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Continuous limits of large plant-pollinator random networks and some applications*

Sylvain Billiard[†], H el ene Leman[‡], Thomas Rey[§] and Viet Chi Tran[¶]

January 13, 2022

This work is dedicated to S. M el eard and has been presented at her 60th birthday’s conference (2018).

Abstract

We study a stochastic individual-based model of interacting plant and pollinator species through a bipartite graph: each species is a node of the graph, an edge representing interactions between a pair of species. The dynamics of the system depends on the between- and within-species interactions: pollination by insects increases plant reproduction rate but has a cost which can increase plant death rate, depending on pollinators density. Pollinators reproduction is increased by the resources harvested on plants. Each species is characterized by a trait corresponding to its degree of generalism. This trait determines the structure of the interactions graph and the quantity of resources exchanged between species. Our model includes in particular nested or modular networks. Deterministic approximations of the stochastic measure-valued process by systems of ordinary differential equations or integro-differential equations are established and studied, when the population is large or when the graph is dense and can be replaced with a graphon. The long-time behaviors of these limits are studied and central limit theorems are established to quantify the difference between the discrete stochastic individual-based model and the deterministic approximations. Finally, studying the continuous limits of the interaction network and the resulting PDEs, we show that nested plant-pollinator communities are expected to collapse towards a coexistence between a single pair of species of plants and pollinators.

Keywords: ecological mutualistic community, birth and death process, interacting particles, limit theorem, kinetic limit, graphon, integro-differential equation, stationary solution.

AMS Codes: 92D40, 92D25, 05C90, 60J80, 60F17, 47G20.

Communities of interacting species, such as plants and pollinators, are systems characterized by a large diversity of both their components (dozens of species are typically involved) and the topology of their interaction networks [19]. How does the structure of the interaction networks affect the dynamics of species and the stability of communities is a common and long-standing question in the ecological literature (*e.g.* [40, 46, 38]). Addressing this question is challenging because the number of species in a community is large, and so is the number of possible edges. Describing ecological networks from

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observations thus needs much effort, without being ensured that the inferred networks are representative of the studied communities (interactions can indeed depend on space and time, but also on the abundances of the species which makes them harder or not to observe). From a theoretical point of view, the study of the dynamics and stability of communities most often relies either on the numerical analysis of large systems of ordinary differential equations, or on the study of the system near equilibrium in simplified communities (see *e.g.* [40, 41, 7, 15, 18, 26, 44, 45, 46, 38] and [2] for a review). This makes difficult the identification of general properties of ecological communities. Overall, despite being more than 50 years old, the question of how correctly modelling ecological networks and communities is still challenging. In this paper, we develop a new theoretical framework that could help in addressing the previous questions, based on the fact that networks are hierarchically structured. Interactions can indeed be considered at different scales: between individuals, between species or at the level of the whole community [29]. At all scales however, several studies showed evidence that the structure of the interaction networks is due to traits variation between or within species' such as size, symmetry or time of activity *e.g.* [16, 48, 47, 4]. Starting from a stochastic individual-based model, our goal is to provide simplifications of an ecological network deriving the continuous limits of both the population sizes and the interaction graph structured by a trait.

We focus on a particular ecological community: plant and pollinator species. The interactions between individuals of each species are modelled by a bipartite random network. Interactions affect the demographic rates of plant and pollinator individuals because of resources exchanges. On the one hand, plants benefit from pollinators visitations to increase their reproduction rate. On the other hand, pollinators consume nectar, leaves, pollen, etc. which increases their reproduction or survival rates. However, producing such resources is costly for the plants, which can negatively affect plant demographic rates, proportionally to pollinators density [30, 32].

The interaction rates between plant and pollinator individuals are modelled by a random graph where the species are the nodes of the graph. The existence of an edge between a plant and a pollinator species indicates that individuals of these two species can interact. The resulting graph is bipartite, since there is by definition no direct edges between insect species or between plant species. The topology of the graph depends on a trait that represents the degree of generalism of the species. Any pair of plant-pollinator species is connected independently from the other pairs with a probability that depends on the traits of the two considered species. This simple model corresponds to Erdős-Rényi graphs, where the probability of connection is the same for every pairs. Such a model can also generate particular structures such as nested or modular graphs which are commonly found in ecological networks [46, 29].

In Section 1, we present the stochastic individual based model, how the random interactions graph is modelled, and how interactions affect demographic rates. Considering large populations but with a fixed number of species, we show in Section 2 how the dynamics can be approximated by a system of ODEs (close to the ones commonly studied in the ecological literature). The fluctuations between the approximated deterministic limit and the stochastic individual based process are established.

In Section 3, we derive a continuous approximation of the random graph when the numbers of plant and pollinator species, say n and m , are also large. When the graph is dense (*i.e.* the order of the number of edges is in $O(n \times m)$), the complex random network can be replaced by a continuous object, namely a graphon [14, 39]. In this case, the high-dimensional system of ODEs can be replaced by two partial integro-differential equations: one for the plants and the other for the pollinators. The latter equations fall into the broader class of kinetic equations, the most well known and studied being the seminal Boltzmann and Vlasov equations. The use of such mesoscopic scale, namely intermediate between a microscopic agent based approach [25], and an averaged macroscopic one (over space) such as [42], is not a novelty for modeling competitive interactions between species [21, 35, 9, 10], *i.e.* with a large but not infinite number of species with trait structure. Indeed, such approach can be traced back as early as the book of [43] for the mathematical modeling of evolutionary ecology. However, the kinetic treatment of large random networks and their approximations by integro-differential equations

is new to our knowledge. Finally, in Section 4, the large-time behaviors of the ODE system or of the integro-differential equations are studied and simulations are produced to explore several situations.

1 Stochastic individual based model with species interactions

In this section, we introduce a stochastic individual-based model of plant and pollinator species. In this model, the number of species and the number of individuals in each species are finite. Each species is defined by a trait, for instance a morphological or functional trait, which determines its degree of generalism. This trait shapes the interaction network: generalist plant species can be visited by a large number of insect species and generalist pollinator species can visit a large number of plant species. Even though several coevolved traits can be considered in the model (*e.g.* orchids have flower with a particular morphology, color, phenology, etc.), we will focus on a single trait for the sake of simplicity. The dynamics is driven by the births and deaths of individuals at random times that depend 1) on their position in the plant-pollinator network, determined by their species' trait, 2) by the weights of the interactions between pairs of species, and 3) by the population sizes of the species. The evolution of these interacting populations is described by a stochastic differential equation (SDE) involving Poisson point measures and an acceptance-rejection algorithm as in the Gillespie algorithm [27] (see Fournier and Méléard [25] for the mathematical formulation of the Gillespie algorithm by mean of SDEs in cases with interactions).

1.1 Description of the plant-pollinator community

We suppose n and m plant and pollinator species, respectively, which are characterized by some traits $x \in [0, 1]$ and $y \in [0, 1]$. For $i \in \{1, \dots, n\} = \llbracket 1, n \rrbracket$ and $j \in \{1, \dots, m\} = \llbracket 1, m \rrbracket$, we respectively denote x^i and y^j the trait of the plant species i and of the pollinator species j . These traits can represent for instance their degree of generalism, *i.e.* their tendency to interact with a large number of other species: a species is considered as generalist when its trait (x^i or y^j) is close to 1, or specialist when it is close to 0.

1.2 The plant-pollinator interaction network as a bipartite random graph

Plants and pollinators interact through a bipartite network where each species is a vertex, and an interaction is an edge. We denote $i \sim j$ or $j \sim i$ when individuals of the plant species i can interact with individuals of the pollinator species j . There are no edges between two plant or two pollinator species because the network only represents interactions between plants and pollinators. Yet, when specifying the birth and death rates, competition kernels within and between plant species, and within and between pollinator species, will be introduced in the model.

The bipartite graph can be represented by an $n \times m$ adjacency matrix $G^{n,m}$, with

$$G_{ij}^{n,m} = \begin{cases} 1 & \text{if the pollinator species } j \text{ can interact with the plant species } i, \\ 0 & \text{otherwise.} \end{cases}$$

Regarding the structure of the network, we consider a stochastic bipartite graph that generalizes the Erdős-Rényi random graph ([13, 22, 20]). We assume that the probability $\phi(x^i, y^j)$ there is an edge $i \sim j$ between plant species i and pollinator species j only depends on the traits x^i and y^j of these two species. Different pairs are supposed to be connected independently, the interaction graph is thus built such that:

Assumption 1.1. *Conditionally on $(x^i, y^j)_{i,j \in \llbracket 1, n \rrbracket \times \llbracket 1, m \rrbracket}$, the random variables $(G_{ij}^{n,m})_{(i,j) \in \llbracket 1, n \rrbracket \times \llbracket 1, m \rrbracket}$ are independent and distributed as Bernoulli random variables with parameters $(\phi(x^i, y^j))_{(i,j) \in \llbracket 1, n \rrbracket \times \llbracket 1, m \rrbracket}$.*

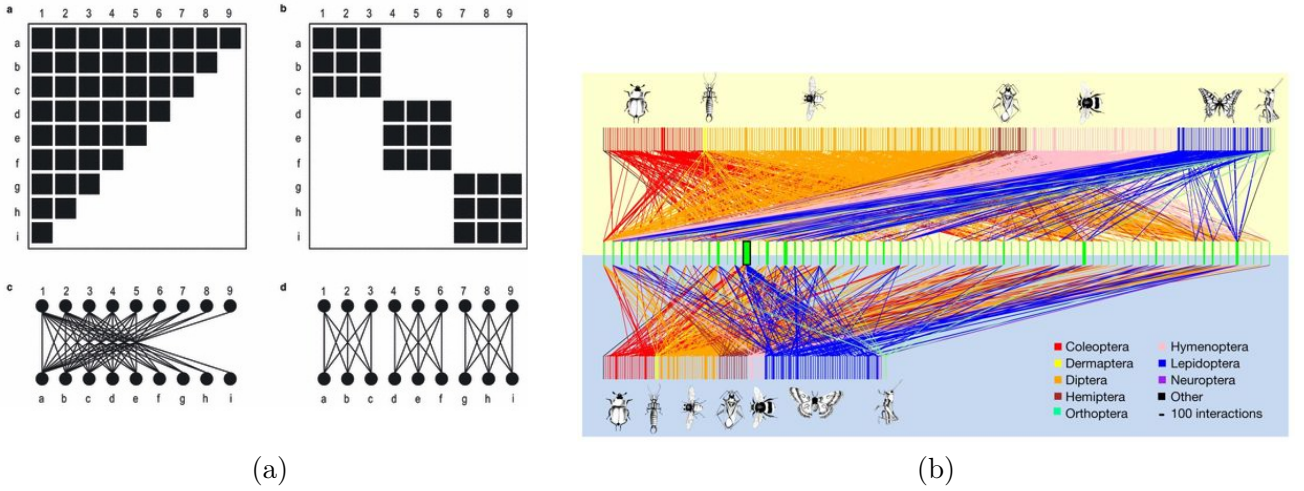


Figure 1: (a): Nested (left) or modular (right) bipartite networks, from Fontaine et al. [24]. (b) Pollination network for diurnal and nocturnal insect species, from Knop et al. [37]

Example 1.2. Case 1. If there exists $\phi_0 \in (0, 1)$ such that for all i and j , $\phi(x^i, y^j) = \phi_0$, then the stochastic network is a bipartite Erdős-Rényi graph. The degrees of nodes representing pollinators (resp. plants), i.e. the numbers of edges, do not depend on the species traits. Degrees are thus independent binomial r.v. with parameters (m, ϕ_0) (resp. (n, ϕ_0)) and the total number of edges follows a binomial distribution with parameters (nm, ϕ_0) .

Case 2. The probability of an edge $i \sim j$ between two species i and j depends on their degree of generalism, for instance by assuming:

$$\phi(x^i, y^j) = x^i y^j. \quad (1.1)$$

Under this assumption, two generalist species (x^i and y^j close to 1) have a higher probability to be connected than two specialist species (x^i and y^j close to 0). Nested graphs result from such an assumption (Fig. 1 a-left).

Case 3. When plant and pollinator species can be structured in groups, for instance because of pollination syndrome or spatio-temporal segregation, the probability of an edge $i \sim j$ $\phi(x^i, y^j) = \phi_{IJ}$ depends only on classes $I \ni i$ and $J \ni j$. The resulting random graph is a Stochastic Block Model (SBM [33], see e.g. [1] for a review), often called modular networks in community ecology (Fig. 1 a-right).

If species i and j interact, i.e. if $G_{ij}^{n,m} = 1$, we denote by $c_{ij}^{n,m}$ the weight of the interaction $i \sim j$. The quantity $c_{ij}^{n,m}$ describes the intensity and frequency of the relation between the pollinator species j and the plant species i . From the point of view of the plant, $c_{ij}^{n,m}$ can be interpreted as a measure of the pollination services received from the pollinators. From the point of view of the pollinators, $c_{ij}^{n,m}$ measures the quantity and quality of nutrients collected from the plants.

