

# Does phenology explain plant–pollinator interactions at different latitudes? An assessment of its explanatory power in plant–hoverfly networks in French calcareous grasslands

Natasha de Manincor, Nina Hautekeete, Yves Piquot, Bertrand Schatz, Cédric Vanappelghem, François Massol

## ▶ To cite this version:

Natasha de Manincor, Nina Hautekeete, Yves Piquot, Bertrand Schatz, Cédric Vanappelghem, et al.. Does phenology explain plant–pollinator interactions at different latitudes? An assessment of its explanatory power in plant–hoverfly networks in French calcareous grasslands. Oikos, 2020, 129 (5), pp.753-765. 10.1111/oik.07259 . hal-02942299

## HAL Id: hal-02942299 https://hal.science/hal-02942299

Submitted on 6 Nov 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Peer Community In

**RESEARCH ARTICLE** 



Cite as: Natasha de Manincor, Nina Hautekeete, Yves Piquot, Bertrand Schatz, Cédric Vanappelghem, François Massol. Does phenology explain plant-pollinator interactions at different latitudes? An assessment of its explanatory power in planthoverfly networks in French calcareous grasslands. Zenodo 10.5281/zenodo.2543768 version 4, peer-reviewed and recommended by PCI Ecology (2019).

Posted: 22th November 2019

Recommender: Anna Eklöf

Staniczenko

Reviewers: Ignasi Bartomeus and Phillip P.A.

Correspondence: natasha.demanincor@gmail.com Does phenology explain plant-pollinator interactions at different latitudes? An assessment of its explanatory power in plant-hoverfly networks in French calcareous grasslands

Natasha de Manincor<sup>1</sup>, Nina Hautekeete<sup>1</sup>, Yves Piquot<sup>1</sup>, Bertrand Schatz<sup>2</sup>, Cédric Vanappelghem<sup>3</sup>, François Massol<sup>1,4</sup>

<sup>1</sup> Université de Lille, CNRS, UMR 8198 - Evo-Eco-Paleo, F-59000 Lille, France <sup>2</sup> CEFE, EPHE-PSL, CNRS, University of Montpellier, University of Paul Valéry Montpellier 3, IRD, Montpellier, France

<sup>3</sup> Conservatoire d'espaces naturels Nord et du Pas-de-Calais, 160 rue Achille Fanien - ZA de la Haye, 62190 LILLERS

<sup>4</sup> Univ. Lille, CNRS, Inserm, CHU Lille, Institut Pasteur de Lille, U1019 - UMR 8204 - CIIL - Center for Infection and Immunity of Lille, F-59000 Lille, France

This article has been peer-reviewed and recommended by *Peer Community in Ecology* 

#### ABSTRACT

For plant-pollinator interactions to occur, the flowering of plants and the flying period of pollinators (i.e. their phenologies) have to overlap. Yet, few models make use of this principle to predict interactions and fewer still are able to compare interaction networks of different sizes. Here, we tackled both challenges using Bayesian Structural Equation Models (SEM), incorporating the effect of phenological overlap in six plant-hoverfly networks. Insect and plant abundances were strong determinants of the number of visits, while phenology overlap alone was not sufficient, but significantly improved model fit. Phenology overlap was a stronger determinant of plant-pollinator interactions in sites where the average overlap was longer and network compartmentalization was weaker, i.e. at higher latitudes. Our approach highlights the advantages of using Bayesian SEMs to compare interaction networks of different sizes along environmental gradients and articulates the various steps needed to do so.

*Keywords:* Bayesian model, interaction probability, latent block model, latitudinal gradient, mutualistic network, phenology overlap, species abundance, structural equation model.



## Introduction

Understanding how phenology determines species interactions is a central question in the case of mutualistic networks. In plant-pollinator networks, phenology shapes their temporal and spatial limits, thus defining the area and the period along the season in which interactions preferably occur (Olesen et al. 2011; Ogilvie & Forrest 2017). Since plant and pollinator phenologies are not equally affected by changes in environmental cues, partial or total phenological mismatches can occur as a result of environmental changes such as climate change (Parmesan 2007; Rafferty 2017). Phenological advances indeed increase at higher latitudes, as a response to the acceleration of warming temperature along the same gradient (Post et al. 2018), increase phenological mismatch, and have the potential to threaten the synchrony needed for effective pollination (Hutchings et al. 2018). Such environmental changes can thus drastically alter pollinator interactions through modified temporal overlap between pollinators and their floral resources leading, in extreme cases, to local extinctions (Memmott et al. 2007) and the ensuing absence of the partner species at the location and/or time at which the interaction should have taken place (Willmer 2012; Miller-Struttmann et al. 2015; Rafferty et al. 2015; Hutchings et al. 2018).

Because phenological match is crucial to plant-pollinator interactions, and thus ultimately to pollinators' fitness, pollinators have to adapt to phenological shifts either through interaction with other plant species (Rafferty *et al.* 2015) or through changes of their own phenology (Bartomeus *et al.* 2011). Phenology can then influence dynamical network properties, such as the stability and the coexistence of species, through changes in network topology (Encinas-Viso *et al.* 2012). Moreover, phenology predictably affects network compartmentalization as different phenophases likely correspond to different compartments when networks are considered on an annual scale (Martín González *et al.* 2012).

Despite considerable theoretical advances, there are few models available to predict the probability of interaction in plant-pollinator networks (Staniczenko *et al.* 2017; Cirtwill *et al.* 2019) and fewer still able to make comparisons between networks. Due to their complexity and variation among years (Chacoff *et al.* 2017), most studies of mutualistic networks have focused on predicting and comparing classic network metrics (nestedness, connectance, modularity, etc.) which are all influenced by network size, i.e. the number of plant and insect species (Fortuna *et al.* 2010; Staniczenko *et al.* 2013; Poisot & Gravel 2014; Astegiano *et al.* 2015). Moreover, few studies have compared interaction networks along environmental gradients (Devoto *et al.* 2005; Schleuning *et al.* 2012; Sebastián-González *et al.* 2015; Pellissier *et al.* 



2017). In order to compare networks of different sizes, a better alternative is to switch from network-derived metrics to the comparison of the probability of interaction given by regression models, which can consider multiple factors and latent variables and assume that the sampled data are just part of a larger unobserved dataset (Grace *et al.* 2010).

Calcareous grasslands are characterized by highly diverse plant communities with a high proportion of entomophilous species (Baude *et al.* 2016), thus they are a convenient model for such studies. Most plant-insect pollinator networks involve bee species (Anthophila), but recent studies have also pointed out the importance of hoverflies (Diptera: Syrphidae), which pollinate a large spectrum of wild flowering species (Klecka *et al.* 2018a) and crops (Jauker & Wolters 2008; Rader *et al.* 2011). They usually behave opportunistically, i.e. from being pollen generalists to specialists, only limited by morphological constraints (Iler *et al.* 2013; Klecka *et al.* 2018a; Lucas *et al.* 2018). Indeed, their generalist behaviour, at the species level, could be the result of individually specialized diets, since most pollen retrieved on hoverfly individuals usually comes from a single plant taxon (Lucas *et al.* 2018) and depends on flower availability and phenology (Cowgill *et al.* 1993; Colley & Luna 2000; Lucas *et al.* 2018). Moreover, some hoverflies have preferences regarding plant colour, morphology and inflorescence height (Branquart & Hemptinne 2000; Colley & Luna 2000; Lunau 2014; Klecka *et al.* 2018b, a).

Here we study the consequences of environmental gradients on plant-pollinator interactions, focusing on how phenology overlap affects interactions between plants and insects in six calcareous grassland sites distributed along a latitudinal gradient. We obtained plant and insect phenologies, abundances, and interactions in all sites from April to October 2016. We modelled plant-pollinator interaction networks following a Bayesian Structural Equation Modelling approach (SEM) using latent variables, i.e. unobserved variables (Grace *et al.* 2010). SEM is a multivariate technique used to test several hypotheses in ecological studies. SEM analysis involves cause-effect equations to evaluate multiple causal relationship (Grace 2006; Eisenhauer *et al.* 2015) using observed and latent variables to explain some other observed variables (Grace 2006). SEM can be used to choose among competing models (Grace & Bollen 2008). Thus, SEM are well suited for studying the complexity of ecological networks. To test whether phenology affects network compartmentalization, we looked for species subgroups using a latent block model (LBM) which is among the best clustering methods for weighted networks (Leger *et al.* 2015).

