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Interacting Partially Observable DBN to model the dynamics of partially observable metapopulations : opportunities and open challenges

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Abstract

In ecology, among the mathematical approaches used to model population dynamics, Hidden Markov Models (HMM) are well adapted to the case where the species of interest is difficult to observe. For a broader application of HMM in ecology, two limits need to be overcome. While HMMs are often used to deal with detection errors, another important situation is when only some life stages of the population can be observed while the others remain hidden. Also, understanding ecological patterns of dispersal requires a model at the metapopulation level rather than for a single population. Therefore, there is a need to extend the HMM framework to the case of several couples of hidden and observed life stages interacting via dispersal, which depends on the studied species (plant, fungus, animal). Such interactions have to be modeled explicitly. In this work, we propose a conceptual guide to model and estimate metapopulation parameters using the framework of Partially Observable Dynamic Bayesian Networks (PO-DBN). We show that only four interaction structures are needed to describe the main metapopulation models. We illustrate the four structures with examples of species dynamics and we show how to build the associated interacting PO-DBN. Finally, we consider parameter estimation using the EM algorithm. We establish that for two structures the complexity of EM remains linear in the number of patches, which means that estimation is easily accessible for the associated metapopulations. For the two other structures, the EM complexity is exponential and

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we discuss methods from approximate inference to overcome this difficulty. This study provides the practical foundations for modeling and estimating the dynamics of a metapopulation with hidden life stages.

Keywords: Metapopulation dynamics, Hidden life stages, Modelling, Dynamic Bayesian Network, Estimation

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1. Introduction

When studying a particular population, it is fundamental to consider that this population is part of a larger entity with interactions through dispersal. The metapopulation concept allows to consider such interactions. Levins et al. (1969) defines a metapopulation as a group of populations that can become locally extinct and recolonize unoccupied sites. In other words, a metapopulation is a set of populations of the same species that evolve in distinct sites (also called patches), while interacting with each other via colonization. The maintenance of the species at the regional scale depends on the balance between local extinction and colonization of new unoccupied sites through propagule exchanges. Therefore, the study of a metapopulation enables to take into account both the local and the regional dynamics of the species. Understanding metapopulation dynamics improve our knowledge on the main levers used by the species for survival, and on how they will adapt to new situations (e.g. habitat change or loss Amarasekare and Possingham, 2001). For instance, for biodiversity conservation purpose, it can help identifying important colonization paths to protect, while in pest control it can help targeting control actions (Ovaskainen and Hanski, 2004).

The Levins model (Levins et al., 1969), modeling the dynamics of the fraction of occupied sites as a function of population colonization and extinction probabilities, is the reference model for studying metapopulation dynamics. In the 2000's, this model was improved by introducing Stochastic Patch Occupancy Models (SPOM), which make spatial dependence explicit (Ovaskainen and Hanski, 2004) by considering that all patches are connected but with different weights. A major limitation of these models is the assumption that all individuals in the population are observable. This is because the original aim of these models was not to estimate key parameters from data, but rather to study the quasi-stationary state of the metapopulation (before total extinction, which is the stationary state). SPOMS have been used to estimate parameters involved in the dynamics of the species under study

(Rampal et al., 2004), however still in a context of complete observation of the populations at each site.

In practice, populations studied are not always perfectly observable. During the monitoring, the objective is to detect the presence of the species or to count the number of individuals in the population, but species can be rare or cryptic and easily missed, or it can be confused with another. We will refer to these situations as detection errors. In other cases, some individuals in the population are more difficult to observe than other. Indeed, a population is composed of individuals at different life stages, and for some species, one or several life stages are not easily accessible to the observer. This is typically the case for plants: standing flora are visible, while seeds in the seed bank are hidden. It is also the case for many animals species like fishes, insects or crustaceans, where the first life stages are usually difficult to localize and/or to sample. For instance, in the case of salmon (Mobley et al., 2021), eggs are deposited in spawning grounds that are very difficult to observe. We will refer to such populations as Partially Observable Population (POP).

Hidden Markov Models (HMM, Cappé et al., 2005) are widely used in ecology (McClintock et al., 2020; Glennie et al., 2023) because they are particularly adapted to estimate the dynamics of a single population from data with detection error. Indeed, in the inference process, HMMs explicitly take into account the fact that the process of interest is hidden and the observation brings information on the hidden process. Examples of HMM to model detection errors are numerous: Dubart et al. (2019) for snails, Royle and Kéry (2007) for birds, or Louvrier et al. (2018) for wolves. See alsoGimenez et al. (2014) or Louvrier et al. (2018) for explanations about the reformulation of occupancy models into HMM. But, in the case where some life stages are hidden there are not many attempts to use HMM. We can mention Pluntz et al. (2018), but the model is actually an extension of the classical HMM. One reason is that the dependency structure between hidden and observed variables in a HMM is too simple to model the case where these two sets of variables correspond to different life stages, due to the cycling over life stages.

In addition, most of HMM for population dynamics study a single population in a patch, with possibly a constant colonization parameter but which is independent of the true state of the other patches in the regional metapopulation. To the best of our knowledge, only two studies used a HMM-related model with an explicit interaction between the different patchs of a metapopulation, and estimated metapopulation parameters from data: Dubart et al.

(2019) for snails in the context of detection error, and Le Coz et al. (2019) for weeds with hidden seed bank.

Therefore, while species with hidden life stage are ubiquitous, there is clearly a lack of modeling framework to be able to estimate from monitoring data the key parameters driving metapopulation dynamics for such species. As mentioned before, one possible explanation is that, for the within patch dynamics, the HMM structure is too simple. Besides, taking explicitly into account colonization from one patch to another requires also to model which specific life stages are involved in this process. Indeed, not all life stages of a population participate to dispersal, as shown for invertebrate species in Benton and Bowler (2012), and these stages can be hidden. For example, adult salmon disperse by swimming movement, so dispersal concerns the observable life stage only, while fungus disperses through ascospores present in the field soil, which are not visible. This makes the hidden life stages an important consideration, although they are very rarely considered in the context of metapopulation dynamics inference.

This paper focuses on metapopulations in which certain stages of development are hidden. We will refer to them as Metapopulation with Partially Observable Populations (M-POP), i.e. metapopulations in which the populations are POPs. In this work, we propose a conceptual guide for modeling and estimating parameters involved in the dynamics of a M-POP. We consider an extension of Dynamic Bayesian Networks (DBN, Dean and Kanazawa, 1989) with hidden states, which we refer to as Partially Observable DBNs (PO-DBNs). PO-DBN generalize HMM in the sense that the Markovian assumption is still made but there is no constraint of the dependency structure between the observed and hidden variables at time $t+1$ and observed and hidden variables at time t. So, they are particularly suited to model a POP dynamics by taking into account hidden stages dynamics and life cycle.Then a M-POP can be modeled by interacting PO-DBN (one per population) which interact through dispersal.

In an interacting PO-DBN, the interaction structure between the different PO-DBN depends on the dispersal mode of the species under study. The variables (hidden or observed) involved depend on the life stage at the origin of the dispersal (hidden or observed life stage) and the life stage impacted by the arrival of new individuals (again, hidden or observed life stage). For instance, in the case of plants with seed bank, the observed life stage corresponds to the standing flora and the hidden life stage to seeds in the seed bank. Dispersal from one patch to another one starts from the standing flora and reaches the seed bank of the colonized patch. Therefore, in the corresponding interacting PO-DBN structure, the hidden state of a patch at time $t+1$ will depend on the observed states of neighbouring patches at time t.

After presenting why PO-DBN and interacting PO-DBN are well adapted to the modeling of POP and M-POP dynamics respectively (sections 2 and 3) we demonstrate that the main M-POP dynamics can be described from only four basics interactions structures of interacting PO-DBN. In section 4 we illustrate the four structures with concrete examples of species dynamics and we show how to build the probability distributions defining the associated interacting PO-DBN. Finally, in section 5 we consider parameter estimation for these models and we discuss how to use the EM algorithm. We establish that for two structures the complexity of EM remains linear in the number of patches, which means that estimation is easily accessible for the associated metapopulations. For the two other structures, the complexity is exponential and we present methods from approximate inference that can be used to overcome this computational limit.

2. From Partially Observable Populations to PO-DBN

In this section, we focus on the modeling of a POP dynamics, i.e. a single population in a given patch. We show how the framework of PO-DBN is well suited to model the different types of dynamics that can exist between the observed life stage and the hidden life stage and we present examples from the literature that follows this line to model weeds dynamics.

2.1. Partially Observable Populations

In ecology, a population is a group of individuals of the same species in a given location (patch). Individuals can be present at different life stages. The life cycle of animal species is classically divided into three stages: juveniles, growing individuals and finally in adults (Caswell, 1989). The life cycle of plants is classically decomposed into three similar stages: seed, growing plant and mature plant (Capdevila et al., 2022). Each stage plays an important role in the dynamics of the species and a multitude of external factors influence the survival of the species during one or more stages of its development. For instance, for plants species, two types of strategies are used to escape unfavorable (biotic or abiotic) environments: dormancy and colonization. Indeed, when external conditions are unfavorable for their development (e.g. cold winter), they can enter dormancy: a phase during which the plant development and metabolism is strongly reduced. The species can also colonize new patches, i.e. spreads in a new environment.

In order to study the dynamics of a population, for instance to understand which survival strategy is preferred, one needs to collect data from the population (counts, abundance, presence/absence) at successive time steps. However, some life stages can be more difficult to observe than others. Practically, in the case of plants, seeds in the seed bank are seldom sampled because of the burden in time and cost, while standing plants are classically sampled. We refer to a population where only some life stages are observable as a Partially Observable Population (POP). Note that it is different from an imperfect sampling where some individuals are missed independently from their life stage, or misidentified to another species, which we refer to as detection errors. In this paper we focus on population where only individuals in specific life stages can be observed.

2.2. Why are PO-DBN adapted to model POP dynamics?

Dynamic Bayesian Networks (DBNs, Dean and Kanazawa, 1989) can be used to study multidimensional time series with structured dependencies. They describe the evolution over discrete time of a process $S = (S_t)_{t \in \mathbb{N}}$ composed of N variables: $S = (S_t^1, S_t^2, ..., S_t^N)_{t \in \mathbb{N}, N \in \mathbb{N}}$. A DBN is Markovian, i.e the current state S_t depends only on the previous state S_{t-1} and not on all the past sequence. Thus, a DBN is completely determined by the initial distribution of the state at time $t = 0$ and the transition distribution from states S_{t-1} to state S_t. As DBN are graphical models (Koller and Friedman, 2009), it is possible to represent the dependencies between the different variables through a directed graph whose nodes are the model's variables and arcs go from parent nodes toward child nodes. This is an advantage since this graphical representation can easily been build from biological knowledge on the species dynamics. Then in a second step, the joint distribution probability of $S = (S_t^1, S_t^2, ..., S_t^N)_{t \in \mathbb{N}, N \in \mathbb{N}}$ is defined as the product of the distribution probability of each variable conditionally to its parents.

We refer to as Partially Observable Dynamic Bayesian Networks (PO-DBNs), the case where only some variables in S_t are observed and the others are hidden. PO-DBN are therefore particularly well suited to model POP. In particular, in this paper we focus on populations whose dynamics are divided into two distinct life stages: an observed and a hidden one, and we will show

how to use PO-DBN to estimate the key parameters driving the population dynamics, like survival or colonization.

2.2.1. How to model POP dynamics with a PO-DBN?

To describe POP dynamics, we focus on a special case of PO-DBN in which $N = 2$ and we consider that S_t is composed of two variables: one observed and one hidden, describing the state of the POP at time t: $S_t = \begin{pmatrix} O_t \\ H_t \end{pmatrix}$. The variable H_t, corresponds to the state of the unobservable life stage (e.g. the larval stage of an insect or the seed stage of a plant), and O_t is the state of the observable life stage (e.g. the adult insect or the flowering stage of a plant). Note that there may be more than two life stages but we assume that they can be grouped into two sets, observable and hidden. The states of these two processes can take different forms. They can be presence/absence data (= 1/0), count data or abundance classes data. We denote the state space of $H = (H_t)_{t\in\mathbb{N}}$ by Ω_H and the state space of $O = (O_t)_{t\in\mathbb{N}}$ by Ω_O.

The PO-DBN associated to the POP dynamics is defined by two probability distributions :

- The initial distribution of S_0 at $t = 0$, denoted π, and defined, for all $s_0 = \begin{pmatrix} o_0 \\ h_0 \end{pmatrix} \in \Omega_O \times \Omega_H$, as:

  $$\pi(s_0) = \pi(h_0, o_0) = \mathbb{P}(H_0 = h_0, O_0 = o_0).$$

  We will show in the next section how this probability can be decomposed into two terms, according to the dependency structure of the PO-DBN.

- The transition distribution, which corresponds to the probability of S_t conditionally to S_{t-1} noted T, and defined as, for all $s_{t-1} = \begin{pmatrix} o_{t-1} \\ h_{t-1} \end{pmatrix} \in \Omega_O \times \Omega_H, s_t = \begin{pmatrix} o_t \\ h_t \end{pmatrix} \in \Omega_O \times \Omega_H$:

  $$T(s_{t-1}, s_t) = \mathbb{P}(S_t = \begin{pmatrix} o_t \\ h_t \end{pmatrix} |S_{t-1} = \begin{pmatrix} o_{t-1} \\ h_{t-1} \end{pmatrix})$$

  For greater clarity, we denote this probability $T(h_{t-1}, o_{t-1}|h_t, o_t)$.

