plants with seed banks.

Regarding parameter estimation, the naive procedure that consists of applying the EM algorithm on the reformulation of the MHMM-DF as a HMM with a single multidimensional chain has an exponential time and space complexity in terms of the number of patches. However, parameter estimation with exponential time and space complexity can only be done for a MHMM-DF with a small number of hidden states and a small number of patches. Thus, we demonstrate that for the MHMM-DF structure, estimation using the EM algorithm is achievable with a linear time and space complexity in terms of the number of patches. This linear complexity is obtained thanks to independence between dormant populations at time n and patch c and dormant populations in other patches at previous times, conditional on observed non-dormant populations. The same independence property is used for the Viterbi algorithm (Forney, 1973), which enables the recovery of the

state of the species' dormant populations for all time steps with the same complexity. The Viterbi algorithm unlike the EM algorithm finds the most probable sequence of hidden states using a set of parameters, whereas the EM finds the set of parameters which is the most probable to have generated the observable data. Additionally, the model can be used to predict the subsequent states of the species' non-dormant population.

We used simulated data to illustrate the quality of estimations provided by the EM algorithm for MHMM-DF, and of hidden state estimations and predictions provided by the Viterbi algorithm. Finally, using model selection techniques, we demonstrate how the framework can be used to discriminate between dynamics with and without dormancy or with and without colonisation.

2. Multidimensional HMM with data feedback

The MHMM-DF is a Dynamic Bayesian Network (Ghahramani, 1998). In the following sections we define the dependency structure of a MHMM-DF and model the interactions between dormant and non-dormant populations with a parametric version of the MHMM-DF.

2.1. Definition

Let us consider a set $\mathcal{C}$ of C patches. At time $n \in \{1, \dots, N\}$ on patch $c \in \mathcal{C}$ two variables are defined: $X_{c,n}$ is the abundance class of the dormant population (hidden) and $Y_{c,n}$ is the abundance class of the non-dormant population (observed). Their domains are $\Omega_X = \{0, 1, \dots, |\Omega_X| - 1\}$ and $\Omega_Y = \{0, 1, \dots, |\Omega_Y| - 1\}$, respectively. In order to simplify the expression of probabilities, we will resort to extra notations summarised in Table 1. The sequence of hidden variables of patch c forms the hidden chain c . A Multidimensional HMM with Data Feedback (MHMM-DF) of C dimensions models the joint dynamics of the C chains when the following two assumptions are fulfilled. First, for a given patch c at a given time n , the non-dormant population state $Y_{c,n+1}$ only depends on the dormant population state $X_{c,n}$. The second assumption is that the dormant population state $X_{c,n+1}$ depends on the dormant population state of the same chain at the previous time step $X_{c,n}$, and on all non-dormant population states at time $n + 1$, Y_{n+1}^C . This direct dependence of hidden variables on observable variables is the data feedback part of the model. The dependences in the MHMM-DF are represented in Fig. 1 for two chains or patches.

Variable	Domain	Definition
$X_{c,n}$	$\Omega_X = \{0, 1, \dots, \Omega_X - 1\}$	abundance class of dormant population in patch c at time n
$Y_{c,n}$	$\Omega_Y = \{0, 1, \dots, \Omega_Y - 1\}$	abundance class of non-dormant population in patch c at time n
X_n^C	Ω_X^C	$\{X_{c,n}, 1 \leq c \leq C\}$
Y_n^C	Ω_Y^C	$\{Y_{c,n}, 1 \leq c \leq C\}$
X_n^C	Ω_X^{nC}	$\{X_n^C, 1 \leq n \leq N\}$
Y_n^C	Ω_Y^{nC}	$\{Y_n^C, 1 \leq n \leq N\}$

Table 1: Variables of the MHMM-DF.

158 The dynamics of a MHMM-DF is fully defined by three probabilities.
 159 The first one is the initial probability of the hidden states, $\mathbb{P}(X_0^C = x_0^C)$. For
 160 the sake of simplicity we will assume here that $\mathbb{P}(X_0^C = x_0^C) = \prod_{c=1}^C \pi(x_{c,0})$.
 161 The emission probability, defined as $\phi(x_{c,n-1}, y_{c,n}) = \mathbb{P}(Y_{c,n} = y_{c,n} | X_{c,n-1} =$
 162 $x_{c,n-1})$, models the awakening process, which corresponds to the generation
 163 of the local non-dormant population from the local dormant population. Fi-
 164 nally, the transition probability of the hidden variable of chain c , defined as
 165 $A(x_{c,n-1}, x_{c,n}, y_n^C) = \mathbb{P}(X_{c,n} = x_{c,n} | X_{c,n-1} = x_{c,n-1}, Y_n^C = y_n^C)$, models the
 166 generation of the current dormant population at patch c , given the previous
 167 dormant population state and the non-dormant population state both lo-
 168 cally and in the neighbourhood. Note that in ϕ and A , variable ordering first
 169 corresponds to hidden variables and then to observed ones, and not to the
 170 temporal ordering of the events. In Section 3, we describe these probabilities
 171 in the case of annual plants.

172 With these notations, the joint probability distribution of the hidden and
 173 observed variables of the C chains is:

$$\prod_{c=1}^C \pi(x_{c,0}) \prod_{n=1}^N A(x_{c,n-1}, x_{c,n}, y_n^C) \phi(x_{c,n-1}, y_{c,n}). \quad (1)$$

174

175 2.2. Model parameterisation

176 The estimation of ϕ and A functions in a non-parametric approach could
 177 be difficult, in particular, when the amount of available data is low. We
 178 present here a possible parameterisation for ϕ and A for the case where
 179 hidden and observed variables are abundance classes.

Figure 1: Dependency graph in a Multidimensional HMM with Data Feedback. Case of two hidden chains (grey nodes). Blue edges are involved in the emission probability ϕ and red ones in the transition probability A . Each chain emits its own observations and then observations from all chains influence the next hidden state of a chain.

180 For a given value $x_{c,n-1}$, $\phi(x_{c,n-1}, y_{c,n})$ is modelled as a Binomial distri-
 181 bution with parameters $|\Omega_Y|$, and $p_{x_{c,n-1}}$. The probability $p_{x_{c,n-1}}$ is then
 182 modelled as a logistic regression: $p_{x_{c,n-1}} = \frac{1}{1+\exp(-(\mu_0+\mu_1 x_{c,n-1}/|\Omega_X|))}$, where μ_0
 183 and μ_1 are hyper parameters. Thus:

$$\begin{aligned} \phi(x_{c,n-1}, y_{c,n}) &= \binom{|\Omega_Y|-1}{y_{c,n}} \left[\frac{1}{1 + \exp(-(\mu_0 + \mu_1 \frac{x_{c,n-1}}{|\Omega_X|}))} \right]^{|\Omega_Y|-1} \\ &\quad \times \left[\exp(-(\mu_0 + \mu_1 \frac{x_{c,n-1}}{|\Omega_X|})) \right]^{|\Omega_Y|-y_{c,n}-1}. \end{aligned} \quad (2)$$

184 The choice of a Binomial distribution combined with a logistic regression
 185 is motivated by the need for a parsimonious model (i.e., a model with few
 186 parameters). Additionally, a Binomial distribution combined with a logistic
 187 regression enables us to have a mean that increases when the class of the
 188 explanatory variables increases.

189 The transition distribution A can also be modelled as a Binomial distri-
 190 bution. The parameters are $(|\Omega_X|, p_{x_{c,n-1}, y_n^c})$, and the second parameter is

again modelled as a logistic regression. It is natural to distinguish the influence of $y_{c,n}$ from the influence of the observations on the chains other than chain c , so we propose to model $p_{x_{c,n-1}, y_n^C}$ as a function of $x_{c,n-1}$, $y_{c,n}$ and $y_n^{C \setminus c}$, where $y_n^{C \setminus c} = \{y_{c',n}, c' \in \mathcal{C}, c' \neq c\}$ is the set of observations of all the patches except c at time n .

Extracting a subset of $y_n^{C \setminus c}$ can be done in order to analyse a specific colonisation process. This will be the case, for example, in a metapopulation process where only populations from geographically-close patches can colonise a given patch. In other situations, it can be reasonable to assume that colonisation is possible with the same intensity from all patches. Colonisation scenarios can be modelled in the MHMM-DF framework by building an appropriate A function. Their suitability to data can be compared using model selection techniques. Here, for illustration purposes, we focused on models for which each patch contributes equally to colonisation.

In order to limit the number of parameters in the regression model for $p_{x_{c,n}, y_n^C}$, we propose to aggregate $y_n^{C \setminus c}$ in a one dimension variable. There are several options to summarise the information in $y_n^{C \setminus c}$. For instance, we will refer to *mean colonisation* as the colonisation process that considers that only the mean value of the non-dormant population state in patches other than c influences the dormant population state in patch c . The function that summarises the information is called f_{mean} and associates the set of observed states of non-dormant population $y_n^{C \setminus c}$ to its mean value (rounded to the first smaller integer to remain in Ω_Y). It is a measure of the mean colonisation capacity in the neighbourhood. The output of f_{mean} is then used to define the logistic regression model for $p_{x_{c,n}, y_n^C}$ as follows:

$$p_{x_{c,n}, y_n^C} = \frac{1}{1 + \exp(-(\nu_0 + \nu_1 \times \frac{x_{c,n-1}}{|\Omega_X|} + \nu_2 \times \frac{y_{c,n}}{|\Omega_Y|} + \nu_3 \times \frac{f_{\text{mean}}(y_n^{C \setminus c})}{|\Omega_Y|}))}. \quad (3)$$

Note that each explanatory variable was normalised.

Finally, we modelled the initial distribution of the species dormant population in patch c by using a parameterised Binomial distribution with parameters $|\Omega_X|$ and p_τ where:

$$p_\tau = \frac{1}{1 + \exp(-\tau)}. \quad (4)$$

Hyperparameters	Interpretation for annual plants
Initial distribution $\mathbb{P}(x_{c,0}) = \pi(x_{c,0})$	
τ	Mean trend
Awakening process $\mathbb{P}(y_{c,n} x_{c,n-1}) = \phi(x_{c,n-1}, y_{c,n})$	
μ_0	Exogenous colonisation of non-dormant population
	Not relevant for plants
μ_1	Influence of seed bank state on next adult plant population
Seed bank dynamics $\mathbb{P}(x_{c,n} x_{c,n-1}, y_n^C) = (x_{c,n-1}, x_{c,n}, y_n^C)$	
ν_0	Exogenous colonisation by seed rain
ν_1	Influence of the previous seed bank state on the current one (dormancy)
ν_2	Influence of local seed production on the current seed bank state
ν_3	Influence of neighbouring seed production on the current seed bank state

Table 2: Parameterisation of a MHMM-DF using Binomial Logistic Regressions. The hyperparameters are the parameters of the logistic regression.

221 This parameterisation of the MHMM-DF requires seven hyper parameters
222 that are listed in Table 2. Using classical results of identifiability for HMM,
223 we established that the MHMM-DF is generically identifiable as soon as $C >$
224 2 under the mild assumption that N must be greater than 7 (see Appendix
225 B).

226 3. Modelling the dynamics of annual plants with a MHMM-DF

227 The MHMM-DF is well adapted to describe the regional and local dynam-
228 ics of annual plants like weeds. In order to model a species dynamics with a
229 MHMM-DF, two assumptions must be made. The first assumption imposes
230 immobility on the species' dormant populations in a patch. This assump-
231 tion is usually verified for annual plants since seeds are immobile once in the
232 seed bank. The second assumption is that the species' non-dormant popu-
233 lation cannot directly influence another non-dormant population. A species'
234 non-dormant population can only influence the species' dormant populations.
235 Thus, a non-dormant population will either die, become sterile or transform
236 into a dormant population at the end of each time step. This assumption

is verified for annual plants when the time step is at least a year since the species' non-dormant population does not live longer than a year. This implies a complete renewal of the plant's non-dormant population between each time step.

In a MHMM-DF for annual plant dynamics, the hidden variables or the species dormant populations $(X_{c,n})_{(c,n) \in \{1,\dots,C\} \times \{1,\dots,N\}}$ correspond to the seed bank's state at time n in patch c . The observable variables or the species' non-dormant populations $(Y_{c,n})_{(c,n) \in \{1,\dots,C\} \times \{1,\dots,N\}}$ correspond to the adult plant's state at time n in patch c . The seed bank state is influenced by dormancy, colonisation and the current state of adult flora in the patch. All these processes are represented with red arrows in Fig. 1. The blue arrows correspond to germination and survival up to adulthood.

For a parametric MHMM-DF with indistinguishable effects of neighbours, each hyperparameter is associated with a specific process of a plant's dynamics, with the exception of τ , which is associated with the initial probability of dormant populations. With a parametric MHMM-DF, the annual plant dynamics is described by multiple processes: survival of seeds in the seed bank corresponding to the dormancy process (ν_1); local production of seeds entering the local seed bank corresponding to the influence of the local non-dormant population on the local dormant population (ν_2); and neighbouring production of seeds entering the local seed bank corresponding to the spatial colonisation process (ν_3) and the germination process corresponding to (μ_1). The exogenous colonisation process has two hyperparameters, μ_0 and ν_0 . The exogenous production of seeds entering the regional seed bank by seed rain corresponds to the exogenous colonisation of dormant populations (ν_0). The process modelled with the hyperparameter μ_0 corresponds to exogenous colonisation of non-dormant populations. This process is not present with annual plants. Even if this process cannot be removed, the smaller μ_0 is, the smaller the probability of non-dormant populations being colonised by the exterior will be. For instance, with $\mu_0 = -5.7$, the probability of exogenous colonisation of a non-dormant population occurring when all past populations are extinct is 0.004.

4. Estimation

A classical algorithm to estimate the parameters of a HMM model is the EM algorithm (Dempster et al., 1977). This iterative algorithm alternates an Expectation step and a Maximisation step, and converges towards

273 a local maximum of the log-likelihood. The E-step for HMM is the well-
 274 known Forward-Backward algorithm (Rabiner, 1989), which takes advantage
 275 of the linear structure of a HMM (see Fig. A.9) and variable elimination
 276 to efficiently compute all conditional probabilities of the hidden variables
 277 given the observations. However, when the hidden variables are multidimen-
 278 sional, the size of the domains and the structure of interaction can make the
 279 forward-backward algorithm intractable. Since chains only depend on one
 280 another through observations in MHMM-DF, we have demonstrated that
 281 independently running a forward-backward per chain is possible. While re-
 282 maining exact, it significantly reduces the computational complexity of the
 283 E step from exponential in terms of the number of patches $O(|\Omega_X|^{2C}N)$ to
 284 linear $O(|\Omega_X|^2CN)$. In this section, the EM algorithm is described for one-
 285 dimensional HMM and then detailed for MHMM-DF.

286 4.1. EM algorithm for HMM

287 A HMM (see Fig. A.9) is defined by: the initial probability $\pi(x_0)$, the
 288 emission probability $\phi(x_n, y_n)$ and the transition probability $A(x_{n-1}, x_n)$. As
 289 can be observed the transition probability does not depend on observations,
 290 and is $A(x_{n-1}, x_n) = \mathbb{P}(X_n = x_n | X_{n-1} = x_{n-1})$. Let us denote $\lambda = (\pi, \phi, A)$
 291 corresponding to the model's parameters.