The comparison of 16 SEMs and the analysis of LBMs of sampled networks evinced that phenology overlap is an important determinant of plant-pollinator interactions,



but is less informative than species abundances and performs heterogeneously among sites. Our results suggest that the use of SEMs to compare networks of different sizes along an environmental gradient is an innovative approach which can help understand the structure of plant-pollinator networks.

## Methods

#### Study sites

We sampled plant and hoverfly species in six areas (Fig. S1) of 1 hectare each in different French regions: two sites in Hauts-de-France (Les Larris de Grouches-Luchuel, thereafter noted LAR, 50°11'22.5"N 2°22'02.9"E and Regional natural reserve Riez de Noeux les Auxi, noted R, 50°14'51.85"N 2°12'05.56"E, in départements Pas-de-Calais and Somme), two sites in Normandie (Château Gaillard – le Bois Dumont, noted CG, 49°14'7.782"N 1°24'16.445"E and les Falaises d'Orival, noted FAL, 49°04'40.08"N 1°33'07.254"E, départements: Eure and Seine Maritime) and two sites in Occitanie (Fourches, noted F, 43°56'07.00"N 3°30'46.1"E and Bois de Fontaret, noted BF, 43°55'17.71"N 3°30'06.06"E, départment: Gard). The six sites are included in the European NATURA 2000 network, a network of preserved areas designated to protect a number of habitats and species representative of European biodiversity. The four sites in Hauts-de-France and Normandie are managed by the Conservatoire d'espaces naturels of Normandie, Picardie and Nord – Pas-de-Calais and the sites in Occitanie by the CPIE Causses méridionaux. We sampled each site once a month from April to October 2016, except for the site of Riez that was sampled from May to October.

#### Plant-hoverfly observations and sampling

To collect information at the community level, in each site and at each session we realized: (i) a botanic inventory of the flowering species, recorded their abundances and the total flower covering in the area and (ii) a pollinator sampling using a hand net along a variable transect walk.

Flowering plants were identified at the species level. We recorded the abundances of all flowering species. At first, we estimated the total percentage of surface covered by all flowering species in the selected area. We then estimated the relative abundance of each flowering species. We used Braun-Blanquet coefficients of abundance-dominance, ranked from i to 5 (most abundant coefficient class) (van der Maarel 1975, 1979; Mucina *et al.* 2000), to rank flowering species. We converted the coefficients to percentage intervals and then in mean values of percentage cover classes (Table S1): coefficient **5** = 75-100%, coeff **4** = 50-75%, coeff **3**=25-50%, coeff **2** = 10-25%, coeff **1** =



1-10%, coeff + = few individuals less than < 1%, coeff i = 1 individual. All inventories were realized by the same surveyors to avoid biases.

Pollinator observations were performed by the same team of 3-5 persons each day. The surveyors walked slowly around any potential attractive resource patch included in the selected 1-hectare area for 4h each day. We split the sampling period into 2 hours in the morning (about 10-12h) and 2 hours in the afternoon (about 14-16h) to cover the daily variability of both pollinator (bees and hoverflies, which are more active in the morning than in the afternoon; D'Amen et al. 2013) and flower communities. Sampling took place when we had suitable weather conditions for pollinators (following Westphal et al. 2008). We sampled all flower-visiting insects and we recorded observed interactions. All sampled insects were immediately put individually in a killing vial with ethyl acetate and were later prepared and pinned in the laboratory and identified at the species level by expert taxonomists. Even if we collected both bees and hoverflies, in this study we focus on hoverflies only (since at the moment of the study bees were not identified at the species level yet). Overall, we sampled for 41 days, equivalent to about 164 hours in the field (all the surveyors collected at the same time). For all analyses described here, we only used the list of visited herbaceous plant species and hoverflies which were found visiting a plant. Despite their rarity and even if hoverflies are known to prefer open flowers (Branquart & Hemptinne 2000), we also considered the interactions between hoverflies and plant species of the Fabaceae family because we observed in the field that they visited Fabaceae species that were already opened by other insects, e.g. by large bee species, such as Eucera sp. (de Manincor, personal observation).

#### Plant – hoverfly networks

For each site, we constructed an interaction network consisting of all pairs of interacting plant and insect species, pooling data from all months. A pair of species (i,j) was connected with intensity  $v_{ij}$  when we recorded  $v_{ij}$  visits of insect species i on plant species j in the site. We calculated the network specialization index, H2' (Blüthgen *et al.* 2006) using the H2fun function implemented in the bipartite package (Dormann *et al.* 2009; R Core Team 2018). We obtained the *d*-value (Kullback-Leibler divergence between the interactions of the focal species and the interactions predicted by the weight of potential partner species in the overall network) and the *dmax*-value (maximum d-value theoretically possible given the observed number of interactions in the network) using the dfun function in the bipartite package (Dormann *et al.* 2009). We did not use the d' values provided by this package as they sometimes yielded spurious results based on the computation of the minimal d value (e.g. reporting low d' for species with only one partner in the network).We then



manually calculated the standardized specialization index d' (Blüthgen *et al.* 2006) for each plant and insect species as the ratio of the *d*-value to its corresponding *dmax*-value.

We calculated the modularity of the network and the associated partition of species into modules using the cluster leading eigen method for modularity optimization implemented in the igraph package (Csardi & Nepusz 2006; Newman 2006). Modularity optimization can help identify strong, simple divisions of a network into relatively independent sub-networks by looking for highly interconnected subnetworks. However, modules are not meant to inform about more subtle groupings among the species, e.g. particular avoidance of interactions between insects of group A and plants of group 1. In order to detect such groups, we implemented latent block models (LBM) using the BM poisson method for Poisson probability distribution implemented in the blockmodels package (Leger et al. 2015). Blocks are calculated separately for the two groups (insect and plant) based on the number of visits (i.e. a weighted network). The algorithm finds the best divisions of insects and plants through fitting one Poisson parameter in each block of the visit matrix, thus essentially maximizing the ICL (Integrated Completed Likelihood; Biernacki et al. 2000; Daudin et al. 2008). The LBM script is given in Supplementary Information (Appendix S3). All analyses were performed in R version 3.3.3 (R Core Team 2018).

#### Plant and hoverfly abundances and phenology overlap

We calculated plant abundance using information about the abundance-dominance recorded in the field following the methodology of Braun-Blanquet presented above. We transformed the coefficients of abundance in percentages (Table S1): we used the mean of the percentage corresponding to each class. We then calculated the relative abundance ( $A_P$ ) of each flowering plant species as the ratio of the focal species cumulated abundance to total flower abundance during its flowering season. For hoverflies, we used the recorded number of visiting individuals (total abundance) and their presence (recorded months) along the season to calculate their average abundance during months when they were present ( $A_H$ ).

We refer to plant phenology as their flowering period and insect phenology as the flying period. We considered only flowering plants which had been visited by pollinators. For the pollinators, we considered only hoverflies which were found in interaction. To build the species phenology tables for both plants and hoverflies, we merged the information provided by two sources of data (field data and the literature): we used the observed phenology of both plants and insects during the field session as the only source of information for plants (plants visited by insects and plants found in



the botanic inventory in the site at that date), and we complemented the hoverfly phenology with information provided by the Syrph the Net Database (Speight *et al.* 2016). We then built the phenology overlap (PO) matrix based on the species phenology tables by calculating the number of phenologically active months that are shared by each pair of insect and plant species along the season.

#### **Bayesian Structural Equation Modelling (SEM)**

SEM is a confirmatory technique that involves cause-effect equations to evaluate multivariate hypotheses in ecological networks (Grace 2006). The primary interest of SEM analyses lies in its ability to compare different causal models between the same sets of explanatory and explained variables. Another important feature of SEM is that they can relate data through latent variables, *i.e.* variables which are not measured in the model and which represent underlying causes or effects, coupled with observed variables (Grace 2006; Grace *et al.* 2010). SEM can now be assessed using Bayesian approaches and parameters estimated using MCMC (Markov Chain Monte Carlo)(Grace *et al.* 2010; Fan *et al.* 2016).