Without more assumption beyond Markovianity, we can represent the dependencies between the states of the population at time $t-1$, S_{t-1}, and at time t, S_t, on the diagram shown in Figure 1.

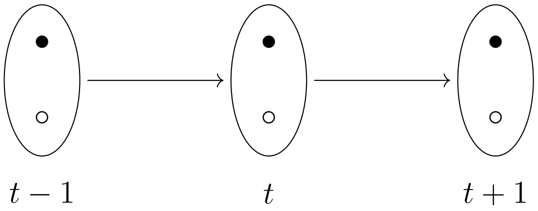

Figure 1: Simplified graphical representation of the interactions between hidden states and observed states in the PO-DBN of a POP. An empty circle represents an hidden life stage (H_t) and a fulfilled one is an observed life stage (O_t). The oval form represents S_t.

Remark 1. *A model with the dependency structure of Figure 1 has been proposed by Pieczynski (2003) under the name of Pairwise Markov Chain. It is presented as an extension of the HMM.*

In order to take into account the specific dependencies between the observed and the hidden life stages of a given species, the transition distribution T can be decomposed as a product of two transitions : the first one corresponding to the transition distribution of the hidden state, noted T_H, and the second one corresponding to the transition distribution of the observed one, noted T_O. We detail these two terms in the next section.

2.2.2. Examples of PO-DBN associated to the POP dynamics

The graphical representation of the PO-DBN shows the dependencies between the hidden and observed life stages of each population. From it, we can construct the model's probability distributions π, T_H and T_O. We will see that depending of the species, T_H and T_O will not involve the same variables in the conditionning.

T_H and T_O define what we will referred to as the internal dependency structure of the POP described by the PO-DBN.

By looking at two particular PO-DBNs for POP dynamics with the two most general structures, whose internal dependency structures are shown in Figure 2, we explain in detail how to write the probability distributions π, T_H and T_O associated. The two figures illustrate the same model, i.e. the same transition distribution from s_{t-1} to s_t. This transition can be decomposed in two different ways, using Bayes rule, and depending on the population dynamics in question, we will choose the decomposition which is easier to interpret in terms of the dependencies between the hidden and observed state of life.

(a) PO-DBN associated to a POP dynamics with dependencies from the hidden life stage to the observed one

(b) PO-DBN associated to a POP dynamics with dependencies from observed life stage to the hidden one

Figure 2: Graphical representation of the internal dependency structures of the two most general PO-DBN associated to a POP dynamics. Between time steps $t-1$ and t, the dashed arcs are involved in the transition of observation, T_O, and the filled ones are involved in the transition of the hidden state, T_H.

For the internal dependency structure shown in Figure 2a, the probability distributions π, T_H and T_O are derived from the graphical representation by identification of the parents of O_t and H_t:

- A time $t = 0$, node O_0 is the child of node H_0 and node H_0 has no parent node. Thus, in the structure 2a the initial distribution can be written as follows:

$$\begin{aligned}\pi(h_0, o_0) &= \mathbb{P}(H_0 = h_0, O_0 = o_0)\\ &= \mathbb{P}(O_0 = o_0 | H_0 = h_0)\mathbb{P}(H_0 = h_0).\end{aligned}$$

- At time t, node O_t is the child node of H_t, O_{t-1} and H_{t-1}. And, H_t is the child node of H_{t-1} and O_{t-1}. So, the transition distributions T_H and T_O can be written as follows:

$$T_H(h_t|h_{t-1}, o_{t-1}) = \mathbb{P}(H_t = h_t|H_{t-1} = h_{t-1}, O_{t-1} = o_{t-1}),$$

  and,

$$T_O(o_t|h_t, h_{t-1}, o_{t-1}) = \mathbb{P}(O_t = o_t|H_t = h_t, H_{t-1} = h_{t-1}, O_{t-1} = o_{t-1}).$$

For the structure shown in Figure 2b, the distributions are as follows :

- The initial probability can be rewritten as:

$$\pi(h_0, o_0) = \mathbb{P}(H_0 = h_0 | O_0 = o_0)\mathbb{P}(O_0 = o_0).$$

- The transition probabilities T_H and T_0 are equal to:

$$T_H(h_t | h_{t-1}, o_{t-1}, o_t) = \mathbb{P}(H_t = h_t | O_t = o_t, H_{t-1} = h_{t-1}, O_{t-1} = o_{t-1}),$$

  and,

$$T_O(o_t | h_{t-1}, o_{t-1}) = \mathbb{P}(O_t = o_t | H_{t-1} = h_{t-1}, O_{t-1} = o_{t-1}).$$

In practice, the internal dependencies structures of the PO-DBN for a POP are often less complex, resulting in simpler expressions of the T_H and T_O distributions. Indeed, depending on population dynamics, some dependencies no longer exist. So, we examine now a simpler internal dependency structure that corresponds to the graphical representation of Figure 3, and we detail the expression of the probability distributions π, T_H and T_O.

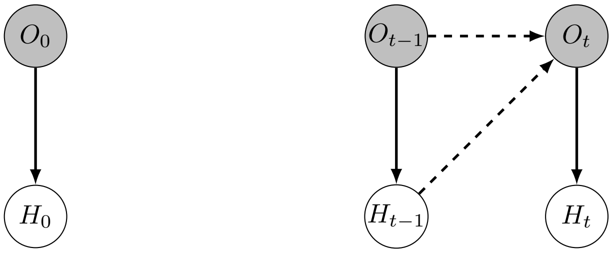

Figure 3: Graphical representation of the internal dependency structure of the PO-DBN structure associated to a theoretical POP dynamics. Between time steps $t-1$ and t, the dashed arcs are involved in the transition of observation, T_O, and the filled ones are involved in the transition of the hidden state, T_H.

- A time $t = 0$, node H_0 is the child of node O_0 and node O_0 has no parent node. Thus, the initial distribution can be decomposed as follows:

$$\begin{aligned}\pi(h_0, o_0) &= \mathbb{P}(H_0 = h_0, O_0 = o_0) \\ &= \mathbb{P}(H_0 = o_0 | O_0 = h_0)\mathbb{P}(O_0 = o_0).\end{aligned}$$

- At time t, node H_t is the child node of O_t. And, O_t is the child node of O_{t-1} and H_{t-1}. So, the transition distributions T_H and T_O are defined as follows:

  $$T_H(h_t|o_t) = \mathbb{P}(H_t = h_t|O_t = o_t),$$

  and,

  $$T_O(o_t|h_{t-1}, o_{t-1}) = \mathbb{P}(O_t = o_t|H_{t-1} = h_{t-1}, O_{t-1} = o_{t-1}).$$

If we remove some arcs in Figure 2a, we can recover the case of HMM, widely used in ecology, whose internal dependency structure is shown in Figure 4. Therefore HMM are special cases of PO-DBN.

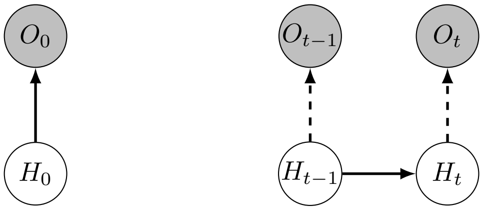

Figure 4: Graphical representation of the internal dependency structure of a HMM. Between time steps $t-1$ and t, the dashed arcs are involved in the transition of observation, T_O, and the filled ones are involved in the transition of the hidden state, T_H.

In this structure, the distributions of probability defining the model are as follow.

- The initial probability is decomposed as:

  $$\pi(h_0, o_0) = \mathbb{P}(O_0 = o_0|H_0 = h_0)\mathbb{P}(H_0 = h_0).$$

- The transition probabilities T_H and T_0 are the following:

  $$T_H(h_t|h_{t-1}) = \mathbb{P}(H_t = h_t|H_{t-1} = h_{t-1}),$$

  which is the transition matrix of the HMM and,

  $$T_O(o_t|h_t) = \mathbb{P}(O_t = o_t|H_t = h_t),$$

  usually referred to as the emission distribution of the HMM.

2.2.3. Estimation of the PO-DBN of a POP

In order to estimate the key parameters of the PO-DBN associated to the POP, in the case where the state spaces are not too large, π, T_H and T_O can be modeled as non-parametric. Otherwise, and in any cases, the distribution π, T_H and T_O can be defined via some parameters linked to the species dynamics. Estimation is based on classical algorithms for data with latent variables: EM and the Forward-Backward algorithm (see section 5.1 and Appendix A, and also Murphy, 2002, for more general PO-DBN) . Since for the PO-DBN of a POP, $N = 2$, EM can be ran without encountering problems due to space or time complexity.

2.3. Literature examples of PO-DBNs to model and estimate the weeds dynamic

We present here existing works using PO-DBN for describing POP dynamics (even if not named as such by the authors), in which the hidden states and observed states represent different life stages of the population.

The first model, presented by Pluntz et al. (2018) is a model designed to estimate the key parameters involved in weeds dynamics, which are the probabilities of colonization (c), seed survival (s), seed production (d) and germination (g). The observed variable $O_t \in \{0, 1\}$ is 1 if standing flora is observed at time t and 0 otherwise. The hidden state $H_t \in \{0, 1\}$ designates the presence or absence of seeds in the soil. The model is an extension of the classical HMM of Figure 4 where the current unobserved life stage depends not only on the previous one but also on the previous observed population. This is necessary in order to model the fact that the standing flora (observed) produces new seeds that will enter the seed bank (hidden). This event represents seed production, and it occurs with probability d. The PO-DBN internal dependency structure is represented in the Figure 5 and is a sub case of Figure 2a.

The parameters s, c and d are both involved in the expression of T_H and g is involved in the expression of T_O . Finally, the seed production, of probability d is fixed to 1. So, except d all the parameters are estimated using the EM algorithm and the method has been implemented on real data to determine the roles of seed banking and colonization in weed species dynamics.

The model proposed by Louvet et al. (2021) is similar to that of Pluntz et al. (2018) model. However, it offers additional insights into the effect of the seed bank, which is characterized by the Seed Bank Characteristic

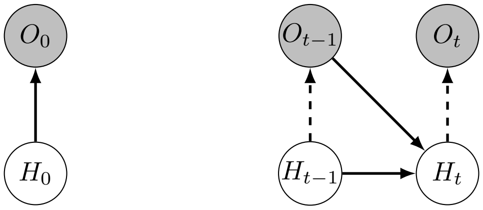

Figure 5: Graphical representation of the internal dependency structure of the PO-DBN used to model weeds dynamics in Pluntz et al. (2018). The observed life-stage is the standing flora, and the unobserved life stage is the seed bank. Note that there is a delay of one time step on O_t compared to the structure in Pluntz et al. (2018), but they are equivalent up to a shift of 1 in the indices of the observed variables. Between time steps $t-1$ and t,the dashed arcs are involved in the transition of observation, T_O, and the filled ones are involved in the transition of the hidden state, T_H.

Event (SBCE) probability. The model proposed by Kazakou et al. (2021) is bayesian and, puts an additional layer to the model of Pluntz et al. (2018) in which the parameters depend on conditions external to the plant. Parameter estimation is obtained using an EM algorithm in Louvet et al. (2021) and an MCMC algorithm in Kazakou et al. (2021).

The limit of these models comes from the fact that they represent colonization as a constant probability (seed rain) that influences the dynamics of the unobserved life stage. It does not take into account the real population state of neighbouring patches over time. The framework presented in the next section allows us to go beyond this limit.

3. From Metapopulation with Partially Observable Populations to interacting PO-DBN

Now we move from the modeling of a POP to the modeling of several POP in interactions as in a metapopulation with some life stages unobserved. We first define formally the notion of M-POP. Then we present the framework of interacting PO-DBN and the general procedure to build one for a given M-POP. A example from literature is described, again on weeds dynamics.

3.1. Metapopulation with Partially Observable Populations

A metapopulation is a set of spatially distributed populations of a same species, interacting with each other. In a metapopulation, each population evolves in a homogeneous spatial unit that is different from its neighbours, called a patch.

We refer to a metapopulation in which in each patch only some life stages of the population are observable as a Metapopulation with Partially Observable Populations (M-POP). In a M-POP, interactions between the populations of different patchs, which represent colonization, can occur between hidden or observed life stages.

In the following, we will assume that the hidden and observed life stages are identical in each patch. Besides, we assume that the mode of colonization is identical between all populations of the M-POP. So, the internal dependency structure of the PO-DBN associated to the POP will be the same in each patch. Then we show how to link the PO-DBN of the different patches.

3.2. How to model M-POP dynamics with interacting PO-DBN ?

Let us consider a M-POP divided into C distinct populations, where $C \geq 1$. Each population is identified by a number $c \in \{1, ..., C\}$ and its local dynamics is modeled by the associated PO-DBN. Its states (observed and hidden) can be influenced by the populations in the neighbouring patches of c (if dispersal is limited by distances for instance). The set of indices of the patches neighbours to patch c is denoted N_c.