292 Let us define $Q(\lambda | \lambda') = E[\ln(\mathbb{P}(X^N, Y^N | \lambda) | Y^N = y^N, \lambda')]$. The function
 293 Q can be expressed in terms of π , ϕ and A :

$$\begin{aligned} Q(\lambda | \lambda') &= \sum_{n=0}^N \sum_{x_n \in \Omega_X} \gamma_n(x_n) \ln(\phi(x_n, y_n)) \\ &+ \sum_{x_0 \in \Omega_X} \gamma_0(x_0) \ln(\pi(x_0)) \\ &+ \sum_{n=1}^N \sum_{x_{n-1} \in \Omega_X} \sum_{x_n \in \Omega_X} \xi_n(x_{n-1}, x_n) \ln(A(x_{n-1}, x_n)) \end{aligned}$$

294 where $\gamma_n(x_n) = \mathbb{P}(X_n = x_n | Y^N = y^N, \lambda_t)$ and $\xi_n(x_{n-1}, x_n) = \mathbb{P}(X_{n-1} =$
 295 $x_{n-1}, X_n = x_n | Y^N = y^N, \lambda_t)$.

296 We denote λ_t as the current estimator at iteration t of the algorithm. The
 297 E-steps and M-steps are defined as follows:

298
 299 **E-step:** compute all the probabilities $\gamma_n(x_n)$ and $\xi_n(x_{n-1}, x_n)$.

300 **M-step:** update the parameter λ by maximising $Q(\lambda | \lambda_t)$.

301

302 The direct application of the EM algorithm to a HMM where the hidden
 303 variable is of dimension C (i.e., $x_n = (x_{1,n}, \dots, x_{c,n})$) requires a number
 304 of computations that is exponential in C . Therefore, for multidimensional
 305 hidden states HMMs, the E step is generally intractable. However, for the
 306 structure of a MHMM-DF, we can derive an exact E-step that is only linear
 307 in terms of C .

308 4.2. E step for MHMM-DF

309 In a MHMM-DF, the C hidden chains are independent conditionally to
 310 all the observations:

$$\mathbb{P}(X^{C,N} = x^{C,N} | Y^{C,N} = y^{C,N}) = \prod_{c=1}^C \mathbb{P}(X_c^N = x_c^N | Y^{C,N} = y^{C,N}).$$

311 This can be graphically seen in Fig. 1 where all the paths going from a hidden
 312 variable of chain c to a hidden variable of chain c' go through an observed
 313 variable. This implies that the function $Q(\lambda | \lambda')$ can be written in terms of
 314 the following probabilities :

$$\begin{aligned} \xi_{c,n}(x_{c,n-1}, x_{c,n}) &= \mathbb{P}(X_{c,n} = x_{c,n}, X_{c,n-1} = x_{c,n-1} | Y^{C,N} = y^{C,N}, \lambda_t), \\ \rho_{c,n-1}(x_{c,n-1}) &= \mathbb{P}(X_{c,n-1} = x_{c,n-1} | Y^{C,N} = y^{C,N}, \lambda_t). \end{aligned}$$

315 The proof is provided in Appendix C. Consequently, we could consider ap-
 316 plying one forward-backward algorithm per chain. A direct mimicking of the
 317 forward-backward algorithm for a one-dimensional HMM would suggest that
 318 we define the auxiliary variable for chain c as :

$$\begin{aligned} \alpha_{c,n}(x_{c,n}) &= \mathbb{P}(Y^{C,n} = y^{C,n}, X_{c,n} = x_{c,n} | \lambda_t) \\ \beta_{c,n}(x_{c,n}) &= \mathbb{P}(Y_{n+1}^C = y_{n+1}^C, \dots, Y_N^C = y_N^C | X_{c,n} = x_{c,n}, \lambda_t) \end{aligned}$$

320 where $y^{C,n} = \{y_{c,n'}\}_{1 \leq c \leq C, 1 \leq n' \leq n}$ corresponds to the observations in all patches
 321 from the initial time step until step n . As opposed to the case $C = 1$, the
 322 variables $Y_{n+1}^C, \dots, Y_N^C$ are not independent of $Y^{C,n}$ conditionally on $X_{c,n}$. As
 323 a consequence, the property $\alpha_{c,n}(x_{c,n})\beta_{c,n}(x_{c,n}) \propto \mathbb{P}(X_{c,n} = x_{c,n}, y^{C,N} | \lambda_t)$,
 324 which is crucial to calculate ρ and ξ in a HMM, does no longer hold. How-
 325 ever, the property can be recovered by defining the auxiliary variables of the
 326 E-step as:

$$\alpha_{c,n}(x_{c,n}) = \mathbb{P}(Y^{C,n} = y^{C,n}, X_{c,n} = x_{c,n} | \lambda_t),$$

327

$$\beta_{c,n}(x_{c,n}) = \mathbb{P}(Y_{n+1}^C = y_{n+1}^C, \dots, Y_N^C = y_N^C | Y^{C,n} = y^{C,n}, X_{c,n} = x_{c,n}, \lambda_t).$$

328

This way, the product $\alpha_{c,n}(x_{c,n})\beta_{c,n}(x_{c,n})$ is equal to $\mathbb{P}(X_{c,n} = x_{c,n}, y^{C,N} | \lambda_t)$.

329

The auxiliary variables can be defined by their recursive equations :

$$\alpha_{c,n}(x_{c,n}) \propto \sum_{x_{c,n-1} \in \Omega_X} \alpha_{c,n-1}(x_{c,n-1}) \phi_t(x_{c,n-1}, y_{c,n}) A_t(x_{c,n-1}, x_{c,n}, y_n^C).$$

330

A complete proof is given in Appendix C. Equality is obtained by multiplying the right part of the equation by the constant factor $K_{c,n} = \mathbb{P}(y_n^{C \setminus c} | y^{C,n-1})$.

332

$K_{c,n}$ is the probability of the observations in all patches except c at time n ,

333

conditionally on all the observations up to time $n - 1$. Let us define:

$$\tilde{\alpha}_{c,n}(x_{c,n}) = \sum_{x_{c,n-1} \in \Omega_X} \tilde{\alpha}_{c,n-1}(x_{c,n-1}) \phi_t(x_{c,n-1}, y_{c,n}) A_t(x_{c,n-1}, x_{c,n}, y_n^C)$$

334

where $\tilde{\alpha}_{c,0}(x_{c,0}) = \alpha_{c,0}(x_{c,0})$.

335

Similarly we can show that

$$\beta_{c,n}(x_{c,n}) \propto \sum_{x_{c,n+1} \in \Omega_X} \beta_{c,n+1}(x_{c,n+1}) A_t(x_{c,n}, x_{c,n+1}, y_{n+1}^C) \phi_t(x_{c,n}, y_{c,n+1}).$$

336

Let us define:

$$\tilde{\beta}_{c,n}(x_{c,n}) = \sum_{x_{c,n+1} \in \Omega_X} \tilde{\beta}_{c,n+1}(x_{c,n+1}) A_t(x_{c,n}, x_{c,n+1}, y_{n+1}^C) \phi_t(x_{c,n}, y_{c,n+1})$$

337

with $\tilde{\beta}_{c,N}(x_{c,N}) = \beta_{c,N}(x_{c,N})$.

338

All the $\tilde{\alpha}$ and $\tilde{\beta}$ can be calculated recursively. Thus, the probabilities of

339

interest for the E-step are calculated using the following equalities:

$$\rho_{c,n}(x_{c,n}) = \frac{\tilde{\beta}_{c,n}(x_{c,n}) \tilde{\alpha}_{c,n}(x_{c,n})}{\sum_{x \in \Omega_X} \tilde{\beta}_{c,n}(x) \tilde{\alpha}_{c,n}(x)},$$

$$\xi_{c,n}(x_{c,n-1}, x_{c,n}) = \frac{A_t(x_{c,n-1}, x_{c,n}, y_n^C) \tilde{\beta}_{c,n}(x_{c,n}) \tilde{\alpha}_{c,n-1}(x_{c,n-1}) \phi_t(x_{c,n-1}, y_{c,n})}{\sum_{(x, x') \in \Omega_X^2} A_t(x', x, y_n^C) \tilde{\beta}_{c,n}(x) \tilde{\alpha}_{c,n-1}(x') \phi_t(x', y_{c,n})}.$$

340 We were also able to derive the expression of the likelihood in terms of
 341 the quantities $\tilde{\alpha}_{c,n}$ and $\tilde{\beta}_{c,n}$.

$$\begin{aligned} \mathbb{P}(y^{C,N}) &= \left[\sum_{x_{c,n} \in \Omega_X} \tilde{\alpha}_{c,n}(x_{c,n}) \tilde{\beta}_{c,n}(x_{c,n}) \right] \\ &\times \left[\prod_{j=1}^N \prod_{l \in \{1, \dots, C\} \setminus c} \sum_{x_{l,j-1} \in \Omega_X} \phi(x_{l,j-1}, y_{l,j}) \frac{\tilde{\alpha}_{l,j-1}(x_{l,j-1})}{\sum_{x \in \Omega_X} \tilde{\alpha}_{l,j-1}(x)} \right]. \quad (5) \end{aligned}$$

342 See Appendix D for a proof.

343 4.3. M step for MHMM-DF

344 We present here the equations for the M step for a MHMM-DF model
 345 with indistinguishable effects of the neighbours, as defined in Section 2.2. In
 346 this case, the M-step corresponds to an update of the current estimators of
 347 the hyperparameters τ , $\mu = (\mu_0, \mu_1)$ and $\nu = (\nu_0, \dots, \nu_3)$ associated with
 348 $(\pi_\tau, \phi_\mu, A_\nu)$. If (τ_t, ν_t, μ_t) are the current parameter estimators, and $\rho_{c,n}$
 349 and $\xi_{c,n}$ are the corresponding functions computed during the E step, then
 350 $(\tau_{t+1}, \nu_{t+1}, \mu_{t+1})$ are obtained by maximizing $Q(\lambda|\lambda_t)$:

$$\begin{aligned} Q(\lambda|\lambda_t) &= \sum_{c=1}^C \sum_{x \in \Omega_X} \ln(\pi(x)) \rho_{c,0}(x) \\ &+ \sum_{c=1}^C \sum_{n=1}^N \sum_{(x_n, x_{n-1}) \in \Omega_X^2} \ln(A(x_{n-1}, x_n, y_n^C)) \xi_{c,n}(x_{n-1}, x_n) \\ &+ \sum_{x_{n-1} \in \Omega_X} \ln(\phi(x_{n-1}, y_{c,n})) \rho_{c,n-1}(x_{n-1}). \end{aligned}$$

351 The solution λ that maximizes $Q(\lambda|\lambda_t)$ is a zero of the partial derivatives of
 352 Q . Thus:

$$\begin{aligned} \frac{\partial Q}{\partial \tau} &= \sum_{c=1}^C \sum_{x_{c,0} \in \Omega_X} \left[(x_{c,0}) + \frac{(1 - |\Omega_X|)}{1 + \exp(-\tau)} \right] \rho_{c,0}(x_{c,0}) \\ &= \frac{C(1 - |\Omega_X|)}{1 + \exp(-\tau)} - C + \sum_{c=1}^C \sum_{x_{c,0} \in |\Omega_X|} x_{c,0} \rho_{c,0}(x_{c,0}), \end{aligned}$$

$$\begin{aligned}\frac{\partial Q}{\partial \mu_0} &= \sum_{c=1}^C \sum_{n=1}^N \sum_{x_{c,n-1} \in \Omega_X} [(y_{c,n}) + (1 - |\Omega_Y|)p_{x_{c,n-1}}] \rho_{c,n-1}(x_{c,n-1}), \\ \frac{\partial Q}{\partial \mu_1} &= \sum_{c=1}^C \sum_{n=1}^N \sum_{x_{c,n-1} \in \Omega_X} [(y_{c,n}) + (1 - |\Omega_Y|)p_{x_{c,n-1}}] \frac{x_{c,n-1}}{|\Omega_X|} \rho_{c,n-1}(x_{c,n-1})\end{aligned}$$

353 where we recall that $p_{x_{c,n-1}} = \frac{1}{1 + \exp(-(\mu_1 \frac{x_{c,n-1}}{|\Omega_X|} + \mu_0))}$.

$$\begin{aligned}\frac{\partial Q}{\partial \nu_0} &= \sum_{c=1}^C \sum_{n=1}^N \sum_{(x_n, x_{n-1}) \in \Omega_X^2} q_{x_{c,n}, y_n^C} \xi_{c,n}(x_{c,n-1}, x_{c,n}), \\ \frac{\partial Q}{\partial \nu_1} &= \sum_{c=1}^C \sum_{n=1}^N \sum_{(x_n, x_{n-1}) \in \Omega_X^2} \frac{x_{c,n-1}}{|\Omega_X|} q_{x_{c,n}, y_n^C} \xi_{c,n}(x_{c,n-1}, x_{c,n}), \\ \frac{\partial Q}{\partial \nu_2} &= \sum_{c=1}^C \sum_{n=1}^N \sum_{(x_n, x_{n-1}) \in \Omega_X^2} \frac{y_{c,n}}{|\Omega_Y|} q_{x_{c,n}, y_n^C} \xi_{c,n}(x_{c,n-1}, x_{c,n}), \\ \frac{\partial Q}{\partial \nu_3} &= \sum_{c=1}^C \sum_{n=1}^N \sum_{(x_n, x_{n-1}) \in \Omega_X^2} \frac{f_{\text{mean}}(y_n^{C \setminus c})}{|\Omega_Y|} q_{x_{c,n}, y_n^C} \xi_{c,n}(x_{c,n-1}, x_{c,n})\end{aligned}$$

354 where $q_{x_{c,n}, y_n^C} = [(x_{c,n}) + (1 - |\Omega_X|) \frac{1}{1 + \exp(-(\nu_0 + \nu_1 \frac{x_{c,n-1}}{|\Omega_X|} + \nu_2 \frac{y_{c,n}}{|\Omega_Y|} + \nu_3 \frac{f_{\text{mean}}(y_n^{C \setminus c})}{|\Omega_Y|}))}]$.

355 Note that each group of hyperparameters τ , ν and μ can be updated in-
 356 dependently of one another, since the group of partial derivatives associated
 357 with one of them does not involve the others. The numerical method used to
 358 search for the zeros is the limited-memory Broyden–Fletcher–Goldfarb–Shanno
 359 algorithm of Byrd et al. (1995).

360 5. Hidden state estimation and prediction

361 When managing annual plants, knowing the past history of the seed bank
 362 is valuable information that can be used to target control or conservation
 363 actions. In a MHMM-DF model, the species' dormant population of patch
 364 c at all time steps up to N can be recovered by computing the most likely
 365 sequence given the observed sequences of non-dormant populations in all

patches. In this section, we show how to efficiently compute this sequence by deriving the Viterbi algorithm for MHMM-DF chain-by-chain. Prediction of the state of the adult flora the next season is also valuable information for management. We also describe how to predict the most likely non-dormant state of the species at time $N + 1$ based on the observations of the previous years.