In our study, we modelled hoverfly-plant interaction networks using a SEM approach (Fig. 1) with latent variables linking the number of visits per plant-pollinator species pair to abundance and phenology overlap (PO) data through a first latent table representing probabilities of interactions, another latent table representing the possible interactions between plant and pollinators (as a realization of the aforementioned interaction probability matrix), and a third latent table yielding the expected number of visits per plant-pollinator species pair (*i.e.* the intensity of interactions). We used the term latent tables to describe latent variables organized as insect x plant tables, such as the expected number of visit matrix.



**Figure 1.** Summary diagram of the SEM model. We estimated 4 effects: the effect of plant abundance (AP  $\rightarrow \lambda ij$ , coefficient  $\lambda P$ ), the effect of insect (hoverflies) abundance on the intensity of visits (AH  $\rightarrow \lambda ij$ ,  $\lambda H$ ), the effect of phenology overlap on the intensity of visits (PO  $\rightarrow \lambda ij$ ,  $\lambda PO$ ) and the effect of phenology overlap on the probability of interaction (PO  $\rightarrow Iij$ ,  $\mu PO$ ). The phenology overlap (PO) is the number of phenologically active months that are shared by each pair of insect and plant species along the season. The intensity of visits ( $\lambda ij$ ) and the probability of interaction are latent variables in the model. Effect-i and effect-p are random effects calculated by the model which represent the insect and plant species identities. The Iij (Possible interactions) is a binary variable and the Vij (visits observed) follow a Poisson distribution with an expected value given when the probability of interaction is predicted as "true". Rectangles represent observed variables while ovals represent unobserved influences.





In this model, we considered that PO had an effect on possible interactions ( $I_{ij}$ ) and the number of visits ( $\lambda_{ij}$ ) – a longer overlap is intuitively expected to drive a higher probability of interaction and a larger number of visits. Interaction probabilities were also assumed to depend on two random effects (plant and insect species identities,  $E_i$ and  $E_j$ ), to represent heterogeneity of species degrees (*i.e.* the number of links) in the network. We modelled the possibility of interaction  $I_{ij}$  between insect species *i* and plant species *j* (*i.e.*  $I_{ij} = 1$  when species *i* and *j* can interact) as a Bernoulli random variable of probability  $\mu_{ij}$  given by:

$$logit(\mu_{ij}) = \mu_0 + \mu_{PO} PO_{ij} + E_i + E_j$$

where logit is the usual logistic transformation (log(x/(1-x)),  $\mu_0$  is the intercept of this relation,  $\mu_{PO}$  is the coefficient measuring the effect of PO, and  $E_j$  and  $E_j$  are the random effects associated with insect species i and plant species j respectively.

The number of visits  $V_{ij}$  was assumed to depend on plant and hoverfly abundances, as more abundant species are expected to be more often sampled (and thus more often recorded "in interaction"). Please note that we only linked abundances to the number of visits,  $V_{ij}$ , and not to the possibility of interaction  $I_{ij}$ , because the aim of the latter latent table is to capture "forbidden links", while detectability and sampling effects are supposed to be captured by the statistical model of the number of interactions. We integrated species abundances as predictor variables in order to assess the effect of PO on the number of visits, such as species abundances.  $V_{ij}$  was modelled as a Poisson random variable to allow for sampling variability, with a conditional mean  $\lambda_{ij}$  (the intensity of visits that can occur) given by:

$$\log(\lambda i j) = \lambda_0 + \lambda_H A_{H,i} + \lambda_P A_{P,j} + \lambda_{PO} \log(1 + PO_{ij})$$

where  $\lambda_0$  is the intercept of this relation,  $\lambda_H$  is the coefficient measuring the effect of hoverfly abundance  $A_H$ ,  $\lambda_P$  is that of plant abundance  $A_P$ , and  $\lambda_{PO}$  is the coefficient of the effect of PO.

Possible interactions ( $I_{ij}$ ) and the intensity of visits ( $\lambda_{ij}$ ) are multiplied to obtain the unconditional mean number of recorded visits, *i.e.*  $V_{ij}$  is then obtained as a Poisson draw of mean  $I_{ij} \lambda_{ij}$ .

Overall we estimated four main parameters: the effect of phenology overlap on the probability of interaction ( $PO \rightarrow I_{ij}$ ,  $\mu_{PO}$ ), the effect of phenology overlap on the intensity of interactions ( $PO \rightarrow \lambda_{ij}$ ,  $\lambda_{PO}$ ), the effect of plant abundance on the intensity of interactions ( $A_P \rightarrow \lambda_{ij}$ , coefficient  $\lambda_P$ ) and the effect of insect (hoverflies) abundance on the intensity of interactions ( $A_H \rightarrow \lambda_{ij}$ ,  $\lambda_{H}$ ).



We used the jags function (R2jags package), which provides an interface from R to the JAGS library for Bayesian data analysis, to estimate model parameters. JAGS (Plummer 2003) uses a Markov Chain Monte Carlo algorithm to generate samples from the posterior distribution of the parameters. We ran two Markov chains with  $10^6$  iterations per chain to check for model convergence. The code of the model is given in Supplementary Material (Appendix S1 and S2).

#### Model and parameter comparison

We estimated the 16 models that included all combinations of 0 and 4 of the abovementioned effects to understand which effects were more likely to play a role in the structuring of the network. The goodness-of-fit of these models were compared using the leave-one-out cross-validation criterion (LOO) calculated using the R package 100 using Pareto smoothed importance sampling for regularizing importance weights (Vehtari et al. 2017). The LOO criterion is a fully Bayesian method to compare models of different complexities and to estimate prediction accuracy using the log-likelihood evaluated at the posterior simulations of the parameter values (Vehtari et al. 2017). Models can thus be ranked according to their LOO scores, with the best model being the one with the lowest LOO value. The LOO criterion is analogous to the classic Akaike and Bayesian Information Criteria, which are used to compare frequentist models, but can instead be applied to Bayesian models, without suffering the instability issues of the Deviance Information Criterion which used to be the main information criterion for Bayesian models(Vehtari et al. 2017). To rank the models, we then calculated the  $\Delta LOO$  (noted  $\Delta_i$ ) as  $\Delta_i = LOO_i - LOO_{min}$  (following Burnham & Anderson 2004), where  $LOO_{min}$  is the minimum of the  $LOO_i$  values among the 16 models. We used  $\Delta_i$  to obtain model weights  $\omega_i$ , following the Akaike weight methodology (Burnham & Anderson 2002):

$$\omega_i = \frac{e^{-\Delta_i/2}}{\sum e^{-\Delta_i/2}}$$

We then summed weights ( $w_H$ ) over all models that incorporated a given focal parameter to ascertain the plausibility of the effect associated to this parameter. We used this sum to evaluate the null hypothesis (H0) that a given factor has no effect on the plant-pollinator interactions by comparing the sum of weights to null expectations, based on the fact that each tested effect is incorporated in exactly half of the tested models. The effect is considered *plausible* when  $w_H > 0.5$ , *implausible* otherwise, *likely* when  $w_H > 0.73$ , and *unlikely* when it corresponds to a value of 0.27 or lower, following Massol *et al.* (2007).



#### Predictive power analysis

We tested the predictive power of the models we built by making predictions for the  $I_{ii}$  table and checking their validity using a binarized version of the visit table  $V_{ii}$ . Predictions were obtained by defining a threshold on interaction probability  $\mu_{ij}$ : values found above the threshold were predicted as occurring interactions, values below the threshold as no interaction. The threshold probability value was found by maximizing the sum of model specificity and sensitivity. We computed accuracy statistics (sensitivity, specificity, omission rate, area under the ROC curve [AUC]) in two situations: (i) when predicting data for the site that was used to build the model (selfvalidation; e.g. predicting interaction data in the site of Riez based on the model developed for this site) and (ii) when predicting data for the other site from the same region (cross-validation; e.g. predicting data for the LAR site based on the model for the R site). We performed theses analyses using the SDMTools package in R. We only used the set of best models (LOO < 4) found for each site to predict the interactions in the other site through a multimodel averaging approach. We obtained the threshold probability using optim.tresh function with option max.sensitivity+specificity.