By extending the notations of the Section 2.2.1 to the case of C patches, we denote as $S_{c,t} = \begin{pmatrix} O_{c,t} \\ H_{c,t} \end{pmatrix}$ the state of the POP of patch c at time t ($O_{c,t}$ for the local observable life stage and $H_{c,t}$ for the local hidden life stage). We note $S_{1:C,t} = \begin{pmatrix} O_{1:C,t} \\ H_{1:C,t} \end{pmatrix}$ the state of the M-POP (composed of all POP in the M-POP), where $S_{1:C,t} = (S_{1,t}, S_{2,t}, \dots, S_{C,t})$ and $O_{1:C,t} = (O_{1,t}, O_{2,t}, \dots, O_{C,t})$.

Colonization between patches must be taken into account in the transition distributions T_O and T_H in each patch. Indeed, on a patch c the new state $S_{c,t}$ of POP c depends not only on the state local $S_{c,t-1}$ but also on the state of the neighbouring POPs denoted as $S_{N_c,t-1}$. Furthermore, depending on the species studies, the life stage from which colonization originates is observed or hidden, and similarly colonization impacts only the hidden or the observed life stage, meaning that T_O and T_H will depend only on the hidden part or the observed part of $S_{N_c,t-1}$.

So, to model a M-POP the idea is to start from a set of C identical PO-DBN and to link them by interaction arcs that form the Interaction Structure.

We will refer to this model (without more formal definition) as an interacting PO-DBN. The graphical representation of the conditional independencies in an interacting PO-DBN is constructed from the repetition (for all patches) of the same internal dependency structure (as populations of the same species are assumed to develop in the same way). These internal dependency structures are in interaction via arcs that go from $O_{c',t-1}$ or $H_{c',t-1}$ at patch c' to $O_{c,t}$ or $H_{c,t}$ in another patch c at $t+1$, if c' is in N_c. These arcs represent the mode of dispersion associated with the M-POP under study. This final structure (internal dependency structure plus interaction structure) is designated as the total interaction structure.

3.3. Example of an interacting PO-DBNs for M-POP from literature

Continuing the example of weeds, colonization of the seed bank is due to seeds produced by standing flora that disperse and reach neighbouring patches and enter their seed bank. However in the model of Pluntz et al. (2018), the real state of the neighbouring patches is not considered and colonization is summarized by the parameter c constant over time. This does not fully reflect the metapopulation's dynamics.

To overcome this limitation, Le Coz et al. (2019) and Cheptou et al. (2022) have extended the model proposed by Pluntz et al. (2018) to model the dynamics of annual plants and seed banks with an interacting PO-DBN (even if not named as such in the article). Similarly to Pluntz et al. (2018), the observed life stage is the standing flora (divided into abundance classes), and the hidden one represents the seed bank (also divided into abundance classes). This model combines the dynamics of a considered weed population in each field, represented by the internal dependency structure shown on Figure 5 to an interaction structure between the populations of each field representing colonization. Colonization occurs from the standing flora of a patch to the seed bank of another patch, as shown in Figure 6. In this model the state of the seed bank in field c depends explicitly on the state of the standing flora in the neighbouring fields, which changes through time (as opposed to a seed rain model). We will come back to this interacting PO-DBN in section 4.2 where we will provide the expression of T_O and T_H.

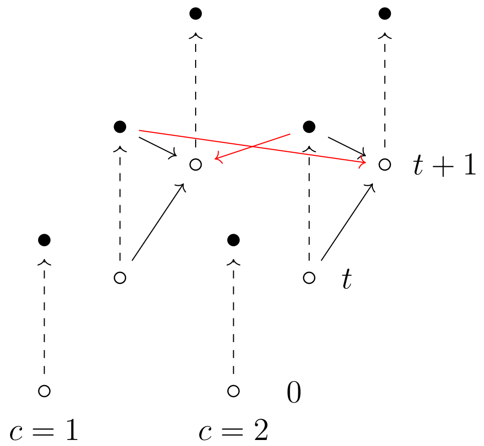

Figure 6: Graphical representation of the total dependency structure of the interacting PO-DBN used to model weeds dynamics in Le Coz et al. (2019). Case of a metapopulation of two patches. Filled circle represent standing flora (observed life stage), and empty ones represents the seed-bank unobserved life stage. In this representation, the dashed arcs are involved in the T_O transition, and the filled arcs are involved in the T_H transition. Red arcs correspond to the interaction structure while black arcs correspond to the internal dependency structure.

4. Four structures of interacting PO-DBNs to describe the main M-POP dynamics

From the two previous section, it appears clearly that interacting PO-DBNs offer a promising modeling option in ecology for describing the dynamics of M-POPs because they enable the study of species whose some life stages may not be observable on each patch, as well as the explicit modeling of inter-patch colonization. In order to deepen our understanding on how to use them for modeling and estimating M-POP dynamics, we will address the two open questions in the following sections.

- What are the relevant interaction structures when modeling the dynamics of a M-POP ? (Section 4)
- Can we easily access parameter estimation for these models, in other words, what is the computational complexity of estimation in interacting PO-DBNs ? (Section 5)

Consider the dynamics of a M-POP, containing C distinct populations interacting with each other. As all specie do not have the same dispersal strategy, in order to identify the interaction structure of the associated interacting PO-DBN we need to identify whether the life stage from which colonization originated is observed or hidden, and similarly whether the colonized life stage is hidden or observed. If we consider a species that uses only one dispersal mode there are only four possible interaction structures:

- colonisation from the observed life stage of patch c toward the observed life stage of patch c' (from $O_{c,t-1}$ to $O_{c',t}$), as shown in Figure 7;

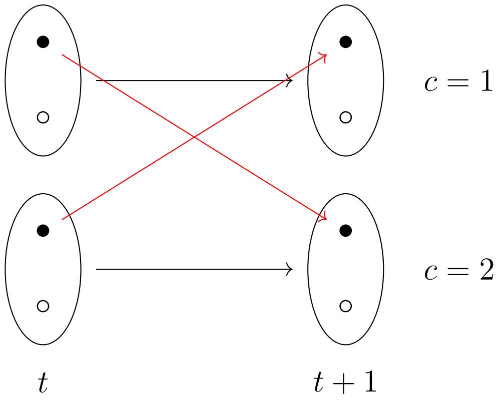

Figure 7: General representation of the interacting PO-DBN with interactions between observed life stages of the $C = 2$ populations. An empty circle represents an hidden life stage and a filled one is an observed life stage.

- colonisation from the observed life stage of patch c to the hidden life stage of patch c' (from $O_{c,t-1}$ to $H_{c',t}$), as shown in Figure 8;
- colonization from the hidden life stage of patch c to the observed life stage of patch c' (from $H_{c,t-1}$ to $O_{c',t}$), as shown in Figure 9;
- colonisation from the hidden life stage of patch c towards the hidden life stage of patch c' (from $H_{c,t-1}$ to $H_{c',t}$), as shown in Figure 10.

It is possible to combine these four types of interaction to create more complex interaction structures, in order to model species with several dispersal modes.

In Figures 7 to 10 the internal dependency structure in each patch is not detailed because it will be different from one species to another. In the following, we describe a concrete example of M-POP for each of the four interaction structures and we provide the definition of π, T_O and T_H for the associated interacting PO-DBN.

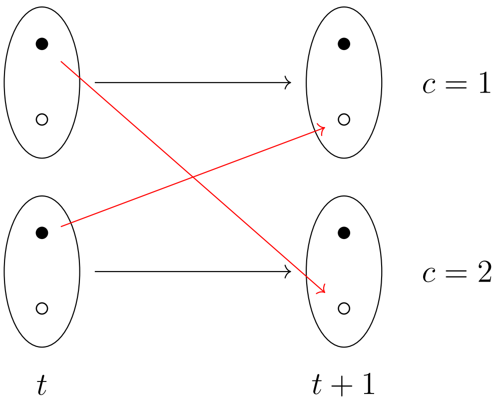

Figure 8: General representation of the interacting PO-DBN with interactions from observed life stages to hidden life stages of the $C = 2$ populations. An empty circle represents an hidden life stage and a filled one is an observed life stage.

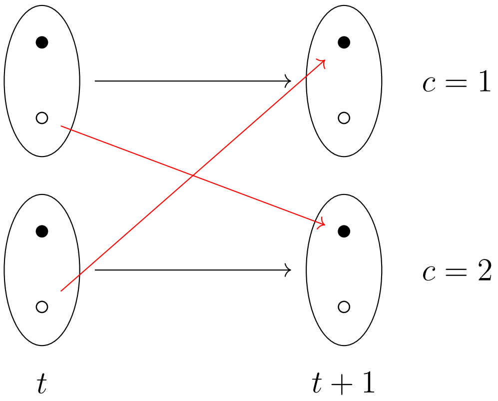

Figure 9: General representation of the interacting PO-DBN with interactions from hidden life stages to observed life stages of the $C = 2$ populations. An empty circle represents an hidden life stage and a filled one is an observed life stage.

4.1. Interactions between observed life stages

Let us consider the case of sea trouts dynamics. The number of trouts migrating upstream is declining every year due to global warming, but also to changes in the watercourses that hinder their migration. It would therefore be helpful to have a model at the level of the metapopulation in order to predict the dynamic of the trouts populations or their genetic connectivity.

In a metapopulation of sea trouts (Mobley et al., 2021), in each patch, a river, the population is composed of two life stages: adults and trouts

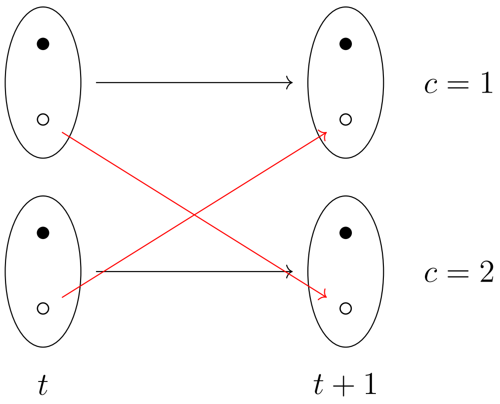

Figure 10: General representation of the interacting PO-DBN with interactions between hidden life stages of the $C = 2$ populations. An empty circle represents an hidden life stage and a filled one is an observed life stage.

eggs. The only observable life stage is that of adults. They are observed when they go up the rivers to lay their eggs in spawning grounds, which are difficult to observe. Then, they move to colonize other patches (i.e. other rivers). Therefore, the dynamics of two patches are linked by movements from the observed life stage of a patch to the observed life stage of another patch. This corresponds to the first general interaction structure presented in Figure 7 in the case of $C = 2$ processes. To build an interacting PO-DBN for the sea trouts, we also need to specify the internal dependency structure. Since eggs become adults in the same river and adults can come back to the river they come from, we obtain the total dependency structure of Figure 11 in the case of 2 rivers. If there are more than two patches, some rivers may be too far from each other for colonization to be possible, and, in this case, each river c is only in interaction with some other rivers $c' \in N_c$ and the arc corresponding in the interaction structure is only present between the PO-DBN of patch c and those in N_c.

Based on the structure in Figure 11, n interacting PO-DBN model for a sea trouts M-POP would be as follows. Let us define $H_{c,t}$ as the presence or not of eggs hidden in the spawning ground of the river c and $O_{c,t}$ as the presence or not of adult trouts in the the same river. Since, the states are 'presence/absence' we denote the state spaces as $\Omega_H = \{0, 1\}$ and $\Omega_O = \{0, 1\}$.

The three probability distributions π, T_H and T_O of the interacting PO-

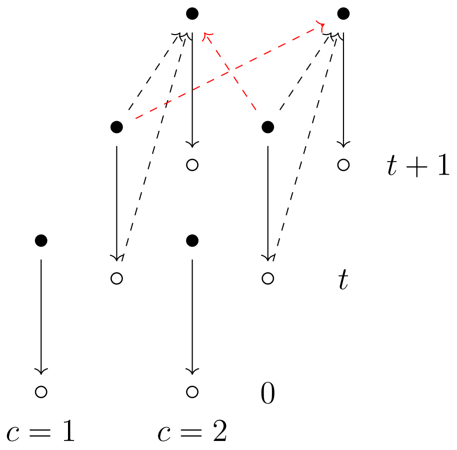

Figure 11: Total dependency structure of the interacting PO-DBN associated to sea trouts with interactions between observed life stages of the $C = 2$ populations. An empty circle represents the state of eggs (hidden) and a filled one is the state of adults (observable) in the river. In this representation, the dashed arcs are involved in the T_O transition, and the filled arcs are involved in the T_H transition. Red arcs correspond to the interaction structure while black arcs correspond to the internal dependency structure.

DBN associated to the sea trout dynamics are defined as follows :

- *Initial distribution.* There is one initial probability per river c. If we assume that it is the same for each river it can be denoted $\pi(h_{c,0}, o_{c,0})$, where for all $c \in \{1, ..., C\}$, and for all $h_{c,0} \in \Omega_H$ and for all $o_{c,0} \in \Omega_O$:

$$\begin{aligned}\pi(h_{c,0}, o_{c,0}) &= \mathbb{P}(H_{c,0} = h_{c,0}, O_{c,0} = o_{c,0}) \\ &= \mathbb{P}(H_{c,0} = h_{c,0} | O_{c,0} = o_{c,0}) \mathbb{P}(O_{c,0} = o_{c,0}).\end{aligned}$$

  It is decomposed into two probabilities: the probability of presence/absence of adults at $t = 0$, and the probability of presence/absence of eggs at $t = 0$ conditionally to the presence/absence of adults. Obviously, $\mathbb{P}(H_{c,0} = 1 | O_{c,0} = 0) = 0$.