5.1. Hidden state estimation

The Viterbi algorithm (Forney, 1973) finds the most likely sequence of hidden states. When applied to the MHMM-DF model, it makes it possible to recover the state of a species' dormant population for any patch at any time. The most likely sequence of hidden states is the sequence of hidden states that maximises the joint probability of all the hidden variables conditional on the observations (i.e. non-dormant population). Thus, the following must be computed:

$$\operatorname{argmax}_{x^{C,N} \in \Omega_X^{C \times N}} \mathbb{P}(X^{C,N} = x^{C,N} | Y^{C,N} = y^{C,N})$$

which is equivalent to computing:

$$\operatorname{argmax}_{x^{C,N} \in \Omega_X^{C \times N}} \mathbb{P}(X^{C,N} = x^{C,N}, Y^{C,N} = y^{C,N}).$$

As for the forward-backward algorithm, a direct application of the Viterbi algorithm is not possible due to the size of $\Omega_X^{C \times N}$. However, here again we show that we can find the most likely sequence of hidden states independently, chain-by-chain. Independent recovery can be done due to the following property of MHMM-DF:

$$\max_{x^{C,N} \in \Omega_X^{C \times N}} \mathbb{P}(X^{C,N} = x^{C,N}, Y^{C,N} = y^{C,N}) = \prod_{c=1}^C \max_{x_c^N \in \Omega_X^N} \mathbb{P}(X_c^N = x_c^N, Y^{C,N} = y^{C,N}).$$

Proof of this property can be found in Appendix E. Let us now consider a single chain, c , and see how we can recursively compute the most likely state of the hidden sequence for this chain. We first define:

$$\delta_{c,n}(x_{c,n}) = \max_{x_c^{n-1} \in \Omega_X^{n-1}} \mathbb{P}(X_c^{n-1} = x_c^{n-1}, X_{c,n} = x_{c,n}, Y^{C,n} = y^{C,n}),$$

where $x_c^{n-1} = (x_{c,1}, \dots, x_{c,n-1})$. $\delta_{c,n}$ can be reformulated as:

$$\delta_{c,n}(x_{c,n}) = \max_{x_{c,n-1} \in \Omega_X} K_{c,n} \delta_{c,n-1}(x_{c,n-1}) \phi(x_{c,n-1}, y_{c,n}) A(x_{c,n-1}, x_{c,n}, y_n^C)$$

387 where $K_{c,n}$ is the same constant as defined in the E-step for MHMM-DF. A
 388 detailed proof can be found in Appendix E. In order to avoid the constant,
 389 we define, for all c and all n , $\tilde{\delta}_{c,n}$ as:

$$\tilde{\delta}_{c,n}(x_{c,n}) = \max_{x_{c,n-1} \in \Omega_X} \tilde{\delta}_{c,n-1}(x_{c,n-1}) \phi(x_{c,n-1}, y_{c,n}) A(x_{c,n-1}, x_{c,n}, y_n^C)$$

390 where $\tilde{\delta}_{c,0} = \delta_{c,0}$. Then, in order to compute the most likely state of the
 391 hidden chain at patch c , we used the following intermediate quantity:

$$\psi_{c,n}(x_{c,n}) = \operatorname{argmax}_{x_{c,n-1} \in \Omega_X} \tilde{\delta}_{c,n-1}(x_{c,n-1}) \phi(x_{c,n-1}, y_{c,n}) A(x_{c,n-1}, x_{c,n}, y_n^C).$$

392 The Viterbi procedure is then as follows for each patch c :

393 1. Initialization for all $x_{c,0} \in \Omega_X$:

$$\tilde{\delta}_{c,0}(x_{c,0}) = \pi(x_{c,0}),$$

394

$$\psi_{c,0}(x_{c,0}) = 0.$$

395 2. Forward recursion for $n \in \{1, \dots, N\}$:

$$\tilde{\delta}_{c,n}(x_{c,n}) = \max_{x_{c,n-1} \in \Omega_X} \tilde{\delta}_{c,n-1}(x_{c,n-1}) \phi(x_{c,n-1}, y_{c,n}) A(x_{c,n-1}, x_{c,n}, y_n^C),$$

396

$$\psi_{c,n}(x_{c,n}) = \operatorname{argmax}_{x_{c,n-1} \in \Omega_X} \tilde{\delta}_{c,n-1}(x_{c,n-1}) \phi(x_{c,n-1}, y_{c,n}) A(x_{c,n-1}, x_{c,n}, y_n^C).$$

397 Once the recursion is done, we can collect the hidden state of patch c at
 398 time N by looking at the state that maximises $\tilde{\delta}_{c,N}$. In a recursive manner,
 399 we can then collect the hidden state of patch c at times $N - 1$ to 1. Thus,
 400 the species' dormant populations state can be recovered with the following
 401 procedure:

402 1. Initialization :

$$\hat{x}_{c,N} = \operatorname{argmax}_{x_{c,N} \in \Omega_X} \tilde{\delta}_{c,N}(x_{c,N}) = \operatorname{argmax}_{x_{c,N} \in \Omega_X} \max_{x_c^{N-1} \in \Omega_X^{N-1}} \mathbb{P}(X_c^N = x_c^N, Y^{C,N} = y^{C,N}).$$

403 2. Backward recursion for $n \in \{N - 1, \dots, 0\}$:

$$\hat{x}_{c,n} = \psi_{c,n}(\hat{x}_{c,n+1})$$

404 where $\hat{x}_{c,n}$ is the most likely state for $X_{c,n}$.

405 5.2. Prediction

406 We predict the species non-dormant population state in patch c at time
 407 $N + 1$ as the state with maximum probability given the observed past non-
 408 dormant populations:

$$\hat{y}_{c,N+1} = \operatorname{argmax}_{y_{c,N+1} \in \Omega_Y} \mathbb{P}(Y_{c,N+1} = y_{c,N+1} | Y^{C,N} = y^{C,N}).$$

409 This predictor is easily obtained using the quantity $\rho_{c,N}$ computed in the E
 410 step of EM for MHMM-DF:

$$\hat{y}_{c,N+1} = \operatorname{argmax}_{y_{c,N+1} \in \Omega_Y} \sum_{x_{c,N} \in \Omega_X} \rho_{c,N}(x_{c,N}) \phi(x_{c,N}, y_{c,N+1})$$

411 where $\hat{y}_{c,N+1}$ is the most likely state for $Y_{c,N+1}$. A detailed proof can be found
 412 in Appendix F.

413 6. Numerical experiments

414 Three types of experiments are done using simulated data. The first ex-
 415 periment evaluates the quality of the estimators and characterises situations
 416 for which estimation may be difficult. The second experiment is model selec-
 417 tion. It illustrates how MHMM-DFs with the EM algorithm can be used to
 418 discriminate between different types of dynamics from observations. The last
 419 experiment evaluates the quality of predictions and hidden state estimation.
 420 The code used is available on Figshare and the digital object identifier is
 421 10.6084/m9.figshare.7796612.

422 All the following simulations are done with $C = 10$ patches and $N = 100$
 423 time steps, where $|\Omega_X| = |\Omega_Y| = 5$. For a given value of the vector (μ, ν) ,
 424 we simulated the states of dormant and non-dormant populations with mean
 425 colonisation and only used observations of non-dormant populations for pa-
 426 rameter estimation, hidden state estimation and prediction. The follow-
 427 ing numerical experiments were programmed with R. The M step of the
 428 EM algorithm uses the R function `optimr` with the limited-memory Broy-
 429 den–Fletcher–Goldfarb–Shanno algorithm. Since the EM algorithm finds a
 430 local maximum, we ran eight EM algorithms initialised with randomly gen-
 431 erated vectors of hyperparameters and selected the resulting vector of esti-
 432 mators with the highest likelihood. Most of the 8 starting point converged to
 433 the same result. The EM algorithm stops if the number of iterations exceeds
 434 100 or if $\max(\max(|\nu_t - \nu_{t-1}|), \max(|\mu_t - \mu_{t-1}|), |\tau_t - \tau_{t-1}|) < 0.01$.

Figure 2: Evolution of the root mean squared error of the hyperparameters estimators when the true values are $(\tau, \mu_0, \mu_1, \nu_0, \nu_2, \nu_3) = (-1, -3.7, 6.5, -3, 4, 2)$ and ν_1 varies from 0 to 6.5 with a 0.5 step. See Table 2 for definitions of parameters.

436 The experiments are focused on the hyperparameters associated with A
 437 and ϕ . We used 14 vectors of hyperparameters (see Table 2 for definitions of
 438 parameters) for which we only had ν_1 , associated with the dormancy process
 439 (i.e., influence of the previous state of the dormant population on the cur-
 440 rent one), which varies from 0 to 6.5. The hyperparameters of the awakening
 441 process is fixed to $\mu = (-3.7, 6.5)$. The parameter μ_0 was chosen to have a
 442 small probability of generating non-dormant population when the dormant
 443 population is extinct (abundance class 0). We then chose $\mu_1 = 6.5$ to simu-
 444 late situations where the influence of dormant populations on non-dormant
 445 populations is strong. The hyperparameter associated with the initial proba-
 446 bility is fixed at $\tau = -1$. The hyperparameters associated with A are fixed at
 447 $\nu = (-3, \nu_1, 4, 2)$: low probability of external colonisation by propagule rain,

Figure 3: Evolution of the coefficient of variation of the hyperparameters estimators when the true values are $(\tau, \mu_0, \mu_1, \nu_0, \nu_2, \nu_3) = (-1, -3.7, 6.5, -3, 4, 2)$ and ν_1 varies from 0 to 6.5 with a 0.5 step. See Table 2 for definitions of parameters.

448 and intermediate strengths for the influence of the local and neighbouring
449 non-dormant plant populations on the dormant populations. For each of the
450 14 vectors, ten population trajectories were simulated, and for each trajec-
451 tory the hyperparameters estimators were computed. The ten simulations
452 were used to calculate the variance of the hyperparameters estimators, as
453 well as the bias, the root mean squared error and the coefficient of variance.

454 When the hyperparameter ν_1 associated with dormancy takes interme-
455 diate values all parameters are correctly estimated as seen from the root
456 mean squared error (Fig. 2). However, when ν_1 is either high or low, the
457 variance, root mean squared error and bias of the estimators are large (see
458 Figs. G.13, 2 and G.14), except for ν_0 and μ_0 (constant terms of the logistic
459 regressions) which are always well estimated. When simulating data with
460 a small ν_1 (low survival of the dormant population), extinction of dormant

Figure 4: Evolution of the dormant population visited states in relation to A 's hyperparameters estimators when the true values are $(\tau, \mu_0, \mu_1, \nu_0, \nu_2, \nu_3) = (-1, -3.7, 6.5, -3, 4, 2)$ and ν_1 varies from 0 to 6.5 with a 0.5 step. See Table 2 for definitions of parameters.

461 populations is the most visited state and the observable neighbours are often
 462 extinct. Multiple simulations with small ν_1 generated data with neighbours
 463 only in the extinction state thus making ν_3 unidentifiable. Logically the
 464 unidentifiable parameter ν_3 has a high coefficient of variance as shown in
 465 Fig. 3 and a high root mean squared error shown in Fig. 2. On the other
 466 hand when ν_1 is large, the dormant population is predominantly in the max-
 467 imum state because all non-dormant populations will either maintain their
 468 previous state, though survival, or grow. This tendency was confirmed by
 469 computing state frequencies from simulations (see Fig. 4). Therefore, when
 470 ν_1 is low, the poor quality of the estimator of μ_1 (influence of the dormant
 471 population state on the non-dormant population state) could be explained
 472 by the fact that we seldom observe the awakening process in the data (i.e.,
 473 $x_{c,n} > 0$ and $y_{c,n+1} > 0$), making estimation harder. When ν_1 is high, (high

Figure 5: Evolution of the root mean squared error of the hyperparameters estimators when the true values are $(\tau, \mu_0, \mu_1, \nu_0, \nu_1, \nu_2) = (-1, -3.7, 6.5, -3, 4, 4)$ and ν_3 varies from 0 to 6.5 with a 0.5 step. See Table 2 for definitions of parameters.

474 survival of the dormant population) and all dormant populations frequently
475 visit the maximum state, it becomes difficult to distinguish which process
476 (dormancy, colonisation, local generation of dormant population) drives the
477 dynamics since many different vectors of hyperparameters may generate the
478 same data. When ν_1 takes intermediate values, the species is not predomi-
479 nantly visiting one extreme state, and the species survival strategy can easily
480 be estimated. We observed the same phenomena for ν_3 , the hyperparamete-
481 ter associated with mean colonisation (see Figs. G.15, 6 and 5). However,
482 in this case, variance remains low for low values of ν_3 because experiments
483 were run for $\nu_1 = 4$, a value that ensures that the seed survival process
484 occurs. Appendix H shows an example of a confidence interval for varying
485 ν_3 and additionally explains how to calculate confidence intervals for each
486 hyperparameter.

Figure 6: Evolution of the Coefficient of variation of the hyperparameters estimators when the true values are $(\tau, \mu_0, \mu_1, \nu_0, \nu_1, \nu_2) = (-1, -3.7, 6.5, -3, 4, 4)$ and ν_3 varies from 0 to 6.5 with a 0.5 step. See Table 2 for definitions of parameters.

487 6.2. Model selection

488 Model selection compares different models and chooses the one that best
489 explains the data. Using simulated data, we used model selection techniques
490 to compare a model with mean spatial colonisation against a model without
491 spatial colonisation. Additionally, we repeated the experiment with a model
492 without dormancy against a model with dormancy. Using the Akaike Infor-
493 mation Criterion (AIC, Akaike 2011, Akaike 1981), we tried to determine
494 whether a specific process is negligible in the species dynamics. When the
495 AIC is calculated for each model, the model with the smallest AIC will be
496 selected. However, if the difference in AIC between the models is not greater
497 than 2, we then assume that we cannot determine which model is best suited
498 for the data (Burnham and Anderson, 2004). In addition to the AIC, we
499 looked at the sum of the Kullback-Leibler distance between the estimated

500 transition probability and the exact transition probability for each model.
 501 The model with the smallest value for the sum of the Kullback-Leibler is the
 502 best suited for the data. The parametric MHMM-DF, which will be referred
 503 to as the full model, has seven hyperparameters, whereas the model without
 504 spatial colonisation ($\nu_3 = 0$) and the model without dormancy ($\nu_1 = 0$) both
 505 have six hyperparameters.

506 To select between the full model and the model without dormancy, we
 507 simulated 30 trajectories of population states, with 100 time steps and ten
 508 patches, where the hyperparameters were: $\mu = (-3.7, 6.5)$, $\tau = -1$ and $\nu =$
 509 $(-3, \nu_1, 4, 2)$, where $\nu_1 \in \{0, 1, 2, 3\}$. Since the AIC penalizes models with
 510 more parameters, for $\nu_1 = 0, 1, 2, 3$, the full model was chosen respectively
 511 0 times, 0 times, 5 times and 22 times out of 30. On the other hand, the
 512 model without dormancy was chosen 20 times, 21 times, 4 times and 0 times
 513 out of 30, respectively. In the remaining cases, the difference in AIC was
 514 smaller than 2. The Kullback-Leibler based selection method chose the full
 515 model 19 times, 20 times, 22 times and 30 times out of 30, for $\nu_1 = 0, 1, 2, 3$
 516 respectively. As seen in Fig. G.13, when $\nu_1 = 0, 1$ or 2 estimators have a
 517 high variance. Additionally, the most visited state for dormant populations
 518 is the extinction state, as seen in Fig. 4. In our experiment, the dynamics
 519 considered are highly similar since simulating under one of the dynamics
 520 will give similar observations. However, when the hyperparameters are $\mu =$
 521 $(-3.7, 6.5)$, $\tau = -1$ and $\nu = (-3, \nu_1, 8, 2)$, for $\nu_1 \in \{0, 1, 2, 3\}$, the full model
 522 was chosen 0 times, 11 times, 25 times and 22 times out of 30, respectively.
 523 As can be seen the results are more precise with a higher ν_2 (influence of the
 524 local non-dormant population on the dormant population). This is due to
 525 the variance of the estimators being lower when $\nu_2 = 8$ than when $\nu_2 = 4$.

526 To select a model between the full model and the model with spatial
 527 colonisation, we simulated 30 sets of data with hyperparameters : $\mu =$
 528 $(-3.7, 6.5)$, $\tau = -1$ and $\nu = (-3, 4, 4, \nu_3)$, where $\nu_3 \in \{0, 1, 2, 3\}$. When sim-
 529 ulating with ν_3 fixed to 0, the species dynamics does not have spatial coloni-
 530 sation. For $\nu_3 = 0, 1, 2, 3$, the full model was chosen one time, *three* times,
 531 24 times and 28 times out of 30, respectively. However, for $\nu_3 = 0, 1, 2, 3$ the
 532 difference in AIC was smaller than 2 respectively 19 times, 22 times, 6 times
 533 and 2 times out of 30. The Kullback-Leibler model selection chose the full
 534 model respectively 7 times, 25 times, 30 times and 23 times out of 30. The
 535 Kullback-Leibler method often favors the full model as opposed to the AIC
 536 method. This is due to the AIC penalizing models with more parameters
 537 and thus being less likely to chose a model which overfits the data.