Assumption 1.3. For all $n, m \in \mathbb{N}^2$, conditionally on $(x^i, y^j)_{(i,j) \in \llbracket 1, n \rrbracket \times \llbracket 1, m \rrbracket}$, $(c_{ij}^{n,m})_{(i,j) \in \llbracket 1, n \rrbracket \times \llbracket 1, m \rrbracket}$ is assumed to be a sequence of independent random variables such that

- the expected values only depend on the traits of the plants and pollinators through a function $c^{n,m} : [0, 1]^2 \rightarrow \mathbb{R}$: for all $i \in \llbracket 1, n \rrbracket$, $j \in \llbracket 1, m \rrbracket$:

$$\mathbb{E}_{x,y} \left[c_{ij}^{n,m} \right] = c^{n,m}(x^i, y^j), \quad (1.2)$$

with $\mathbb{E}_{x,y}[A] = \mathbb{E}[A | (x^i, y^j)_{(i,j) \in \llbracket 1, n \rrbracket \times \llbracket 1, m \rrbracket}]$,

- and the variances decrease with n and m such that:

$$V_{max} := \sup_{n \in \mathbb{N}, m \in \mathbb{N}} \sup_{(i,j) \in [1,n] \times [1,m]} \text{Var}_{x,y}((m+n)c_{i,j}^{n,m}) < \infty. \quad (1.3)$$

1.3 Stochastic dynamics of the plant-pollinator community

The dynamics of the plant and pollinator populations within the community is ruled by random point birth and death events. We assume that the size of the population of plants and pollinators is scaled by a factor $K > 0$, called the carrying capacity in ecology. This carrying capacity K is a measure of the size of the system, in other words, it controls the total abundance of the whole community that can be sustained by the environment. A continuous limit of the stochastic dynamics will be obtained when the species abundances tend to infinity, in other words when $K \rightarrow \infty$.

Given the scaling factor K , we denote $P_t^{K,i}$ and $A_t^{K,j}$ the size of the plant and pollinator species i and j at time t . The plant and pollinator populations at time t can be represented by the following point measures:

$$\mathbf{P}_t^{K,n,m}(dx) = \frac{1}{nK} \sum_{i=1}^n P_t^{K,i} \delta_{x^i}(dx), \quad \mathbf{A}_t^{K,n,m}(dy) = \frac{1}{mK} \sum_{j=1}^m A_t^{K,j} \delta_{y^j}(dy). \quad (1.4)$$

The interactions between plants and pollinators are characterized by an exchange of resources [32]. The quantity of resources gained by plants or pollinators R is modeled through a "mass-action model". At time t , in the population scaled by K , a single individual of the plant species i interacting with pollinator species j is supposed to gain a quantity of resources (here the pollination service) proportional to the abundance of pollinators $A_t^{K,j}/K$ weighted by the interaction efficiency $c_{ij}^{n,m}$, such that the total resource gained by a plant individual of species i through the pollination interactions is

$$R_t^{A,K,i} := \sum_{j \sim i} \frac{c_{ij}^{n,m} A_t^{K,j}}{K}. \quad (1.5)$$

Similarly, for a given pollinator of the species j , the resources gained from the interaction with the plant species at time t in the population parameterized by K is assumed to be:

$$R_t^{P,K,j} = \sum_{i \sim j} \frac{c_{ij}^{n,m} P_t^{K,i}}{K}. \quad (1.6)$$

The dynamics of the community is supposed to be governed by the birth and death rates of the plant and pollinator populations. We denote $b^P(R)$ and $b^A(R)$ the individual birth rate of plant and pollinator species, respectively, each depending on the quantity of resources exchanged R^P or R^A . Similarly, we denote $d^P(R)$ and $d^A(R)$ the individual death rates. Finally,

$$g^P(R) := b^P(R) - d^P(R) \quad \text{and} \quad g^A(R) := b^A(R) - d^A(R), \quad (1.7)$$

are the component of the growth rate due to the interactions between plants and pollinators.

The plants and pollinators dynamics are also assumed to be affected by logistic competition among plants and among pollinators (within and between species competition). We suppose that competition strength depends on the traits x and y . This can represent the fact that plants or pollinators with similar traits tend to share similar ecological niche, or phenology, etc. A plant with trait $x \in [0,1]$ suffers an additional death rate term due to competition such that

$$k \star \mathbf{P}_t^{K,n,m}(x) := \int_{[0,1]} k(x, x') d\mathbf{P}_t^{K,n,m}(dx') = \frac{1}{nK} \sum_{i=1}^n k(x, x^i) P_t^{K,i}, \quad (1.8)$$

where $k(x, x')$ quantifies the competition pressure exerted by another plant of trait x' . Similarly, a pollinator with trait $y' \in [0, 1]$ suffers an additional death rate due to competition with pollinators of trait y is

$$h \star \mathbf{A}_t^{K,n,m}(y) := \int_{[0,1]} h(y, y') d\mathbf{A}_t^{K,n,m}(dy') = \frac{1}{mK} \sum_{j=1}^m h(y, y^j) A_t^{K,j}, \quad (1.9)$$

where $h(y, y')$ quantifies the competition of individuals with trait y' on individuals with trait y .

The following assumptions on the functions involved in the model will be needed, both for modeling and mathematical purposes.

Assumption 1.4. (i) The birth rates b^P and b^A are assumed to be bounded on \mathbb{R}^+ by constants $M^P > 0$ and $M^A > 0$ respectively. Moreover, all the rate functions b^P , b^A , d^P and d^A are assumed to be locally Lipschitz continuous on $[0, \infty)$.

(ii) The competition kernels k and h are assumed to be continuous on $[0, 1]^2$.

1.4 Stochastic differential equations

Following works by Méléard and co-authors [25, 17], it is possible to describe the evolution of the population measures $(\mathbf{P}_t^{K,n,m}, \mathbf{A}_t^{K,n,m})_{t \in \mathbb{R}_+}$ defined in (1.4) by stochastic differential equations (SDEs) driven by Poisson point measures. Let us first present these SDEs and then explain their heuristic meaning.

Definition 1.5. Suppose that assumptions 1.1, 1.3 and 1.4 hold. Let $Q_B^P(ds, dk, d\theta)$, $Q_D^P(ds, dk, d\theta)$, $Q_B^A(ds, dk, d\theta)$ and $Q_D^A(ds, dk, d\theta)$ be Poisson point measures on $\mathbb{R}_+ \times E := \mathbb{R}_+ \times \llbracket 1, n \rrbracket \times \mathbb{R}_+$ with intensity measure $q(ds, dk, d\theta) = ds n(dk) d\theta$ where ds and $d\theta$ are Lebesgue measures on \mathbb{R}_+ and where $n(dk)$ is Lebesgue measure on $\mathbb{N}^* = \{1, 2, \dots\}$.

For $i \in \{1, \dots, n\}$ and $j \in \{1, \dots, m\}$, one has

$$\begin{aligned} P_t^{K,i} = & P_0^{K,i} + \int_0^t \int_E \mathbb{1}_{i=k} \mathbb{1}_{\theta \leq b^P(R_{s-}^{A,K,i})} P_{s-}^{K,i} Q_B^P(ds, dk, d\theta) \\ & - \int_0^t \int_E \mathbb{1}_{i=k} \mathbb{1}_{\theta \leq [d^P(R_{s-}^{A,K,i}) + k \star \mathbf{P}_{s-}^{K,n}(x^i)]} P_{s-}^{K,i} Q_D^P(ds, dk, d\theta) \end{aligned} \quad (1.10)$$

$$\begin{aligned} A_t^{K,j} = & A_0^{K,j} + \int_0^t \int_E \mathbb{1}_{j=k} \mathbb{1}_{\theta \leq b^A(R_{s-}^{P,K,j})} A_{s-}^{K,j} Q_B^A(ds, dk, d\theta) \\ & - \int_0^t \int_E \mathbb{1}_{j=k} \mathbb{1}_{\theta \leq [d^A(R_{s-}^{P,K,j}) + h \star \mathbf{A}_{s-}^{K,m}(y^j)]} A_{s-}^{K,j} Q_D^A(ds, dk, d\theta). \end{aligned} \quad (1.11)$$

The above SDEs correspond to the mathematical formulation of the individual-based simulations classically used in ecology and originated with Gillespie's algorithm [27, 28]. The Poisson point measures Q_B^P and Q_D^A (resp. Q_D^P and Q_B^A) give the random times of possible birth (resp. death) events. The indicators $\mathbb{1}_{i=k}$ or $\mathbb{1}_{j=k}$ in the integral ensure that the equations for $P^{K,i}$ or $A^{K,j}$ are indeed modified when the birth or death events affect the plant population i or pollinator population j . The indicators in θ correspond to an acceptance-rejection algorithm so that the birth and death times occur with the correct rates. Note that in these SDEs, the network is hidden in the definitions of the terms $R_s^{A,K,i}$ and $R_s^{P,K,j}$ (see (1.5) and (1.6)).

In order to approximate the individual-based model with ODEs or integro-differential equations, we can reformulate the SDEs (1.10) and (1.11) by expressing the processes $P^{K,i}$ and $A^{K,j}$ as semimartingales. The following proposition also states the existence and uniqueness of a solution to (1.10)-(1.11).

Proposition 1.6. *Consider here n , m and K fixed. Assume 1.4 and that*

$$\mathbb{E} \left[\langle \mathbf{P}_0^{K,n,m}, \mathbf{1} \rangle^2 + \langle \mathbf{A}_0^{K,n,m}, \mathbf{1} \rangle^2 \right] < +\infty,$$

then the processes defined by (1.10) and (1.11) are well defined on \mathbb{R} . Moreover, for all $T \geq 0$,

$$\mathbb{E} \left[\sup_{t \in [0, T]} \langle \mathbf{P}_t^{K,n,m}, \mathbf{1} \rangle^2 + \langle \mathbf{A}_t^{K,n,m}, \mathbf{1} \rangle^2 \right] < +\infty. \quad (1.12)$$

For any $f : [0, 1] \rightarrow \mathbb{R}$ measurable test function, we have:

$$\begin{aligned} \langle \mathbf{P}_t^{K,n,m}, f \rangle &= \frac{1}{n} \sum_{i=1}^n \frac{1}{K} P_t^{K,i} f(x^i) \\ &= \langle \mathbf{P}_0^{K,n,m}, f \rangle + \int_0^t \frac{1}{nK} \sum_{i=1}^n f(x^i) \left[g^P(R_{s-}^{A,K,i}) - k \star \mathbf{P}_s^{K,n,m}(x^i) \right] P_s^{K,i} ds \\ &\quad + \frac{1}{nK} \sum_{i=1}^n f(x^i) M_t^{K,i}, \end{aligned} \quad (1.13)$$

where $(M^{K,i})_{i \in \{1, \dots, n\}}$ are square integrable martingales with predictable quadratic variation processes:

$$\langle M^{K,i} \rangle_t = \int_0^t (b^P(R_s^{A,K,i}) + d^P(R_s^{A,K,i}) + k \star \mathbf{P}_s^{K,n,m}(x^i)) P_s^{K,i} ds. \quad (1.14)$$

A similar expression holds for the pollinator populations. For any $f : [0, 1] \rightarrow \mathbb{R}$ measurable test function, we have:

$$\begin{aligned} \langle \mathbf{A}_t^{K,n,m}, f \rangle &= \frac{1}{m} \sum_{j=1}^m \frac{1}{K} A_t^{K,j} f(y^j) \\ &= \langle \mathbf{A}_0^{K,n,m}, f \rangle + \int_0^t \frac{1}{mK} \sum_{j=1}^m f(y^j) \left[g^A(R_{s-}^{P,K,j}) - h \star \mathbf{A}_s^{K,n,m}(y^j) \right] A_s^{K,j} ds \\ &\quad + \frac{1}{mK} \sum_{j=1}^m f(y^j) M_t^{K,j}, \end{aligned} \quad (1.15)$$

where $(M^{K,j})_{j \in \{1, \dots, m\}}$ are square integrable martingales with predictable quadratic variation processes:

$$\langle M^{K,j} \rangle_t = \int_0^t (b^A(R_s^{P,K,j}) + d^A(R_s^{P,K,j}) + h \star \mathbf{A}_s^{K,n,m}(y^j)) A_s^{K,j} ds.$$

The proof follows from usual stochastic calculus with Poisson point processes (*e.g.* [34]), as developed in [6, 25] for example. We however give a sketch of proof in Appendix A.1.

Thus the processes $(\mathbf{P}_t^{K,n,m})_{t \in \mathbb{R}_+}$ and $(\mathbf{A}_t^{K,n,m})_{t \in \mathbb{R}_+}$ are well-defined in the set $\mathbb{D}(\mathbb{R}_+, \mathcal{M}_F([0, 1]))$ of right-continuous left-limited (càdlàg) processes with values in the set of finite measures on $[0, 1]$. The space $\mathcal{M}_F([0, 1])$ embedded with the weak topology is a Polish space and the set of càdlàg functions is embedded with the Skorokhod topology (*e.g.* [11]) which makes it Polish as well.