## Results

#### Plant-hoverfly networks and phenology overlap

At the end of the field campaign we had collected 1584 hoverflies and recorded 1668 interactions between 76 hoverfly species and 115 plant species overall (Table 1, Table S2). The number of sampled hoverfly and plant species varied between sites and among regions. In Normandie we generally sampled a higher number of hoverflies than in the other two regions (Table 1) and the maximum number of visits recorded in the site of FAL was 47 (between Helophilus pendulus and Scabiosa columbaria, Fig. S2) and in the site of CG was 22 (between Eristalis tenax and S. columbaria and between Sphaerophoria scripta and Leontodon hispidus, Fig. 2). We observed the highest diversity of both plants and hoverflies in Occitanie and the lowest diversity of hoverflies in Hauts-de-France. Despite the high species diversity in Occitanie, the total number of interactions recorded in these sites (BF and F) is not the highest recorded in the field (Table 1): the maximum number of visits in the site of BF was 10 (between Spherophoria scripta and Helichrysum stoechas, Fig. S3) and 12 in the site of F (between Syrphus ribesii and Bellis perennis, Fig. 3). In the two southern sites we also recorded the lowest connectance values (BF: 0.07 and F: 0.08) of all six sites, with the highest connectance observed in the site of R (R 0.16; LAR 0.13; CG 0.13; FAL 0.12). The maximum number of visits recorded in the site of LAR was 12 (between Syrphus



*ribesii* and *L. hispidus*, Fig. S4) and in the site of R was 17 (between *Syritta pipiens* and *Asperula cynanchica*, Fig. S5).

In spite of differences in diversity and the number of interactions, the overall level of specialization (H2 index) did not show a high variation among the 6 networks (range: 0.32 – 0.37). However, we found that the sites in Occitanie (BF and F) had a higher average degree of specialization (d') for both insect (BF 0.63 and F 0.57) and plant species (BF 0.58 and F 0.48). The sites in Occitanie also had a higher modularity (BF 0.51 and F 0.48) than the ones in Normandie (CG 0.34 and FAL 0.23) and Hauts-de-France (LAR 0.37 and R 0.34; Table 1). Given that these statistics only compare 6 sites, none of these assessments can be properly statistically tested, but the importance of the differences among sites is highly suggestive of a difference in average specialization and modularity. We found that plant phenology is generally shorter in all sites than that of hoverflies (Table 1). The phenology overlap was shorter in Occitanie (BF and F) than in the other sites (Table 1).

Illustrations of the block clustering provided by the LBM analysis (Latent Block Model) are shown in Fig. 2 and 3 in the main text and in Fig. S2 to S5 in Supplementary Information. We found different numbers of blocks in plants and hoverflies among sites: the BF site had 2 insect blocks and 2 plant blocks (Fig. S3); the F site had 4 of both (Fig. 3); the CG and R sites had 3 blocks for the plants and 4 blocks for the insects in (Fig. 2 and S5); the FAL site had 4 plant blocks and 3 insect blocks (Fig. S2); the LAR site had 3 blocks for the plants and 2 for the insects (Fig. S4).



**Table 1.** Summary table of results obtained in each site (Bois de Fontaret [BF] and Fourches [F] in Occitanie, Château Gaillard [CG] and Falaises [FAL] in Normandie, Larris [LAR] and Riez [R] in Hauts-de-France). H2 ' and d' indices refer to specialization indices described by Blüthgen *et al.* (2006) and implemented in the R package bipartite (Dormann *et al.* 2009). The modularity score was obtained using the leading-eigenvector method described by Newman (2006) and implemented in the igraph package (Csardi & Nepusz 2006). LBM refers to latent block modelling as implemented in the R package blockmodels (Leger *et al.* 2015).

		Collected data			Specialization index		Species phenology			Modularity analysis	LE	BM		
Site	Region	Sampled insects	Insect species	Plant species	Recorded Interactions	H2' index	d' Insects (average + sd)	d' Plants (average + sd)	Insect (average + sd)	Plant (average + sd)	Phenology overlap (PO) (average + sd)	modularity score	blocks I	blocks P
BF	Occitanie	197	40	43	198	0.37	$0.63 \pm 0.17$	$0.58 \pm 0.17$	$5.25 \pm 1.51$	$2.14 \pm 1.04$	1.77 ± 1.03	0.53	2	2
F	Occitanie	223	36	49	286	0.33	$0.57 \pm 0.18$	$0.48 \pm 0.19$	$5.61 \pm 1.54$	2.08 ± 1.13	$1.78 \pm 1.14$	0.48	4	4
CG	Normandie	295	32	25	297	0.34	$0.40 \pm 0.21$	$0.47 \pm 0.18$	$6.03 \pm 1.00$	3.28 ± 1.24	3.02 ± 1.17	0.34	4	3
FAL	Normandie	363	34	30	374	0.32	$0.40 \pm 0.18$	$0.41 \pm 0.18$	$6.06 \pm 1.13$	3.57 ± 1.59	3.23 ± 1.51	0.23	3	4
LAR	Hauts-de- France	220	24	33	220	0.36	0.48 ± 0.19	0.45 ± 0.15	6.38 ± 0.82	3.18 ± 1.38	2.99 ± 1.36	0.37	2	3
R	Hauts-de- France	286	22	29	293	0.32	0.39 ± 0.16	0.40 ± 0.16	5.55 0.74	3.38 ± 1.47	3.11 ± 1.45	0.34	4	3
	Total	1584	76	117	1668									



**Figure 2.** Block clustering provided by LBM in the site of Chateau Gaillard (CG, Normandie) overlaid on a heatmap of species phenology overlap. The LBM algorithm finds the best division for the group of insects and plants independently through fitting Poisson parameters in each block maximizing the likelihood (ICL). Insect species are displayed in rows and plant species in columns, following their degree (number of partners). The blocks of insects and the blocks of plants are separated by solid black lines. Colours correspond to the number of months that are shared by each pair of plant and insect species (PO, phenology overlap), with higher PO corresponding to darker colours. Numbers are the number of visits observed in the field for a given plant-insect pair. Complete species names are reported in Table S2.





**Figure 3.** Block clustering provided by LBM in the site of Fourches (F, Occitanie), overlaid on a heatmap of species phenology overlap. Insect species are displayed in rows and plant species in columns, following their degree (number of partners). The blocks of insects and the blocks of plants are separated by solid black lines. Colours correspond to the number of months that are shared by each pair of plant and insect species (PO, phenology overlap), with higher PO corresponding to darker colours. Numbers are the number of visits observed in the field for a given plant-insect pair. Complete species names are reported in Table S2.





#### Model ranking and comparison of parameters in each site

For each site we compared the 16 models using the LOO criterion (Table 2,  $\Delta$ LOO values). We found that models 1, 2 and 4 had consistently better goodness-of-fit than the others. The model incorporating all effects except the effect of phenological overlap on the probability of interaction (Model 4:  $\lambda_{ii} \sim A_H + A_P + PO$ , Table 2) was the best model in the sites of CG, FAL and LAR. In the two southern sites (BF and F), we found that the model incorporating all effects except that of phenological overlap on the intensity of visits (Model 1:  $\lambda_{ii} \sim A_H + A_P / I_{ij} \sim$  PO, Table 2), was the best one. The model incorporating all effects (Model 0:  $\lambda_{ii} \sim A_H + A_P + PO / I_{ij} \sim PO$ , Table 2) was found as the best one only in the site of R, but was a suitable model ( $\Delta LOO < 4$ ) in all the other sites (Table 2). We also compared the sum of model weights of the four parameters among sites (Table 2, Effects weight). We found that the effect of insect abundance on the intensity of interaction  $(A_H \rightarrow \lambda_{\mu})$  is always likely (*i.e.* the sum of their weights is always higher than 0.73, Table 2) and of large effect size in all sites (standardised coefficient higher than 1, Fig. 4). Likewise, we found that the effect of plant abundance on the intensity of interaction ( $A_P \rightarrow \lambda_{ii}$ ) was always likely and had large effect size in most part of sites, except in the site of F ( $w_H$  = 0.59, Table 2; standardised coefficient = 0.67, Fig. 4). The effects of phenological overlap on the probability of interaction (PO  $\rightarrow I_{ij}$ ) and the intensity of visits (PO  $\rightarrow \lambda_{ij}$ ), however, had variable plausibility among sites. The effect of phenological overlap on the probability of interaction was *likely* only in half of the sites (Table 2 and Fig. 4). The effect of phenological overlap on the intensity of visits was not plausible only in the two southern sites (BF and F) and plausible in the other four sites (LAR, R CG and FAL, Table 2 and Fig. 4). In all sites, the standardised coefficients of PO effects were always less than 1, thus showing a low effect size of phenology on interaction probability and intensity (Fig. 4).