Figure 7: Mean percentage of correctly recovered and predicted populations for ν_1 (influence of the previous dormant population state) varying from 0 to 6.5.

539 We looked at the mean percentage of correctly recovered dormant popula-
 540 tion states and the mean percentage of correctly predicted next non-dormant
 541 population states. For a vector of hyperparameter, we simulated population
 542 trajectories in ten patches over 100 time steps with $|\Omega_X| = |\Omega_Y| = 5$. We
 543 then simulated the non-dormant populations in the ten patches at the 101st
 544 time step, 100 times. We used the observed non-dormant population states
 545 of the first 100 time steps to estimate the hyperparameters using the EM al-
 546 gorithm. The estimators were then used to recover the dormant populations
 547 in the first 100 time steps over all the patches. Additionally, the estimators
 548 were used to predict the non-dormant populations in all patches for the 101st
 549 time step. The predictions were then evaluated using the 100 simulations of
 550 the 101st time step. Twenty-eight different vectors of hyperparameters, for
 551 which there were ten trajectories of populations, were simulated. For the first

Figure 8: Mean percentage of correctly recovered and predicted populations for ν_0 (influence of external colonisation) varying from -6.5 to 0 .

14 vectors of hyperparameters, all hyperparameters were fixed except for the hyperparameter associated with dormancy, which varied from 0 to 6.5 . The hyperparameters were : $\mu = (-3.7, 6.5)$, $\tau = -1$ and $\nu = (-3, \nu_1, 4, 2)$. The next 14 vectors of hyperparameters all had fixed values, with $\nu_1 = 4$, except for ν_0 , which varied from -6.5 to 0 .

We observed that the quality of hidden state estimation is rarely below 70% (see Figs. 7 and 8) and is better with high values of ν_1 (Fig. 7), i.e. when dormant population survival is high. On the other hand, the quality of prediction is low for high values of ν_1 . In this case, the dormant populations frequently visit the maximum state. There is almost no stochasticity in the dynamics of dormant populations (the variance of A is low) thus making their recovery easier. On the other hand, the percentage of correct prediction dropped to 40% when ν_1 was large. The poor quality of prediction is

566 directly linked to the high variance in the non-dormant population distribu-
567 tion. Since the dormant population is predominantly in the maximum state,
568 the non-dormant population distribution, conditional on the dormant popu-
569 lation being in the maximum state, is a binomial distribution with parameters
570 $(|\Omega_Y|, \frac{1}{1+\exp(-(\mu_0-\mu_1(|\Omega_X|-1)/|\Omega_X|)))})$ and its state distribution is as follows: the
571 non-dormant population has a 44% chance to be in the maximum state, a
572 39% chance to be in state 3, a 13% chance to be in state 2, a 2% chance to be
573 in state 1 and a 0.1% chance to be extinct. As the model predicts the most
574 probable state, it is not surprising to only have 40% of correct predictions.

575 For low ν_1 the situation is easier since the simulated dormant and non-
576 dormant populations frequently visit the extinction state. In addition, the
577 effect of the hyperparameter ν_0 , which corresponds to exogenous colonisation
578 of the dormant population by propagule rain, contribute to adding extra
579 noise in the species dynamics: hidden state estimation and next non-dormant
580 population predictions are easier for low values of this parameter.

581 Finally, to illustrate the scalability of the EM algorithm, the same exper-
582 iment was reproduced with ten time steps with 100 patches with 30 simula-
583 tions. The non-dormant population at the 11th time step was then simulated
584 100 times. The exact values of the hyperparameters were : $\mu = (-3.7, 6.5)$,
585 $\tau = -1$ and $\nu = (-3, 3, 4, 2)$. We obtained 80% of correct prediction of
586 the non-dormant population states and 68.9% of correct recovery of dormant
587 population states. This is slightly less than when estimating from 10 patches
588 and 100 time steps, maybe because estimation is easier from a small number
589 of patched but long trajectories of observations than for the opposite.

590 7. Discussion

591 We propose the MHMM-DF framework that can describe, from abun-
592 dance classes of non-dormant populations, the local and regional dynamics
593 of annual plants that can undergo a potentially infinite dormancy. In a
594 non-parametric approach, the MHMM-DF can be defined using only three
595 probabilities: the initial probability, the transition probability from past pop-
596 ulations to current dormant populations and the emission probability from
597 past dormant populations to current non-dormant populations. For the sake
598 of sparsity, we have proposed to model these probabilities as Binomial dis-
599 tributions with the probability parameter modelled as a logistic function de-
600 pendent on hyperparameters. Each hyperparameter is associated with a spe-
601 cific process in the species dynamics. They describe the colonisation process

602 from neighbouring patches, the exogenous colonisation process from propag-
603 ule rain, the dormancy process, the influence of the locally newly produced
604 dormant individuals and the awakening process from dormant populations
605 to non-dormant populations.

606 The colonisation process from neighbouring patches for plants is asso-
607 ciated with one hyperparameter and is described as the indistinguishable
608 influence of neighbour non-dormant population states on a dormant popu-
609 lation state in a patch. Several options exist to aggregate the neighbour
610 states into a single variable and we proposed the mean colonisation. How-
611 ever, this choice has drawbacks. The mean colonisation can assign the same
612 value in Ω_Y for very contrasted configurations of neighbours states. Addi-
613 tionally, when the number of patches increases, it increases the tendency for
614 the mean colonisation process to be identical for every patch. To circumvent
615 the first limit, we proposed the alphabetic colonisation (detailed in Appendix
616 I), which only assigns the same aggregated value to two vectors of neighbour
617 states if both vectors are equal though patch permutation. The influence of
618 the neighbour patches are still indistinguishable. However contrasted distri-
619 butions of the abundance classes of the neighbourhood will lead to different
620 aggregated values. In practice, to create an ordinal variable from the vector
621 of neighbours, we ranked the distributions of the abundance classes according
622 to alphabetic (or lexicographic) order. We demonstrated that the parametric
623 MHMM-DF with mean or alphabetic colonisation is generically identifiable
624 for a least three patches.

625 Different colonisation processes can be implemented preferably if identifi-
626 ability is verified. Instead of considering one hyperparameter for the spatial
627 colonisation process, the colonisation process could include a hyperparam-
628 eter per number of non-dormant populations in each state as modelled in
629 Gyllenberg and Hanski (1997). Each hyperparameter associated with the
630 colonisation process would measure the influence of the number of neigh-
631 bour non-dormant populations in a specific state. However, establishing the
632 model's identifiability is not straightforward, and moreover the model would
633 require more data for estimation.

634 Modelling the awakening process with a logistic regression for the proba-
635 bility parameter of the binomial distribution implies that, when the dormant
636 population is extinct, the probability of the non-dormant population being
637 extinct is smaller than 1. In other words, non-dormant populations may be
638 colonised by exterior non-dormant populations. However, since plants are
639 sessile, colonisation of non-dormant populations by exogenous factors should

not be possible. Thus the use of the logit function can be questioned when modelling the awakening process. One option is to set the probability of exterior colonisation of non-dormant populations to a very low value instead of estimating it. Alternatively, we could model the awakening probability as a zero-inflated Binomial distribution. The zero-inflated Binomial distribution would force the non-dormant population to be extinct when the dormant one is extinct, and in the other situations, the awakening process would still be a Binomial distribution with logit regression. This is obtained by setting the mixture parameter of this zero-inflated model to 1 in the case of absence of a dormant population and to 0 otherwise. The generic identifiability is still satisfied for this model.

The MHMM-DF framework is built under biological assumptions, where the dependencies between the species populations represent known biological processes. These biological processes are often modelled using precise information about the number of individuals (David et al., 2010). Even though, this type of modelling is rewarding, since predictions are more accurate, they are often computationally intensive when dealing with hidden dynamics and may have unidentifiable parameters. Modelling with abundance classes helps reduce the computational complexity. The parametric MHMM-DF is used to infer the input of each process on the species dynamics by learning statistical relationships, as opposed to mechanistic approaches that would require precise knowledge beforehand about mechanisms and environmental factors that influence the species dynamics.

The MHMM-DF relies on two main assumptions about the species dynamics. The model assumes dormant populations to be sessile and assumes that non-dormant populations do not influence one another directly. The first assumption implies that dormant populations can not travel between patches, which reduces the time and space complexity of the E step from exponential to linear in terms of patches, $O(|\Omega_X|^2 NC)$, where C is the number of patches, N is the number of time steps, and $|\Omega_X|$ is the number of states of a dormant population. Reducing the computational complexity of the E step implies that dealing with a large number of patches is not an issue with a MHMM-DF. The second assumption implies that once a non-dormant population is observed, the non-dormant population will be renewed in the next time step. These two assumptions are verified for annual plants. Even though the MHMM-DF was created to model the dynamics of plants in patches, the model is general and could be applied to different organisms.

In specific ecosystems, the assumption of seed immobility in the seed bank

678 is questionable. If it is relevant for most natural populations, where seeds
 679 are only mobile during dispersal, seeds in the seed bank of riparian ecosys-
 680 tems may move because of floods. Furthermore, in agricultural systems,
 681 tools or machines may transfer seeds from one seed bank to another. The
 682 second assumption, which assumes no interaction between past and current
 683 non-dormant populations, can easily be removed without hindering the com-
 684 plexity of the E step. Removing the assumption enables us to model the local
 685 non-dormant population’s survival between two time steps and the migration
 686 of non-dormant populations between patches. The associated parametric
 687 MHMM-DF with both survival and migration of non-dormant populations
 688 would have nine hyperparameters and is identifiable. Adding the survival
 689 process of non-dormant populations is relevant for plants since it would en-
 690 able us to study the dynamics of perennial plants. Even though, including
 691 the migration process is not relevant to plant dynamics, a model with migra-
 692 tion could be applied to many more species such as fresh water snails whose
 693 dormancy process would be seen as aestivation during dry seasons (Lamy
 694 et al., 2013).

695 MHMM-DF can have multiple uses such as estimating a species’ dynam-
 696 ics via hyperparameters, discriminating between two different types of dy-
 697 namics, predicting the state of the next non-dormant populations and even
 698 recovering all past states of dormant populations. The results show that the
 699 estimators, obtained using the EM algorithm, have a low variance and low
 700 bias when the species’ populations are not predominantly visiting either the
 701 extinction state or the maximum state. On the other hand, distinguishing
 702 the input resulting from each process is difficult when dormant populations
 703 frequently visit an extreme state since many different vectors of hyperparam-
 704 eters have a similar likelihood. When only observing the non-dormant popu-
 705 lations, the predictions and hidden state estimations obtained were globally
 706 of good quality. When a population is inferred to be or to become extinct,
 707 errors in predictions and hidden state estimations seem to be dependent on
 708 exogenous colonisation. Additionally, errors in predictions and hidden state
 709 estimations depend on the variance of the Binomial distribution. The model
 710 selection technique is able to discriminate between dynamics with dormancy
 711 and dynamics without dormancy, or even dynamics with colonisation and
 712 dynamics without colonisation. In order to fully validate the parameterisa-
 713 tion, the model should now be tested on real data. For instance, studying the
 714 dynamics of weed species with the model could be a subsequent extension.

715 Since multiple exterior factors can influence species dynamics, such as

temperature for plant germination (Taab, 2009; Seglias et al., 2018; El-Keblawy et al., 2017; Ueno, 2002; Gómez-González et al., 2018; Zhang et al., 2017), the logit function, associated with the awakening process, can include covariables to increase the model’s realism. For weed species in agricultural fields, the species dynamics could be made to depend on crop type (Borgy et al., 2015). It would be also relevant to model different sizes or types of neighbourhood, since the distance of seed dispersal or even the paths vary between species (Nathan, 2000). Indeed colonisation may be related to specific dissemination agents, such as rivers for riparian ecosystems or agricultural machines for weed species. In the latter case, dispersal is not defined by a distance from the source but by the path formed by the successive patches in which the agricultural machines travelled before entering the current patch. In practice, the size or the paths for dispersal are not known. Using model selection and several MHMM-DF models associated to different neighbourhoods, it would be possible to determine which model is best suited for a specific species.

The framework presented is the first step towards modelling the local and regional dynamics of species with an undetectable life form. The MHMM-DF can be used to describe the dynamics of annual plants by only observing standing plants. Estimating the hyperparameters associated with an annual plant will help to identify which process has the greatest influence on the seed bank’s state. Moreover, groups of species with similar survival strategies can be identified using a classification based on their estimators.

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Akaike, H. (1981). Likelihood of a model and information criteria. *Journal of Econometrics* 16(1), 3 – 14.

Akaike, H. (2011). *Akaike’s Information Criterion*, pp. 25–25. Berlin, Heidelberg: Springer Berlin Heidelberg.

Allman, E. S., C. Matias, and J. A. Rhodes (2009). Identifiability of parameters in latent structure models with many observed variables. *The Annals of Statistics* 37(6A), 3099 – 3132.

- 749 Amarasekare, P. and H. Possingham (2001). Patch dynamics and metapop-
750 ulation theory: the case of successional species. *Journal of Theoretical*
751 *Biology* 209(3), 333 – 344.
- 752 Borgy, B., X. Reboud, N. Peyrard, R. Sabbadin, and S. Gaba (2015). Dy-
753 namics of weeds in the soil seed bank : A hidden Markov model to estimate
754 life history traits from standing plant. *PLoS ONE* 10, e0139278.
- 755 Brand, M., N. Oliver, and A. Pentland (1997). Coupled hidden Markov mod-
756 els for complex action recognition. *Computer Vision and Pattern Recog-*
757 *niton*, 994 – 999.
- 758 Bullock, J., K. Shea, and O. Skarpaas (2006). Measuring plant dispersal: an
759 introduction to field methods and experimental design. *Plant Ecology* 186,
760 217–234.
- 761 Burnham, K. P. and D. R. Anderson (2004). Multimodel inference: un-
762 derstanding AIC and BIC in model selection. *Sociological methods & re-*
763 *search* 33(2), 261–304.
- 764 Byrd, R., P. Lu, J. Nocedal, and C. Zhu (1995, 9). A limited memory
765 algorithm for bound constrained optimization. *SIAM Journal of Scientific*
766 *Computing* 16, 1190 – 1208.
- 767 Cohen, D. (1966). Optimizing reproduction in a randomly varying environ-
768 ment. *Journal of Theoretical Biology* 12(1), 119–129.
- 769 David, O., A. Garnier, C. Larédo, and J. Lecomte (2010). Estimation of
770 plant demographic parameters from stage-structured censuses. *Biomet-*
771 *rics* 66(3), 875–882.
- 772 Dempster, A., N. Laird, and D. Rubin (1977). Maximum likelihood from
773 incomplete data via the EM algorithm. *Journal of the Royal Statistical*
774 *Society* 39(1), 1–38.
- 775 Dornier, A., V. Pons, and C. PO. (2011). Colonization and extinction
776 dynamics of an annual plant metapopulation in an urban environment.
777 *Oikos* 120(8), 1240–1246.
- 778 El-Keblawy, A., H. Shabana, T. Navarro, and S. Soliman (2017). Effect
779 of maturation time on dormancy and germination of *Citrullus colocynthis*

780 (cucurbitaceae) seeds from the arabian hyper-arid deserts. *BMC Plant*
781 *Biology* 17(1), 263.

782 Forney, G. (1973). The Viterbi algorithm. *IEEE* 63(1), 268 – 278.

783 Freckleton, R. and A. Watkinson (2002). Large-scale spatial dynamics of
784 plants: metapopulation regional ensembles and patchy populations. *Journal of Ecology* 90, 419–434.
785

786 Fréville, H., R. Choquet, R. Pradel, and P. Cheptou (2013). Inferring seed
787 bank from hidden Markov models: new insights into metapopulation dy-
788 namics in plants. *Journal of Ecology*, 1572–1580.