2 Community dynamics limit when abundances are large but the number of species is fixed

In this section, we consider the numbers of species n and m as fixed while the plant and pollinator populations size tend to $+\infty$.

2.1 Law of large numbers

Proposition 2.1. *We consider a sequence $(\mathbf{P}^{K,n,m}, \mathbf{A}^{K,n,m})_{K \in \mathbb{N}}$ of processes as in Definition 1.5, with initial conditions such that*

$$\sup_{K \in \mathbb{N}} \mathbb{E} \left[\langle \mathbf{P}_0^{K,n,m}, \mathbf{1} \rangle^3 + \langle \mathbf{A}_0^{K,n,m}, \mathbf{1} \rangle^3 \right] < +\infty, \quad (2.1)$$

and such that there exist $(\tilde{P}_0^1, \dots, \tilde{P}_0^n)$ and $(\tilde{A}_0^1, \dots, \tilde{A}_0^m)$ satisfying the following convergences almost surely:

$$\lim_{K \rightarrow +\infty} \frac{P_0^{K,i}}{K} = \tilde{P}_0^i, \quad \lim_{K \rightarrow +\infty} \frac{A_0^{K,j}}{K} = \tilde{A}_0^j.$$

Then, for all $T \geq 0$, the following convergence holds almost surely for all $i \in \llbracket 1, n \rrbracket$ and $j \in \llbracket 1, m \rrbracket$:

$$\lim_{K \rightarrow \infty} \sup_{t \leq T} \sup_{i,j} \left\{ \left| \frac{P_t^{K,i}}{K} - \tilde{P}_t^i \right|, \left| \frac{A_t^{K,j}}{K} - \tilde{A}_t^j \right| \right\} = 0, \quad (2.2)$$

where $(\tilde{P}_t^1, \dots, \tilde{P}_t^n)_{t \geq 0}$ and $(\tilde{A}_t^1, \dots, \tilde{A}_t^m)_{t \geq 0}$ are the unique solution of the system, which exists on \mathbb{R}^{n+m} :

$$\begin{aligned} \forall 1 \leq i \leq n, \quad \frac{d\tilde{P}_t^i}{dt} &= \left(g^P \left(\sum_{j \sim i} \tilde{R}_t^{A,ij} \right) - \frac{1}{n} \sum_{\ell=1}^n k(x^i, x^\ell) \tilde{P}_t^\ell \right) \tilde{P}_t^i \\ \forall 1 \leq j \leq m, \quad \frac{d\tilde{A}_t^j}{dt} &= \left(g^A \left(\sum_{i \sim j} \tilde{R}_t^{P,ij} \right) - \frac{1}{m} \sum_{\ell=1}^m h(y^j, y^\ell) \tilde{A}_t^\ell \right) \tilde{A}_t^j, \end{aligned} \quad (2.3)$$

where, for all $t \in \mathbb{R}^+$, $\tilde{R}_t^{P,ij} = c_{ij}^{n,m} \tilde{P}_t^i$ and $\tilde{R}_t^{A,ij} = c_{ij}^{n,m} \tilde{A}_t^j$.

Eq. (2.3) is similar to a classical Lotka-Volterra system applied to mutualistic interactions with competition. In our case, the species community is structured by the plants traits x^i and the pollinators traits y^j which determine the probability and strength of the interactions. In addition, how interactions translate into births and deaths (the so-called *numerical response* in ecological terms) is embedded in functions g^A and g^P (demographic growth) and k and h (competitive kernels). Those functions can take any form (see section 4 for some examples). As a consequence, Eqs. (2.3) can capture a large variety of ecological situations. In particular, many ODE models published in the ecological literature are special cases of Eqs. (2.3) (e.g. [46, 8, 38]). Our analysis thus shows that ODE models can be commonly seen as a limits of stochastic individual-based models as defined in Section 1.

Proof. Since the numbers n and m of species are supposed constant, working with the vector processes $(P_t^{K,i}, A_t^{K,j})_{i \in \llbracket 1, n \rrbracket, j \in \llbracket 1, m \rrbracket}$ with values in \mathbb{R}_+^{n+m} (and not the measure-valued processes) is here sufficient. Notice that under the assumption (2.1), we can obtain by computations similar to the Step 1 of the proof of Proposition 1.6 that:

$$\sup_{K \in \mathbb{N}} \mathbb{E} \left[\sup_{t \in [0, T]} \langle \mathbf{P}_t^{K,n,m}, \mathbf{1} \rangle^3 + \langle \mathbf{A}_t^{K,n,m}, \mathbf{1} \rangle^3 \right] < +\infty. \quad (2.4)$$

The global existence and uniqueness of solution to (2.3) can be proved by classical results for ordinary differential equations: it follows from the local boundedness and Lipschitz property of the functions on the right-hand side. Then this proposition is a direct application of Theorem 2.1 p.456 in the book by Ethier and Kurtz [23]. \blacksquare

As a consequence:

Corollary 2.2. *Under the assumptions of Proposition 2.1, and for any $T > 0$, the sequence of measure-valued processes $(\mathbf{P}^{K,n}, \mathbf{A}^{K,m})_{K \in \mathbb{N}}$ converges a.s. and uniformly in the Skorohod space $\mathbb{D}([0, T], \mathcal{M}_F([0, 1])^2)$ to the process $(\tilde{\mathbf{P}}^n, \tilde{\mathbf{A}}^m)$ defined by:*

$$\tilde{\mathbf{P}}_t^n(dx) = \frac{1}{n} \sum_{i=1}^n \tilde{P}_t^i \delta_{x^i}(dx), \quad \tilde{\mathbf{A}}_t^m(dy) = \frac{1}{m} \sum_{j=1}^m \tilde{A}_t^j \delta_{y^j}(dy).$$

In this corollary, the space $\mathcal{M}_F([0, 1])^2$ can be embedded with the total variation topology which is stronger than the weak topology: as n, m , the sequences (x^1, \dots, x^n) and (y^1, \dots, y^m) remain unchanged, all the measures are absolutely continuous with respect to the same counting measures $\sum_{i=1}^n \delta_{x^i}$ or $\sum_{j=1}^m \delta_{y^j}$. Also, the uniform convergence in the Skorohod space for any $T > 0$ yields the convergence for the Skorohod topology on \mathbb{R}_+ .

For the remainder, let us denote by $\Phi^{P,n,m} = (\Phi_1^{P,n,m}, \dots, \Phi_n^{P,n,m})$ and $\Phi^{A,n,m} = (\Phi_1^{A,n,m}, \dots, \Phi_m^{A,n,m})$ the applications from \mathbb{R}_+^{n+m} into \mathbb{R}^n and \mathbb{R}^m respectively such that (2.3) rewrites for all $i \in \{1, \dots, n\}$ and $j \in \{1, \dots, m\}$:

$$\frac{d\tilde{P}_t^i}{dt} = \Phi_i^{P,n,m}(\tilde{P}_t, \tilde{A}_t) \quad \text{and} \quad \frac{d\tilde{A}_t^j}{dt} = \Phi_j^{A,n,m}(\tilde{P}_t, \tilde{A}_t). \quad (2.5)$$

2.2 Central limit theorem

Let us introduce the fluctuation processes:

$$\eta_t^{K,P} = \sqrt{K} \begin{pmatrix} P_t^{K,1}/K - \tilde{P}_t^1 \\ \vdots \\ P_t^{K,n}/K - \tilde{P}_t^n \end{pmatrix}, \quad \text{and} \quad \eta_t^{K,A} = \sqrt{K} \begin{pmatrix} A_t^{K,1}/K - \tilde{A}_t^1 \\ \vdots \\ A_t^{K,m}/K - \tilde{A}_t^m \end{pmatrix}. \quad (2.6)$$

Proposition 2.3. *Consider the process of Definition 1.5, assume that the functions b^A, b^P, d^A and d^P are of class \mathcal{C}^1 , that (2.1) holds, and that the initial conditions $(\eta_0^{K,P}, \eta_0^{K,A})_{K \geq 0}$ converge in distribution towards a deterministic vector $(\tilde{\eta}_0^P, \tilde{\eta}_0^A)$ when $K \rightarrow +\infty$. Under the same assumptions as Proposition 2.1, one has*

$$(\eta_t^{K,P}, \eta_t^{K,A})_{t \geq 0} \xrightarrow{K \rightarrow \infty} (\tilde{\eta}_t^P, \tilde{\eta}_t^A)_{t \geq 0},$$

where the converge holds in law in the Skorohod space $\mathbb{D}(\mathbb{R}_+, \mathbb{R}^{n+m})$ and where the processes $(\tilde{\eta}_t^P, \tilde{\eta}_t^A) = (\tilde{\eta}_t^{P,i}, \tilde{\eta}_t^{A,j})_{i \in \{1, \dots, n\}, j \in \{1, \dots, m\}}$ are solutions of the following SDEs driven by $n + m$ independent standard Brownian motions $(W^{P,i}, W^{A,j})_{1 \leq i \leq n, 1 \leq j \leq m}$ in \mathbb{R} :

for all $1 \leq i \leq n$ and $1 \leq j \leq m$,

$$\begin{aligned} \tilde{\eta}_t^{P,i} &= \tilde{\eta}_0^{P,i} + \int_0^t \sqrt{\left(b^P(\tilde{R}_s^{A,i}) + d^P(\tilde{R}_s^{A,i}) + \frac{1}{n} \sum_{\ell=1}^n k(x^i, x^\ell) \tilde{P}_s^\ell \right)} \tilde{P}_s^i dW_s^{P,i} \\ &\quad + \int_0^t \left[\sum_{\ell=1}^n \frac{\partial \Phi_i^{P,n,m}}{\partial p^\ell}(\tilde{P}_s, \tilde{A}_s) \tilde{\eta}_s^{P,\ell} + \sum_{\ell=1}^m \frac{\partial \Phi_i^{P,n,m}}{\partial a^\ell}(\tilde{P}_s, \tilde{A}_s) \tilde{\eta}_s^{A,\ell} \right] ds, \\ \tilde{\eta}_t^{A,j} &= \tilde{\eta}_0^{A,j} + \int_0^t \sqrt{\left(b^A(\tilde{R}_s^{P,j}) + d^A(\tilde{R}_s^{P,j}) + \frac{1}{m} \sum_{\ell=1}^m h(y^j, y^\ell) \tilde{A}_s^\ell \right)} \tilde{A}_s^j dW_s^{A,j} \\ &\quad + \int_0^t \left[\sum_{\ell=1}^n \frac{\partial \Phi_j^{A,n,m}}{\partial p^\ell}(\tilde{P}_s, \tilde{A}_s) \tilde{\eta}_s^{P,\ell} + \sum_{\ell=1}^m \frac{\partial \Phi_j^{A,n,m}}{\partial a^\ell}(\tilde{P}_s, \tilde{A}_s) \tilde{\eta}_s^{A,\ell} \right] ds. \end{aligned} \quad (2.7)$$

Proof of Proposition 2.3. It is a direct application of Theorem 2.3 from Chapter 11 of [23]. The proof can also be carried from the semi-martingale expressions of $P_t^{K,i}$ and $A_t^{K,j}$ (1.13)-(1.15) and (2.5). To understand (2.7), consider for example the i th component of $\eta_t^{K,P}$, $\eta_t^{K,P,i}$. The other terms can be treated similarly. We sketch here this alternative proof:

$$\begin{aligned}
\eta_t^{K,P,i} &= \eta_0^{K,P,i} + \sqrt{K} \int_0^t \frac{1}{n} \sum_{\ell=1}^n k(x^\ell, x^i) \left(\frac{P_s^{K,\ell}}{K} \frac{P_s^{K,i}}{K} - \tilde{P}_s^\ell \tilde{P}_s^i \right) ds + \sqrt{K} \frac{M_t^{K,i}}{K} \\
&+ \sqrt{K} \int_0^t \left[g^P \left(\sum_{j \sim i} c_{ij}^{n,m} \frac{A_s^{K,j}}{K} \right) P_s^{K,i} - g^P \left(\sum_{j \sim i} c_{ij}^{n,m} \tilde{A}_s^j \right) \tilde{P}_s^i \right] ds \\
&= \eta_0^{K,P,i} + \frac{1}{n} \sum_{\ell=1}^n k(x^\ell, x^i) \int_0^t \left[\eta_s^{K,\ell} \frac{P_s^{K,i}}{K} + \tilde{P}_s^\ell \eta_s^{K,i} \right] ds + \sqrt{K} \frac{M_t^{K,i}}{K} \\
&+ \int_0^t \left[g^P \left(\sum_{j \sim i} c_{ij}^{n,m} \frac{A_s^{K,j}}{K} \right) \eta_s^{K,i} + \sqrt{K} \tilde{P}_s^i \left(g^P \left(\sum_{j \sim i} c_{ij}^{n,m} \frac{A_s^{K,j}}{K} \right) - g^P \left(\sum_{j \sim i} c_{ij}^{n,m} \tilde{A}_s^j \right) \right) \right] ds,
\end{aligned} \tag{2.8}$$

for the martingale $M^{K,i}$ appearing in (1.13) with quadratic variation (1.14). Because the birth and death rates are assumed to be of class \mathcal{C}^1 , so is g^P and a Taylor expansion can be used for the last term:

$$\begin{aligned}
\sqrt{K} \left(g^P \left(\sum_{j \sim i} c_{ij}^{n,m} \frac{A_s^{K,j}}{K} \right) - g^P \left(\sum_{j \sim i} c_{ij}^{n,m} \tilde{A}_s^j \right) \right) &= (g^P)' \left(\sum_{j \sim i} c_{ij}^{n,m} \tilde{A}_s^j \right) \times \sum_{j \sim i} c_{ij}^{n,m} \sqrt{K} \left(\frac{A_s^{K,j}}{K} - \tilde{A}_s^j \right) + \varepsilon_K \\
&= (g^P)' \left(\sum_{j \sim i} c_{ij}^{n,m} \tilde{A}_s^j \right) \times \sum_{j \sim i} c_{ij}^{n,m} \eta_s^{K,j} + \varepsilon_K,
\end{aligned} \tag{2.9}$$

where ε_K is a remainder term. From (2.8) and (2.9), we recognize that:

$$\eta_t^{K,P,i} = \eta_0^{K,P,i} + \sqrt{K} \frac{M_t^{K,i}}{K} + \int_0^t \left[\sum_{\ell=1}^n \frac{\partial \Phi_i^{P,n,m}}{\partial p^\ell} (\tilde{P}_s, \tilde{A}_s) \tilde{\eta}_s^{P,\ell} + \sum_{\ell=1}^m \frac{\partial \Phi_i^{P,n,m}}{\partial a^\ell} (\tilde{P}_s, \tilde{A}_s) \tilde{\eta}_s^{A,\ell} \right] ds + \varepsilon_K.$$