- *Transition distribution.* For Figure 11, we have that the presence of eggs in the spawning ground of river c depends only on the presence of adult sea trout in that river, while the presence of adults at time t depends on the presence of adult at time $t-1$ in river c and in neighbour rivers, and on the presence of eggs at time $t-1$ in river c (eggs that have hatched into adults).

The two transition distributions T_H and T_O are therefore defined as follows: for all $c \in \{1, ..., C\}$, and for all $(h_{1:C,t-1}, o_{1:C,t-1}) \in \Omega_H \times \Omega_O$ and $(h_{c,t}, o_{c,t}) \in \Omega_H^C \times \Omega_O^C$,

$$T_H(h_{c,t}|o_{c,t}) = \mathbb{P}(H_{c,t} = h_{c,t}|O_{c,t} = o_{c,t}).$$

It represents the probability that there are eggs (or not) in spawning grounds of river c conditionally to the arrival (or not) of the sea trouts in river c. And,

$$\begin{aligned} &T_O(o_{c,t}|\{o_{c',t-1}, c' \in N_c\}, o_{t-1,c}, h_{t-1,c}) = \\ &\quad \mathbb{P}(O_{c,t} = o_{c,t}|\{O_{c',t-1} = o_{c',t-1}, c' \in N_c\}, O_{c,t-1} = o_{c,t-1}, H_{c,t-1} = h_{c,t-1}), \end{aligned}$$

which designates the probability of presence or absence of adults in river c at time t conditionally to arrival of adults by migration or to the presence of eggs at $t-1$ that have hatched into adults.

The sea trouts metapopulation is an example of the general interaction structure shown in Figure 7. This structure can be relevant to any M-POP where individuals in the first life stages remain unseen and only adults are visible and can colonize new patches. For instance, it can describe the dynamic of river fishes that go to ocean and go up into the rivers.

4.2. Interactions from observed life stages to hidden life stages

Let us continue the description of the case of a weed metapopulation, started in section 3.3. Weed control is a major challenge in agriculture, because weeds can lead to competition with crops, thus decreasing crop yield. In the same time weeds are beneficial for auxiliary and pollinator insects (Bretagnolle and Gaba, 2015). In order to regulate weeds populations, without totally eradicating them, interacting PO-DBNs can allow us to estimate the colonizing and dormancy profile of each species.

For a metapopulation of weeds, we recall that in each patch (i.e. a field), the population is composed of two life stages : seeds in seed bank and standing flora, and only the standing flora is visible. The seeds in seed bank can remain in the soil or grow and become standing flora. Seeds produced by the standing flora either enter the local seed bank or are dispersed by the wind before entering the soil and feeding the seed bank of other patches (i.e. other fields). Thus, the dynamics of two patches are linked by interactions from the observed life stage of a patch to the hidden life stage of another patch.

This corresponds to the second general interaction structure, presented in Figure 8, where $C = 2$. If there are more than two patches, some fields may be too far from each other for colonization to be possible, and, in this case, each field c is only in interaction with a subset of fields $c' \in N_c$ and the arc corresponding in the interaction structure is only present between c and the PO-DBN of patches in N_c.

Then, combining this interaction structure with the internal dependency structure specific to weeds leads to the total dependency structure of Figure 6. Let us know define more formally the interacting PO-DBN model for a weed M-POP. Let us define $H_{c,t}$ as the presence or absence of seeds hidden in the soil , and $O_{c,t}$ as the presence or absence of standing flora observed on the surface of field c at time t. Since, the states are 'presence/absence', the state spaces are $\Omega_H = \{0,1\}$ and $\Omega_O = \{0,1\}$. The three probability distributions π, T_H and T_O of the PO-DBN associated to a weed dynamics are defined as follows :

- *Initial distribution.* There is one initial probability per patch c. We denote $\pi(h_{c,0}, o_{c,0})$, where for all $c \in \{1, ..., C\}$, for all $h_{c,0} \in \Omega_H$ and for all $o_{c,0} \in \Omega_O$:

  $$\begin{aligned}\pi(h_{c,0}, o_{c,0}) &= \mathbb{P}(H_{c,0} = h_{c,0}, O_{c,0} = o_{c,0}) \\ &= \mathbb{P}(O_{c,0} = o_{c,0} | H_{c,0} = h_{c,0}) \mathbb{P}(H_{c,0} = h_{c,0}),\end{aligned}$$

  where the two terms designate respectively the probability of presence or absence of standing flora conditionally to the presence or absence of seeds in the soil, and the probability of presence or absence of seeds in the soil, at the start of the study. Obvioulsy, $\mathbb{P}(O_{c,0} = 1 | H_{c,0} = 0) = 0$. The probability $\mathbb{P}(O_{c,0} = 1 | H_{c,0} = 1) =$ is the probability of success of germination and growth of the plant.

- *Transition distribution.* The presence of seeds in the soil and of standing flora in the patch c at time t depends not only on the presence of seeds in the soil and of standing flora in the patch c at time $t-1$ but also on the standing flora of the other patch c' at time $t-1$. The two transition distributions T_H and T_O are derived as follows. For all $c \in \{1, ..., C\}$, for all $(h_{1:C,t-1}, o_{1:C,t-1}) \in \Omega_H \times \Omega_O$ and $(h_{c,t}, o_{c,t}) \in$

$\Omega_H \times \Omega_O$,

$$T_H(h_{c,t}|h_{c,t-1}, o_{c,t-1}, \{o_{c',t-1}, c' \in N_c\}) = \\ \mathbb{P}(H_{c,t} = h_{c,t}|H_{c,t-1} = h_{c,t-1}, O_{c,t-1} = o_{c,t-1}, \{O_{c',t-1} = o_{c',t-1}, c' \in N_c\}).$$

It represents the probability of presence/absence of seeds in the seed bank of field c at time t conditionally to the presence of seeds at time $t-1$ in field c and to the presence/absence of standing plants in neighbouring fields at $t-1$. For instance, if $o_{c,t-1} = 0$, $o_{c',t-1} = 0$ for all $c' \in N_c$, and $h_{c,t-1} = 1$ $T_H(1|h_{c,t-1}, o_{c,t-1}, \{o_{c',t-1}, c' \in N_c\})$ represents the probability of survival of the seed bank from $t-1$ to t.

The transition for the local observation is

$$T_O(o_{c,t}|h_{c,t}) = \mathbb{P}(O_{c,t} = o_{c,t}|H_{c,t} = h_{c,t}),$$

It designates the probability of presence/absence of standing plants at time t conditionally to the presence/absence of seeds in the seed bank at t.

We have described an example of an interacting PO-DBN with the general interaction structure shown in Figure 8. It also applies to any annual plant whose newly produced seeds are dispersed by the wind, by animals (e.g. hoarding by squirrels or transport by fur), by humans or by gravity.

4.3. Interactions from hidden life stages to observed life stages

In order to reduce pesticide use in the management of plant diseases in crops fields, it is necessary to understand the epidemics dynamics at the local and regional scales. A model at the metapopulation level would be useful to inform management tools (Cros et al., 2017) and to design efficient management strategies. We illustrate the general dependency structure of Figure 9 on the case of oilseed rape phoma stem canker. This is a fungal disease that infects and destroys oilseed rape crops (West et al., 2001). In a given field (i.e., a patch), two life stages can be distinguished: ascospores on the field surface in stubble, which are very difficult to detect (considered as the hidden life stage), and, phoma that has infected a leaf, visible by the leaf spots (observable life stage). Starting from leaf spots, phoma then spreads throughout the plant, ultimately leading to its death and the production of infected stubble. This stubble, remaining on the soil surface after oilseed rape has been harvested, produce ascospores, which are then dispersed by the wind, infecting young plants in local and other patches (i.e., other fields). The interaction structure is that of Figure 9 since dispersal starts from ascospores (hidden) and the result of colonization is visible on infected leaves (observed). The complete interaction structure associated to the phoma dynamics is represented, for $C = 2$ patches, in Figure 12. As for the other examples, if there are more than two patches, the arcs corresponding to the interaction structures may not be present between all patches but only between those that are spatially neighbours.

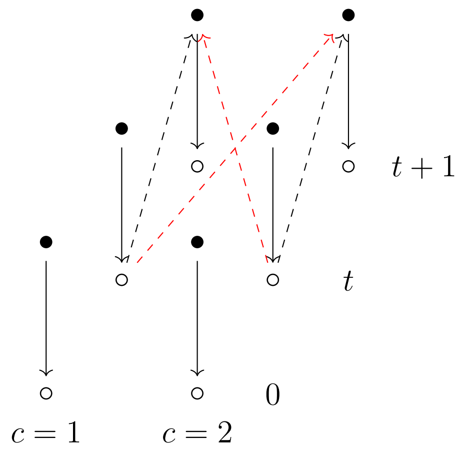

Figure 12: Total dependency structure of the interacting PO-DBN associated to the phoma dynamics on oilseed rape, with interactions from hidden life stages towards observed life stages. An empty circle represents the ascospores in stubble on the ground (hidden) and a filled one represents the infected leaves (observed). In this representation, the dashed arcs are involved in the T_O transition, and the filled arcs are involved in the T_H transition. Red arcs correspond to the interaction structure while black arcs correspond to the internal dependency structure.

The probabilities defining an interacting PO-DBN model for this M-POP would be as follows. Let us define $H_{c,t}$ as the abundance of ascospores on the stubble on the field c surface and $O_{c,t}$ as a severity index derived from the spots on the leaves of field c. The state spaces are $\Omega_H = \{0, 1, ..., s\}$ and $\Omega_O = \{0, 1, ..., d\}$, where 0 means 'absence' and s or d are respectively the maximal abundance class or severity index.

The three distribution probabilities π, T_H and T_O of the interacting PO-DBN associated to the phoma dynamics are defined as follows:

- *Initial distribution.* There is one initial probability per process c. If we assume that it is the same for each field it is denoted $\pi(h_{c,0}, o_{c,0})$, where for all $c \in \{1, ..., C\}$, and for all $h_{c,0} \in \Omega_H$ and for all $o_{c,0} \in \Omega_O$:

  $$\begin{aligned}\pi(h_{c,0}, o_{c,0}) &= \mathbb{P}(H_{c,0} = h_{c,0}, O_{c,0} = o_{c,0}) \\ &= \mathbb{P}(H_{c,0} = h_{c,0} | O_{c,0} = o_{c,0}) \mathbb{P}(O_{c,0} = o_{c,0}).\end{aligned}$$

  The two probabilities designate respectively the probability of the ascospores abundance conditionally to the severity index of the leaf infection and the probability of the severity index of the leaf infection, at initial time.

- *Transition distribution.* From Figure 12, we have that the abundance of hidden ascospores on the field c at time t depends on the severity index represented by the leaf spots visible at the same time (same year) on the same field, while the severity index on the field c at time t is taken conditionally to the abundance of infected stubble on patch c and on patches in N_c at time $t-1$. The two transition distributions T_H and T_O are defined as follows: for all $c \in \{1, ..., C\}$, and for all $(h_{1:C,t-1}, o_{1:C,t-1}) \in \Omega_H^C \times \Omega_O^C$ and $(h_{c,t}, o_{c,t}) \in \Omega_H \times \Omega_O$,

  $$T_H(h_{c,t} | o_{c,t}) = \mathbb{P}(H_{c,t} = h_{c,t} | O_{c,t} = o_{c,t}).$$

  It represents the probability of the abundance of the infected stubble (ascospores) conditionally to the severity index the same year on patch c. And,

  $$\begin{aligned}T_O(o_{c,t} | \{h_{c',t-1}, c' \in N_c\}) = \mathbb{P}(O_{c,t} = o_{c,t} | \{&H_{c',t-1} = h_{c',t-1}, c' \in N_c\}, \\ &H_{c,t-1} = h_{c,t-1}),\end{aligned}$$

  which designates the probability of the severity index conditionally to the hidden infected stubble in the neighbour fields and in the local field the previous time step.

Remark 2. *In practice, in agriculture, oilseed rape is cultivated in rotation with other crops such as wheat and barley. In this case, since phoma cannot infect wheat and barley, the internal dependency structure and the interaction structure would present less arcs compared to Figure 12.*

The structure of Figure 12 could also be applied to other metapopulations such as a fungus whose mode of dispersal is projection. It also can be applied to mussel dynamics, in which juveniles (too small to be visible) are transported by host fishes from one patch to another, then drop out as adults (and therefore too large to be transported again) and become visible in their arrival patch, where they will produce new juveniles that will be transported to another patch.

4.4. Interactions between the hidden life stages

Flooding favors the movement of certain species, both animal and plant. In this example, we consider plant species with low wind dispersal and for which flooding, i.e. moving seeds by water, is the only dispersal mode. In order to predict the spatial repartition of these species, it is important to take into account the effect of flooding on their dynamics when modeling (Hölzel and Otte, 2001).

During flooding, some of the seeds in the patch's soil may be carried by the water to other patches downstream of the flooding site, while others may remain in the patch soil. Following the flood, the displaced or non-displaced seeds germinate and become standing floras. Therefore the dynamics of two patches are linked by movements of the hidden life stage of a patch to another patch. This corresponds to the general interaction structure presented on Figure 10 in the case of $C = 2$ patches. The detailed interaction structure associated to the dynamic of these plants is shown in Figure 13 for two patches. If there are more than two patches, some patches may be too far from each other for colonization to be possible. In this case, each patch c is only in interaction with some other patches $c' \in N_c$ and the arc corresponding in the interaction structure is only present between the PO-DBN associated to the specie in patch c and those in N_c. Then the internal dependency structure in a patch leads to an interacting PO-DBN with total dependency structure shown in Figure 13.