789 Ghahramani, Z. (1998). *Learning dynamic Bayesian networks*, pp. 168–197.
790 Berlin, Heidelberg: Springer Berlin Heidelberg.

791 Ghahramani, Z. and M. Jordan (1997). Factorial hidden Markov models.
792 *Mach. Learn.* 29(2-3), 245–273.

793 Gotelli, N. J. (1991). Metapopulation models: The rescue effect, the
794 propagule rain, and the core-satellite hypothesis. *The American Naturalist* 138(3), 768–776.
795

796 Gyllenberg, M. Hastings, A. and I. Hanski (1997). 5 - Structured metapop-
797 ulation models. In I. Hanski and M. E. Gilpin (Eds.), *Metapopulation*
798 *Biology*, pp. 93 – 122. San Diego: Academic Press.

799 Gómez-González, S., M. Paniw, K. Antunes, and F. Ojeda (2018). Heat
800 shock and plant leachates regulate seed germination of the endangered
801 carnivorous plant *drosophyllum lusitanicum*. *Web Ecology* 18(1), 7–13.

802 Han, Z., T. Lui, Q. Sun, R. Li, J. Xie, and B. Li (2014). Application of com-
803 pound interest laws in biology: Reunification of existing models to develop
804 seed bank dynamics model of annual plants. *Ecological Modelling* 278, 67–
805 73.

806 Hanski, I. (1994). A practical model of metapopulation dynamics. *Journal*
807 *of Animal Ecology* 63(1), 151–162.

808 Hanski, I. (1998). Metapopulation dynamics. *Nature* 396, 41–49.

- 809 Jarry, M., M. Khaladi, M. Hossaert-McKey, and D. McKey (1995). Modelling
810 the population dynamics of annual plants with seed bank and density
811 dependent effects. *Acta Biotheoretica* 43(1-2), 53–65.
- 812 Lamy, T., O. Gimenez, J. Pointier, P. Jarne, and P. David (2013). Metapop-
813 ulation dynamics of species with cryptic life stages. *the American Natu-
814 ralist* 181(4), 479–491.
- 815 Levin, S., D. Cohen, and A. Hastings (1984). Dispersal strategies in patchy
816 environments. *Theoretical Population Biology* 26(2), 165–191.
- 817 Levins, R., D. Vagaggini, P. Zarattini, and G. Mura (1969). Some demo-
818 graphic and genetic consequences of environmental heterogeneity for bio-
819 logical control. *Bulletin of the Entomological Society of America* 15(3),
820 237–240.
- 821 Manna, F., R. Pradel, R. Choquet, H. Fréville, and P. Cheptou (2017). Dis-
822 entangling the role of seed bank and dispersal in plant metapopulation
823 dynamics using patch occupancy surveys. *Ecology* 98(10), 2662–2672.
- 824 Mistro, D., L. Rodrigues, and A. Schmid (2005). A mathematical model
825 for dispersal of an annual plant population with a seed bank. *Ecological
826 Modelling* 188, 52–61.
- 827 Nathan, R. Muller-Landau, H. (2000). Spatial patterns of seed dispersal,
828 their determinants and consequences for recruitment. *Trends in Ecology
829 & Evolution* 15(7), 278–285.
- 830 Oakes, D. (1999). Direct calculation of the information matrix via the EM.
831 *Journal of the Royal Statistical Society: Series B (Statistical Methodol-
832 ogy)* 61(2), 479–482.
- 833 Pluntz, M., S. L. Coz, N. Peyrard, R. Pradel, R. Choquet, and P.-O. Cheptou
834 (2018). A general method for estimating seed dormancy and colonisation in
835 annual plants from the observation of existing flora. *Ecology Letters* 21(9),
836 1311–1318.
- 837 Quintana-Ascencio, P. F., E. S. Menges, C. W. Weekley, M. I. Kelrick, and
838 B. Pace-Aldana (2011). Biennial cycling caused by demographic delays in
839 a fire-adapted annual plant. *Population Ecology* 53(1), 131–142.

- 840 Rabiner, L. (1989). A tutorial on hidden Markov models and selected appli-
841 cations in speech recognition. In *Proceedings of the IEEE*, Volume 77, pp.
842 257–286.
- 843 Seglias, A. and Williams, E., A. Bilge, and A. Kramer (2018). Phylogeny
844 and source climate impact seed dormancy and germination of restoration-
845 relevant forb species. *Plos one* 13(2), e019193.
- 846 Soubeyrand, S., A. Laine, I. Hanski, and A. Penttinen (2009). Spatiotemporal
847 structure of host-pathogen interactions in a metapopulation. *American*
848 *Naturalist* 174(3), 308–320.
- 849 Taab, A. (2009). *Seed Dormancy and Germination in Solanum nigrum and*
850 *S. physalifolium as Influenced by Temperature Conditions*. Ph. D. thesis,
851 Swedish University of Agricultural Sciences Uppsala.
- 852 Ueno, K. (2002). Effects of desiccation and a change in temperature on
853 germination of immature grains of wheat (triticum aestivum l.). *Euphyt-*
854 *ica* 126(1), 107 – 113.
- 855 Wainwright, M. and M. Jordan (2008). Graphical models, exponential fam-
856 ilies, and variational inference. In *Foundations and Trends in Machine*
857 *Learning*, Volume 1, pp. 1–305.
- 858 Zhang, R., J. Baskin, C. Baskin, Q. Mo, L. Chen, X. Hu, and Y. Wang
859 (2017). Effect of population, collection year, after-ripening and incubation
860 condition on seed germination of stipa bungeana. *Scientific reports* 7(1),
861 13893.

862 **Appendices**

863 **A. Graphical structure of HMM, CHMM and FHMM**

Figure A.9: Hidden Markov Chain. Y_n variables are observed at each time step n while X_n variables (grey nodes) are not. The dynamics of the hidden variables is not influenced by the observed variables.

Figure A.10: Factorial Hidden Markov Model.

864 B. Proof of generic identifiability for a MHMM-DF with the mean 865 colonisation process

866 A HMM model with N time steps is generically identifiable if the set of
867 values of θ such that $\mathbb{P}(Y^N = y^N | \theta) = \mathbb{P}(Y^N = y^N | \theta')$ has null Lebesgue
868 measure. We use the results for HMM here to demonstrate the generic iden-
869 tifiability of the MHMM-DF models with the mean colonisation process. The
870 proof relies on Theorem 6 from Allman et al. 2009:

871 **Theorem 1 (Theorem 6 of Allman et al. (2009)).** *The parameters of*
872 *a HMM with r hidden states and s observable states are generically identi-*
873 *fiable from the marginal distribution of $2L + 1$ consecutive variables provided*
874 *L satisfies*

Figure A.11: Coupled Hidden Markov Model.

$$\binom{L + s - 1}{s - 1} \geq r.$$

875 This results holds for a HMM, with a dependency structure identical to Fig.
876 A.9. We can convert a MHMM-DF model into a HMM with hidden variable
877 H_n and observed variables O_n (see Fig. B.12) by grouping the observed and
878 hidden variables of all patches, $H_n = (X_n^C, Y_{n+1}^C)$, and by setting $O_n = Y_{n+1}^C$.
879 Note that the observed variables are duplicated. We will denote ϕ^{hmm} and
880 A^{hmm} as respectively the emission and the transition probabilities of the
881 HMM $(H_n, O_n)_{n \in \{0, \dots, N-1\}}$. ϕ^{hmm} is deterministic, and A^{hmm} depends on the
882 probabilities ϕ and A of the MHMM-DF.

883 When applying Theorem 1 to the HMM defined by (H_n, O_n) we obtain
884 the following theorem

885 **Theorem 2.** *The parameters (ϕ^{hmm}, A^{hmm}) of the HMM model correspond-*
886 *ing to the conversion of a MHMM-DF are generically identifiable from seven*
887 *consecutive observations, if $|\Omega_X| \leq |\Omega_Y|$, and if $C > 2$.*

888 **Proof.**

Figure B.12: Conversion of a MHMM-DF into a HMM. When grouping the observed and hidden variables of the MHMM-DF and duplicating the observed variables, the dependency structure is identical to a classical HMM.

889 The number of possible hidden states is $r = |\Omega_X|^C |\Omega_Y|^C$, the number of
 890 possible observable states is $s = |\Omega_Y|^C$ and $L = 3$. We must show that the
 891 following inequality is satisfied:

$$\binom{|\Omega_Y|^C + 2}{|\Omega_Y|^C - 1} \geq |\Omega_X|^C |\Omega_Y|^C.$$

892 The inequality can be reformulated as:

$$(|\Omega_Y|^C + 2)(|\Omega_Y|^C + 1) \geq |\Omega_X|^C.$$

893 Since we assume that $|\Omega_X| \leq |\Omega_Y|$, the inequality is true.

894 $\square$

895 This theorem demonstrates the generic identifiability of A_{hmm} and ϕ_{hmm} ,
 896 considered as non-parameterised, but not yet the generic identifiability of ϕ
 897 and A . We now consider the model with a non-distinguishable effect of the
 898 neighbours, defined by ϕ_μ and A_ν and provide sufficient conditions for their
 899 generic identifiability. We need to prove that $(A_{\mu,\nu}^{hmm}, \phi_{\mu,\nu}^{hmm}) = (A_{\mu',\nu'}^{hmm}, \phi_{\mu',\nu'}^{hmm})$
 900 implies $(\mu, \nu) = (\mu', \nu')$.
 901

902 In the HMM representation of a MHMM-DF, the emission matrix ϕ_{hmm}
 903 is deterministic and is independent of μ, ν . Therefore, we need to show that
 904 $A_{\mu,\nu}^{hmm} = A_{\mu',\nu'}^{hmm}$ implies $(\mu, \nu) = (\mu', \nu')$. We recall that $A_{\mu,\nu}^{hmm}(h_n, h_{n-1}) =$
 905 $\mathbb{P}(h_n | h_{n-1}, \nu, \mu)$. The HMM's transition probability is:

$$\begin{aligned}
\mathbb{P}(h_n|h_{n-1}, \nu, \mu) &= \mathbb{P}(x_n^C, y_{n+1}^C | x_{n-1}^C, y_n^C) \\
&= \mathbb{P}(y_{n+1}^C | x_n^C) \mathbb{P}(x_n^C | x_{n-1}^C, y_n^C) \\
&= \prod_{c=1}^C \mathbb{P}(y_{c,n+1} | x_{c,n}) \mathbb{P}(x_{c,n} | x_{c,n-1}, y_n^C) \\
&= \prod_{c=1}^C \binom{|\Omega_Y| - 1}{y_{c,n+1}} \\
&\quad \times \left[\frac{1}{1 + \exp(-(\mu_0 + \mu_1 \frac{x_{c,n}}{|\Omega_X|}))} \right]^{|\Omega_Y| - 1} \left[\exp(-(\mu_0 + \mu_1 \frac{x_{c,n}}{|\Omega_X|})) \right]^{|\Omega_Y| - y_{c,n+1} - 1} \\
&\quad \times \binom{|\Omega_X| - 1}{x_{c,n}} \left[\frac{1}{1 + \exp(-(\nu_0 + \nu_1 \frac{x_{c,n-1}}{|\Omega_X|} + \nu_2 \frac{y_{c,n}}{|\Omega_Y|} + \nu_3 (\frac{f_{\text{mean}}(y_n^{C \setminus c})}{|f_{\text{mean}}(\Omega_Y^{C-1})|})))} \right]^{|\Omega_X| - 1} \\
&\quad \times \left[\exp(-(\nu_0 + \nu_1 \frac{x_{c,n-1}}{|\Omega_X|} + \nu_2 \frac{y_{c,n}}{|\Omega_Y|} + \nu_3 (\frac{f_{\text{mean}}(y_n^{C \setminus c})}{|f_{\text{mean}}(\Omega_Y^{C-1})|}))) \right]^{|\Omega_X| - x_{c,n} - 1}
\end{aligned}$$

906 **Theorem 3.** *The hyperparameter $(\mu, \nu) = (\mu_0, \mu_1, \nu_0, \nu_1, \nu_2, \nu_3)$ of a MHMM-*
907 *DF with the mean colonisation process is generically identifiable from seven*
908 *consecutive observations if the following conditions hold: if $|\Omega_X| \leq |\Omega_Y|$,*
909 *$|\Omega_Y| > 1$ and $C > 2$.*

910 **Proof.**

911 As explained above, we need to find conditions under which $\mathbb{P}(h_n|h_{n-1}, \nu, \mu) =$
912 $\mathbb{P}(h_n|h_{n-1}, \nu', \mu')$ implies $(\mu, \nu) = (\mu', \nu')$. Let us show one-by-one the equal-
913 ity for each hyperparameter. We start with μ_0 . Let us define $L1$ as the
914 transition probability from $(x_{n-1}^C, y_n^C) = (\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix})$ to $(x_n^C, y_{n+1}^C) =$

915 $(\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}).$

$$\begin{aligned}
L1(\mu_0, \nu_0) &= \binom{|\Omega_Y| - 1}{0}^C \left[\frac{1}{1 + \exp(-\mu_0)} \right]^{(|\Omega_Y| - 1)C} [\exp(-\mu_0)]^{(|\Omega_Y| - 1)C} \\
&\quad \times \binom{|\Omega_X| - 1}{0}^C \left[\frac{1}{1 + \exp(-\nu_0)} \right]^{(|\Omega_X| - 1)C} [\exp(-\nu_0)]^{(|\Omega_X| - 1)C}.
\end{aligned}$$

916 We now define $L2$ as the transition probability from $(x_{n-1}^C, y_n^C) = \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}$

917 to $(x_n^C, y_{n+1}^C) = \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} |\Omega_Y| - 1 \\ 0 \\ \dots \\ 0 \end{pmatrix}$:

$$\begin{aligned} L2(\mu_0, \nu_0) &= \begin{pmatrix} |\Omega_Y| - 1 \\ 0 \end{pmatrix}^{C-1} \begin{pmatrix} |\Omega_Y| - 1 \\ |\Omega_Y| - 1 \end{pmatrix} \left[\frac{1}{1 + \exp(-\mu_0)} \right]^{(|\Omega_Y| - 1)C} [\exp(-\mu_0)]^{(|\Omega_Y| - 1)(C-1)} \\ &\quad \times \begin{pmatrix} |\Omega_X| - 1 \\ 0 \end{pmatrix}^C \left[\frac{1}{1 + \exp(-\nu_0)} \right]^{(|\Omega_X| - 1)C} [\exp(-\nu_0)]^{(|\Omega_X| - 1)C}. \end{aligned}$$

918 If $L1(\mu_0, \nu_0) = L1(\mu'_0, \nu'_0)$ and $L2(\mu_0, \nu_0) = L2(\mu'_0, \nu'_0)$ then $L1(\mu_0, \nu_0)/L2(\mu_0, \nu_0) =$
 919 $L1(\mu'_0, \nu'_0)/L2(\mu'_0, \nu'_0)$, which implies $e^{-(|\Omega_Y| - 1)\mu_0} = e^{-(|\Omega_Y| - 1)\mu'_0}$. Thus $\mu'_0 = \mu_0$.
 920 Since $\mu'_0 = \mu_0$, we can now identify ν_0 using $L1$:

$$\begin{aligned} L1(\mu_0, \nu_0) &= L1(\mu_0, \nu'_0) \\ &\Leftrightarrow \left(\left(\frac{1}{1 + \exp(-\nu_0)} \right) \exp(-\nu_0) \right)^{(|\Omega_X| - 1)C} = \left(\left(\frac{1}{1 + \exp(-\nu'_0)} \right) \exp(-\nu'_0) \right)^{(|\Omega_X| - 1)C} \\ &\Leftrightarrow (1 + \exp(-\nu_0)) \exp(\nu_0) = (1 + \exp(-\nu'_0)) \exp(\nu'_0) \\ &\Leftrightarrow \nu_0 = \nu'_0. \end{aligned}$$