Using the Aldous-Rebolledo criterion (*e.g.* [36]) it is possible to prove that the distributions of the processes $(\eta^{K,P}, \eta^{K,A})_K$ form a tight family with a unique limiting value that solves the SDEs (2.7). \blacksquare

Systems of SDEs have already been introduced in the literature to describe the evolution of communities, but they are to our knowledge of a different nature. In (2.7) the noise relates to the fluctuation of the stochastic individual-based model around its deterministic limit (2.5) for $K \rightarrow +\infty$. In other works, such as in [15] for instance, the white noise corresponds to a diffusive limit obtained when considering a different longer time-scale, as in the Donsker theorem (see *e.g.* [17, Section 4.2]): the random noise comes from the rapid successions of birth and death events in this accelerated time-scale. In recent works, following the steps of May [40], [3, 26] introduce a system of equations, coupled *via* a smooth random vector field, which describes the approximated dynamical system around an equilibrium state: in this case, the noise models the complexity and nonlinearity of interactions.

3 Continuous limits when abundances and the number of species are large

We now consider that the numbers of plant and pollinator species in the network tend to infinity. Taking the limit $n, m \rightarrow +\infty$, we obtain equations describing the evolution of a population consisting

in a *continuum* of species.

First, recall that the plant-pollinator network is defined by its adjacency matrix $(G_{ij}^{n,m})_{(i,j) \in [1,n] \times [1,m]}$ that is supposed to satisfy Assumption 1.1 for all n and $m \in \mathbb{N}$.

Let the traits of plants and pollinators be chosen according to i.i.d. random variables with cumulative distribution functions F_P and F_A respectively. To order species according to their respective trait, we proceed as follows: let $(\tilde{u}_i)_{i \geq 1}$ and $(\tilde{v}_j)_{j \geq 1}$ be two sequences of i.i.d. random variables with uniform distribution in $[0, 1]$; for any $n, m \in \mathbb{N}^2$, let $(u^{i,n})_{i=1..n}$ be the ordered n^{th} first values of $(\tilde{u}_i)_{i \geq 1}$ and $(v^{j,m})_{j=1..m}$ be the ordered m^{th} first values of $(\tilde{v}_j)_{j \geq 1}$, then for any $i \in \{1, \dots, n\}$ and $j \in \{1, \dots, m\}$,

$$x^{i,n} = F_P^{-1}(u^{i,n}) \quad \text{and} \quad y^{j,m} = F_A^{-1}(v^{j,m}).$$

The indices n and m will be dropped when no confusion is possible.

Assumption 3.1. *We assume that there exists for any $n, m \in \mathbb{N}^2$ a continuous function $c^{n,m}$ satisfying the condition (1.2) of Assumption 1.3. Additionally, we assume that there exists a function $c : [0, 1]^2 \mapsto \mathbb{R}$ to which the sequences of functions $nc^{n,m}(\cdot, \cdot)$ and $mc^{n,m}(\cdot, \cdot)$ converge uniformly, in $L^\infty([0, 1]^2)$, when n and m tend to $+\infty$.*

The idea in this assumption is that the function $c(\cdot, \cdot)$ is a ‘‘harvesting function’’ underlying the matrix $(c_{ij}^{n,m})_{i \in [1,n], j \in [1,m]}$ of harvesting coefficients.

Notice also that Assumption 3.1 implies that n and m grow to infinity with a similar speed. To state this idea in specific terms, we assume that there exists a sequence $(\alpha_n)_{n \geq 1}$ such that

$$m = \alpha_n n \quad \text{and} \quad \lim_{n \rightarrow \infty} \alpha_n = 1. \quad (3.1)$$

In what follows, we write $n \rightarrow \infty$, $m \rightarrow \infty$ or $n, m \rightarrow \infty$ indistinctly.

Proposition 3.2. *Let us assume Assumptions 1.1, 1.4 and 3.1 hold and that there exist deterministic continuous bounded densities \bar{p}_0 and \bar{a}_0 such that the following weak convergences hold:*

$$\lim_{n \rightarrow +\infty} \frac{1}{n} \sum_{i=1}^n \tilde{P}_0^i \delta_{x^i} \stackrel{w}{=} \bar{p}_0(x) dx, \quad \lim_{m \rightarrow +\infty} \frac{1}{m} \sum_{j=1}^m \tilde{A}_0^j \delta_{y^j} \stackrel{w}{=} \bar{a}_0(y) dy \quad \text{a.s.} \quad (3.2)$$

For any $T \geq 0$, and for $n, m \rightarrow +\infty$, the sequence of measure-valued processes

$$\left(\tilde{\mathbf{P}}_t^{n,m}(dx), \tilde{\mathbf{A}}_t^{n,m}(dy) \right)_{t \geq 0} := \left(\frac{1}{n} \sum_{i=1}^n \tilde{P}_t^i \delta_{x^i}, \frac{1}{m} \sum_{j=1}^m \tilde{A}_t^j \delta_{y^j} \right)_{t \geq 0}, \quad n, m \geq 1$$

converge in law in $\mathcal{C}([0, T], \mathcal{M}_F([0, 1]^2))$ to a deterministic process $(\bar{\mathbf{P}}, \bar{\mathbf{A}})$ in $\mathcal{C}([0, T], \mathcal{M}_F([0, 1]^2))$, such that:

- (i) for all $t \geq 0$, $\bar{\mathbf{P}}_t$ and $\bar{\mathbf{A}}_t$ admit densities \bar{p}_t and \bar{a}_t with respect to the Lebesgue measure on $[0, 1]$,
- (ii) $(\bar{\mathbf{P}}, \bar{\mathbf{A}})$ is the unique solution, for $f \in \mathcal{C}([0, 1], \mathbb{R})$, of

$$\begin{aligned} \int_0^1 f(x) d\bar{\mathbf{P}}_t(x) &= \int_0^1 f(x) d\bar{p}_0(x) dx \\ &\quad + \int_0^t \int_0^1 f(x) \left[g^P \left(\int_0^1 c(x, y) \phi(x, y) \bar{a}_s(y) dy \right) - k \star \bar{p}_s(x) \right] \bar{p}_s(x) dx ds, \\ \int_0^1 f(y) d\bar{\mathbf{A}}_t(y) &= \int_0^1 f(y) d\bar{a}_0(y) dy \\ &\quad + \int_0^t \int_0^1 f(y) \left[g^A \left(\int_0^1 c(x, y) \phi(x, y) \bar{p}_s(x) dx \right) - h \star \bar{a}_s(y) \right] \bar{a}_s(y) dy ds, \end{aligned} \quad (3.3)$$

where we recall that $k \star \nu$ denotes the product of any measure ν on $[0, 1]$ by the kernel k , i.e. $k \star \nu(x) = \int_0^1 k(x, x') d\nu(x')$. In all this statement, the space $\mathcal{M}_F^2([0, 1])$ is endowed with its weak topology.

The proof of this Proposition is given in Appendix A.2

Equation (3.3) is analogous to the ODE system given in Equation (2.3). However, here species are not considered as discrete but continuously distributed along a continuous trait. Modelling the dynamics of a plant-pollinator community with the PDEs given in Equation (3.3) is thus a functional rather than a species representation of the same system. The term $c\phi$ reflects both the topology (ϕ) and the intensity (c) of plant-pollinator interactions throughout the community depending on the traits values x and y involved.

Proposition 3.3. *Under the same assumptions as Proposition 3.2 and if the densities p_0 and a_0 are continuous functions of $[0, 1]$, then for any $t \geq 0$, $p_t, a_t \in C^0([0, 1], \mathbb{R})$.*

This proposition is a classical consequence of Gronwall's Lemma, and we will not detail its proof.

Remark 3.4. *Note that one can formally write a strong form of (3.3). This leads to the following system of integral equations on the densities \bar{p}_t and \bar{a}_t :*

$$\begin{aligned}\partial_t \bar{p}_t(x) &= \left[g^P \left(\int_0^1 c(x, y) \phi(x, y) \bar{a}_t(y) dy \right) - k \star \bar{p}_t(x) \right] \bar{p}_t(x), \\ \partial_t \bar{a}_t(y) &= \left[g^A \left(\int_0^1 c(x, y) \phi(x, y) \bar{p}_t(x) dx \right) - h \star \bar{a}_t(y) \right] \bar{a}_t(y),\end{aligned}\tag{3.4}$$

with initial conditions \bar{p}_0 and \bar{a}_0 .

4 Study of the limiting dynamical systems

Let us now study the behaviour of the limiting dynamical systems that have been obtained: the ODE system (2.3) when $K \rightarrow +\infty$, and the kinetic PDEs (3.3) when additionally $n, m \rightarrow +\infty$.

4.1 Stationary states of the ODE system (2.3)

In this section, we give some results about the dynamics of solutions to Systems (2.3), for general forms of g^P and g^A . Notice that any stationary points $(\tilde{P}_\infty^1, \dots, \tilde{P}_\infty^n, \tilde{A}_\infty^1, \dots, \tilde{A}_\infty^m)$ of (2.3) are solutions to the following system:

$$\begin{aligned}\forall 1 \leq i \leq n, \tilde{P}_\infty^i = 0 \text{ or } g^P \left(\sum_{j \sim i} c_{ij}^{n,m} \tilde{A}_\infty^j \right) &= \frac{1}{n} \sum_{\ell=1}^n k(x^i, x^\ell) \tilde{P}_\infty^\ell, \\ \forall 1 \leq j \leq m, \tilde{A}_\infty^j = 0 \text{ or } g^A \left(\sum_{i \sim j} c_{ij}^{n,m} \tilde{P}_\infty^i \right) &= \frac{1}{m} \sum_{\ell=1}^m h(y^j, y^\ell) \tilde{A}_\infty^\ell.\end{aligned}\tag{4.1}$$

The community with no individuals is an obvious stationary point called the *null equilibrium* in the rest of the paper:

$$\tilde{P}_\infty^i = 0 \text{ for all } i \in \{1, \dots, n\} \quad \text{and} \quad \tilde{A}_\infty^j = 0 \text{ for all } j \in \{1, \dots, m\},$$

is a stationary state of (2.3). The local stability of this stationary state depends only on the sign of $g^P(0)$ and $g^A(0)$.

Remark 4.1. *According to the expression of the non trivial equilibria, a plant-pollinator community can exist, i.e. $\tilde{P}_\infty^i > 0$ and $\tilde{A}_\infty^j > 0$, as soon as the interactions between plants and pollinators translate into positive growth rate for both plants and pollinators. Despite this condition is little restrictive, a non-trivial equilibrium is possible only if trajectories have to converge to it, (i.e. a non-trivial equilibrium has to be stable). The stability of an equilibrium can be more tricky to study and obtained in general.*

Lemma 4.2. *If $g^P(0) \vee g^A(0) < 0$, the null equilibrium is locally stable. If $g^P(0) \vee g^A(0) > 0$, the null equilibrium is locally unstable.*

Proof. The Jacobian matrix around the null equilibrium can be directly computed:

$$\begin{pmatrix} g^P(0) & 0 & 0 & \dots & 0 & 0 \\ 0 & g^P(0) & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & g^A(0) & 0 \\ 0 & 0 & \dots & 0 & 0 & g^A(0) \end{pmatrix},$$

whose eigenvalues are $g^P(0)$ with multiplicity n and $g^A(0)$ with multiplicity m . This ends the proof. ■

4.2 Study of a plant-pollinator interaction with a trade-off for the plan

As explained in Remark 4.1, more precise functional forms for the birth and death rates are needed to carry further computation.