Let us define $H_{c,t}$ as the abundance of seeds in seed bank of the patch c and $O_{c,t}$ as the abundance of standing flora visible on the same patch. The state spaces are $\Omega_H = \{0, 1, ..., s\}$ and $\Omega_O = \{0, 1, ..., d\}$, where 0 means 'empty' and s or d represent the maximal abundance class.

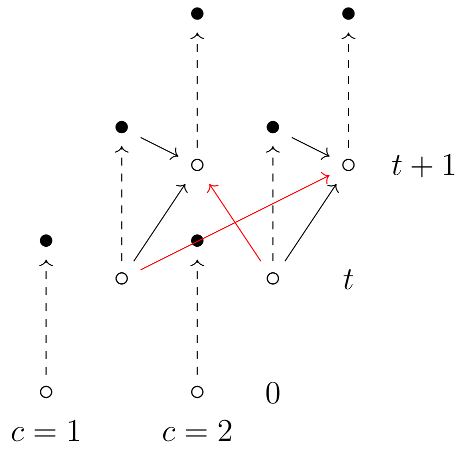

Figure 13: Total dependency structure of the interacting PO-DBN associated to the flooding dynamics with interactions between hidden states. An empty circle represents the seed in seed-bank (hidden) and a filled one represents the standing flora (observed). In this representation, the dashed arcs are involved in the T_O transition, and the filled arcs are involved in the T_H transition. Red arcs correspond to the interaction structure while black arcs correspond to the internal dependency structure.

The three distribution probabilities π , T_H and T_O of the interacting PO-DBN associated to the specie dynamics are defined as follows :

- *Initial distribution.* There is one initial probability per process c. If we assume that it is the same for each patch it is denoted $\pi(h_{c,0}, o_{c,0})$, where for all $c \in \{1, ..., C\}$, and for all $h_{c,0} \in \Omega_H$ and for all $o_{c,0} \in \Omega_O$:

  $$\begin{aligned}\pi(h_{c,0}, o_{c,0}) &= \mathbb{P}(H_{c,0} = h_{c,0}, O_{c,0} = o_{c,0})\\ &= \mathbb{P}(O_{c,0} = o_{c,0} | H_{c,0} = h_{c,0})\mathbb{P}(H_{c,0} = h_{c,0}).\end{aligned}$$

  The two terms designate respectively the probability of abundance of standing flora conditionally to the abundance of seeds, and the probability of abundance of seeds in the soil at time $t = 0$.

- *Transition distribution.* In Figure 13, we can see that the abundance of seeds in the soil of patch c at time t depends local abundance of standing flora at $t-1$, and on the presence of seeds in the soil in patch c and also in patches in N_c (displaced via flooding) at $t-1$. The abundance of standing flora in patch c at time t depends on the presence of seeds in the soil in the same patch at time t . The two transition distributions T_H and T_O are therefore as follows: for all $c \in \{1, ..., C\}$, for all $(h_{1:C,t-1}, o_{1:C,t-1}) \in \Omega_H \times \Omega_O$ and $(h_{c,t}, o_{c,t}) \in \Omega_H^C \times \Omega_O^C$,

$$\begin{aligned} T_H(h_{c,t}|h_{c,t-1}, \{h_{c',t-1}, c' \in N_c\}, o_{c,t-1}) = \mathbb{P}(H_{c,t} = h_{c,t}|H_{c,t-1} = h_{c,t-1}, \\ \{H_{c',t-1} = h_{c',t-1}, c' \in N_c\}, \\ O_{c,t-1} = o_{c,t-1}), \end{aligned}$$

It represents the probability of the abundance of seeds in the soil conditionally to the seeds abundance in patch c and in neighbour patches time $t-1$ and the abundance of standing flora in the same patch at time $t-1$. And,

$$T_O(o_{c,t}|h_{c,t-1}) = \mathbb{P}(O_{c,t} = o_{c,t}|H_{c,t} = h_{c,t}),$$

which is the probability of standing flora abundance conditionally to the abundance of seeds in the same patch, representing the growth of plants.

The model with the general interaction structure shown in Figure 10 can be applied to other metapopulations which are displaced by an external effect when they are in their hidden life stage, such as when seeds in the soil are moved from one patch to another by tractor wheel. Besides, the metapopulation dynamics of subterranean animals that can move from one patch to another via underground passages can also be described by such structure.

Remark 3. *Another example of the general interaction structure shown in Figure 10 is known in the literature as Coupled HMM (CHMM, Brand et al., 1997). A CHMM in an interacting PO-DBN whose total interaction structure shown in Figure 14. It is well adapted to deal with the case of detection errors, in which the observation is a "noisy" version of reality, described by the hidden state.*

As illustrated in the four examples, the construction of the interacting PO-DBN associated to the dynamics of the species under study is a relatively straightforward process. It comprises three fundamental steps:

1. At the POP scale, the internal dependency structure is built from the dynamics of the POP.

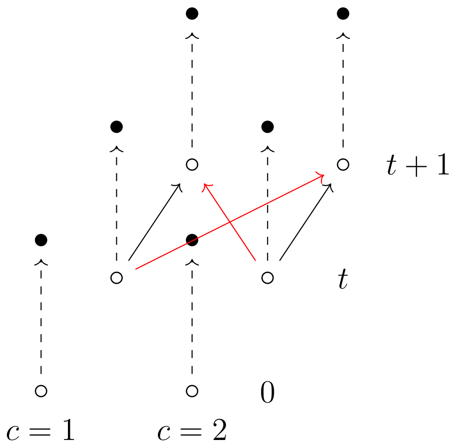

Figure 14: Graphical representation of a Coupled HMM. An empty circle represents a hidden state and a filled one represents an observed one. In this representation, the dashed arcs are involved in the T_O transition, and the filled arcs are involved in the T_H transition. Red arcs correspond to the interaction structure while black arcs correspond to the internal dependency structure.

2. At the M-POP scale, the type of interactions between each POP are identified from the type of dispersal used and arcs are added between the PO-DBN of each patch to obtain the total dependency structure of the interacting PO-DBN associated to the dynamics of the M-POP under study.
3. Ultimately, the graphical representation of the total dependency structure is used in order to identify which variables are parents of $O_{c,t}$ on one hand and of $H_{c,t}$ on the other hand, in order to determine the variables involved in the conditioning part of T_H and T_O.

5. Estimation of the parameters of a M-POP

In this section, we begin by recalling how parameter estimation is classically performed for a PO-DBN with one of the structure shown in Figure 2 or with simpler internal dependency structure (i.e. with some arcs absent). This is the model for a single POP on a patch. Then we show how the computational complexity can become prohibitive when using a direct application of the same estimation method to an interacting PO-DBN, depending on the interaction structure. We explain why for the structures of Figure 7 and Figure 8 simplifications occur and estimation remains tractable meaning that for the corresponding M-POP it will be easy to implement an estimation procedure with low time or space complexity. Finally we discuss which methods for approximate resolution can be mobilized to bypass the computational lock associated to interacting PO-DBN with structures of Figures Figure 9 and Figure 10.

5.1. Parameters estimation for the PO-DBN of a POP

Since a PO-DBN is in the family of models with hidden variables, the classical method to estimate the parameters is the Expectation-Maximization algorithm (EM, Dempster et al., 1977). The EM algorithm is an iterative algorithm and each iteration is composed of two steps. We detail here these two steps on the PO-DBN of Figure 2a to point out where the computational difficulty could arise when moving to one of the four types of interacting PO-DBN model of a M-POP presented in the previous section.

In the following, we denote the vector of the observations between $t = 0$ and $t = M$ by $O_{0:M} = (O_0, O_1, O_2, ..., O_M)$. In the same way, the vector of the hidden states between $t = 0$ and $t = M$ is denoted $H_{0:M} = (H_0, H_1, ..., H_M)$. The set of model parameters is θ. For the non-parametric PO-DBN with the dependency structure shown in Figure 2a, θ is composed of the initial distribution π and the two transition distributions T_H and T_O.

Let us consider $\theta^{(m)}$ the parameter estimates at iteration m of EM and define $Q(\theta|\theta^{(m)})$ the intermediate quantity, as the expectation of the complete log-likelihood, where

$$Q(\theta|\theta^{(m)}) = \mathbb{E}_{\theta^{(m)}} \left[\ln \mathbb{P}_\theta(O_{0:M}, H_{0:M})|O_{0:M} = o_{0:M}\right].$$

The two steps in each iteration are the following ones:

1. **Expectation Step (E step):** computation of the marginal conditional distributions involved in the expression of the intermediate quantity $Q(\theta|\theta^{(m)})$.
2. **Maximization step (M step):** updating of the set of parameters θ thanks to the quantities found in the E Step, by resolving $\theta^{(m+1)} = \arg\max_\theta Q(\theta|\theta^{(m)})$.

These two steps are repeated until the algorithm converges. EM converges towards a local maximum of the likelihood $\mathbb{P}_\theta(O_{0:M} = o_{0:M})$. In the case of the PO-DBN of Figure 2a, similarly to EM for estimating a HMM, the

E-step relies on the Forward-Backward algorithm (Baum et al., 1970). Two auxiliary quantities are computed recursively from which all other conditional probabilities needed in the E step can be computed. Their expressions are:

$$\begin{aligned}\alpha_t(h_t) &= \mathbb{P}_{\theta^{(m)}}(O_{0:t} = o_{0:t}, H_t = h_t),\\ \beta_t(h_t) &= \mathbb{P}_{\theta^{(m)}}(O_{t+1:M} = o_{t+1:M} | H_t = h_t, O_t = o_t).\end{aligned}$$

Remark 4. *Compared to the forward-backward variables of the EM for HMM the difference lies in the fact that the observation* o_t *appears in the conditioning of* β_t*.*

The quantities αs are computed by a forward recurrence

$$\alpha_t(h_t) = \sum_{h_{t-1}} T_O(o_t \mid h_{t-1}, h_t, o_{t-1}) T_H(h_t \mid h_{t-1}, o_{t-1}) \alpha_{t-1}(h_{t-1}),$$

with $\alpha_0(h_0) = \pi(z_0, y_0)$. And the quantities βs by a backward recurrence

$$\beta_t(h_t) = \sum_{h_{t+1}} \beta_{t+1}(h_{t+1}) T_O(o_{t+1} \mid h_{t+1}, h_t, o_t) T_H(h_{t+1} \mid h_t, o_t),$$

with $\beta_M(z_M) = 1$. One can see that for a given t and K possible values for the hidden state (i.e. $|\Omega_H| = K$) there are $2K$ values to compute and each computation involves K sums. Therefore computing all the $\alpha_t(h_t)$ and $\beta_t(h_t)$ requires $2MK^2$ sums. It means that the time complexity of the E-step is quadratic in K, the number of possible states of the unobserved life stage of the POP.

Regarding now the M-step, in the non-parametric case, the maximization leads to analytical expressions for updating the parameters. In the parametric case, depending on the case, there may not be analytical expression and one must resort to numerical optimization.

5.2. Why can estimation become intractable for interacting PO-DBN?

The most straightforward way to estimate the parameters of an interacting PO-DBN would be to consider it as a PO-DBN model with structure of Figure 1 with multidimensional hidden and observed variables (by grouping all patches) and to apply the EM algorithm to this PO-DBN. Indeed, if we consider the vector of all hidden states at time t, $H_{1:C,t} = \{H_{1,t}, H_{2,t}, \ldots, H_{C,t}\}$ and the vector of all observations at time t $O_{1:C,t} =$

$\{O_{1,t}, O_{2,t}, \dots, O_{C,t}\}$, then $(H_{1:C,t}, O_{1:C,t})$ is a PO-DBN and the dimension of the hidden state space is $K' = |\Omega_H|^C$. Therefore the computational complexity of the E-step becomes $2M(K')^2$ and is exponential in the number of patches of the M-POP. This can quickly becomes prohibitive, beyond a few patches.

5.3. For which interaction structure can we obtain a tractable complexity for interacting PO-DBN estimation?

When representing an interacting PO-DBN by a multidimensional PO-DBN as above we reach the worse complexity of the E step. We do not take into account that the corresponding M-POP is structured in patches and that not all 4 dispersal paths are used. In the four total dependency structures presented in section 4, each structure uses a single dispersal path (e.g from hidden life stage of a patch to observed life stage of another). In some cases, this can lead to a reduction of the E step complexity.

Such a simplification will be possible when, conditionally to all the observation $o_{1:C,0:M}$, the state of each hidden sequence, $H_{c,0:M} = \{H_{c,0}, H_{c,1}, \dots, H_{c,M}\}$, is independent of the state of each other sequence $H_{c',0:M}$ for $c' \neq c$. We will refer to this property as Independence of Hidden Chains Conditionally to the Observations (IHCCO). We will see that only two of the four interaction structures described in section 4 satisfy this property. In this case the actual auxiliary quantities computed during the E step will not be $\alpha_t(h_{1:C,t})$, $\beta_t(h_{1:C,t})$ which both depend on the state of all hidden chains at time t, but auxiliary quantities defined at the chain level, $\alpha_{c,t}(h_{c,t})$, $\beta_{c,t}(h_{c,t})$, leading to a complexity which is $C \times 2MK^2$, i.e. linear in the number of patches (see Appendix B and Appendix C).