921 Let us now show the identifiability of μ_1 . We consider $L3$, the expression
 922 defined by the transition probability from $(x_{n-1}^C, y_n^C) = \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}$ to

923 $(x_n^C, y_{n+1}^C) = \begin{pmatrix} |\Omega_X| - 1 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}$. Note that from now on, in the expres-

924 sions used to derive identifiability, we omit the terms that are known to be
 925 equal for two distinct values of the current hyperparameter considered for
 926 identifiability. Therefore

$$\begin{aligned}
L3(\nu_0, \mu_0, \mu_1) &\propto \left[\frac{1}{1 + \exp(-\mu_0)} \right]^{(|\Omega_Y|-1)(C-1)} [\exp(-\mu_0)]^{(|\Omega_Y|-1)(C-1)} \\
&\times \left[\frac{1}{1 + \exp(-(\mu_0 + \frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1))} \right]^{(|\Omega_Y|-1)} \\
&\times \left[\exp(-(\mu_0 + \frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1)) \right]^{(|\Omega_Y|-1)} \\
&\times \left[\frac{1}{1 + \exp(-\nu_0)} \right]^{(|\Omega_X|-1)C} [\exp(-\nu_0)]^{(|\Omega_X|-1)(C-1)}.
\end{aligned}$$

927

Thus

$$\begin{aligned}
L3(\nu_0, \mu_0, \nu_1') &= L3(\nu_0, \mu_0, \nu_1) \\
&\Leftrightarrow \\
\left[\frac{1}{1 + \exp(-(\mu_0 + \frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1'))} \right] \left[\exp(-\frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1') \right] &= \left[\frac{1}{1 + \exp(-(\mu_0 + \frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1))} \right] \left[\exp(-\frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1) \right] \\
&\Leftrightarrow \\
\frac{\exp(-\frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1) + \exp(-\mu_0 - \frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1 - \frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1')}{\mu_1} &= \frac{\exp(-\frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1') + \exp(-\mu_0 - \frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1 - \frac{(|\Omega_X|-1)}{|\Omega_X|} \mu_1')}{\mu_1'} \\
&\Leftrightarrow \\
\mu_1 &= \mu_1'.
\end{aligned}$$

928

We establish the identifiability of ν_1 by using $L4$, the transition probabil-

929

ity from $(x_{n-1}^C, y_n^C) = (\begin{pmatrix} |\Omega_X| - 1 \\ \dots \\ |\Omega_X| - 1 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix})$ to $(x_n^C, y_{n+1}^C) = (\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix})$.

$$\begin{aligned}
L4(\mu_0, \nu_0, \nu_1) &\propto \left[\frac{1}{1 + \exp(-\mu_0)} \right]^{(|\Omega_Y|-1)C} [\exp(-\mu_0)]^{(|\Omega_Y|-1)C} \\
&\times \left[\frac{1}{1 + \exp(-(\nu_0 + \nu_1 \frac{(|\Omega_X|-1)}{|\Omega_X|}))} \right]^{(|\Omega_X|-1)C} \\
&\times \left[\exp(-(\nu_0 + \nu_1 \frac{(|\Omega_X|-1)}{|\Omega_X|})) \right]^{(|\Omega_X|-1)C}.
\end{aligned}$$

930

Thus :

$$\begin{array}{ccc}
 L4(\mu_0, \nu_0, \nu_1') & = & L4(\mu_0, \nu_0, \nu_1) \\
 & \Leftrightarrow & \\
 \left[\frac{1}{1 + \exp(-(\nu_0 + \nu_1' \frac{(|\Omega_X| - 1)}{|\Omega_X|}))} \right] \left[\exp(-\nu_1' \frac{(|\Omega_X| - 1)}{|\Omega_X|}) \right] & = & \left[\frac{1}{1 + \exp(-(\nu_0 + \nu_1 \frac{(|\Omega_X| - 1)}{|\Omega_X|}))} \right] \left[\exp(-\nu_1 \frac{(|\Omega_X| - 1)}{|\Omega_X|}) \right] \\
 & \Leftrightarrow & \\
 \nu_1 & = & \nu_1'.
 \end{array}$$

931 We have established identifiability for all hyperparameters except ν_2 and
 932 ν_3 . When $C = 2$ it can be seen that $f_{\text{mean}}(Y_n^{C \setminus c}) = Y_{c',n}$ with $c \neq c'$. By using
 933 the following states defined below one can not show identifiability of ν_2 and
 934 ν_3 . Let us assume $C > 2$. For these two hyperparameters, we consider the

935 following two transition probabilities: $L5$ from $(x_{n-1}^C, y_n^C) = (\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 1 \\ 0 \\ \dots \\ 0 \end{pmatrix})$
 936 to $(x_n^C, y_{n+1}^C) = (\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix})$ and $L6$ from $(x_{n-1}^C, y_n^C) = (\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 1 \\ \dots \\ 1 \end{pmatrix})$ to
 937 $(x_n^C, y_{n+1}^C) = (\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix})$.

$$\begin{aligned}
 L5(\nu_0, \nu_2) & \propto \left[\frac{1}{1 + \exp(-(\nu_0 + \frac{1}{|\Omega_Y|} \nu_2))} \right]^{(|\Omega_X| - 1)} \left[\frac{1}{1 + \exp(-\nu_0)} \right]^{(|\Omega_X| - 1)(C - 1)} \\
 & \times \left[\exp(-(\nu_0 + \frac{1}{|\Omega_Y|} \nu_2)) \right]^{(|\Omega_X| - 1)} [\exp(-\nu_0)]^{(|\Omega_X| - 1)(C - 1)}.
 \end{aligned}$$

938

Therefore:

$$\begin{array}{ccc}
 L5(\nu_0, \nu_2') & = & L5(\nu_0, \nu_2) \\
 & \Leftrightarrow & \\
 \exp(\frac{1}{|\Omega_Y|} \nu_2') & = & \exp(\frac{1}{|\Omega_Y|} \nu_2) \\
 & \Leftrightarrow & \\
 \nu_2' & = & \nu_2.
 \end{array}$$

$$L6(\nu_0, \nu_2, \nu_3) \propto \left[\frac{1}{1 + \exp(-(\nu_0 + \frac{1}{|\Omega_Y|}\nu_2 + \frac{1}{|\Omega_Y|}\nu_3))} \right]^{(|\Omega_X|-1)C} \\ \times \left[\exp(-(\nu_0 + \frac{1}{|\Omega_Y|}\nu_2 + \frac{1}{|\Omega_Y|}\nu_3)) \right]^{(|\Omega_X|-1)C}.$$

939 Therefore

$$\begin{aligned} L6(\nu_0, \nu_2, \nu'_3) &= L6(\nu_0, \nu_2, \nu_3) \\ &\Leftrightarrow \\ \exp(\frac{1}{|\Omega_Y|}\nu'_3) &= \exp(\frac{1}{|\Omega_Y|}\nu_3) \\ &\Leftrightarrow \\ \nu'_3 &= \nu_3. \end{aligned}$$

940 The MHMM-DF with mean colonisation is identifiable with at least two
941 hidden states and at least two observable states with at least three patches
942 and with the number of hidden states smaller or equal to the number of
943 observable states.

944

□

945 C. Expression of E step for MHMM-DF

946 We derive the recursive expression of the forward-backward algorithm for
947 a chain c used in the E-step of EM for MHMM-DF. First, we show how
948 the function Q can be expressed in terms of the probabilities $\rho_{c,n}(x_{c,n})$ and
949 $\xi_{c,n}(x_{c,n-1}, x_{c,n})$ defined as

$$\begin{aligned} \xi_{c,n}(x_{n-1}, x_n) &= \mathbb{P}(X_{c,n} = x_n, X_{c,n-1} = x_{n-1} | Y^{C,N} = y^{C,N}, \lambda_t), \\ \rho_{c,n}(x_n) &= \mathbb{P}(X_{c,n} = x_n | Y^{C,N} = y^{C,N}, \lambda_t) \end{aligned}$$

950 where $\lambda_t = (\pi_t, \phi_t, A_t)$ is the current estimator. We describe here how these
951 probabilities can be computed from auxiliary quantities defined recursively
952 and independently for each chain.

$$\begin{aligned}
Q(\lambda \mid \lambda_t) &= E[\ln(\mathbb{P}(Y^{C,N}, X^{C,N} \mid \lambda)) \mid y^{C,N}, \lambda_t] \\
&= E[\ln(\prod_{c=1}^C \mathbb{P}(X_{c,0} \mid \lambda) \prod_{n=1}^N \mathbb{P}(X_{c,n} \mid X_{c,n-1}, Y_n^C, \lambda) \mathbb{P}(Y_{c,n} \mid X_{c,n-1}, \lambda)) \mid y^{C,N}, \lambda_t] \\
&= \sum_{c=1}^C \sum_{x \in \Omega_X} \ln(\pi(x)) \mathbb{P}(X_{c,0} = x \mid Y^{C,N} = y^{C,N}, \lambda_t) \\
&+ \sum_{c=1}^C \sum_{n=1}^N \sum_{(x_n, x_{n-1}) \in \Omega_X^2} \ln(A(x_{n-1}, x_n, y_n^C)) \mathbb{P}(x_n, x_{n-1} \mid y^{C,N}, \lambda_t) \\
&+ \sum_{c=1}^C \sum_{n=1}^N \sum_{x_{n-1} \in \Omega_X} \ln(\phi(x_{n-1}, y_{c,n})) \mathbb{P}(X_{c,n-1} = x_{n-1} \mid Y^{C,N} = y^{C,N}, \lambda_t) \\
&= \sum_{c=1}^C \sum_{x \in \Omega_X} \ln(\pi(x)) \rho_{c,0}(x) \\
&+ \sum_{c=1}^C \sum_{n=1}^N \sum_{(x_n, x_{n-1}) \in \Omega_X^2} \ln(A(x_{n-1}, x_n, y_n^C)) \xi_{c,n}(x_{n-1}, x_n) \\
&+ \sum_{c=1}^C \sum_{n=1}^N \sum_{x_{n-1} \in \Omega_X} \ln(\phi(x_{n-1}, y_{c,n})) \rho_{c,n-1}(x_{n-1}).
\end{aligned}$$

953 Let us define $\alpha_{c,n}(x_{c,n}) = \mathbb{P}(y^{C,n}, x_{c,n} \mid \lambda_t)$ and $\beta_{c,n}(x_{c,n}) = \mathbb{P}(y_{n+1}^C, \dots, y_N^C \mid y^{C,n}, x_{c,n}, \lambda_t)$.
954 For a given chain c , the $\alpha_{c,n}$ can be computed recursively from $\alpha_{c,n-1}$ (inde-
955 pendently of $\alpha_{c',n}$ for $c' \neq c$):

$$\begin{aligned}
\alpha_{c,n}(x_{c,n}) &= \mathbb{P}(y^{C,n}, X_{c,n} = x_{c,n} \mid \lambda_t) \\
&= \sum_{x_{c,n-1} \in \Omega_X} \mathbb{P}(y^{C,n}, X_{c,n} = x_{c,n}, X_{c,n-1} = x_{c,n-1} \mid \lambda_t) \\
&= \sum_{x_{c,n-1} \in \Omega_X} \mathbb{P}(y^{C,n-1}, X_{c,n-1} = x_{c,n-1} \mid \lambda_t) \\
&\quad \times \mathbb{P}(y_n^C, X_{c,n} = x_{c,n} \mid y^{C,n-1}, x_{c,n-1}, \lambda_t) \\
&= \sum_{x_{c,n-1} \in \Omega_X} \alpha_{c,n-1}(x_{c,n-1}) \mathbb{P}(y_n^C \mid y^{C,n-1}, x_{c,n-1}, \lambda_t) A_t(x_{c,n-1}, x_{c,n}, y_n^C) \\
&= \sum_{x_{c,n-1} \in \Omega_X} \alpha_{c,n-1}(x_{c,n-1}) \phi_t(x_{c,n-1}, y_{c,n}) A_t(x_{c,n-1}, x_{c,n}, y_n^C) \\
&\quad \times \mathbb{P}(y_n^{C \setminus c} \mid y^{C,n-1}, y_{c,n}, x_{c,n-1}, \lambda_t).
\end{aligned}$$

956 Since $Y_n^{C \setminus c}$ is independent of $X_{c,n-1}$ and $Y_{c,n}$, conditional on $y^{C,n-1}$, we
 957 have $\mathbb{P}(y_n^{C \setminus c} | y^{C,n-1}, y_{c,n}, x_{c,n-1}) = \mathbb{P}(y_n^{C \setminus c} | y^{C,n-1}) = K_{c,n}$, where $K_{c,n}$ is a con-
 958 stant in $x_{c,n-1}$ and $x_{c,n}$. Therefore,

$$\alpha_{c,n}(x_{c,n}) \propto \sum_{x_{c,n-1} \in \Omega_X} \alpha_{c,n-1}(x_{c,n-1}) \phi_t(x_{c,n-1}, y_{c,n}) A_t(x_{c,n-1}, x_{c,n}, y_n^C).$$

959 In practice, instead of computing $\alpha_{c,n}(x_{c,n})$, we can compute $\tilde{\alpha}_{c,n}(x_{c,n})$
 960 defined as:

$$\tilde{\alpha}_{c,n}(x_{c,n}) = \sum_{x_{c,n-1} \in \Omega_X} \tilde{\alpha}_{c,n-1}(x_{c,n-1}) \phi(x_{c,n-1}, y_{c,n}) A_t(x_{c,n-1}, x_{c,n}, y_n^C)$$

961 with $\tilde{\alpha}_{c,0}(x_{c,0}) = \alpha_{c,0}(x_{c,0})$.

962 Similarly, there is a recursive expression of $\beta_{c,n}$ involving $\beta_{c,n-1}$:

$$\begin{aligned} \beta_{c,n}(x_{c,n}) &= \mathbb{P}(y_{n+1}^C, \dots, y_N^C | y^{C,n}, x_{c,n}, \lambda_t) \\ &= \sum_{x_{c,n+1} \in \Omega_X} \mathbb{P}(y_{n+1}^C, \dots, y_N^C, x_{c,n+1} | y^{C,n}, x_{c,n}, \lambda_t) \\ &= \sum_{x_{c,n+1} \in \Omega_X} \mathbb{P}(y_{n+2}^C, \dots, y_N^C, x_{c,n+1} | y^{C,n+1}, x_{c,n}, \lambda_t) \mathbb{P}(y_{n+1}^C | y^{C,n}, x_{c,n}, \lambda_t) \\ &= \sum_{x_{c,n+1} \in \Omega_X} \mathbb{P}(y_{n+2}^C, \dots, y_N^C | y^{C,n+1}, x_{c,n}, x_{c,n+1}, \lambda_t) A_t(x_{c,n}, x_{c,n+1}, y_{n+1}^C) \\ &\quad \times \phi_t(x_{c,n}, y_{c,n+1}) \mathbb{P}(y_{n+1}^{C \setminus c} | y^{C,n}, y_{c,n+1}, x_{c,n}, \lambda_t) \\ &= K_{c,n+1} \sum_{x_{c,n+1} \in \Omega_X} \mathbb{P}(y_{n+2}^C, \dots, Y_N^C | y^{C,n+1}, x_{c,n}, x_{c,n+1}, \lambda_t) \\ &\quad \times A_t(x_{c,n}, x_{c,n+1}, y_{n+1}^C) \phi(x_{c,n}, y_{c,n+1}). \end{aligned}$$

963 Since the vector $(Y_{n+2}^C, \dots, Y_N^C)$ is independent of $X_{c,n}$ given $y^{C,n+1}, x_{c,n+1}$,
 964 we have:

$$\beta_{c,n}(x_{c,n}) \propto \sum_{x_{c,n+1} \in \Omega_X} \beta_{c,n+1}(x_{c,n+1}) A_t(x_{c,n}, x_{c,n+1}, Y_{n+1}^C) \phi_t(x_{c,n}, y_{c,n+1}).$$

965 Similarly to the forward part of the algorithm, we compute the backward
 966 part with $\tilde{\beta}_{c,n}$ defined as:

$$\tilde{\beta}_{c,n}(x_{c,n}) = \sum_{x_{c,n+1} \in \Omega_X} \tilde{\beta}_{c,n+1}(x_{c,n+1}) A_t(x_{c,n}, x_{c,n+1}, y_{n+1}^C) \phi(x_{c,n}, y_{c,n+1})$$

967 with $\tilde{\beta}_{c,N}(x_{c,N}) = \beta_{c,N}(x_{c,N})$.