In this Section, we give results for the following particular forms for the individual growth rate functions:

$$\begin{aligned} g^P(R^A) &= b^P(R^A) - d^P(R^A) = \frac{\alpha_P R^A}{\beta_P + \gamma_P R^A} - (d_P + \delta_P R^A), \\ g^A(R^P) &= b^A(R^P) - d^A(R^P) = \frac{\alpha_A R^P}{\beta_A + \gamma_A R^P} - d_A, \end{aligned} \tag{4.2}$$

where R^A and R^P are the total resources collected by respectively plants and pollinators (Eqs. (1.5) and (1.6)). Parameters α_P , α_A , β_P , β_A , γ_P , γ_A , d_A , d_P and δ_P are assumed positive. Note that according to Lemma 4.2, the null equilibrium is stable in this particular case.

On the right-hand side of Equation (4.2), the death rate is an increasing function of the resources exchanged R for plants. This reflects an interaction trade-off for the plant, *i.e.* it is supposed that there is a cost for interacting with pollinators due to nectar production, leaves consumption, etc. Graphical representations of g^P and g^A are given in Figure 2. The form given here to the growth rates (or

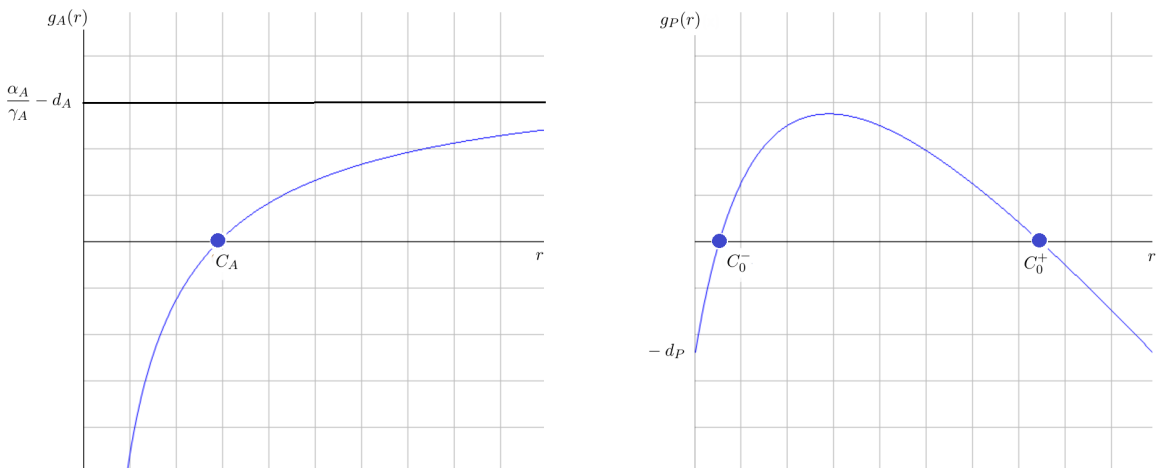


Figure 2: Graphical representation of g_A and g_P

numerical responses) g^P and g^A can be found in [30]. It assumes that there is no competition between plants for collecting resources from pollinators, and that there is no competition between pollinators

for collecting resources from plants.

We state an additional assumption on the parameters of both functions to avoid the case where one growth rate is never positive.

Assumption 4.3. *Assume that there exist $r^P > 0$ and $r^A > 0$ such that*

$$g^P(r^P) > 0 \quad \text{and} \quad g^A(r^A) > 0.$$

4.2.1 Case $n = m = 1$

Let us first consider the particular case of a single plant species interacting with a single pollinator species. In other words, we consider the system (2.3) with $n = m = 1$ and omit the indices and exponents $i = 1$ and $j = 1$ for the sake of simplicity (so that \tilde{P}_t^1 becomes P_t and $c_{11}^{1,1}$ becomes c for instance). We also assume that the two species interact, *i.e.* $G_{11} = 1$. Otherwise, computations are trivial: the community goes to extinction as only death events occur. We have then:

$$\begin{aligned} \frac{dP_t}{dt} &= (g^P(cA_t) - kP_t) P_t \\ \frac{dA_t}{dt} &= (g^A(cP_t) - hA_t) A_t \end{aligned} \tag{4.3}$$

(see [32] for a similar ODE model in the ecology literature).

As discussed in Lemma 4.2, the null equilibrium is a locally stable equilibrium of the system (4.3). Let us search for positive equilibrium. To help the study, we may draw some phase plan of the system, for the choice of parameters $\alpha_A = 25$, $\alpha_P = 9$, $\beta_A = \beta_P = \gamma_A = \gamma_P = 1$ and $\delta_P = 3$, and some various d_A and d_P . (see Figure 3).

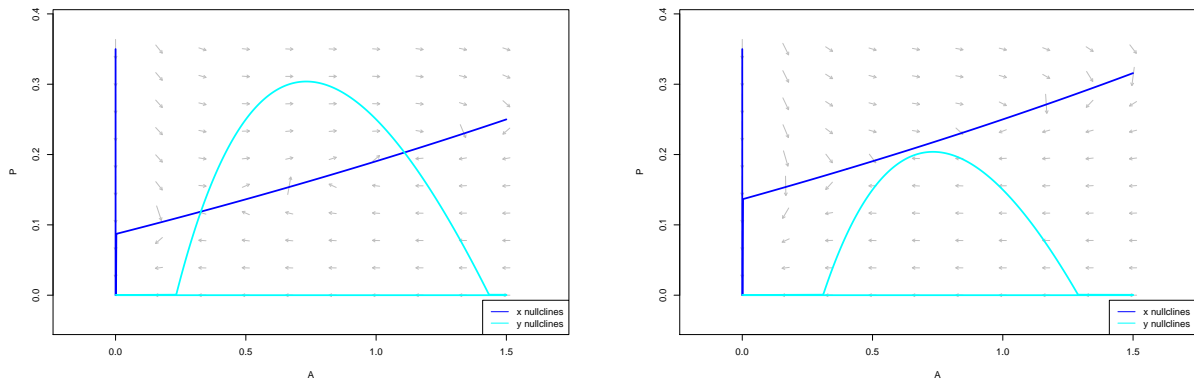


Figure 3: Phase plan and nullclines of the system of ODE (4.3): nullclines for the pollinators dynamics in blue; nullclines for the plants dynamics in cyan. Right: $d_A = 2$ and $d_P = 1$, the system has 3 stationary states: the null equilibrium, 1 stable positive equilibrium and 1 unstable positive equilibrium. Left: $d_A = 3$ and $d_P = 1.2$, the unique equilibrium of the system is the null equilibrium.

Precisely, we prove the following lemma that gives the number of equilibria and their stability.

Lemma 4.4. *In addition to the null-equilibrium, System (4.3) has 0, 1 or 2 equilibria, depending on the values of the parameters. Moreover, in this last case, the system has 1 stable positive equilibrium and 1 unstable positive equilibrium.*

To conclude on the dynamics of the trajectories of System (4.3), we performed simulations. In summary, it appeared that, depending on the parameters values, either all trajectories are attracted by

the null equilibrium (Fig 3(left)), or trajectories converge to 0 or some positive equilibrium, depending on the initial conditions (Fig 3(right)). We never observed cycles. Moreover, the competitive terms ensure that trajectories remain bounded.

Proof of Lemma 4.4. Any stationary point (P_∞, A_∞) is solution to

$$\begin{aligned} g^P(cA_\infty) &= kP_\infty & \text{or} & & P_\infty &= 0 \\ g^A(cP_\infty) &= hA_\infty & \text{or} & & A_\infty &= 0. \end{aligned} \quad (4.4)$$

Recall that either both or no coordinates are null. In view of (4.4), the existence of a positive equilibrium requires at least that $\sup_{x \in \mathbb{R}^+} g^P(x) > 0$ and $\sup_{y \in \mathbb{R}^+} g^A(y) > 0$. This is true under Assumption 4.3. Denote by C_0^- and C_0^+ the two zeros of g^P . From (4.4), we deduce that, if there exists a positive stationary state, it satisfies

$$\begin{cases} P_\infty = \frac{1}{k}g^P(cA_\infty) \\ A_\infty = \frac{1}{h}g^A\left(\frac{c}{k}g^P(cA_\infty)\right), \text{ and } cA_\infty \in (C_0^-, C_0^+). \end{cases}$$

It remains to find the number of zeros of $f(x) = \frac{1}{h}g^A\left(\frac{c}{k}g^P(cx)\right) - x$ on $\left(\frac{C_0^-}{c}, \frac{C_0^+}{c}\right)$. A rapid differentiation gives

$$f''(x) = \frac{c^3}{hk}(g^P)''(cx)(g^A)'\left(\frac{c}{k}g^P(cx)\right) + \frac{c^3}{(hk)^2}(g^P)'(cx)^2(g^A)''\left(\frac{c}{k}g^P(cx)\right) < 0,$$

since g^A is increasing and g^P and g^A are concave functions. Thus, f' is decreasing and

$$f'(x) = \frac{c^2}{hk}(g^P)'(cx)(g^A)'\left(\frac{c}{k}g^P(cx)\right) - 1,$$

converges to $+\infty$ (resp. $-\infty$) when x goes to C_0^-/c (resp. C_0^+/c). Finally, f is increasing then decreasing and admits a unique maximum. Since f converges to $-\infty$ when x goes to C_0^-/c and C_0^+/c , it admits

- 2 zeros if $\max_{x \in (C_0^-/c, C_0^+/c)} f(x) > 0$, and System (4.4) has 2 positive equilibrium,
- 1 zero if $\max_{x \in (C_0^-/c, C_0^+/c)} f(x) = 0$, and System (4.4) has 1 positive equilibrium,
- no zero otherwise, and System (4.4) has no positive equilibrium.

Finally, in the case of 2 positive equilibrium, which will be denoted by (P_∞^-, A_∞^-) and (P_∞^+, A_∞^+) with $A_\infty^- < A_\infty^+$, the Jacobian matrix can be computed in order to study their stability:

$$J^\pm = \begin{pmatrix} -kP_\infty^\pm & cP_\infty^\pm(g^P)'(cA_\infty^\pm) \\ cA_\infty^\pm(g^A)'(cP_\infty^\pm) & -hA_\infty^\pm \end{pmatrix}.$$

The trace is negative, thus the stability of the stationary states depend on the sign of the determinant.

$$\det(J^\pm) = P_\infty^\pm A_\infty^\pm \left(hk - c^2(g^P)'(cA_\infty^\pm)(g^A)'(cP_\infty^\pm) \right) = -P_\infty^\pm A_\infty^\pm hk f'(A_\infty^\pm),$$

and its sign depends only on the sign of $f'(A_\infty^\pm)$. According to the previous study on function f , we deduce that $\det(J^+)$ is negative, and $\det(J^-)$ is positive. In other words, System (4.4) admits 1 stable positive equilibrium and 1 unstable positive equilibrium.

In the case when System (4.4) admits a unique positive equilibrium, the same study implies that this equilibrium is a non-hyperbolic equilibrium. ■

4.2.2 Behaviour of the kinetic equations (3.3)

Recall that we are still working with the growth rates defined in (4.2).

The stationary solutions of (3.3) are couples of measures $\bar{P}^\infty(dx)$ and $\bar{A}^\infty(dy)$ in $\mathcal{M}_F([0, 1])$ such that, for all positive, bounded and continuous function f on $[0, 1]$:

$$0 = \int_0^1 f(x) \left[g^P \left(\int_0^1 \psi(x, y) \bar{A}^\infty(dy) \right) - k \star \bar{P}^\infty(x) \right] \bar{P}^\infty(dx), \quad (4.5)$$

$$0 = \int_0^1 f(y) \left[g^A \left(\int_0^1 \psi(x, y) \bar{P}^\infty(dx) \right) - h \star \bar{A}^\infty(y) \right] \bar{A}^\infty(dy) \quad (4.6)$$

where

$$\psi(x, y) := c(x, y)\phi(x, y). \quad (4.7)$$

The null measures constitute a trivial solution to (4.5)-(4.6), which is stable in our particular case (4.2). Let us discuss non-zero solutions.