**Table 2.** (i) Comparison of SEM models using the leave-one-out cross-validation criterion (LOO); (ii) evidence ratios (ER) of model effects in each site. (i) Models are ranked depending on the number of parameters used (from 0 to 4). The best models are the ones with  $\Delta LOO=0$  (underlined and bold values). The other suitable models are the ones with  $\Delta LOO < 4$  (underlined and italic values).  $\lambda_{ij}$  is the intensity of visits,  $I_{ij}$  is the probability of interaction,  $A_H$  is the insect abundance,  $A_P$  is the plant abundance and PO is the phenology overlap. (ii) We compared 4 model effects: PO  $\rightarrow I_{ij}$ , effect of the phenology overlap on the probability of interaction; PO  $\rightarrow \lambda_{ij}$  effect of the phenology overlap on the intensity of visits;  $A_H \rightarrow \lambda_{ij}$  and  $A_P \rightarrow \lambda_{ij}$  effects of the hoverflies and plant abundances on the intensity of interaction. The w<sub>H</sub> limits for unlikelihood is 0.27, plausibility 0.5 and likelihood 0.73. Underlined and bold values represent the likely hypothesis only.

			Sites						
			BF	F	CG	FAL	LAR	R	
	Model	Nb of parameters	ΔLOO values						
0	$\lambda_{ij} \sim A_H + A_P + PO / I_{ij} \sim PO$	4	<u>2.98</u>	<u>2.04</u>	<u>3.54</u>	<u>2.54</u>	<u>2.86</u>	<u>0.00</u>	
1	$\lambda_{ij} \sim A_H + A_P / I_{ij} \sim PO$	3	<u>0.00</u>	<u>0.00</u>	36.75	64.04	10.37	<u>2.90</u>	
2	$\lambda_{ij} \sim A_P + PO / I_{ij} \sim PO$	3	8.66	78.23	106.46	184.02	44.60	17.00	
3	$\lambda_{ij} \sim A_H + PO / I_{ij} \sim PO$	3	6.63	<u>1.71</u>	8.09	73.62	11.24	11.42	
4	$\lambda_{ij} \sim A_H + A_P + PO$	3	<u>2.86</u>	8.06	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>2.24</u>	
5	$\lambda_{ij}$ ~ PO / $I_{ij}$ ~ PO	2	14.69	73.20	109.85	223.86	55.67	23.09	
6	$\lambda_{ij} \sim A_H / I_{ij} \sim PO$	2	<u>1.45</u>	<u>1.31</u>	33.53	119.04	27.23	19.76	
7	$\lambda_{ij} \sim A_P / I_{ij} \sim PO$	2	9.84	72.16	156.61	256.04	47.99	21.53	
8	$\lambda_{ij} \sim A_H + PO$	2	11.49	8.18	5.25	71.97	10.28	13.80	
9	$\lambda_{ij} \sim A_P + PO$	2	10.71	88.67	103.46	182.14	44.36	17.94	
10	$\lambda_{ij} \sim A_H + A_P$	2	24.36	14.04	36.10	66.82	10.51	4.26	
11	<i>Ι<sub>ij</sub></i> ~ ΡΟ	1	11.78	68.52	154.26	272.98	64.12	32.39	
12	$\lambda_{ij} \sim PO$	1	19.99	86.20	108.46	219.66	54.64	25.73	
13	$\lambda_{ij} \sim A_H$	1	25.58	14.41	36.12	123.30	28.27	22.78	
14	$\lambda_{ij} \sim A_P$	1	32.99	87.70	157.74	256.39	48.82	22.87	
15	-	0	34.39	83.89	155.68	274.80	64.78	33.52	
Model effects			Effects weight (W <sub>H</sub> )						
	$PO \rightarrow I_{ij}$		<u>0.88</u>	<u>0.98</u>	0.15	0.22	0.20	<u>0.74</u>	
	$PO \rightarrow \lambda_{ij}$		0.26	0.35	<u>1.00</u>	<u>1.00</u>	<u>0.99</u>	<u>0.79</u>	
	$A_H \rightarrow \lambda_{ij}$		<u>0.99</u>	<u>1.00</u>	<u>1.00</u>	<u>1.00</u>	<u>1.00</u>	<u>1.00</u>	
	$A_P \rightarrow \lambda_{ij}$		<u>0.74</u>	0.59	<u>0.93</u>	<u>1.00</u>	<u>0.99</u>	<u>1.00</u>	



**Figure 4.** Summary diagram of the best models in all sites. The thickness of the arrows is scaled to Akaike weights (thin ER < 0.73; thick ER > 0.73, cf. Table 2). Standardised coefficients of the model average (computed based on the Akaike weighted model average) are reported next to the arrows. PO is the phenology overlap,  $I_{ij}$  is the probability of interaction,  $\lambda_{ij}$  is the intensity of visits,  $A_H$  and  $A_P$  are the hoverflies and plant abundances respectively.





When assessing the predictive power of the best models, we observed that the sensitivity and specificity values, both for the self-validation and the cross-validation, were higher than 0.5 (Table S3), which means that the interactions predicted by the models are better than predicted by chance. While area under the curve (AUC) values were all higher than 0.75 for self-validation, cross-validation tests yielded intermediate values (AUC between 0.62 and 0.73), reflecting the fact that abundances and phenology are certainly not sufficient to make accurate predictions on the occurrence of plant-pollinator interactions.

## Discussion

Latitude affects the seasonality, with advancing species phenologies at higher latitudes, and thus, can be a limiting factor for the phenological coupling of interacting species (Post et al. 2018). In this study we explored the effect of phenology overlap on a large network of species interactions in calcareous grasslands and how this effect could vary along a latitudinal gradient in France using empirical data on six planthoverfly networks. We identified plants and insects at the species level to build detailed interaction networks and hence avoid spurious generalisation levels. In order to better understand the determinants of variation in species interactions in space and time, we used the latitudinal gradient to consider variations linked to environmental cues and the entire flowering period to allow for seasonal variation (Valverde et al. 2016; Pellissier et al. 2017). One of the main problems of comparing networks along gradients is the dependence of network metrics on network size (Staniczenko et al. 2013; Astegiano et al. 2015; Tylianakis & Morris 2017). In this study, to avoid the problem of comparing networks with different dimensions, we decided to focus on the determinants of the probability of interaction and the number of visits, rather than the overall structure. We employed Bayesian Structural Equation Models (SEM) which is an emergent approach increasingly used to investigate complex networks of relationship in ecological studies (Grace et al. 2010; Eisenhauer et al. 2015; Fan et al. 2016; Theodorou et al. 2017). In our study we used SEM to link the numbers of visits to phenology overlap (PO) and species abundance through latent probabilities of species interaction and expected numbers of visits per plant-pollinator species pair. We tested different models with variable numbers of effects and compared them in each site. In our models, we used species abundances to construct a sensible null model to test whether phenology overlap could help explain the probability and intensity of interactions when the effects of species abundances are already taken into account. In all sites, we found that models that included both PO and abundances had always better goodness-of-fit than models that included only abundances.



Abundances indeed provided a sensible null model since the goodness-of-fit of models that did not include abundances were always quite worse than the ones which did.