968 The two probabilities $\rho_{c,n}(x_{c,n}) = \mathbb{P}(X_{c,n} = x_{c,n} | y^{C,N}, \lambda_t)$ and $\xi_{c,n}(x_{c,n-1}, x_{c,n}) =$
 969 $\mathbb{P}(X_{c,n} = x_{c,n}, X_{c,n-1} = x_{c,n-1} | y^{C,N}, \lambda_t)$ necessary to compute Q are obtained
 970 from $\tilde{\alpha}_{c,n}$ and $\tilde{\beta}_{c,n}$ as follows:

$$\rho_{c,n}(x_{c,n}) = \frac{\mathbb{P}(X_{c,n} = x_{c,n}, y^{C,N} | \lambda_t)}{\mathbb{P}(y^{C,N} | \lambda_t)} = \frac{\beta_{c,n}(x_{c,n})\alpha_{c,n}(x_{c,n})}{\sum_{x \in \Omega_X} \beta_{c,n}(x)\alpha_{c,n}(x)} = \frac{\tilde{\beta}_{c,n}(x_{c,n})\tilde{\alpha}_{c,n}(x_{c,n})}{\sum_{x \in \Omega_X} \tilde{\beta}_{c,n}(x)\tilde{\alpha}_{c,n}(x)},$$

$$\xi_{c,n}(x_{c,n-1}, x_{c,n}) = \frac{\mathbb{P}(X_{c,n} = x_{c,n}, X_{c,n-1} = x_{c,n-1}, y^{C,N} | \lambda_t)}{\mathbb{P}(y^{C,N} | \lambda_t)}.$$

971 It is possible to express the numerator in terms of $\tilde{\alpha}_{c,n}$ and $\tilde{\beta}_{c,n}$:

$$\begin{aligned} \mathbb{P}(x_{c,n}, x_{c,n-1}, y^{C,N}) &= \mathbb{P}(X_{c,n} = x_{c,n}, X_{c,n-1} = x_{c,n-1}, y_n^C | \lambda_t) \\ &\quad \times \mathbb{P}(\{y_l^C\}_{l \neq n} | x_{c,n}, x_{c,n-1}, y_n^C, \lambda_t) \\ &= A_t(x_{c,n-1}, x_{c,n}, y_n^C) \mathbb{P}(X_{c,n-1} = x_{c,n-1}, y_n^C | \lambda_t) \\ &\quad \times \mathbb{P}(y^{C,n-1} | x_{c,n}, x_{c,n-1}, y_n^C, \lambda_t) \\ &\quad \times \mathbb{P}(y_{n+1}^C, \dots, y_N^C | x_{c,n}, x_{c,n-1}, y^{C,n}, \lambda_t) \\ &= A_t(x_{c,n-1}, x_{c,n}, y_n^C) \mathbb{P}(X_{c,n-1} = x_{c,n-1}, y_n^C | \lambda_t) \\ &\quad \times \mathbb{P}(y^{C,n-1} | x_{c,n-1}, y_n^C, \lambda_t) \beta_{c,n}(x_{c,n}) \\ &= A_t(x_{c,n-1}, x_{c,n}, y_n^C) \beta_{c,n}(x_{c,n}) \mathbb{P}(X_{c,n-1} = x_{c,n-1}, y^{C,n} | \lambda_t) \\ &= A_t(x_{c,n-1}, x_{c,n}, y_n^C) \beta_{c,n}(x_{c,n}) \mathbb{P}(X_{c,n-1} = x_{c,n-1}, y^{C,n-1} | \lambda_t) \\ &\quad \times \mathbb{P}(y_n^C | x_{c,n-1}, y^{C,n-1}, \lambda_t) \\ &= A_t(x_{c,n-1}, x_{c,n}, y_n^C) \beta_{c,n}(x_{c,n}) \alpha_{c,n-1}(x_{c,n-1}) \phi_t(x_{c,n-1}, y_{c,n}) K_{c,n} \\ &\propto A_t(x_{c,n-1}, x_{c,n}, Y_n^C) \tilde{\beta}_{c,n}(x_{c,n}) \tilde{\alpha}_{c,n-1}(x_{c,n-1}) \phi_t(x_{c,n-1}, y_{c,n}). \end{aligned}$$

972 This leads to

$$\xi_{c,n}(x_{c,n-1}, x_{c,n}) = \frac{A_t(x_{c,n-1}, x_{c,n}, y_n^C) \tilde{\beta}_{c,n}(x_{c,n}) \tilde{\alpha}_{c,n-1}(x_{c,n-1}) \phi_t(x_{c,n-1}, y_{c,n})}{\sum_{(x, x') \in \Omega_X^2} A_t(x', x, y_n^C) \tilde{\beta}_{c,n}(x) \tilde{\alpha}_{c,n-1}(x') \phi_t(x', y_{c,n})}.$$

973 D. Expression of the likelihood of a MHMM-DF

974 Since the forward-backward algorithm only requires quantity proportional
 975 to the likelihood, we never compute the likelihood of the data during EM.

976 However, there are situations where we are interested in computing the like-
 977 lihood, such as for model selection. We derive here the likelihood expression
 978 in terms of $\tilde{\alpha}_{c,n}$ and $\tilde{\beta}_{c,n}$.

$$\begin{aligned}
 \mathbb{P}(y^{C,N}) &= \sum_{x_{c,n} \in \Omega_X} \mathbb{P}(X_{c,n} = x_{c,n}, y^{C,N}) \\
 &= \sum_{x_{c,n} \in \Omega_X} \alpha_{c,n}(x_{c,n}) \beta_{c,n}(x_{c,n}) \\
 &= \sum_{x_{c,n} \in \Omega_X} [\prod_{j=1}^n K_{c,j}] \tilde{\alpha}_{c,n}(x_{c,n}) [\prod_{j'=n+1}^N K_{c,j'}] \tilde{\beta}_{c,n}(x_{c,n}) \\
 &= [\prod_{j=1}^N K_{c,j}] \sum_{x_{c,n} \in \Omega_X} \tilde{\alpha}_{c,n}(x_{c,n}) \tilde{\beta}_{c,n}(x_{c,n}).
 \end{aligned}$$

979 One must calculate $\prod_{j=1}^N K_{c,j}$ in order to calculate the likelihood. First,
 980 let us show that: $\frac{\tilde{\alpha}_{c,n}(x_{c,n})}{\sum_{x \in \Omega_X} \tilde{\alpha}_{c,n}(x)} = \mathbb{P}(X_{c,n} = x_{c,n} | y^{C,n})$. We know that $\alpha_{c,n}(x) \propto$
 981 $\tilde{\alpha}_{c,n}(x)$ and that $\alpha_{c,n}(x) = \mathbb{P}(X_{c,n} = x_{c,n}, y^{C,n}) = \mathbb{P}(X_{c,n} = x_{c,n} | y^{C,n}) \mathbb{P}(y^{C,n})$.
 982 Therefore, $\tilde{\alpha}_{c,n}(x) \propto \mathbb{P}(X_{c,n} = x_{c,n} | y^{C,n})$. Hence, if we normalise we obtain
 983 $\frac{\tilde{\alpha}_{c,n}(x_{c,n})}{\sum_{x \in \Omega_X} \tilde{\alpha}_{c,n}(x)} = \mathbb{P}(X_{c,n} = x_{c,n} | y^{C,n})$. We are left with computing $\prod_{j=1}^N K_{c,j}$.

$$\begin{aligned}
 \prod_{j=1}^N K_{c,j} &= \prod_{j=1}^N \mathbb{P}(y_j^{C \setminus c} | y^{C,j-1}) \\
 &= \prod_{j=1}^N \sum_{x_{j-1}^{C \setminus c} \in \Omega_X^{C-1}} \mathbb{P}(y_j^{C \setminus c}, X_{j-1}^{C \setminus c} = x_{j-1}^{C \setminus c} | y^{C,j-1}) \\
 &= \prod_{j=1}^N \sum_{x_{j-1}^{C \setminus c} \in \Omega_X^{C-1}} \mathbb{P}(y_j^{C \setminus c} | X_{j-1}^{C \setminus c} = x_{j-1}^{C \setminus c}, y^{C,j-1}) \mathbb{P}(X_{j-1}^{C \setminus c} = x_{j-1}^{C \setminus c} | y^{C,j-1}) \\
 &= \prod_{j=1}^N \sum_{x_{j-1}^{C \setminus c} \in \Omega_X^{C-1}} \prod_{l \in \{1, \dots, C\} \setminus \{c\}} \mathbb{P}(y_{l,j} | X_{l,j-1} = x_{l,j-1}) \mathbb{P}(X_{l,j-1} = x_{l,j-1} | y^{C,j-1}) \\
 &= \prod_{j=1}^N \sum_{x_{j-1}^{C \setminus c} \in \Omega_X^{C-1}} \prod_{l \in \{1, \dots, C\} \setminus \{c\}} \phi(x_{l,j-1}, y_{l,j}) \frac{\tilde{\alpha}_{l,j-1}(x_{l,j-1})}{\sum_{x \in \Omega_X} \tilde{\alpha}_{l,j-1}(x)}.
 \end{aligned}$$

984 One can notice that each term in the product over l involves only $x_{l,j-1}$ and
 985 not all the elements in $x_{j-1}^{C \setminus c}$. We can therefore rewrite the last equality as:

$$\prod_{j=1}^N K_{c,j} = \prod_{j=1}^N \prod_{l \in \{1, \dots, C\} \setminus \{c\}} \sum_{x_{l,j-1} \in \Omega_X} \phi(x_{l,j-1}, y_{l,j}) \frac{\tilde{\alpha}_{l,j-1}(x_{l,j-1})}{\sum_{x \in \Omega_X} \tilde{\alpha}_{l,j-1}(x)}.$$

986 Finally

$$\mathbb{P}(y^{C,N}) = \left[\prod_{j=1}^N \prod_{l \in \{1, \dots, C\} \setminus \{c\}} \sum_{x_{l,j-1} \in \Omega_X} \phi(x_{l,j-1}, y_{l,j}) \frac{\tilde{\alpha}_{l,j-1}(x_{l,j-1})}{\sum_{x \in \Omega_X} \tilde{\alpha}_{l,j-1}(x)} \right] \left[\sum_{x_{c,n} \in \Omega_X} \tilde{\alpha}_{c,n}(x_{c,n}) \tilde{\beta}_{c,n}(x_{c,n}) \right].$$

987 E. The Viterbi algorithm for MHMM-DF

988 In this section, we show how to compute the most likely sequences of
 989 hidden states of all of the patches, independently for each patch. We want to
 990 maximise $\mathbb{P}(X^{C,N} = x^{C,N} | Y^{C,N} = y^{C,N})$ which is equivalent to maximising
 991 $\mathbb{P}(X^{C,N} = x^{C,N}, Y^{C,N} = y^{C,N})$. The latter can be factored over the C chains
 992 as follows:

$$\begin{aligned}
 \mathbb{P}(X^{C,N} = x^{C,N}, Y^{C,N} = y^{C,N}) &= \mathbb{P}(X^{C,N} = x^{C,N} | Y^{C,N} = y^{C,N}) \times \mathbb{P}(Y^{C,N} = y^{C,N}) \\
 &= \mathbb{P}(Y^{C,N} = y^{C,N}) \prod_{c=1}^C p(X_c^N = x_c^N | Y^{C,N} = y^{C,N}) \\
 &= \mathbb{P}(Y^{C,N} = y^{C,N}) \prod_{c=1}^C \frac{p(X_c^N = x_c^N, Y^{C,N} = y^{C,N})}{\mathbb{P}(Y^{C,N} = y^{C,N})} \\
 &= \frac{1}{(\mathbb{P}(Y^{C,N} = y^{C,N}))^{C-1}} \prod_{c=1}^C p(X_c^N = x_c^N, Y^{C,N} = y^{C,N}) \\
 &\propto \prod_{c=1}^C \mathbb{P}(X_c^N = x_c^N, Y^{C,N} = y^{C,N}).
 \end{aligned}$$

993 This implies that:

$$\begin{aligned}
 \max_{x^{C,N} \in \Omega_X^{C \times N}} \mathbb{P}(X^{C,N} = x^{C,N}, Y^{C,N} = y^{C,N}) &= \max_{x^{C,N} \in \Omega_X^{C \times N}} \prod_{c=1}^C \mathbb{P}(X_c^N = x_c^N, Y^{C,N} = y^{C,N}) \\
 &= \prod_{c=1}^C \max_{x_c^N \in \Omega_X^N} \mathbb{P}(X_c^N = x_c^N, Y^{C,N} = y^{C,N}).
 \end{aligned}$$

994 Thus we can perform recovery separately per patch. Let us note $\delta_{c,n}(x_{c,n}) =$
 995 $\max_{x_c^{n-1} \in \Omega_X^{n-1}} \mathbb{P}(X_c^n = x_c^n, Y^{C,n} = y^{C,n})$. Here is the recursive definition of $\delta_{c,n}$ in
 996 terms of $\delta_{c,n-1}$:

$$\begin{aligned}
 \delta_{c,n}(x_{c,n}) &= \max_{x_c^{n-1} \in \Omega_X^{n-1}} \mathbb{P}(x_c^{n-1}, y^{C,n-1}) \mathbb{P}(x_{c,n}, y_n^C | x_c^{n-1}, y^{C,n-1}) \\
 &= \max_{x_{c,n-1} \in \Omega_X} \delta_{c,n-1}(x_{c,n-1}) \mathbb{P}(x_{c,n}, y_n^C | x_{c,n-1}, y^{C,n-1}) \\
 &= \max_{x_{c,n-1} \in \Omega_X} \delta_{c,n-1}(x_{c,n-1}) \mathbb{P}(y_n^C | x_{c,n-1}, y^{C,n-1}) A(x_{c,n-1}, x_{c,n}, y_n^C) \\
 &= \max_{x_{c,n-1} \in \Omega_X} \delta_{c,n-1}(x_{c,n-1}) \phi(x_{c,n-1}, y_{c,n}) \mathbb{P}(y_n^{C \setminus c} | x_{c,n-1}, y^{C,n-1}) A(x_{c,n-1}, x_{c,n}, y_n^C) \\
 &= \max_{x_{c,n-1} \in \Omega_X} \delta_{c,n-1}(x_{c,n-1}) \phi(x_{c,n-1}, y_{c,n}) K_{c,n} A(x_{c,n-1}, x_{c,n}, y_n^C).
 \end{aligned}$$

997 **F. Prediction of the next non-dormant population state for MHMM-**
 998 **DF**

999 The prediction of a species population state in patch c at time $N + 1$,
 1000 given the sequences of observations of the non-dormant states in all patches
 1001 up to time N , is defined as:

$$\begin{aligned}
 \hat{y}_{c,N+1} &= \operatorname{argmax}_{y_{c,N+1} \in \Omega_Y} \mathbb{P}(Y_{c,N+1} = y_{c,N+1} | Y^{C,N} = y^{C,N}) \\
 &= \operatorname{argmax}_{y_{c,N+1} \in \Omega_Y} \sum_{x_{c,N} \in \Omega_X} \mathbb{P}(Y_{c,N+1} = y_{c,N+1}, X_{c,N} = x_{c,N} | Y^{C,N} = y^{C,N}) \\
 &= \operatorname{argmax}_{y_{c,N+1} \in \Omega_Y} \sum_{x_{c,N} \in \Omega_X} \mathbb{P}(x_{c,N} | y^{C,N}) \mathbb{P}(y_{c,N+1} | x_{c,N}, y^{C,N}) \\
 &= \operatorname{argmax}_{y_{c,N+1} \in \Omega_Y} \sum_{x_{c,N} \in \Omega_X} \rho_{c,N}(x_{c,N}) \phi(x_{c,N}, y_{c,N+1}).
 \end{aligned}$$

Figure G.13: Evolution of the variance of the hyperparameters estimators when the true values are $(\tau, \mu_0, \mu_1, \nu_0, \nu_2, \nu_3) = (-1, -3.7, 6.5, -3, 4, 2)$ and ν_1 varies from 0 to 6.5 with a 0.5 step. See Table 2 for definitions of parameters.