Proposition 4.5. *Assume that*

- *the competitive kernels k and h are constant functions;*
- *for all $x_0, y_0 \in [0, 1]$, $y \mapsto \psi(x_0, y)$ and $x \mapsto \psi(x, y_0)$ are increasing functions;*

then, System (3.3) does not admit non-null stationary state with densities w.r.t Lebesgue measure. Moreover, any non-null stationary state in $L^1([0, 1]^2)$ is a couple of measures $(\bar{P}^\infty, \bar{A}^\infty)$ such that

$$\begin{aligned} \exists \bar{a}_0, \bar{p}_1 \in \mathbb{R}_+^*, \bar{p}_2 \in \mathbb{R}_+, \bar{x}_1, \bar{x}_2, \bar{y}_0 \in [0, 1], \quad & \begin{cases} \bar{P}^\infty = \bar{p}_1 \delta_{\bar{x}_1} + \bar{p}_2 \delta_{\bar{x}_2} \\ \bar{A}^\infty = \bar{a}_0 \delta_{\bar{y}_0} \end{cases} \\ \text{with } \begin{cases} g^P(\bar{a}_0 \psi(\bar{x}_1, \bar{y}_0)) = g^P(\bar{a}_0 \psi(\bar{x}_2, \bar{y}_0)) = k(\bar{p}_1 + \bar{p}_2) \\ g^A(\bar{p}_1 \psi(\bar{x}_1, \bar{y}_0) + \bar{p}_2 \psi(\bar{x}_2, \bar{y}_0)) = h \bar{a}_0. \end{cases} & \end{aligned} \quad (4.8)$$

All these stationary states are unstable, except the state

$$\begin{cases} \bar{P}^\infty = \frac{\max_{\mathbb{R}^+} g^P}{k} \delta_{x_0} \\ \bar{A}^\infty = \frac{\arg \max_{\mathbb{R}^+} g^P}{\psi(x_0, 1)} \delta_1 \end{cases} \quad (4.9)$$

if x_0 , solution to

$$g^A \left(\frac{\max_{\mathbb{R}^+} g^P}{k} \psi(x_0, 1) \right) \psi(x_0, 1) = h \cdot \arg \max_{\mathbb{R}^+} g^P, \quad (4.10)$$

exists and is unique.

Finally, assuming that, for all initial conditions with positive densities w.r.t Lebesgue measure, the quantities $\int_0^1 \psi(x, \cdot) p_t(x) dx$, $\int_0^1 p_t(x) dx$, $\int_0^1 \psi(\cdot, y) a_t(y) dy$ and $\int_0^1 a_t(y) dy$ converge when t grow to infinity, then the trajectory converges to equilibrium (4.9).

This proposition ensures the fact that the only possible stable equilibrium is composed of only one plant species and one pollinator species. Simulations below will illustrate this Proposition.

Remark 4.6. *The proof of Proposition 4.5 is not restricted to the specified forms of g^P and g^A , (4.2). The proposition is still true as soon as shapes (successions of increases and decreases) of g^P and g^A are the same as the ones of specified functions (4.2).*

Otherwise, in any case, System (3.3) has no stationary state with densities, all stationary states will be composed of Dirac measures. Moreover, the maximal number of Dirac measures found in such a stationary state corresponds to the maximal number of points that can be found in an inverse image of a positive real for functions g^P and g^A respectively. The stability of these stationary states can then be deduced using the same kind of arguments as these of the following proof.

With this in mind, we can deduce that the number of pollinator species and plant species is reduced to 1 when considering all type of growths given in Figure 2 of [31].

This result shows that when the plant-pollinator network is nested and the competition among plants and among pollinators is constant, then the plant-pollinator community collapses to a single plant-pollinator species pair. This is in line with the numerical analysis of a system of ODEs by [38]. Our results is a formal demonstration of this necessary collapse. It is also more general since we show that it does not depend on the specific form of g^P and g^A . This raises the question whether it is possible, in this type of ecological model, to maintain a stable coexistence of many plant and pollinator species in a single community by modifying the structure of the interaction graph (i.e. with other assumptions for the function ψ), or the structure of the competition graph (i.e. with non-constant competition functions k and h).

Proof. Any stationary state in $L^1([0, 1]^2)$ satisfies that $(\bar{P}^\infty, \bar{A}^\infty)$

$$\begin{cases} g^P \left(\int_0^1 \psi(x, y) \bar{A}^\infty(dy) \right) = \int_0^1 k \bar{P}^\infty(dx'), & \text{for all } x \notin \text{supp} \bar{P}^\infty, \\ g^A \left(\int_0^1 \psi(x, y) \bar{P}^\infty(dx) \right) = \int_0^1 h \bar{A}^\infty(dy'), & \text{for all } y \notin \text{supp} \bar{A}^\infty \end{cases} \quad (4.11)$$

Since $(\bar{P}^\infty, \bar{A}^\infty) \in L^1([0, 1]^2)$, $\int_0^1 k \bar{P}^\infty(dx')$ and $\int_0^1 h \bar{A}^\infty(dy')$ are finite. Then, since, ψ is increasing w.r.t each variable, g^A is increasing and g^P is increasing then decreasing, we deduce (4.8).

Let us denote by \mathcal{S} the set of stationary states given by (4.8) excluding equilibrium (4.9) Let us prove that all states in \mathcal{S} are unstable. To this aim, we develop an argument by contradiction, assuming that it is not true and that there exists at least a stationary state $(\bar{P}^\infty, \bar{A}^\infty) \in \mathcal{S}$. We deal with the case where $\bar{x}_1 < x_0 < \bar{x}_2$, \bar{y}_0 being any value in $[0, 1]$. Other cases ((2) $\bar{x}_2 < x_0 < \bar{x}_1$, $\bar{y}_0 \in [0, 1]$ or (3) $\bar{x}_1 = \bar{x}_2 = x_0$, $\bar{y}_0 < 1$) can be treated similarly.

Let consider an initial state that is close (in Wasserstein distance) to $(\bar{P}^\infty, \bar{A}^\infty)$ and that has positive densities w.r.t Lebesgue measures. Thus, p_t exists and is positive for all $t \geq 0$ and we can study $\log(p_t(x))$ for all $t \in \mathbb{R}_+$ and all $x \in [0, 1]^2$:

$$\frac{d}{dt} \log(p_t(x)) = g^P \left(\int_0^1 \psi(x, y) a_t(y) dy \right) - \int_0^1 k p_t(x') dx'.$$

Under our assumption, \mathcal{S} admits at least a stable state and since the initial state is close to this set, we deduce that (p_t, a_t) will converge to some $(\hat{P}^\infty, \hat{A}^\infty) \in \mathcal{S}$, which is close to $(\bar{P}^\infty, \bar{A}^\infty)$ (if not it), sufficiently close to have a similar form. Then for all $x \in [0, 1]$,

$$\begin{aligned} \frac{d}{dt} \log(p_t(x)) &\xrightarrow[t \rightarrow \infty]{} g^P \left(\int_0^1 \psi(x, y) \hat{a}^\infty(y) dy \right) - \int_0^1 k \hat{p}^\infty(x') dx' \\ &= g^P \left(\int_0^1 \psi(x, y) \hat{a}^\infty(y) dy \right) - g^P \left(\int_0^1 \psi(\hat{x}_1, y) \hat{a}^\infty(y) dy \right). \end{aligned}$$

The latter quantity is positive as soon as $x \in (\hat{x}_1, x_0)$, which contradicts the fact that $p_t(x)$ converges to 0 for all $x \notin \{\hat{x}_1, \hat{x}_2\}$.

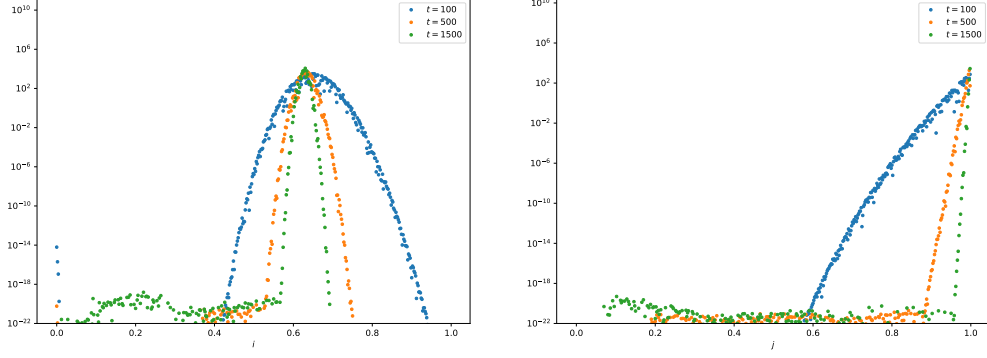


Figure 4: Solutions to (4.12) at time 100 (blue), 500 (orange) and 1500 (green). The left panel represents the distribution of plant species and the right panel the distribution of pollinator species. Parameters are $\alpha_A = 3$, $\alpha_P = 25$, $\beta_A = \beta_P = \gamma_P = 1$, $\gamma_A = 0.3$, $d_P = 1$, $d_A = 3$ and $\delta_P = 3$, with $N = 500$

The last point of Proposition (4.5) can be obtained using the same argument, once the convergences of the four quantities detailed in the statement are assumed. \blacksquare

Let us illustrate numerically Proposition 4.5. Let $(p_i(t))_i$, resp. $(a_j(t))_j$ be an approximation of $(\bar{p}_t(x_i))_i$, resp. $(\bar{a}_t(y_j))_j$, for $x_i = i/N$, $y_j = j/N$, $0 \leq i, j \leq N$. Then the continuous model (3.4) can be approximated using the rectangular rule by the following system of coupled ODEs:

$$\begin{aligned} \frac{dp_i}{dt} &= \left[g^P \left(\frac{1}{N} \sum_{j=0}^N c_{ij} a_j \right) - \frac{1}{N} \sum_{j=0}^N k_{i,j} p_j \right] p_i, \\ \frac{da_j}{dt} &= \left[g^A \left(\frac{1}{N} \sum_{i=0}^N c_{ij} p_i \right) - \frac{1}{N} \sum_{i=0}^N h_{i,j} a_i \right] a_j, \end{aligned} \quad (4.12)$$

where the initial data has been defined as $p_i(0) = \bar{p}_0(x_i)$, $p_i(0) = \bar{p}_0(x_i)$, $a_j(0) = \bar{a}_0(y_j)$. We recognize the ODE system (2.3) obtained when the numbers of plant and pollinator species are finite with $n = m = N$.

We shall consider the case of growth functions (4.2) with $\alpha_A = 3$, $\alpha_P = 25$, $\beta_A = \beta_P = \gamma_P = 1$, $\gamma_A = 0.3$, $d_P = 1$, $d_A = 3$ and $\delta_P = 3$, with $N = 500$ species of plants and pollinators. In order to fit the hypotheses of Proposition 4.5 and insure the convergence towards an explicit equilibrium of the dynamics, the interaction matrix $(c_{ij})_{i,j}$ is nondecreasing in each index i and j , and the competition kernels will be chosen constant. We consider the simple case

$$c_{ij} = \frac{(i+1)(j+1)}{2N^2}.$$

We represent in Figure 4 (in logarithmic scale) the convergence towards the equilibrium state reached when no evolution occurs anymore on the discrete dynamics, for a random initial datum supported in $[0, 1]$. We observe that the conclusion of proposition 4.5 are in agreement, namely the system converges towards an equilibrium which consists of a Dirac delta centered inside the domain for the plants, and on the right border for the pollinators: the last remaining plant specie is moderately specialist ($x \simeq 0.6$) whereas the remaining pollinator is genuinely generalist ($y = 1$).

5 Conclusion

Two of the main goals of ecology are i) to explain how emerged the size, composition and structure of communities, for example plant-pollinator communities, and ii) predict the dynamics and stability of a given community. Such questions involve different hierarchical scales, from the individuals which effectively interact (the microscopic scale), to the species and the whole community (the macroscopic scale).

Theoretical ecology mostly address these questions by studying a system of ODEs where one equation refers to a given species. This approach has several methodological and conceptual drawbacks. First, the system is discretized and structured by species, which precludes the possibility of within-species variability regarding the rate and intensity of interactions, in particular between-species overlaps. Second, the interaction graphs underlying the system of ODEs are most often arbitrarily given without specified mechanisms. Finally, due to the high-dimensionality of the ODEs system, it is difficult to obtain general properties of communities.

Here, we modelled an individual-based plant-pollinator network, where interactions are structured by an individual trait. We found continuous limits of the microscopic system and finally showed that it could be approximated by PDEs. We finally studied the dynamics, stationary state and stability of this continuous limits. Our approach allows to address several limits exposed before: the relationships between the individuals, species and community scales are explicit; interactions variability within and between-species is taken into account; the interaction graph is based on individuals' traits; PDEs approximations allows an explicit and analytical study of the property of a community. We showed in particular that a nested plant-pollinator network is expected to collapse, a phenomenon already observed by previous works, but to our knowledge for the first time formally demonstrated under general conditions. Our approach can thus provide a new and original theoretical framework for ecologists to address long-standing questions.

One of the actual limit of our model is that interactions take place through a "mass-action model", in particular with the use of the resources (1.5)-(1.6) which are already at a macroscopic scale. Returning to an event-based modelling for establishing these functional responses (e.g. [5]) and showing how interactions at the individual level would translate into an interaction graph and into the dynamics of the whole community is an open question.

Code

The code for simulations is available here:

<https://gitlab.com/thoma.rey/PlantPollinatorsNetwork/>

A Proofs

A.1 Bounds on the microscopic representation

Here, we give a sketch of proof of Proposition 1.6. The proof follows from usual stochastic calculus with Poisson point processes, as developed in [25] for example.