We also found that in all sites the most important factor affecting pollinator visits was insect abundance (Table 2). Likewise, we found that plant abundance was also a very important effect in most sites, except in the site of F (Table 2). Since insect abundances are given by visitation data, it is not surprising that the intensity of interactions positively depends on these abundances. Species abundance often explain the linkage level in pollination network studies (Olesen et al. 2008; Bartomeus et al. 2016; Chacoff et al. 2017; Pellissier et al. 2017) but it is often associated with the length of the phenology to better assess the general properties of the interaction network (Vázquez et al. 2009; Olito & Fox 2015). In accordance with this verbal prediction, we indeed found that the best models incorporated the effect of PO on either the probability or the intensity of interactions (Table 2), and the model that only considered species abundance (model 5 in Table 2) was not the best one in any site. Phenology overlap generally cannot predict the probability of interaction on its own (Encinas-Viso et al. 2012; CaraDonna et al. 2017). Our findings do agree with this general predicament since no site favoured a model that only incorporated PO effects and because these effects always display lower effect sizes than the other variables. However, our objective was not to compare the effect of phenology overlap to that of species abundance – for such an endeavour, one would need estimates of species abundances independent of visitation data. Because models which consider the effect of PO on the intensity and/or probability of interactions are the best models for all sites, this evinces a clear effect of PO. In our model, the effect of PO on the probability of interaction and the expected number of visits also vary along the latitudinal gradient (Fig. 4).In general, we observed that southern sites (BF and F) showed shorter plant phenology and phenology overlap (PO) than the other four sites (Table 1). In these sites, plant species richness is higher and fewer visits were sampled, probably because the presence of specialist species with short phenophases may increase the number of forbidden or undetected links (Olesen et al. 2011; Martín González et al. 2012). Conversely, in sites where plant phenology is longer, PO is longer too, as observed in Normandie and Hauts-de-France (CG, FAL, LAR and R, Table 1). Moreover, when plant richness and specialization are lower, a higher number of visits can be observed (Table 1) because generalist species could interact without constraints. Indeed, in Normandie and Hauts-de-France we found that the effect of phenology overlap on the intensity of visits was always likely (PO  $\rightarrow \lambda_{ij}$ , Table 2) and we observed higher numbers of interactions in the first two/three blocks of insects and plants which also corresponded to blocks with longer PO (Fig. 2, S2, S4 and S5). A higher phenological overlap is expected to drive a higher probability of interactions and a larger number of visits (Olesen et al. 2011). In Occitanie, we did not find any effect of PO on the number of



visits because the more densely visited blocks do not correspond to those with longer phenology overlap. Plant phenology can therefore drive the probability and the intensity of interactions in networks in which plant phenology is shorter, thus suggesting that hoverflies may undergo selection for behavioural flexibility in order to maintain synchrony with their foraging resources (Iler *et al.* 2013; Ogilvie & Forrest 2017).

We also found that modularity decreased along the latitudinal gradient, with richer sites (BF and F) displaying higher modularity (as in Sebastián-González et al. 2015) but also the lower connectance. In the two southern sites, higher modularity could be related to shorter phenologies and higher proportions of non-overlapping sets of species, which induce some form of temporal short-term specialisation (Lucas et al. 2018). However, modularity also seems to be influenced by species abundances and degrees (Schleuning et al. 2014), and is expected to increase with link specificity (Morente-López et al. 2018). Indeed, in these sites, species blocks match species degrees (Fig. 3 and S3), with generalist and specialist species forming separate blocks among both plants and insects (Martín González et al. 2012). With lower modularity and more generalist species, we expect a stronger relationship between phenology and the intensity of interactions because interactions are less influenced by insect preferences and more by seasonal rhythm and flower availability (Dormann et al. 2017). Thus, different phenophases might correspond to different compartments (Martín González et al. 2012; Morente-López et al. 2018), as observed in CG, FAL, LAR and R where higher overlap corresponded to higher numbers of observed visits. Although phenology improved model fit (Table 2), its effect size was modest (Fig. 4), which suggests that other types of data such as traits and phylogenies might help predict specific interactions. In our study, we did not consider competition among studied insect species or with other group of insects, such as bees which were present in all sites. Different types of pollinators with different abundances could have contextdependent effects on network topology (Valverde et al. 2016). Moreover, in our study we only considered as "true absence" of the interaction the lack of phenological coupling between species (*i.e.* plant and hoverfly species which are not present at the same moment along the season cannot interact). We did not consider "false absences", i.e. missing links, since not all the potential links among species are recorded in the field (Olesen et al. 2011) which may introduce bias in the estimation of the probability of interactions (Bartomeus et al. 2016; Cirtwill et al. 2019).

To conclude, plant phenology here drives the duration of the phenology overlap between plant and hoverflies, which in turn influences either the probability of interaction or the expected number of visits, as well as network compartmentalization. Longer phenologies correspond to less constrained interactions (lower modularity),



shorter phenologies to more constrained interactions (higher modularity), which in turn restrict the number of visits. Phenology overlap alone was not sufficient to explain interactions, as suggested elsewhere (CaraDonna et al. 2017). Plant and insect abundances played a substantial role to explain the number of visits (as in Chacoff et al. 2017) since abundances may affect partner choice (Trøjelsgaard et al. 2015). Our results, and the ability of the method used here to compare different effects on interaction patterns, suggest that the use of Bayesian SEM to compare networks of different sizes is a valuable tool which can help understand plant-pollinator networks (Eisenhauer et al. 2015). The use of latent variables can help predict the probability of interaction and the expected number of visits while avoiding circularity - the introduction of plant and insect specific random effects played the role of an implicit "degree" effect. Our results demonstrate the importance of considering differences in plant and insect phenologies to better predict their interactions in pollination networks at different latitudes. The use of morphological traits (e.g. tongue length, inter-tegular distance, ...) together with species richness and phylogenies, on top of variables already used, might improve the modelling of interactions and could help better understand some forbidden or missing links in richer communities or considering other pollinators (e.g. wild bees).

## Data accessibility

The data supporting the results are archived on Zenodo (DOI: 10.5281/zenodo.2542845).

## Acknowledgements

Financial support was provided by the ANR ARSENIC project (grant no. 14-CE02-0012), the Region Nord-Pas-de-Calais and the CNRS. We also thank Martin Speight for insect identification, Clément Mazoyer for informatic support and all the students who took part in the field campaign. This work is a contribution to the CPER research project CLIMIBIO. The authors thank the French Ministère de l'Enseignement Supérieur et de la Recherche, the Hauts-de-France Region and the European Funds for Regional Economical Development for their financial support. Version 4 of this preprint has been peer-reviewed and recommended by Peer Community In Ecology (https://doi.org/10.24072/pci.ecology.100034).



## **Conflict of interest disclosure**

The authors of this preprint declare that they have no financial conflict of interest with the content of this article. François Massol and Bertrand Schatz are one of the PCI Ecology recommenders.

## References

- Astegiano, J., Massol, F., Vidal, M.M., Cheptou, P.O. & Guimarães, P.R. (2015). The robustness of plant-pollinator assemblages: Linking plant interaction patterns and sensitivity to pollinator loss. *PLoS One*, 10, e0117243.
- Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S., *et al.* (2011). Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proc. Natl. Acad. Sci. U. S. A.*, 108, 20645–9.
- Bartomeus, I., Gravel, D., Tylianakis, J.M., Aizen, M.A., Dickie, I.A. & Bernard-Verdier, M. (2016). A common framework for identifying linkage rules across different types of interactions. *Funct. Ecol.*, 30, 1894–1903.
- Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., et al. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. Nature, 530, 85–88.
- Biernacki, C., Celeux, G. & Govaert, G. (2000). Assessing a mixture model for clustering with integrated completed likelihood. *IEEE Trans. Pattern Anal. Mach. Intell.*, 22, 719–725.
- Blüthgen, N., Menzel, F. & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecol.*, 6, 9.
- Branquart, E. & Hemptinne, J. (2000). Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). *Ecography (Cop.).*, 23, 732–742.
- Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference A Practical Information-Theoretic Approach*. 2nd Editio. Springer-Verlag, New York.
- Burnham, K.P. & Anderson, D.R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociol. Methods Res.*, 33, 261–304.
- CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M., *et al.* (2017). Interaction rewiring and the rapid turnover of plant pollinator networks. *Ecol. Lett.*, 20, 385–394.
- Chacoff, N.P., Resasco, J. & Vázquez, D.P. (2017). Interaction frequency, network position, and the temporal persistence of interactions in a plant–pollinator network. *Ecology*, 99, 21–28.
- Cirtwill, A.R., Eklof, A., Roslin, T., Wootton, K. & Gravel, D. (2019). A quantitative framework for investigating the reliability of network construction. *Methods Ecol. Evol.*, 10, 902–911.
- Colley, M.R. & Luna, J.M. (2000). Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (Diptera: Syrphidae). *Environ. Entomol.*, 29, 1054–1059.