It is a well established result (Koller and Friedman, 2009) that the conditional independencies of a (Dynamical) Bayesian Network can be identified from the structure of its graphical representation. So it is possible to 'read' in the structures of Figures 7 to 10 if in each of these interacting PO-DBN IHCCO holds or not. How to do this rigorously is explained in (Koller and Friedman, 2009), and it is quite technical. Here we identify two particular patterns that can be found in a structure and we explain only intuitively why IHCCO does not hold if these patterns are present.

The first pattern is when two hidden variables $H_{c,t}$ and $H_{c',t'}$ from two distinct patches have an out-going arc that reaches the same observed variable, let say $O_{c'',t''}$. This forms what is called a V-structure in the DBN

(Koller and Friedman, 2009). If $O_{c'',t''}$ is observed, H_c and $H_{c'}$ are not independent conditionally to this observation since they have both contributed to its emission. Let think of an example where the observation is the sum of the two hidden variables. Then knowledge on the sum of two variables make these two variables dependent. This pattern is present in Figure 9, which represent the interacting PO-DBN for a M-POP with interaction from the hidden life stage to the observed life stage. Let us consider three patches ($C = 3$), it this case both $H_{1,t}$ and $H_{2,t}$ have an out-going arc that reaches the same observed variable, namely $O_{3,t+1}$. So for this type of M-POP, IHCCO does not holds and the complexity of EM will remain exponential in C.

A directed path is a path that follows the direction of the arc in the graphical representation of the interacting PO-DBN. For instance, in Figure 6 there is a directed path from $H_{1,0}$ to $H_{2,2}$ that goes through $O_{1,0}$ and $H_{2,1}$. The second pattern is the existence of a directed path that goes from the hidden variable of one chain $H_{c,t}$ towards the hidden variable of another $H_{c',t'}$ $(t < t')$ without going through any observed variables. If such a path exists then, intuitively knowing the value of $H_{c,t}$ has an influence on the value of $H_{c',t'}$. This pattern is present in Figure 10. When the colonization goes from the hidden population of one patch towards the hidden population of another patch, it creates a directed path from hidden variables of patch c towards hidden variables of patch c' that does not pass through an observed variable (for instance from $h_{c,t}$ towards $h_{c',t+1}$). So for this type of M-POP, IHCCO does not holds and the complexity of EM will remain exponential in C.

For the two remaining cases (Figure 7 and Figure 8) the two patterns are never present. All the directed paths between hidden variables always go through an observation. To get out of chain c and reach chain c', the information carried out by $H_{c,t}$ must pass through some observations which block the influence of $H_{c,t}$ on $H_{c',t'}$. Furthermore, and observation is never the child of two hidden variables from different chains. So there is no way that hidden states at patch c influences hidden states at patch c' conditionally to the observations. For these two M-POP IHCCO holds and it is possible to derive an EM with complexity only linear in C. Details of the E-step for the structure of Figure 11 (which an example of the general structure of Figure 7) and for the structure of Figure 6 (which an example of the general structure of Figure 8) are provided in Appendix B and Appendix C (we also provide the formula for updating the parameters, M-step).

5.4. How to bypass the estimation lock when IHCCO does not hold ?

For the two interaction structures with no conditional independence between the hidden processes conditionally to the observations, three main solutions can be used to handle the complexity of the E-step : Monte-Carlo simulations, variational approximation of the conditional distribution of the C hidden chains given the observations, or ad-hoc simplification of the global transition probability.

Remark 5. *As far as we know, estimation of an interacting PO-DBN with structure of Figure 9 has never been studied, but it could be envisaged using one of these 3 methods. On contrary, these three options have already been proposed for a particular case of the structure of Figure 10, the case of Coupled HMM already mentioned and whose structure is shown in Figure 14.*

5.4.1. Simulation-based EM

Simulation-based EM algorithms are used when Forward-Backward calculations are too complex. In this type of algorithms, the E step is replaced by a simulation step. There exist three main versions of approximate EM based on simulations. In the case of Monte-Carlo EM (MC-EM, Wei and Tanner, 1990), the intermediate quantity $Q(\theta|\theta^{(m)})$ is approximated using a Monte-Carlo estimator. Several samples from the conditional distribution $\mathbb{P}_{\theta^{(m)}}(H_{1:C,0:M} = h_{1:C,0:M} \mid O_{1:C,0:M} = o_{1:C,0:M})$ are generated and Q is approximated by the empirical mean. Stochastic EM (SEM, Celeux and Diebolt, 1985) is a special case of MC-EM where only one draw from $\mathbb{P}_{\theta^{(m)}}(H_{1:C,0:M} = h_{1:C,0:M} \mid O_{1:C,0:M} = o_{1:C,0:M})$ is made. This sampled value is used to restore the hidden variable and the M step consists in maximizing the log-likelihood of the complete data $\mathbb{P}_{\theta^m}(H_{1:C,0:M} = h_{1:C,0:M}, O_{1:C,0:M} = o_{1:C,0:M})$, which can be easier than maximizing Q. The Stochastic Approximation EM (SAEM, Allassonnière and Chevallier, 2021) also requires a single draw at each iteration. At each iteration, one sample is generated, then the function which is maximized Q^{SAEM} is a linear combination of the log-likelihood of the complete data and the function Q^{SAEM} at the previous iteration.

The main advantages of simulation-based EM is that there are rather easy to implement and they come with theoretical guaranties on their convergence. In practice, for the model of interest in this article, the calibration of the algorithm used for simulating the conditional distribution $\mathbb{P}_{\theta^{(m)}}(H_{1:C,0:M} = h_{1:C,0:M} \mid O_{1:C,0:M} = o_{1:C,0:M})$ can be a delicate exercise.

Since there are dynamical stochastic model, it is usually performed using Particle Filtering and more specifically Sequential Monte Carlo (SMC). Particle filtering suffers from degeneracy problems when simulated processes are long, and it is not always obvious which proposal distribution to choose. Nevertheless, it remains widely used, as it is simple to implement and provides good results.

For the CHMM case (Figure 14, particular case of Figure 10 : an MCEM algorithm based on SMC has been proposed, in the context of freeway traffic modeling (Kwon and Murphy, 2000), but there is no available code.

5.4.2. Variational EM

The idea of a variational approximation is to perform computations on a model chosen in a family, $\mathcal{F}$, of probability distributions with simpler dependence structure than that of the true conditional distribution $\mathbb{P}(H_{1:C,0:M} \mid O_{1:C,0:M})$. The family is chosen such that the E step becomes tractable. The element of the family which is selected is the one that leads to the best approximation of the true model. This notion of optimality is defined according to the Kullback-Leibler divergence. When variational approximation is used in the E step of EM, it leads to the Variational EM algorithm (Wainwright and Jordan, 2008). The main advantage of the Variational EM is that it is fast. Indeed, optimizing the Kullback-Leibler divergence is usually fast.

The main limit of the Variational EM is the lack of theoretical guaranties for the models of interest here. Nevertheless the variational approach is more and more used to estimate complex models due to its simplicity and rapidity, and in practice it usually provide good estimators.

In the case of an interacting PO-DBN with structures of Figures 9 and 10, using VEM amounts to the choice of a family $\mathcal{F}$ of models where IHCCO holds. Therefore, the corresponding variational E-step will be of complexity linear in C.

For structures of Figures 10 and 9, the simpler variational approximation is the mean field approximation which consists in choosing for $\mathcal{F}$ the family of fully independent hidden variables. It corresponds to

$$q(h_{1:C,1}, h_{1:C,2}, \ldots, h_{1:C,T}) = \prod_c \prod_t q(h_{c,t})$$

Less naive approximations can sometimes be considered that still enable fast and easy inference. In this spirit, in the case of CHMM, Wainwright and

Jordan (2008) proposed to approximate the true conditional distribution by a product of independent non homogeneous Markov process.

$$q(h_{1:C,1}, h_{1:C,2}, \ldots, h_{1:C,M}) = \prod_{c} \left\{ q_c(h_{c,0}) \prod_{t=1}^{M} q_{c,t}(h_{c,t} \mid h_{c,t-1}) \right\}$$

This solution is implemented in the *CHMM* R package, which provides as well the exact EM (Xiaoqiang et al., 2019). But, as far as we know, there is no such code available for the general structure of Figure 9 and for other particular cases of the Figure 10.

5.4.3. Ad-hoc EM

Another option that has been explored to simplify estimation is to work with a surrogate of the expression of the conditional distribution of interest. The surrogate may not be a proper distribution itself and is not the result of an optimization of some criterion. In that sense, this is different of the variational approach. Examples are from the field of signal analysis, and concern the CHMM model: Brand et al. (1997) for classifying two-handed actions, Montazeri Ghahjaverestan et al. (2016) on clinical data and Zhong and Ghosh (2002) for multichannel EEG analysis. The advantage is to lower the complexity of estimation, like the variational approximation. However they are ad-hoc procedures with no justification of the choice of the surrogate.

6. Discussion

In this article, we focused on interacting PO-DBNs to model the dynamics of metapopulation where some life stages in the each population are not observable. Through concrete examples, we have demonstrated how interacting PO-DBNs are sufficiently rich and flexible to capture the variety of possible metapopulation dynamics, in particular for different dispersal modes. We also discuss parameter estimation in these models in the context of the EM algorithm.

Interacting PO-DBNs are particularly well suited for describing M-POP (metapopulation with partially observed populations) dynamics. First, on a single population, PO-DBNs allow us to model systems whose dependency structure is more complex than that of the classical HMM, which allows us to go beyond detection errors and model the dynamics of a population whose some developmental stages are not all observable. Second, at the metapopulation level, interacting PO-DBNs enable more accurate description of metapopulation dynamics, taking into account interactions among populations through colonization. Additionally, in this framework it is easy to include covariates, like habitat quality or climate influence, to describe the M-POP dynamics more realistically.

M-POP can use different dispersal modes. We formally identified that four interaction structures of interacting PO-DBNs enable to describe the main M-POP with a single dispersal mode and we illustrates them through concrete examples that describe the dynamics of animal and plant species. We acknowledge that more complex interaction structures exist. In this case, the M-POP can be modeled by an interacting PO-DBN whose interaction structure combines several of the four elementary dispersal modes of section 4. As an illustration, let us consider the example of Daphnia, the small crustaceans living in rivers. These populations can be divided into two life stages: adults (observable life stage) and eggs (hidden life stage). During floods, Daphnia can be displaced from one stream to another, enabling adult populations to colonize other patches. Similarly, eggs (which are not visible in the river) can also be transported by floodwaters, but also in birds's feet. Therefore, in the Daphnia case, interactions between different patchs occur between observed life stages, but also between hidden life stages. The interacting PO-DBN would combined arcs of Figure 7 and 10.

Regarding estimation, in the case of interactions between observations or from observed to hidden states, the forward-backward algorithm corresponding to the E step is linear in the number of patchs, therefore EM can be used as such and is not more complicated to implement than an EM for HMM. However, the EM algorithm is not tractable for the two other interaction structures, thus requiring the use of approximate EM algorithms. To the best of our knowledge, these solutions have not been envisaged for these interacting PO-DBNs, with the exception of the structure illustrated in Figure 14 that corresponds to a CHMM. Moreover, in this paper, we have focused on the EM algorithm, but other methods for estimating the parameters of an interacting PO-DBN are available. For example, the ABC (Beaumont et al., 2002) or the MCMC (Robert and Casella, 2005) methods enable Bayesian parameter estimation, but these methods can be difficult to calibrate.

In this article we were interested by the question of understanding the metapopulation dynamics, therefore we focused of the estimation of the interacting PO-DBN parameters. There are other important questions when studying a M-POP dynamics, that could we addressed with the interacting PO-DBN framework. For instance, if the dispersal mode of the species under study is not clearly identified, model selection could be used to identify the interaction structure that best suits the data. If one is interested in the temporal evolution of the hidden life stages of a particular metapopulation it is possible to adapt the Viterbi algorithm for HMM to our four different structures (with the same computational difficulties in practice) to reconstruct the sequences of hidden states in each patch.

In regard to the modeling assumptions, two points of particular significance merit attention. First, we point out the need to collect longitudinal observed data providing information on the hidden system. These data must be a time series, with regular time step, and it can represent an important workload in the field for specific systems. Second, we considered the case of interacting PO-DBNs with finite and discrete hidden state spaces. The estimation methods proposed in this paper are adapted to this situation, but not to continuous hidden state spaces. In contract, the observed state space could be continuous although having as the same time discretized hidden life stages and continuous observed life stages for the same species may appear to be an unsuitable approach.

Even though very general, the framework we propose is not well suited to model the dynamics of any species. For instance, in the case of mammals the evolution between the different life stages (e.g., from juveniles to adults) is not clearly marked by two distinct physical states. and it is not always obvious to define two categories: hidden and observed life stages. The transition is rather smooth and continuous. In this case, it would be necessary to use a different approach to model the metapopulation dynamics.