Proof of Proposition 1.6. Step 1: let us first prove some moment estimates, including (1.12). For a constant $N > 0$, we introduce the stopping time

$$\tau_N^K = \inf \left\{ t \geq 0, \langle \mathbf{P}_t^{K,n}, \mathbf{1} \rangle \geq N \text{ or } \langle \mathbf{A}_t^{K,m}, \mathbf{1} \rangle \geq N \right\}.$$

First notice that neglecting the death terms and upperbounding the birth rate $b^P(R)$ by M^P , we have:

$$\langle \mathbf{P}_t^{K,n}, \mathbf{1} \rangle = \frac{1}{nK} \sum_{i=1}^n P_t^{K,i} \leq \langle \mathbf{P}_0^{K,n}, \mathbf{1} \rangle + \int_0^t \int_E \frac{1}{nK} \mathbb{1}_{\theta \leq M^P} \sup_{u \leq s-} P_u^{K,i} Q_B^P(ds, di, d\theta).$$

Since the right hand side is an increasing process, we can replace the left hand side by $\sup_{s \leq t} \langle \mathbf{P}_s^{K,n}, \mathbf{1} \rangle$. Then, taking the expectation for the stopped process at τ_n^K :

$$\mathbb{E} \left(\sup_{s \leq t \wedge \tau_n^K} \langle \mathbf{P}_s^{K,n}, \mathbf{1} \rangle \right) \leq \mathbb{E} \left(\langle \mathbf{P}_0^{K,n}, \mathbf{1} \rangle \right) + M^P \int_0^t \mathbb{E} \left(\sup_{u \leq s \wedge \tau_n^K} \langle \mathbf{P}_u^{K,n}, \mathbf{1} \rangle \right) ds,$$

implying by Grownall's lemma that:

$$\mathbb{E} \left(\sup_{s \leq t \wedge \tau_n^K} \langle \mathbf{P}_s^{K,n}, \mathbf{1} \rangle \right) \leq \mathbb{E} \left(\langle \mathbf{P}_0^{K,n}, \mathbf{1} \rangle \right) e^{M^P t} < +\infty.$$

Because the right hand side does not depend on N , this yields that $\lim_{K \rightarrow +\infty} \tau_N^K = +\infty$ a.s. (see *e.g.* [25]) and then we obtain by Fatou's lemma that

$$\mathbb{E} \left(\sup_{s \leq t} \langle \mathbf{P}_s^{K,n}, \mathbf{1} \rangle \right) \leq \mathbb{E} \left(\langle \mathbf{P}_0^{K,n}, \mathbf{1} \rangle \right) e^{M^P t} < +\infty. \quad (\text{A.1})$$

Similarly, we can prove that:

$$\mathbb{E} \left(\sup_{s \leq t} \langle \mathbf{A}_s^{K,m}, \mathbf{1} \rangle \right) \leq \mathbb{E} \left(\langle \mathbf{A}_0^{K,m}, \mathbf{1} \rangle \right) e^{M^A t} < +\infty.$$

We can now prove (1.12), for moments of order 2. From (1.10) and using Itô's formula for jump processes (*e.g.* [34, Th.5.1 P.66]), we have with the same method that:

$$\begin{aligned} \langle \mathbf{P}_t^{K,n}, \mathbf{1} \rangle^2 &\leq \langle \mathbf{P}_0^{K,n}, \mathbf{1} \rangle^2 + \int_0^t \int_E \left(\left(\langle \mathbf{P}_{s-}^{K,n}, \mathbf{1} \rangle + \frac{1}{nK} \right)^2 - \langle \mathbf{P}_{s-}^{K,n}, \mathbf{1} \rangle^2 \right) \mathbb{1}_{\theta \leq M^P} P_{s-}^{K,i} Q_B^P(ds, di, d\theta) \\ &\leq \langle \mathbf{P}_0^{K,n}, \mathbf{1} \rangle^2 + \int_0^t \int_E \left(\frac{2}{nK} \sup_{u \leq s-} \langle \mathbf{P}_u^{K,n}, \mathbf{1} \rangle + \frac{1}{n^2 K^2} \right) \mathbb{1}_{\theta \leq M^P} P_{s-}^{K,i} Q_B^P(ds, di, d\theta). \end{aligned}$$

Since the right hand side is an increasing process, we can again replace the left hand side by $\sup_{s \leq t} \langle \mathbf{P}_s^{K,n}, \mathbf{1} \rangle$. Then, taking the expectation gives:

$$\begin{aligned} \mathbb{E} \left(\sup_{s \leq t \wedge \tau_n^K} \langle \mathbf{P}_s^{K,n}, \mathbf{1} \rangle^2 \right) &\leq \mathbb{E} \left(\langle \mathbf{P}_0^{K,n}, \mathbf{1} \rangle^2 \right) + \mathbb{E} \left[\int_0^{t \wedge \tau_n^K} \sum_{i=1}^n \left(\frac{2}{nK} \sup_{u \leq s} \langle \mathbf{P}_u^{K,n}, \mathbf{1} \rangle + \frac{1}{n^2 K^2} \right) M^P P_s^{K,i} ds \right] \\ &\leq \mathbb{E} \left(\langle \mathbf{P}_0^{K,n}, \mathbf{1} \rangle^2 \right) + \int_0^t \left[2M^P \mathbb{E} \left(\sup_{u \leq s \wedge \tau_n^K} \langle \mathbf{P}_u^{K,n}, \mathbf{1} \rangle^2 \right) + \frac{1}{nK} M^P \mathbb{E} \left(\sup_{u \leq s \wedge \tau_n^K} \langle \mathbf{P}_u^{K,n}, \mathbf{1} \rangle \right) \right] ds \\ &\leq \left[\mathbb{E} \left(\langle \mathbf{P}_0^{K,n}, \mathbf{1} \rangle^2 \right) + \frac{t}{nK} M^P \mathbb{E} \left(\sup_{s \leq t \wedge \tau_n^K} \langle \mathbf{P}_s^{K,n}, \mathbf{1} \rangle \right) \right] e^{2M^P t} < +\infty. \end{aligned}$$

Similarly,

$$\mathbb{E} \left(\sup_{s \leq t} \langle \mathbf{A}_s^{K,m}, \mathbf{1} \rangle^2 \right) \leq \left[\mathbb{E} \left(\langle \mathbf{A}_0^{K,m}, \mathbf{1} \rangle^2 \right) + \frac{t}{nK} M^A \mathbb{E} \left(\sup_{s \leq t} \langle \mathbf{A}_s^{K,m}, \mathbf{1} \rangle \right) \right] e^{2M^A t} < +\infty. \quad (\text{A.2})$$

Notice that the upper bound that we obtain do not depend on K .

Step 2: Let us now consider a measurable real function f on $[0, 1]$. Using Itô's formula for SDEs with jumps (see *e.g.* [34, p. 66-67]) and (1.10) provides (1.13) in which:

$$\begin{aligned}
M_t^{K,i} &= \int_0^t \int_E \mathbb{1}_{i=k} \mathbb{1}_{\theta \leq b^P} (\sum_{j \sim i} R_{s-}^{A,K,ij}) P_{s-}^{K,i} Q_B^P(ds, dk, d\theta) - \int_0^t b^P (\sum_{j \sim i} R_s^{K,ij}) P_s^{K,i} ds \\
&\quad - \int_0^t \int_E \mathbb{1}_{i=k} \mathbb{1}_{\theta \leq [d^P (\sum_{j \sim i} R_{s-}^{A,K,ij}) - k \star \mathbf{P}_{s-}^{K,n}(x^i)]} P_{s-}^{K,i} Q_D^P(ds, dk, d\theta) \\
&\quad + \int_0^t [d^P (\sum_{j \sim i} R_s^{A,K,ij}) - k \star \mathbf{P}_s^{K,n}(x^i)] P_s^{K,i} ds
\end{aligned} \tag{A.3}$$

is a square integrable martingale with bracket given by (1.14). A similar computation can be done for $\mathbf{A}^{K,m}$ to obtain (1.15). \blacksquare

A.2 Large number of species limit

Proof of Proposition 3.2. Recall that for $n, m \geq 1$, we have:

$$\begin{aligned}
\int_0^1 f(x) d\tilde{\mathbf{P}}_t^{n,m}(x) &= \int_0^1 f(x) d\tilde{\mathbf{P}}_0^{n,m}(x) dx \\
&\quad + \int_0^t \frac{1}{n} \sum_{i=1}^n f(x^i) \left[g^P \left(\frac{1}{m} \sum_{j=1}^m m c_{i,j}^{n,m} G_{ij} \tilde{A}_s^j \right) - \frac{1}{n} \sum_{\ell=1}^n k(x^i, x^\ell) \tilde{P}_s^\ell \right] \tilde{P}_s^i ds, \\
\int_0^1 f(y) d\tilde{\mathbf{A}}_t^{n,m}(y) &= \int_0^1 f(y) d\tilde{\mathbf{A}}_0^{n,m}(y) dy \\
&\quad + \int_0^t \frac{1}{m} \sum_{j=1}^m f(y^j) \left[g^A \left(\frac{1}{n} \sum_{i=1}^n n c_{i,j}^{n,m} G_{ij} \tilde{P}_s^i \right) - \frac{1}{m} \sum_{\ell=1}^m h(y^j, y^\ell) \tilde{A}_s^\ell \right] \tilde{A}_s^j ds.
\end{aligned} \tag{A.4}$$

where conditionally on $(x^i, y^j)_{1 \leq i \leq n, 1 \leq j \leq m}$, $G_{ij} \sim \text{Bern}(\phi(x^i, y^j))$ and are independent random variables, and $c_{i,j}^{n,m}$ are independent random variables satisfying Equations (1.2) and (1.3).

Step 1: Processes are bounded. Since g^P and g^A are bounded from above respectively by M_P and M_A and since the competition terms for the pollinators are non-positive, choosing $f \equiv 1$ in the previous equation (A.4), we find that a.s.,

$$\langle \tilde{\mathbf{P}}_t^{n,m}, 1 \rangle \leq \langle \tilde{\mathbf{P}}_0^{n,m}, 1 \rangle e^{M_P t} \quad \text{and} \quad \langle \tilde{\mathbf{A}}_t^{n,m}, 1 \rangle \leq \langle \tilde{\mathbf{A}}_0^{n,m}, 1 \rangle e^{M_A t}, \tag{A.5}$$

uniformly in n and m . Moreover, from Assumption (3.2), we have that

$$\lim_{n,m \rightarrow +\infty} \langle \tilde{\mathbf{P}}_0^{n,m}, 1 \rangle = \int_{[0,1]} \bar{p}_0(x) dx \quad \text{and} \quad \lim_{n,m \rightarrow +\infty} \langle \tilde{\mathbf{A}}_0^{n,m}, 1 \rangle = \int_{[0,1]} \bar{a}_0(x) dx \quad \text{a.s..}$$

In other words, $\sup_{n,m} (\langle \tilde{\mathbf{P}}_0^{n,m}, 1 \rangle + \langle \tilde{\mathbf{A}}_0^{n,m}, 1 \rangle)$ is bounded by a finite constant a.s. and for $T > 0$, we define

$$C(T) = \sup_{n,m} \left(\langle \tilde{\mathbf{P}}_0^{n,m}, 1 \rangle e^{M_P T} + \langle \tilde{\mathbf{A}}_0^{n,m}, 1 \rangle e^{M_A T} \right) < +\infty \quad \text{a.s..} \tag{A.6}$$

Thus, the processes $(\tilde{\mathbf{P}}_t^{n,m}(dx), \tilde{\mathbf{A}}_t^{n,m}(dy))_{t \in [0, T]}$ take their values in $(\mathcal{M}_{\leq C(T)}([0, 1]))^2$ which is a compact set.