Figure G.14: Evolution of the bias of the hyperparameters estimators when the true values are $(\tau, \mu_0, \mu_1, \nu_0, \nu_2, \nu_3) = (-1, -3.7, 6.5, -3, 4, 2)$ and ν_1 varies from 0 to 6.5 with a 0.5 step. See Table 2 for definitions of parameters.

1003 H. Confidence Interval computation

1004 The confidence interval of a hyperparameter is calculated using the Fisher
 1005 information matrix $I(\lambda)$. In our case, $I(\lambda)$ is the Fisher information matrix
 1006 of the transition probability and it can be calculated with Q the expectation
 1007 of the log likelihood of the model used in the EM algorithm (Oakes, 1999).
 1008 According to Oakes (1999):

$$I(\lambda) = -\frac{\partial^2 Q(\lambda|\hat{\lambda})}{\partial \lambda^2} \Big|_{\lambda=\hat{\lambda}}$$

1009 The partial derivative according to one group of hyperparameters $(\tau, \nu$
 1010 and $\mu)$ does not involve the two other groups. Thus, $I(\nu), I(\mu), I(\tau)$ can be

Figure G.15: Evolution of the variance of the hyperparameters estimators when the true values are $(\tau, \mu_0, \mu_1, \nu_0, \nu_1, \nu_2) = (-1, -3.7, 6.5, -3, 4, 4)$ and ν_3 varies from 0 to 6.5 with a 0.5 step. See Table 2 for definitions of parameters.

1011 calculated separately. Consequently:

$$I(\nu) = -\frac{\partial^2 Q(\nu|\hat{\nu})}{\partial \nu^2} \Big|_{\nu=\hat{\nu}}$$

1012 Once the Fisher information matrix is calculated, we can calculate a $(100(1 -$
1013 $\epsilon))$ confidence interval for any hyperparameter. The confidence interval for
1014 ν_1 is

$$[\hat{\nu}_1 - Z_{\epsilon/2}(\frac{1}{\sqrt{I(\nu)}})_{\nu_1}, \hat{\nu}_1 + Z_{\epsilon/2}(\frac{1}{\sqrt{I(\nu)}})_{\nu_1}]$$

1015 where $(\frac{1}{\sqrt{I(\nu)}})_{\nu_1}$ corresponds to the $(\nu_1, \nu_1)^{\text{th}}$ entry of the root of the inverse of
1016 the Fisher information. Additionally, $Z_{\epsilon/2}$ corresponds to $Z_{\epsilon/2} = -\varphi^{-1}(\epsilon/2)$
1017 where φ is the cumulative distribution function of the Normal distribution.

1018 Figs. H.16 and H.17 show the confidence intervals for ν_1 and ν_3 when ν_3
1019 is varying. The red dots correspond to the lower bounds of the confidence
1020 interval and the blue dots correspond to the upper bound of the confidence
1021 intervals. The black lines correspond to the real value of the hyper parameter.

Figure H.16: Evolution of the confidence interval of the hyperparameter ν_1 when the true values are $(\tau, \mu_0, \mu_1, \nu_0, \nu_1, \nu_2) = (-1, -3.7, 6.5, -3, 4, 4)$ and ν_3 varies from 0 to 6.5 with a 0.5 step. See Table 2 for definitions of parameters.

1022 I. Alphabetic colonisation

1023 I.1. Definition

We propose here a colonisation process, referred to as *alphabetic colonisation*, which assumes that the impact of colonisation in field c depends only on the number of neighbours in each state of Ω_Y . In other words it depends only on the distribution of the non-dormant population states in $y_n^{c \setminus c}$. For a given patch c , if m_i is the number of patches among the neighbours in

Figure H.17: Evolution of the confidence interval of the hyperparameter ν_3 when the true values are $(\tau, \mu_0, \mu_1, \nu_0, \nu_1, \nu_2) = (-1, -3.7, 6.5, -3, 4, 4)$ and ν_3 varies from 0 to 6.5 with a 0.5 step. See Table 2 for definitions of parameters.

state i , then the impact of colonisation in field c is determined by the vector $(m_0, \dots, m_{|\Omega_Y|-1})$. Each possible vector is associated, through alphabetic (or lexicographic) order, with a unique rank. This rank is then used to define the probability of success $p_{x_{c,n}, y_n^C}$ in the binomial distribution. If we denote the rank associated with $y_n^{C \setminus c}$ by $f_{\alpha}(y_n^{C \setminus c})$, then we have:

$$p_{x_{c,n}, y_n^C} = \frac{1}{1 + \exp(-(\nu_0 + \nu_1 \times \frac{x_{c,n-1}}{|\Omega_X|} + \nu_2 \times \frac{y_{c,n}}{|\Omega_Y|} + \nu_3 \times \frac{f_{\alpha}(y_n^{C \setminus c})}{|f_{\alpha}(\Omega_Y^{C-1})|}))}.$$

1024 where $(\nu_0, \nu_1, \nu_2, \nu_3)$ are hyper parameters and where $|f_{\alpha}(\Omega_Y^{C-1})|$ is the
1025 number of possible outputs of the function f_{mean} .

1026

1027 In order to derive the expression of f_{α} , we first define g a function,

1028 from $|\Omega_Y|^{C-1}$ to $|\Omega_Y|^C$, which sorts the elements of $y_n^{C \setminus c}$ in descending order
 1029 and adds a zero at the last component of the vector. For example, if $C =$
 1030 4 and $\Omega_Y = 5$, $g((1, 4, 1)) = (4, 1, 1, 0)$. Multiple total orders for vectors
 1031 exist; thus, multiple ways of associating a number with a vector of ordered
 1032 observations exist. We chose alphabetical order. For example, this implies
 1033 $(3, 3, 3, 0) < (3, 3, 4, 0) < (4, 1, 1, 0)$. Let us assume $c = C$, without loss of
 1034 generality, then the expression of f_{alpha} is:

$$f_{alpha}(y_n^{C-1}) = \sum_{c'=C-1}^1 \mathbb{1}_{\{g_{c'}(y_n^{C-1}) > g_{c'+1}(y_n^{C-1})\}} \sum_{j=g_{c'+1}(y_n^{C-1})+1}^{g_{c'}(y_n^{C-1})} \binom{|\Omega_Y| - j + c' - 1}{c' - 1},$$

1035 where g_l is l th element of g , and the $\binom{|\Omega_Y| - j + l - 1}{l - 1}$ is the number of unordered
 1036 samplings with replacement of $l - 1$ elements among $|\Omega_Y| - j + 1$. The
 1037 alphabetic colonisation considers more states than the mean colonisation:
 1038 the function f_{alpha} has $\binom{C + |\Omega_Y| - 2}{C - 1}$ different states, whereas f_{mean} has
 1039 only Ω_Y states. However, the computational complexity of calculating the
 1040 state associated with $y_n^{C \setminus c}$ with the alphabetic colonisation is $O(NC((C -$
 1041 $1)\log(C - 1) + |\Omega_Y|^2(C - 1)))$.

1042 I.2. Identifiability

1043 We establish the following identifiability theorem for the alphabetic coloni-
 1044 sation process.

1045 **Theorem 4.** *The hyperparameter $(\mu, \nu) = (\mu_0, \mu_1, \nu_0, \nu_1, \nu_2, \nu_3)$ of a MHMM-*
 1046 *DF with the alphabetic colonisation process is generically identifiable from*
 1047 *seven consecutive observations if the following conditions hold: $|\Omega_X| \leq |\Omega_Y|$,*
 1048 *$|\Omega_Y| > 2$, $C > 2$.*

1049 **Proof.**

1050 Identifiability of $(\mu_0, \mu_1, \nu_0, \nu_1)$ can be proven in the same manner as
 1051 for the model with the mean colonisation process. To prove identifiabil-
 1052 ity ν_2 and ν_3 , we consider the following two transition probabilities: L7 from

$$1053 (x_{n-1}^C, y_n^C) = \left(\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 1 \\ \dots \\ 1 \end{pmatrix} \right) \text{ to } (x_n^C, y_{n+1}^C) = \left(\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix} \right) \text{ and L8 from}$$

$$1054 (x_{n-1}^C, y_n^C) = \left(\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 2 \\ \dots \\ 2 \end{pmatrix} \right) \text{ to } (x_n^C, y_{n+1}^C) = \left(\begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \dots \\ 0 \end{pmatrix} \right):$$

$$L7(\nu_0, \nu_2, \nu_3) \propto \left[\frac{1}{1 + \exp(-(\nu_0 + \frac{1}{|\Omega_Y|}\nu_2 + \frac{f_{alpha}(1, \dots, 1)}{|f_{alpha}(\Omega_Y^{C-1})|}\nu_3))} \right]^{(|\Omega_X|-1)C} \\ \times \left[\exp(-(\nu_0 + \frac{1}{|\Omega_Y|}\nu_2 + \frac{f_{alpha}(1, \dots, 1)}{|f_{alpha}(\Omega_Y^{C-1})|}\nu_3)) \right]^{(|\Omega_X|-1)C}.$$

1055 Therefore:

$$\begin{aligned} L7(\nu_0, \nu'_2, \nu'_3) &= L7(\nu_0, \nu_2, \nu_3) \\ \exp(\frac{1}{|\Omega_Y|}\nu'_2 + \frac{f_{alpha}(1, \dots, 1)}{|f_{alpha}(\Omega_Y^{C-1})|}\nu'_3) &\stackrel{<=>}{=} \exp(\frac{1}{|\Omega_Y|}\nu_2 + \frac{f_{alpha}(1, \dots, 1)}{|f_{alpha}(\Omega_Y^{C-1})|}\nu_3) \\ \frac{1}{|\Omega_Y|}\nu'_2 + \frac{f_{alpha}(1, \dots, 1)}{|f_{alpha}(\Omega_Y^{C-1})|}\nu'_3 &\stackrel{<=>}{=} \frac{1}{|\Omega_Y|}\nu_2 + \frac{f_{alpha}(1, \dots, 1)}{|f_{alpha}(\Omega_Y^{C-1})|}\nu_3. \end{aligned}$$

1056 Similarly:

$$\begin{aligned} L8(\nu_0, \nu'_2, \nu'_3) &= L8(\nu_0, \nu_2, \nu_3) \\ \frac{2}{|\Omega_Y|}\nu'_2 + \frac{f_{alpha}(2, \dots, 2)}{|f_{alpha}(\Omega_Y^{C-1})|}\nu'_3 &\stackrel{<=>}{=} \frac{2}{|\Omega_Y|}\nu_2 + \frac{f_{alpha}(2, \dots, 2)}{|f_{alpha}(\Omega_Y^{C-1})|}\nu_3. \end{aligned}$$

1057 By subtracting $L8 - 2L7$, we obtain:

$$\begin{aligned} L8(\nu_0, \nu_2, \nu_3) - 2L7(\nu_0, \nu_2, \nu_3) &= L8(\nu_0, \nu'_2, \nu'_3) - 2L7(\nu_0, \nu'_2, \nu'_3) \\ &\stackrel{<=>}{=} (\frac{f_{alpha}(2, \dots, 2)}{|f_{alpha}(\Omega_Y^{C-1})|} - \frac{2f_{alpha}(1, \dots, 1)}{|f_{alpha}(\Omega_Y^{C-1})|})\nu_3 \\ &= (\frac{f_{alpha}(2, \dots, 2)}{|f_{alpha}(\Omega_Y^{C-1})|} - \frac{2f_{alpha}(1, \dots, 1)}{|f_{alpha}(\Omega_Y^{C-1})|})\nu'_3. \end{aligned}$$

1058 Thus if $f_{alpha}(2, \dots, 2) - 2f_{alpha}(1, \dots, 1) \neq 0$, identifiability of ν_3 is estab-
1059 lished. From the definition of f_{alpha} we have:

$$f_{alpha}(1, \dots, 1) = \binom{|\Omega_Y| + C - 3}{C - 2},$$

1060

$$f_{alpha}(2, \dots, 2) = \sum_{j=1}^2 \binom{|\Omega_Y| - j + C - 2}{C - 2}.$$

1061 Thus:

$$\begin{aligned}
f_{alpha}(2, \dots, 2) - 2f_{alpha}(1, \dots, 1) &= -2 \binom{|\Omega_Y|+C-3}{C-2} + \sum_{j=1}^2 \binom{|\Omega_Y|-j+C-2}{C-2} \\
&= \binom{|\Omega_Y|+C-4}{C-2} - \binom{|\Omega_Y|+C-3}{C-2} \\
&= \frac{(|\Omega_Y|+C-4)!}{(|\Omega_Y|-2)!(C-2)!} - \frac{(|\Omega_Y|+C-3)!}{(|\Omega_Y|-1)!(C-2)!} \\
&= \frac{(|\Omega_Y|+C-4)!}{(|\Omega_Y|-2)!(C-2)!} \left(1 - \frac{|\Omega_Y|+C-3}{|\Omega_Y|-1}\right).
\end{aligned}$$

1062 Let us show that $f_{alpha}(2, \dots, 2) - 2f_{alpha}(1, \dots, 1) = 0$ implies $C = 2$. As
1063 $\frac{(|\Omega_Y|+C-4)!}{(|\Omega_Y|-2)!(C-2)!} > 0$, if $f_{alpha}(2, \dots, 2) - 2f_{alpha}(1, \dots, 1) = 0$ then $1 - \frac{|\Omega_Y|+C-3}{|\Omega_Y|-1} = 0$.
1064 Thus:

$$\begin{aligned}
1 &= \frac{|\Omega_Y|+C-3}{|\Omega_Y|-1} \\
|\Omega_Y| - 1 &= |\Omega_Y| + C - 3 \\
C &= 2.
\end{aligned}$$

1065 Since $f_{alpha}(2, \dots, 2) - 2f_{alpha}(1, \dots, 1) = 0$ only when $C = 2$, then when $3 \leq C$,
1066 we have $\nu_3 = \nu'_3$. Finally, by using *L8* or *L7*, we easily obtain that if $\nu_3 = \nu'_3$,
1067 then $\nu_2 = \nu'_2$.

1068 Thus, we were able to establish that if $3 \leq C$, then $\mathbb{P}(h_n|h_{n-1}, \nu, \mu) =$
1069 $\mathbb{P}(h_n|h_{n-1}, \nu', \mu')$ implies $(\mu, \nu) = (\mu', \nu')$. To establish generic identifiability,
1070 conditions from Theorem 2 are required: $|\Omega_X| \leq |\Omega_Y|$, and $C > 2$. Addition-
1071 ally, the number of observable states $|\Omega_Y|$ must be greater than 2 since three
1072 states were used to prove generic identifiability. The MHMM-DF with alpha-
1073 betic colonisation is generically identifiable with at least two hidden states
1074 and at least three observable states with at least three patches and with the
1075 number of hidden states smaller or equal to the number of observable states.

1076 $\square$