To conclude, the framework we propose can contribute to bring solutions in conservation biology or invasive species. It sheds a new light on some non-explored populations dynamics and offer the opportunity to study the dynamics of metapopulations with hidden life stages, a domain that, until now, was limited to very specific examples of species (Le Coz et al., 2019) or required very strong assumptions (Levins et al., 1969). The practical use of these models will be possible by developing specific algorithms and codes and providing an easy-to-use modeling tool for ecologists. This article is therefore a mean for encouraging researchers in computational statistics to tackle the challenges raised by estimation in these models and to make the solutions available to the statistical ecology community.

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Disclosure statement

The authors report that there are no competing interests to declare.

Appendix A. E-step of EM for the more general PO-DBN model of a POP

We present here the E-step of the EM algorithm for the PO-DBN whose structure is shown in Figure 2a. The global transition for this model is

$$\begin{aligned}
&\mathbb{P}(H_t = h_t, O_t = o_t \mid H_{t-1} = h_{t-1}, O_{t-1} = o_{t-1}) \\
&\quad = \mathbb{P}(O_t = o_t \mid H_t = h_t, H_{t-1} = h_{t-1}, O_{t-1} = o_{t-1}) \\
&\qquad \times \mathbb{P}(H_t = h_t = h_t \mid H_{t-1} = h_{t-1}, O_{t-1} = o_{t-1}) \\
&\quad = T_O(o_t|h_t, h_{t-1}, o_{t-1}) T_H(h_t|h_{t-1}, o_{t-1}).
\end{aligned}$$

Let M be the number of observation time steps, and $\theta = (\pi, T_H, T_O)$ the model parameters. The complete likelihood, denoted L_{comp}, is given by the following equation:

$$L_{\text{comp}} = \mathbb{P}_\theta(H_{0:M} = h_{0:M}, O_{0:M} = o_{0:M}) = \pi(h_0, o_0) \prod_{t=1}^{M} T_O(o_t \mid h_t, h_{t-1}, o_{t-1}) T_H(h_t|h_{t-1}, o_{t-1}).$$

Appendix A.1. Expression of the intermediate quantity

During iteration m of EM, if $\theta^{(m)}$ is the current estimate of θ, we have to compute (E-step) and them maximize over θ (M-step) the following quantity:

$$Q(\theta, \theta^{(m)}) = \mathbb{E}_{\theta^{(m)}}[\ln(L_{\text{comp}})|O_{0:M} = o_{0:M}].$$

Since

$$\ln(L_{\text{comp}}) = \ln \pi(h_0, o_0) + \sum_{t=1}^{M} \ln T_O(o_t \mid h_t, h_{t-1}, o_{t-1}) + \sum_{t=1}^{M} \ln T_H(h_t|h_{t-1}, o_{t-1}),$$

we have

$$\begin{aligned}
Q(\theta, \theta^{(m)}) = &\sum_{h_0} \mathbb{P}_{\theta^{(m)}}(H_0 = h_0 \mid O_{0:M} = o_{0:M}) \ln \pi(h_0, o_0) \\
&+ \sum_{t=1}^{M} \sum_{h_t, h_{t-1}} \mathbb{P}_{\theta^{(m)}}(H_t = h_t, H_{t-1} = h_{t-1} \mid O_{0:M} = o_{0:M}) \ln T_O(o_t \mid h_t, h_{t-1}, o_{t-1}) \\
&+ \sum_{t=1}^{M} \sum_{h_t, h_{t-1}} \mathbb{P}_{\theta^{(m)}}(H_t = h_t, H_{t-1} = h_{t-1} \mid O_{0:M} = o_{0:M}) \ln T_H(h_t|h_{t-1}, o_{t-1}).
\end{aligned}$$

Appendix A.2. E-step

We can see that evaluating Q requires to compute

- $\rho^{(m)}(h_0) = \mathbb{P}_{\theta^{(m)}}(H_0 = h_0 \mid O_{0:M} = o_{0:M}), \forall h_0 \in \Omega_H$
- $\xi^{(m)}(h_t, h_{t-1}) = \mathbb{P}_{\theta^{(m)}}(H_t = h_t, H_{t-1} = h_{t-1} \mid O_{0:M} = o_{0:M}), \forall 1 \leq t \leq M, \ \forall h_t, h_{t-1} \in \Omega_H$

Similarly to the Forward-Backward algorithm for HMM, each $\rho^{(m)}(h_0)$ and each $\xi^{(m)}(h_t, h_{t-1})$ can be computed via two auxiliary variables defined recursively:

- $\alpha_t^{(m)}(h_t) = \mathbb{P}_{\theta^{(m)}}(O_{0:t} = o_{0:t}, H_t = h_t), \forall 0 \leq t \leq M, \ \forall h_t \in \Omega_H;$
- $\beta_t^{(m)}(h_t) = \mathbb{P}_{\theta^{(m)}}(O_{t+1:M} = o_{t+1:M} | H_t = h_t, O_t = o_t), \ \forall 0 \leq t < M, \ \forall h_t \in \Omega_H.$

Computation of $\rho^{(m)}$ and $\xi_t^{(m)}(h_t, h_{t-1})$ using $\alpha_t^{(m)}$ and $\beta_t^{(m)}$

Note that we have that $\alpha_t^{(m)}(h_t)\beta_t^{(m)}(h_t) = \mathbb{P}_{\theta^{(m)}}(H_t = h_t, O_{0:M} = o_{0:M})$ and the likelihood can be obtained as follows: $\sum_{h_t} \alpha_t^{(m)}(h_t)\beta_t^{(m)}(h_t) = \mathbb{P}_{\theta^{(m)}}(O_{0:M} = o_{0:M})$. So

$$\rho^{(m)}(h_0) = \frac{\alpha_0^{(m)}(h_0)\beta_0^{(m)}(h_0)}{\sum_{h_0} \alpha_0^{(m)}(h_0)\beta_0^{(m)}(h_0)}$$

We also have that

$$\xi_t^{(m)}(h_t, h_{t-1}) = \mathbb{P}_{\theta^{(m)}}(H_t = h_t, H_{t-1} = h_{t-1}, O_{0:M} = o_{0:M}) / \sum_{h_t} \alpha_t^{(m)}(h_t)\beta_t^{(m)}(h_t)$$

and the numerator can be decomposed as

$$\begin{aligned}
&\mathbb{P}_{\theta^{(m)}}(H_t = h_t, H_{t-1} = h_{t-1}, O_{0:M} = o_{0:M}) \\
&= \mathbb{P}_{\theta^{(m)}}(O_{t+1:M} = o_{t+1:M} \mid H_{t-1} = h_{t-1}, H_t = h_t, O_{0:t} = o_{0:t}) \\
&\quad \times \mathbb{P}_{\theta^{(m)}}(H_{t-1} = h_{t-1}, H_t = h_t, O_{0:t} = o_{0:t}) \\
&= \mathbb{P}_{\theta^{(m)}}(O_{t+1:M} = o_{t+1:M} \mid H_t = h_t, O_t = o_t)\mathbb{P}_{\theta^{(m)}}(H_{t-1} = h_{t-1}, H_t = h_t, O_{0:t} = o_{0:t}) \\
&= \beta_t^{(m)}(h_t)T_O^{(m)}(o_t \mid h_t, h_{t-1}, o_{t-1})\mathbb{P}_{\theta^{(m)}}(H_{t-1} = h_{t-1}, H_t = h_t, O_{0:t-1} = o_{0:t-1}) \\
&= \beta_t^{(m)}(h_t)T_O^{(m)}(o_t \mid h_t, h_{t-1}, o_{t-1})T_H^{(m)}(h_t \mid h_{t-1}, o_{t-1})\alpha_{t-1}^{(m)}(h_{t-1})
\end{aligned}$$

Recursive computation of the $\alpha_t^{(m)}$s and $\beta(m)_t s$

The quantities αs can be computed by a forward recurrence and the quantities βs by a backward recurrence, as follows: $\forall 1 \leq t \leq M,\ \forall h_t \in \Omega_H$

$$\alpha^{(m)}(h_t) = \sum_{h_{t-1}} T_O^{(m)}(o_t \mid h_t, h_{t-1}, o_{t-1}) T_H^{(m)}(h_t \mid h_{t-1}, o_{t-1}) \alpha_{t-1}^{(m)}(h_{t-1}),$$

with $\alpha_0^{(m)}(h_0) = \pi^{(m)}(h_0, o_0)$. And, $\forall 0 \leq t < M,\ \forall h_t \in \Omega_H$

$$\beta_t^{(m)}(h_t) = \sum_{h_{t+1}} \beta_{t+1}^{(m)}(h_{t+1}) T_O^{(m)}(o_{t+1} \mid h_{t+1}, h_t, o_t) T_H^{(m)}(h_{t+1} \mid h_t, o_t),$$

with $\beta_M^{(m)}(h_M) = 1$.

Appendix B. EM algorithm for a interacting PO-DBN with interaction structure of Figure 6

We present now the formulas of the EM algorithm for the interacting PO-DBN associated with the structure of Figure 6 presenting an interaction from observations towards hidden states. The formulas below are also presented in Le Coz et al. (2019). Here we have adapted the notations to that of our article, and we consider the case where $N_c = \{1, \dots, C\}$. The complete likelihood for this model, denoted by L_{comp}, is given by:

$$\begin{aligned} L_{\text{comp}} &= \mathbb{P}_\theta(H_{1:C,0:M} = h_{1:C,0:M}, O_{1:C,0:M} = o_{1:C,0:M}) \\ &= \prod_{c=1}^{C} \left[\pi(h_{c,0}) T_O(o_{c,0} \mid h_{c,0}) \prod_{t=1}^{M} T_H(h_{c,t} \mid o_{1:C,t-1}, h_{c,t-1}) T_O(o_{c,t} \mid h_{c,t}) \right]. \end{aligned}$$

Appendix B.1. Expression of the intermediate quantity

The intermediate quantity $Q(\theta|\theta^{(m)})$, can be decomposed into three terms, one depending on the initial distribution π, another depending on the transition matrix T_H and the last one on T_O.

$$\begin{aligned} Q(\theta|\theta^{(m)}) &= \mathbb{E}_{\theta^{(m)}} \left[\ln(L_{\text{comp}}) | O_{1:C,0:M} = o_{1:C,0:M} \right] \\ &= \sum_{c=1}^{C} \sum_{h_{c,0} \in \Omega_H} \ln\left(\pi(h_{c,0})\right) \times \mathbb{P}_{\theta^{(m)}}(H_{c,0} = h_{c,0} | O_{1:C,0:M} = o_{1:C,0:M}) \\ &+ \sum_{c=1}^{C} \sum_{t=1}^{M} \sum_{(h_{c,t}, h_{c,t-1}) \in \Omega_H^2} \ln\left(T_H(h_{c,t} \mid o_{1:C,t-1}, h_{c,t-1})\right) \\ &\times \mathbb{P}_{\theta^{(m)}}(H_{c,t-1} = h_{c,t-1}, H_{c,t} = h_{c,t} | O_{1:C,0:M} = o_{1:C,0:M}) \\ &+ \sum_{c=1}^{C} \sum_{t=0}^{M} \sum_{h_{c,t} \in \Omega_H} \ln\left(T_O(o_{c,t} \mid h_{c,t})\right) \times \mathbb{P}_{\theta^{(m)}}(H_{c,t} = h_{c,t} | O_{1:C,0:M} = o_{1:C,0:M}). \end{aligned}$$

Appendix B.2. E step

In the E step, we calculate the marginal distributions involved in the expression of the intermediate quantity $Q(\theta|\theta^{(m)})$. They are

- $\forall 0 \leq t \leq M, \forall c \in \{1, ..., C\}, \forall h_{c,t} \in \Omega_H,$

$$\rho_{c,t}^{(m)}(h_{c,t}) = \mathbb{P}_{\theta^{(m)}}(H_{c,t} = h_{c,t} | O_{1:C,0:M} = o_{1:C,0:M});$$

- $\forall 1 \leq t \leq M, \forall c \in \{1, ..., C\}, \forall (h_{c,t-1}, h_{c,t}) \in \Omega_H^2$,

  $\xi_{c,t}^{(m)}(h_{c,t-1}, h_{c,t}) = \mathbb{P}_{\theta^{(m)}}(H_{c,t-1} = h_{c,t-1}, H_{c,t} = h_{c,t} | O_{1:C,0:M} = o_{1:C,0:M})$.