Step 2: Relative compactness in $\mathcal{C}([0, T], \mathcal{M}_{\leq C(T)}([0, 1])^2)$

Following [12] (Theorem 7.3) and using the fact that convergence in the Radon metric implies weak convergence of measures, it is sufficient to prove that

(i) $\sup_{n,m \in \mathbb{N}} \left(\langle \tilde{\mathbf{P}}_0^{n,m}, 1 \rangle + \langle \tilde{\mathbf{A}}_0^{n,m}, 1 \rangle \right)$ is bounded almost surely, and

(ii) for any continuous function f on $[0, 1]$, and for any $\varepsilon > 0$,

$$\lim_{\delta \rightarrow 0} \limsup_{n,m \in \mathbb{N}} \mathbb{P} \left(\sup_{|t-s| \leq \delta} |\langle \tilde{\mathbf{P}}_s^{n,m}, f \rangle - \langle \tilde{\mathbf{P}}_t^{n,m}, f \rangle| \geq \varepsilon \right) = 0$$

$$\lim_{\delta \rightarrow 0} \limsup_{n,m \in \mathbb{N}} \mathbb{P} \left(\sup_{|t-s| \leq \delta} |\langle \tilde{\mathbf{A}}_s^{n,m}, f \rangle - \langle \tilde{\mathbf{A}}_t^{n,m}, f \rangle| \geq \varepsilon \right) = 0$$

Point (i) follows from Equation (A.6). Concerning point (ii), notice first that

$$\mathbb{E}[\tilde{R}^{A,n,m}] = \mathbb{E} \left[\frac{1}{m} \sum_{j=1}^m m c_{i,j}^{n,m} G_{ij} \tilde{A}_s^j \right] \leq \frac{1}{m} \sum_{j=1}^m \mathbb{E}[m c_{i,j}^{n,m}] C(T) \leq \max_{n,m \in \mathbb{N}^*} \|m c^{n,m}\|_\infty C(T) < \infty,$$

which is finite from Assumption 3.1. Thus, there exists $\tilde{C} > 0$ such that $\mathbb{P}(\tilde{R}^{A,n,m} > \tilde{C})$ is sufficiently small. Then g^P is bounded on $[0, \tilde{C}]$ by some constant \tilde{M} (since it is a Lipschitz function). Thus, on $\{\tilde{R}^{A,n,m} \leq \tilde{C}\}$, for any positive continuous function f on $[0, 1]$ and any $0 \leq s \leq t \leq T$,

$$|\langle \tilde{\mathbf{P}}_t^{n,m}, f \rangle - \langle \tilde{\mathbf{P}}_s^{n,m}, f \rangle| \leq \int_s^t (\tilde{M} + \|k\|_\infty C(T)) \|f\|_\infty C(T) du.$$

Same computations can be done for the sequence of processes $(\tilde{\mathbf{A}}^{n,m})_{m \in \mathbb{N}^*}$. And these are sufficient to conclude point (ii).

Step 3: Density of the limiting values. Let us then prove that every limiting values of $(\tilde{\mathbf{P}}^{n,m}, \tilde{\mathbf{A}}^{n,m})$, denoted here by $(\bar{\mathbf{P}}, \bar{\mathbf{A}})$, is a process whose time marginals at $t > 0$ admit densities \bar{p}_t and \bar{a}_t with respect to the Lebesgue measure on $[0, 1]$. To achieve this, we dominate the measures $\tilde{\mathbf{P}}_t^{n,m}(dx)$ and $\tilde{\mathbf{A}}_t^{n,m}(dy)$ by measures with densities. For all positive continuous function f on $[0, 1]$, with arguments similar to these of (A.5), we prove that

$$\langle \bar{\mathbf{P}}_t, f \rangle \leq \langle \bar{\mathbf{P}}_0, f \rangle e^{M_P t} = \int_0^1 f(x) (p_0(x) e^{M_P t}) dx, \quad \text{a.s.}$$

$$\langle \bar{\mathbf{A}}_t, f \rangle \leq \langle \bar{\mathbf{A}}_0, f \rangle e^{M_A t} = \int_0^1 f(y) (a_0(y) e^{M_A t}) dy, \quad \text{a.s.}$$

which is sufficient to deduce the existence of densities with respect to Lebesgue measure.

Step 4: Equation satisfied by the limiting value. Let us fix $t > 0$ and f a continuous positive function on $[0, 1]$. We define the map ψ on $\mathcal{C}([0, 1], \mathcal{M}_{\leq C(T)}([0, 1])^2)$, endowed with the uniform convergence, defined by

$$\psi(\mathbf{P}, \mathbf{A}) = \left(\begin{aligned} &\langle \mathbf{P}_t, f \rangle - \langle \mathbf{P}_0, f \rangle - \int_0^t \int_0^1 f(x) [g^P((c\phi) \star \mathbf{A}_s(x)) - k \star \mathbf{P}_s(x)] d\mathbf{P}_s(x) ds \\ &\langle \mathbf{A}_t, f \rangle - \langle \mathbf{A}_0, f \rangle - \int_0^t \int_0^1 f(x) [g^A((c\phi) \star \mathbf{P}_s(x)) - h \star \mathbf{A}_s(x)] d\mathbf{A}_s(x) ds \end{aligned} \right).$$

The continuity of map ψ is straightforward once noticing that the weak convergence on $\mathcal{M}_{\leq C(T)}^2([0, 1])$ is equivalent to convergence of measures in the Kantorovich–Rubinstein distance

$$\mathcal{W}_1(\nu, \mu) = \sup \left\{ \int_0^1 f(x) d(\nu - \mu)(x) \mid f : [0, 1] \mapsto \mathbb{R}^+ \text{ Lipschitz}, Lip(f) \leq 1 \right\},$$

since $[0, 1]$ is a compact space. The function ψ is also bounded since all measures are bounded by $C(T)$.

Then, as $(\bar{\mathbf{P}}, \bar{\mathbf{A}})$ is a weak limiting value of $(\tilde{\mathbf{P}}^{n,m}, \tilde{\mathbf{A}}^{n,m})$, we obtain by definition of the weak convergence that

$$\mathbb{E} \left[\|\psi(\tilde{\mathbf{P}}^{n,m}, \tilde{\mathbf{A}}^{n,m})\|_1 \right] \xrightarrow{n,m \rightarrow +\infty} \mathbb{E} \left[\|\psi(\bar{\mathbf{P}}, \bar{\mathbf{A}})\|_1 \right]. \quad (\text{A.7})$$

On the other hand,

$$\begin{aligned} & \mathbb{E} \left[\|\psi(\tilde{\mathbf{P}}^{n,m}, \tilde{\mathbf{A}}^{n,m})\|_1 \right] \\ &= \mathbb{E} \left[\left| \int_0^t \int_0^1 f(x) \left(g^P \left(\frac{1}{m} \sum_{j=1}^m G_{ij} m c_{i,j}^{n,m} \tilde{A}_s^j \right) - g^P \left((c\phi) \star \tilde{\mathbf{A}}^{n,m} \right) \right) d\tilde{\mathbf{P}}_s^{n,m}(x) ds \right| \right] \end{aligned} \quad (\text{A.8})$$

$$+ \mathbb{E} \left[\left| \int_0^t \int_0^1 f(x) \left(g^A \left(\frac{1}{n} \sum_{j=1}^n G_{ij} n c_{i,j}^{n,m} \tilde{P}_s^j \right) - g^A \left((c\phi) \star \tilde{\mathbf{P}}^{n,m} \right) \right) d\tilde{\mathbf{A}}_s^{n,m}(x) ds \right| \right]. \quad (\text{A.9})$$

Using Assumptions 1.4, the first term (A.8) of the r.h.s can be bounded from above by

$$\begin{aligned} (\text{A.8}) &\leq \int_0^t \frac{C}{n} \sum_{i=1}^n \left[\mathbb{E} \left| \frac{1}{m} \sum_{j=1}^m \tilde{A}_s^j \left(G_{ij} (m c_{i,j}^{n,m} - c(x^i, y^j)) + c(x^i, y^j) (G_{ij} - \phi(x^i, y^j)) \right) \right| \right] ds \\ &\leq C \left[TC(T) \|m c^{n,m} - c\|_\infty \right. \\ &\quad \left. + \int_0^t \frac{1}{n} \sum_{i=1}^n \mathbb{E} \left| \frac{1}{m} \sum_{j=1}^m \tilde{A}_s^j G_{ij} m (c_{i,j}^{n,m} - c^{n,m}(x^i, y^j)) + \tilde{A}_s^j c(x^i, y^j) (G_{ij} - \phi(x^i, y^j)) \right| \right], \end{aligned}$$

with $C := \|f\|_\infty C(T) L^P$ and L^P is the Lipschitz constant of function g^P . Then $\|m c^{n,m} - c\|_\infty$ converges to 0 when n, m grow to ∞ , and it will be sufficiently small for n, m large enough. Finally, from Cauchy-Schwarz inequality, Assumptions 3.1 and 1.1, and denoting by $\text{Var}_{x,y}(A) = \text{Var}(A | (x^i, y^j)_{i \leq n, j \leq m})$, we find for n, m sufficiently large,

$$\begin{aligned} (\text{A.8}) &\leq \varepsilon + \int_0^t \frac{C}{n} \sum_{i=1}^n \mathbb{E} \left[\text{Var}_{x,y} \left(\frac{1}{m} \sum_{j=1}^m \tilde{A}_s^j G_{ij} m c_{i,j}^{n,m} \right) \right]^{1/2} + \mathbb{E} \left[\text{Var}_{x,y} \left(\frac{1}{m} \sum_{j=1}^m \tilde{A}_s^j c(x^i, y^j) G_{ij} \right) \right]^{1/2} \\ &\leq \varepsilon + \int_0^t \frac{C}{n} \sum_{i=1}^n \mathbb{E} \left[\frac{C(T)^2}{m^2} \sum_{j=1}^m V_{max} \right]^{1/2} + \mathbb{E} \left[\frac{C(T)^2 \|c\|_\infty^2}{m^2} \sum_{j=1}^m \phi(x^i, y^j) (1 - \phi(x^i, y^j)) \right]^{1/2} \\ &\leq \varepsilon + CT \frac{C(T) (V_{max}^{1/2} + \|c\|_\infty \|\phi(1 - \phi)\|_\infty^{1/2})}{m^{1/2}} \\ &\leq 2\varepsilon \text{ for } n, m \text{ sufficiently large.} \end{aligned}$$

The second term (A.9) can be treated similarly. This finally proves that $\mathbb{E} \left[\|\psi(\tilde{\mathbf{P}}^{n,m}, \tilde{\mathbf{A}}^{n,m})\|_1 \right]$ converges to 0 when n, m go to ∞ . In addition with (A.7), we deduce that $\psi(\bar{\mathbf{P}}, \bar{\mathbf{A}}) = (0, 0)$ a.s. In other words, the limiting value satisfies Equation (3.3) a.s.

Step 5: Uniqueness of the solution of (3.3). It remains to prove the uniqueness of the solution to (3.3) to conclude. To this aim, let us take $(\mathbf{P}^1, \mathbf{A}^1)$ and $(\mathbf{P}^2, \mathbf{A}^2)$ two deterministic measures, weak

solutions to (3.3) and with identical initial conditions. Let us denote by ρ the Radon metric between two measures ν and μ on $\mathcal{M}_F([0, 1])^2$:

$$\rho(\nu, \mu) = \sup \left\{ \int_0^1 f(x) d(\nu - \mu)(x) \mid f : [0, 1] \mapsto [-1, 1] \text{ continuous} \right\}.$$

With straightforward computations, for any continuous function $f : [0, 1] \mapsto [-1, 1]$, we can find some finite constants C_1, C_2 , independent from t and f , such that

$$\begin{aligned} |\langle \mathbf{P}_t^1 - \mathbf{P}_t^2, f \rangle| &= \left| \int_0^t \int_0^1 f(x) [g^P(c\phi \star \mathbf{A}_s^1(x)) - k \star \mathbf{P}_s^1] d\mathbf{P}_s^1(x) ds \right. \\ &\quad \left. - \int_0^t \int_0^1 f(x) [g^P(c\phi \star \mathbf{A}_s^2(x)) - k \star \mathbf{P}_s^2] d\mathbf{P}_s^2(x) ds \right| \\ &\leq C_1 \int_0^t \rho(\mathbf{P}_s^1, \mathbf{P}_s^2) ds + \int_0^t \int_0^1 (L^P |c\phi \star (\mathbf{A}_s^1 - \mathbf{A}_s^2(x))| + |k \star (\mathbf{P}_s^1 - \mathbf{P}_s^2)(x)|) d\mathbf{P}_s^2(x) ds \\ &\leq C_2 \int_0^t (\rho(\mathbf{P}_s^1, \mathbf{P}_s^2) + \rho(\mathbf{A}_s^1, \mathbf{A}_s^2)) ds, \end{aligned}$$

since $x \mapsto f(x)(g^P(c\phi \star \mathbf{A}_s^1(x)) - k \star \mathbf{P}_s^1(x))$ are continuous bounded functions on $[0, 1]$ for all $s \in [0, T]$, and k and $c\phi$ are continuous bounded functions on $[0, 1]^2$. Same computations can be done with \mathbf{A}^1 and \mathbf{A}^2 , then taking the supremum over all f , we find a constant $C_3 > 0$ such that

$$\rho(\mathbf{P}_t^1, \mathbf{P}_t^2) + \rho(\mathbf{A}_t^1, \mathbf{A}_t^2) \leq C_2 \int_0^t (\rho(\mathbf{P}_s^1, \mathbf{P}_s^2) + \rho(\mathbf{A}_s^1, \mathbf{A}_s^2)) ds.$$

We conclude with Gronwall inequality that $\rho(\mathbf{P}_t^1, \mathbf{P}_t^2) + \rho(\mathbf{A}_t^1, \mathbf{A}_t^2) = 0$ for all $t \in [0, T]$. In other words, $(\mathbf{P}^1, \mathbf{A}^1)$ and $(\mathbf{P}^2, \mathbf{A}^2)$ are identical, and the solution to (3.3) is unique.

This ends the proof. ■

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