- Cowgill, S.E., Wratten, S.D. & Sotherton, N.W. (1993). The selective use of floral resources by the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) on farmland. *Ann. Appl. Biol.*, 122, 223–231.
- Csardi, G. & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal*, Complex Sy, 1695.
- D'Amen, M., Birtele, D., Zapponi, L. & Hardersen, S. (2013). Patterns in diurnal cooccurrence in an assemblage of hoverflies (Diptera: Syrphidae). *Eur. J. Entomol.*, 110, 649–656.
- Daudin, J.J., Picard, F. & Robin, S. (2008). A mixture model for random graphs. *Stat. Comput.*, 18, 173–183.
- Devoto, M., Medan, D. & Montaldo, N.H. (2005). Patterns of interaction between plants and pollinators along an environmental gradient. *Oikos*, 109, 461–472.
- Dormann, C.F., Fründ, J., Blüthgen, N. & Gruber, B. (2009). Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecol. J.*, 2, 7–24.
- Dormann, C.F., Fründ, J. & Schaefer, H.M. (2017). Identifying causes of patterns in ecological networks: opportunities and limitations. *Annu. Rev. Ecol. Evol. Syst.*, 48, 12–20.
- Eisenhauer, N., Bowker, M.A., Grace, J.B. & Powell, J.R. (2015). From patterns to causal understanding: Structural equation modeling (SEM) in soil ecology. *Pedobiologia (Jena).*, 58, 65–72.
- Encinas-Viso, F., Revilla, T.A. & Etienne, R.S. (2012). Phenology drives mutualistic network structure and diversity. *Ecol. Lett.*, 15, 198–208.
- Fan, Y., Chen, J., Shirkey, G., John, R., Wu, S.R., Park, H., *et al.* (2016). Applications of structural equation modeling (SEM) in ecological studies: an updated review. *Ecol. Process.*
- Fortuna, M.A., Stouffer, D.B., Olesen, J.M., Jordano, P., Mouillot, D., Krasnov, B.R., et al. (2010). Nestedness versus modularity in ecological networks: Two sides of the same coin? J. Anim. Ecol., 79, 811–817.
- Grace, J.B. (2006). *Structural Equation Modeling and Natural Systems*. Cambridge University Press, New York.
- Grace, J.B., Anderson, T.M., Olff, H. & Scheiner, S.M. (2010). On the specification of structural equation models for ecological systems. *Ecol. Monogr.*, 80, 67–87.
- Grace, J.B. & Bollen, K.A. (2008). Representing general theoretical concepts in structural equation models: The role of composite variables. *Environ. Ecol. Stat.*, 15, 191–213.
- Hutchings, M.J., Robbirt, K.M., Roberts, D.L. & Davy, A.J. (2018). Vulnerability of a specialized pollination mechanism to climate change revealed by a 356-year analysis. *Bot. J. Linn. Soc.*, 186, 498–509.
- Iler, A., Inouye, D., Høye, T., Miller-Rushing, A., Burkle, L. & Johnston, E. (2013). Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. *Glob. Chang. Biol.*, 19, 2348–2359.
- Jauker, F. & Wolters, V. (2008). Hover flies are efficient pollinators of oilseed rape. *Oecologia*, 156, 819–823.
- Klecka, J., Hadrava, J., Biella, P. & Akter, A. (2018a). Flower visitation by hoverflies (Diptera: Syrphidae) in a temperate plant-pollinator network. *PeerJPreprints*,



19, 780–785.

- Klecka, J., Hadrava, J. & Koloušková, P. (2018b). Vertical stratification of plant– pollinator interactions in a temperate grassland. *PeerJ*, 6, e4998.
- Leger, J.B., Daudin, J.J. & Vacher, C. (2015). Clustering methods differ in their ability to detect patterns in ecological networks. *Methods Ecol. Evol.*, 6, 474–481.
- Lucas, A., Bodger, O., Brosi, B.J., Ford, C.R., Forman, D.W., Greig, C., et al. (2018). Generalisation and specialisation in hoverfly (Syrphidae) grassland pollen transport networks revealed by DNA metabarcoding. J. Anim. Ecol., 87, 1008– 1021.
- Lunau, K. (2014). Visual ecology of flies with particular reference to colour vision and colour preferences. J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol., 200, 497–512.
- van der Maarel, E. (1975). The Braun-Blanquet approach in perspective. *Vegetatio*, 30, 213–219.

van der Maarel, E. (1979). Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio*, 39, 97–114.

- Martín González, A.M., Allesina, S., Rodrigo, A. & Bosch, J. (2012). Drivers of compartmentalization in a Mediterranean pollination network. *Oikos*, 121, 2001–2013.
- Massol, F., David, P., Gerdeaux, D. & Jarne, P. (2007). The influence of trophic status and large-scale climatic change on the structure of fish communities in Perialpine lakes. *J. Anim. Ecol.*, 76, 538–551.
- Memmott, J., Craze, P.G., Waser, N.M. & Price, M. V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecol. Lett.*, 10, 710–717.
- Miller-Struttmann, N.E., Geib, J.C., Franklin, J.D., Kevan, P.G., Holdo, R.M., Ebert-may, D., et al. (2015). Functional mismatch in a bumble bee pollination mutualism under climate change. Science, 349, 1541–4.
- Morente-López, J., Lara-Romero, C., Ornosa, C. & Iriondo, J.M. (2018). Phenology drives species interactions and modularity in a plant flower visitor network. *Sci. Rep.*, 8, 9386.
- Mucina, L., Schaminée, J.H.J. & Rodwell, J.S. (2000). Common data standards for recording relevés in field survey for vegetation classification. *J. Veg. Sci.*, 11, 769–772.
- Newman, M.E.J. (2006). Finding community structure in networks using the eigenvectors of matrices. *Phys. Rev. E Stat. Nonlinear, Soft Matter Phys.*, 74, 036104.
- Ogilvie, J.E. & Forrest, J.R. (2017). Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Curr. Opin. Insect Sci.*
- Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C. & Jordano, P. (2011). Missing and forbidden links in mutualistic networks. *Proc. Biol. Sci.*, 278, 725–732.
- Olesen, J.M., Bascompte, J., Elberling, H. & Jordano, P. (2008). Temporal dynamics in a pollination network. *Ecology*, 89, 1573–1582.
- Olito, C. & Fox, J.W. (2015). Species traits and abundances predict metrics of plantpollinator network structure, but not pairwise interactions. *Oikos*, 124, 428–



436.

- Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Chang. Biol.*, 13, 1860–1872.
- Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., *et al.* (2017). Comparing species interaction networks along environmental gradients. *Biol. Rev.*, 93, 785–800.
- Plummer, M. (2003). JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling.
- Poisot, T. & Gravel, D. (2014). When is an ecological network complex? Connectance drives degree distribution and emerging network properties. *PeerJ*, 2, e251.
- Post, E., Steinman, B.A. & Mann, M.E. (2018). Acceleration of phenological advance and warming with latitude over the past century. *Sci. Rep.*, 8, 3927.
- R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.Rproject.org/.
- Rader, R., Edwards, W., Westcott, D.A., Cunningham, S.A. & Howlett, B.G. (2011).
   Pollen transport differs among bees and flies in a human-modified landscape.
   *Divers. Distrib.*, 17, 519–529.
- Rafferty, N.E. (2017). Effects of global change on insect pollinators: multiple drivers lead to novel communities. *Curr. Opin. Insect Sci.*
- Rafferty, N.E., CaraDonna, P.J. & Bronstein, J.L. (2015). Phenological shifts and the fate of mutualisms. *Oikos*, 124, 14–21.
- Schleuning, M., Fru, J., Klein, A., Abrahamczyk, S., Albrecht, M., Andersson, G.K.S., et al. (2012). Report specialization of mutualistic interaction networks decreases toward tropical latitudes, 1925–1931.
- Schleuning, M., Ingmann, L., Strauß, R., Fritz, S.A., Dalsgaard, B., Matthias Dehling, D., et al. (2014). Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecol. Lett.*, 17, 454–463.
- Sebastián-González, E., Dalsgaard, B., Sandel, B. & Guimarães, P.R. (2015). Macroecological trends in nestedness and modularity of seed-dispersal networks: Human impact matters. *Glob. Ecol. Biogeogr.*, 24, 293–303.
- Speight, M.C.D., Castella, E., Sarthou, J.-P. & Vanappelghem, C. (2016). StN 2016. In: Syrph the Net on CD, Issue 11. Speight, M.C.D., Castella, E., Sarthou, J.-P. & Vanappelghem, C. (Eds.) Syrph the Net Publications, Dublin.
- Staniczenko, P.P.A., Kopp, J.C. & Allesina, S. (2013). The ghost of nestedness in ecological networks. *Nat. Commun.*, 4, 1391–1396.
- Staniczenko, P.P.A., Lewis, O.T., Tylianakis, J.M., Albrecht, M., Coudrain, V., Klein, A.-M., et al. (2017). Predicting the effect of habitat modification on networks of interacting species. Nat. Commun., 8.
- Theodorou, P., Albig, K., Radzevičiūtė, R., Settele, J., Schweiger, O., Murray, T.E., *et al.* (2017). The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. *Funct. Ecol.*, 31, 838–847.
- Trøjelsgaard, K., Jordano, P., Carstensen, D.W. & Olesen, J.M. (2015). Geographical variation in mutualistic networks: Similarity, turnover and partner fidelity. *Proc. R. Soc. B Biol. Sci.*, 282, 20142925.
- Tylianakis, J.M. & Morris, R.J. (2017). Ecological networks across environmental



gradients. Annu. Rev. Ecol. Evol. Syst., 48, 25-48.