They will be computed via the two following auxiliary variables:

- $\forall 0 \leq t \leq M, \forall c \in \{1, ..., C\}, \forall h_{c,t} \in \Omega_H$,

  $$\alpha_{c,t}^{(m)}(h_{c,t}) = \mathbb{P}_{\theta^{(m)}}(O_{1:C,0:t} = o_{1:C,0:t}, H_{c,t} = h_{c,t});$$

- $\forall 0 \leq t < M, \forall c \in \{1, ..., C\}, \forall h_{c,t} \in \Omega_H$,

  $$\beta_{c,t}^{(m)}(h_{c,t}) = \mathbb{P}_{\theta^{(m)}}(O_{1:C,t+1:M} = o_{1:C,t+1:M} | H_{c,t} = h_{c,t}, O_{1:C,t} = o_{1:C,t}).$$

Computation of $\rho_{c,t}^{(m)}$ and $\xi_{c,t}^{(m)}$ using $\alpha_{c,t}^{(m)}$ and $\beta_{c,t}^{(m)}$

The quantities $\rho_{c,t}^{(m)}(h_{c,t})$ and $\xi_{c,t}^{(m)}(h_{c,t-1}, h_{c,t})$ can be expressed as follows:

$$\rho_{c,t}^{(m)}(h_{c,t}) = \frac{\alpha_{c,t}^{(m)}(h_{c,t})\beta_{c,t}^{(m)}(h_{c,t})}{\sum\limits_{h_{c,t} \in \Omega_H} \alpha_{c,t}^{(m)}(h_{c,t})\beta_{c,t}^{(m)}(h_{c,t})},$$

and

$$\xi_{c,t}^{(m)}(h_{c,t-1}, h_{c,t}) = \frac{\beta_{c,t}^{(m)}(h_{c,t}) T_H^{(m)}(h_{c,t} \mid o_{1:C,t-1}, h_{c,t-1}) T_O^{(m)}(o_{c,t} \mid h_{c,t}) \alpha_{c,t-1}^{(m)}(h_{c,t-1})}{\sum\limits_{h_{c,t} \in \Omega_H} \alpha_{c,t}^{(m)}(h_{c,t})\beta_{c,t}^{(m)}(h_{c,t})}.$$

Recursive computation of the $\alpha_{c,t}^{(m)}$s and $\beta_{c,t}^{(m)}$s

In a forward algorithm, we compute $\alpha_{c,t}^{(m)}(h_{c,t})$ by using the following recurrence formula:

$\forall 1 \leq t \leq M, \forall c \in \{1, ..., C\}, \forall h_{c,t} \in \Omega_H$,

$$\alpha_{c,t}^{(m)}(h_{c,t}) \propto \sum_{h_{c,t-1} \in \Omega_H} \alpha_{c,t-1}^{(m)}(h_{c,t-1}) T_H^{(m)}(h_{c,t} \mid o_{1:C,t-1}, h_{c,t-1}) T_O^{(m)}(o_{c,t} \mid h_{c,t}),$$

where $\alpha_{c,0}^{(m)}(h_{c,0}) = \pi^{(m)}(h_{c,0}) T_O^{(m)}(o_{c,0} \mid h_{c,0})$.

In a backward algorithm, we compute $\beta_{c,t}^{(m)}(h_{c,t})$ using the following recurrence formula:

$\forall 0 \leq t < M, \forall c \in \{1, ..., C\}, \forall h_{c,t} \in \Omega_H,$

$$\beta_{c,t}^{(m)}(h_{c,t}) \propto \sum_{h_{c,t+1} \in \Omega_H} \beta_{c,t+1}^{(m)}(h_{c,t+1}) T_O^{(m)}(o_{c,t+1} \mid h_{c,t+1}) T_H^{(m)}(h_{c,t+1} \mid o_{1:C,t}, h_{c,t}),$$

where $\beta_{c,M}^{(m)}(h_{c,M}) = 1$.

Here, as opposed to the recursive formulas for a HMM or for the PO-DBN of Appendix A, there is no equality: equality is up to a constant. In consequence the forward and backward algorithm are performed on auxiliary variables proportional to the original ones. The demonstration is available in Le Coz et al. (2019).

Appendix B.3. M step

In step M, the aim is to solve $\theta^{(m+1)} = \arg\max_{\theta} Q(\theta|\theta^{(m)})$, under the following constraints:

- $\sum_{h_{c,0} \in \Omega_H} \pi(h_{c,0}) = 1;$
- $\sum_{h_{c,t} \in \Omega_H} T_H(h_{c,t} \mid o_{1:C,t-1}, h_{c,t-1}) = 1;$
- $\sum_{o_{c,t} \in \Omega_O} T_O(o_{c,t} \mid h_{c,t}) = 1.$

Using the Lagragian method to take into account these constraints, we can derive the update formulas. We recall that notation $o_{c,t}$ or $o_{1:C,t-1}$ denotes the values of the corresponding random variables observed in the data. They are fixed for a given estimation problem. We obtain:

$\forall y_{1:C} \in \Omega_O^C, \forall x' \in \Omega_H, \forall x \in \Omega_H,$

$$T_H^{(m+1)}(x' \mid y_{1:C}, x) = \frac{\sum_{c=1}^{C} \sum_{t=1}^{M} \xi_{c,t}^{(m)}(x, x') \mathbb{1}_{(y_{1:C} = o_{1:C,t-1})}}{\sum_{x'' \in \Omega_H} \sum_{c=1}^{C} \sum_{t=1}^{M} \xi_{c,t}^{(m)}(x, x'') \mathbb{1}_{(y_{1:C} = o_{1:C,t-1})}},$$

$\forall x \in \Omega_H, \forall y \in \Omega_O,$

$$T_O^{(m+1)}(y \mid x) = \frac{\sum_{c=1}^{C} \sum_{t=0}^{M} \rho_{c,t}^{(m)}(x) \mathbb{1}_{(y=o_{c,t})}}{\sum_{x' \in \Omega_H} \sum_{c=1}^{C} \sum_{t=0}^{M} \rho_{c,t}^{(m)}(x') \mathbb{1}_{(y=o_{c,t})}},$$

and $\forall x \in \Omega_H$,

$$\pi^{(m+1)}(x) = \frac{\sum_{c=1}^{C} \rho_{c,0}(x)}{\sum_{x' \in \Omega_H} \sum_{c=1}^{C} \rho_{c,0}(x')}.$$

Appendix C. EM algorithm for a interacting PO-DBN with interaction structure of Figure 11

We present now the formulas of the EM algorithm for the interacting PO-DBN associated with the structure of Figure 11 presenting an interaction from observations towards observations. The complete likelihood, denoted by L_{comp}, is given by.

$$\begin{aligned} L_{\text{comp}} &= \mathbb{P}_\theta(H_{1:C,0:M} = h_{1:C,0:M}, O_{1:C,0:M} = o_{1:C,0:M}) \\ &= \prod_{c=1}^{C} \left[\pi(o_{c,0}) T_H(h_{c,0} \mid o_{c,0}) \prod_{t=1}^{M} T_H(h_{c,t} \mid o_{c,t}) T_O(o_{c,t} \mid o_{1:C,t-1}, h_{c,t-1}) \right]. \end{aligned}$$

Appendix C.1. Expression of the intermediate quantity

The intermediate quantity $Q(\theta|\theta^{(m)})$ can be decomposed into two terms, one depending on the transition matrix T_H and the last one depending on T_O.

$$\begin{aligned} Q(\theta|\theta^{(m)}) &= \mathbb{E}_{\theta^{(m)}} \left[\ln L_{\text{comp}} | O_{1:C,0:M} = o_{1:C,0:M} \right] \\ &+ \sum_{c=1}^{C} \sum_{t=0}^{M} \sum_{h_{c,t} \in \Omega_H} \ln \left(T_H(h_{c,t} \mid o_{c,t}) \right) \mathbb{P}_{\theta^{(m)}}(H_{c,t} = h_{c,t} | O_{1:C,0:M} = o_{1:C,0:M}) \\ &+ \sum_{c=1}^{C} \sum_{t=1}^{M} \sum_{h_{c,t-1} \in \Omega_H} \ln \left(T_O(o_{c,t} \mid o_{1:C,t-1}, h_{c,t-1}) \right) \mathbb{P}_{\theta^{(m)}}(H_{c,t-1} = h_{c,t-1} | O_{1:C,0:M} = o_{1:C,0:M}) \\ &+ K. \end{aligned}$$

where K is a constant, independent of θ.

Appendix C.2. E step

In the E step, we calculate the marginal distributions involved in the expression of the intermediate quantity $Q(\theta|\theta^{(m)})$. They are, $\forall 0 \le t \le M, \forall c \in \{1, ..., C\}, \forall h_{c,t} \in \Omega_H$,

$$\rho_{c,t}^{(m)}(h_{c,t}) = \mathbb{P}_{\theta^{(m)}}(H_{c,t} = h_t | O_{1:C,0:M} = o_{1:C,0:M}).$$

Note that there is no auxiliary variable similar to the $\xi_{c,t}$ that is computed in Appendix B since in the graphical representation of Figure 11 there is no arc from $h_{c,t-1}$ to $h_{c,t}$.

The quantities $\rho_{c,t}^{(m)}(h_{c,t})$ are computed via the two following auxiliary variables:

- $\forall 0 \leq t \leq M, \forall c \in \{1, ..., C\}, \forall h_{c,t} \in \Omega_H$,
$$\alpha_{c,t}^{(m)}(h_{c,t}) = \mathbb{P}_{\theta^{(m)}}(O_{1:C,0:t} = o_{1:C,0:t}, H_{c,t} = h_{c,t});$$
- $\forall 0 \leq t < M, \forall c \in \{1, ..., C\}, \forall h_{c,t} \in \Omega_H$,
$$\beta_{c,t}^{(m)}(h_{c,t}) = \mathbb{P}_{\theta^{(m)}}(O_{1:C,t+1:M} = o_{c,t+1:M} | H_{c,t} = h_{c,t}, O_{1:C,t} = o_{1:C,t}).$$

Computation of $\rho_{c,t}^{(m)}$ using $\alpha_{c,t}^{(m)}$ and $\beta_{c,t}^{(m)}$

The quantities $\rho_{c,t}^{(m)}(h_{c,t})$ can be expressed as follows:

$$\rho_{c,t}^{(m)}(h_{c,t}) = \frac{\alpha_{c,t}^{(m)}(h_{c,t})\beta_{c,t}^{(m)}(h_{c,t})}{\sum\limits_{h_{c,t} \in \Omega_H} \alpha_{c,t}^{(m)}(h_{c,t})\beta_{c,t}^{(m)}(h_{c,t})}$$

Recursive computation of the $\alpha_{c,t}^{(m)}$s and $\beta_{c,t}^{(m)}$s

In a forward algorithm we compute $\alpha_{c,t}^{(m)}(h_{t,c})$ by using the following recurrence formula:

$$\forall 1 \leq t \leq M, \forall c \in \{1, ..., C\}, \forall h_{c,t} \in \Omega_H,$$
$$\alpha_{c,t}^{(m)}(h_{c,t}) \propto \sum_{h_{c,t-1} \in \Omega_H} \alpha_{c,t-1}^{(m)}(h_{c,t-1}) T_H^{(m)}(h_{c,t} \mid o_{c,t}) T_O^{(m)}(o_{c,t} \mid o_{1:C,t-1}, h_{c,t-1}),$$

where $\alpha_{c,0}^{(m)}(h_{c,0}) = T_O^{(m)}(h_{c,0} \mid o_{c,0})\pi(o_{c,0})$. The initial distribution $\pi(o_{c,0})$ is assumed to be known.

In a backward algorithm, we compute $\beta_{c,t}^{(m)}(h_{c,t})$ using the following recurrence formula:

$$\forall 0 \leq t < M, \forall c \in \{1, ..., C\}, \forall h_{c,t} \in \Omega_H,$$
$$\beta_{c,t}^{(m)}(h_{c,t}) \propto \sum_{h_{c,t+1} \in \Omega_H} \beta_{c,t+1}^{(m)}(h_{c,t+1}) T_H^{(m)}(h_{c,t+1} \mid o_{c,t+1}) T_O^{(m)}(o_{c,t+1} \mid o_{1:C,t}, h_{c,t}),$$

where $\beta_{c,M}^{(m)}(h_{c,M}) = 1$.

Similarly to EM for the interacting PO-DBN of Appendix B, the recursive formulas are up to a constant and in practice the forward-backward algorithm is performed on auxiliary variables proportional to the original ones.

Appendix C.3. M step

In step M, the aim is to solve $\theta^{(m+1)} = \arg\max_{\theta} Q(\theta|\theta^{(m)})$, under the following constraints:

- $\sum\limits_{h_{c,t} \in \Omega_H} T_H(h_{c,t} \mid o_{c,t}) = 1$;
- $\sum\limits_{o_{c,t} \in \Omega_O} T_O(o_{c,t} \mid o_{1:C,t-1}, h_{c,t-1}) = 1$.

Using the Lagragian method to take into account these constraints, we can derive the update formulas. We recall that notation $o_{c,t}$ or $o_{1:C,t-1}$ denotes the values of the corresponding random variables observed in the data. They are fixed for a given estimation problem. We obtain:

$\forall y \in \Omega_O, \forall x \in \Omega_H$,

$$T_H^{(m+1)}(x \mid y) = \frac{\sum\limits_{c=1}^{C} \sum\limits_{t=0}^{M} \rho_{c,t}^{(m)}(x) \mathbb{1}_{(y=o_{c,t})}}{\sum\limits_{x' \in \Omega_H} \sum\limits_{c=1}^{C} \sum\limits_{t=1}^{M} \rho_{c,t}^{(m)}(x')\ \mathbb{1}_{(y=o_{c,t})}},$$

$\forall x \in \Omega_H, \forall y \in \Omega_O, \forall y'_{1:C} \in \Omega_O^C$,

$$T_O^{(m+1)}(y \mid, y'_{1:C}, x) = \frac{\sum\limits_{c=1}^{C} \sum\limits_{t=1}^{M} \rho_{c,t-1}^{(m)}(x) \mathbb{1}_{(y=o_{c,t})} \mathbb{1}_{(y'_{1:C}=o_{1:C,t-1})}}{\sum\limits_{x' \in \Omega_H} \sum\limits_{c=1}^{C} \sum\limits_{t=1}^{M} \rho_{c,t-1}^{(m)}(x') \mathbb{1}_{(y=o_{c,t})} \mathbb{1}_{(y'_{1:C}=o_{1:C,t-1})}}.$$

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