- Valverde, J., Gómez, J.M. & Perfectti, F. (2016). The temporal dimension in individualbased plant pollination networks. *Oikos*, 125, 468–479.
- Vázquez, D.P., Chacoff, N.P. & Cagnolo, L. (2009). Evaluating multiple determinants of the structure of plant-animal mutualistic networks. *Ecology*, 90, 2039–2046.
- Vehtari, A., Gelman, A. & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.*, 27, 1413–1432.
- Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, M., Petanidou, T., et al. (2008). Measuring bee diversity in different European habitats and biogeographic regions. *Ecol. Monogr.*, 78, 653–671.

Willmer, P. (2012). Ecology: Pollinator-plant synchrony tested by climate change. *Curr. Biol.*, 22, R131–R132.

## Appendix

The following Supporting Information is available for this article:

Figure S1. Sites location in France.

**Figure S2.** Block clustering provided by LBM in the site of Bois de Fontaret (BF, Occitanie), overlaid on a heatmap of species phenology overlap.

**Figure S3.** Block clustering provided by LBM in the site of Falaises (FAL, Normandie), overlaid on a heatmap of species phenology overlap.

**Figure S4.** Block clustering provided by LBM in the site of Larris (LAR, Hauts-de-France), overlaid on a heatmap of species phenology overlap.

**Figure S5.** Block clustering provided by LBM in the site of Riez (R, Hauts-de-France), overlaid on a heatmap of species phenology overlap.

 Table S1. Table of transformed plant abundances.

**Table S2.** Table of hoverfly and plant species names and abbreviations used in the LBMFigures.

Table S3. Table of model accuracy.

Appendix S1. Model code.

Appendix S2. Model script for the 16 models.

Appendix S3. Script modularity and latent block model analysis (LBM).





**Figure S1.** Site location in France: in blue the French départements Pas-de-Calais and Somme (Hauts-de-France region), in green the départements Eure and Seine Maritime (Normandie region), in orange the départment Gard (Occitanie region). The six sites correspond to the red dots (with the sites of Fourches and Bois de Fontaret represented by the same dot due to their closeness).





**Figure S2.** Block clustering provided by LBM in the site of Falaises (FAL, Normandie), overlaid on a heatmap of species phenology overlap. Insect species are displayed in rows and plant species in columns, following their degree (number of partners). The blocks of insects and the blocks of plants are separated by solid black lines. Colours correspond to the number of months that are shared by each pair of plant and insect species (PO, phenology overlap), with higher PO corresponding to darker colours. Numbers are the number of visits observed in the field for a given plant-insect pair. Complete species names are reported in Table S2.

Falaises





Bois de Fontaret

**Figure S3.** Block clustering provided by LBM in the site of Bois de Fontaret (BF, Occitanie), overlaid on a heatmap of species phenology overlap. Insect species are displayed in rows and plant species in columns, following their degree (number of partners). The blocks of insects and the blocks of plants are separated by solid black lines. Colours correspond to the number of months that are shared by each pair of plant and insect species (PO, phenology overlap), with higher PO corresponding to darker colours. Numbers are the number of visits observed in the field for a given plant-insect pair. Complete species names are reported in Table S2.





**Figure S4.** Block clustering provided by LBM in the site of Larris (LAR, Hauts-de-France), overlaid on a heatmap of species phenology overlap. Insect species are displayed in rows and plant species in columns, following their degree (number of partners). The blocks of insects and the blocks of plants are separated by solid black lines. Colours correspond to the number of months that are shared by each pair of plant and insect species (PO, phenology overlap), with higher PO corresponding to darker colours. Numbers are the number of visits observed in the field for a given plant-insect pair. Complete species names are reported in Table S2.





**Figure S5.** Block clustering provided by LBM in the site of Riez (R, Hauts-de-France), overlaid on a heatmap of species phenology overlap. Insect species are displayed in rows and plant species in columns, following their degree (number of partners). The blocks of insects and the blocks of plants are separated by solid black lines. Colours correspond to the number of months that are shared by each pair of plant and insect species (PO, phenology overlap), with higher PO corresponding to darker colours. Numbers are the number of visits observed in the field for a given plant-insect pair. Complete species names are reported in Table S2.



**Table S1.** Table of transformed plant abundances. The first column shows the Braun-Blanquet coefficients of, the second column, their percentages, and the third column, the transformed abundances used as the plant abundances in the model.

Coefficient Braun- Blanquet	Abundance percentage interval	Abundance percentage		
i	1 individual	0.1%		
+	< 1 %	0.5%		
1	1-10 %	5%		
2	10-25 %	15%		
3	25-50 %	35%		
4	50-75 %	65%		
5	75-100 %	85%		

**Table S2.** Table of hoverfly and plant species names and abbreviations used in the LBM Figures.

ot th sis
th sis
sis
515
es



Syrphidae	Eumerus sp.	Eumerus sp.	the identification is not possible
Syrphidae	E.corollae	Eupeodes corollae (Fabricius), 1794	F
Syrphidae	E.latifasciatus	Eupeodes latifasciatus (Macquart), 1829	
Svrphidae	E.luniger	Eupeodes luniger (Meigen), 1822	
Svrphidae	F.aurea	Ferdinandea aurea (Rondani), 1844	
Svrphidae	H.hvbridus	Helophilus hybridus (Loew), 1846	
Syrphidae	H nendulus	Helophilus nendulus (L) 1758	
Syrphidae	H trivittatus	Helophilus trivittatus (Eabricius) 1805	
Syrphidae	M mellinum	Melanostoma mellinum (L) 1758	
Syrphidae	M.meinnann M.scalare	Melanostoma scalare (Espricius) 1794	
Syrphildae	WI.Scalare		the identification is not
Syrphidae	Melanostoma sp.	Melanostoma sp.	nossible
Svrphidae	M.auricollis	Meliscaeva auricollis (Meigen), 1822	possible
Syrphidae	M alhifrons	Merodon albifrons (Meigen) 1822	
Syrphidae	M avidus	Merodon avidus (Rossi) 1790	
Syrphidae	M elegans	Merodon elegans (Hurkmans) 1993	
Syrphidae	M equestris	Merodon equestris (Fabricius) 1794	
Syrphidae	M geniculatus	Merodon geniculatus Strohl 1909	
Syrphidae	M moenium	Merodon moenium (Wiedemann) 1822	
Syrphidae	M nigritarsis	Merodon nigritarsis Rondani, 1845	
Syrphidae	M rufuc	Maradan rufus Majaan 1929	
Syrphiluae	101.1 01 05	Merodon serrulatus Wiedemann in Meigen	
Syrphidae	M.serratulus	1877	
Svrphidae	M analis	Microdon anglis (Macquart) 1842	
Syrphidae	M crahroniformis	Milesia crahroniformis (Fabricius) 1775	
Syrphidae	M florea	Myathrona florea (L) 1758	
Syrphidae	N nodagrica	Neoascia podagrica (Espricius) 1775	
Syrphidae	P haemorrhous	Paragus haemorrhous Meigen 1822	
Syrphidae	P tihialis	Paragus tibialis (Fallen) 1817	
Syrpinduc			the identification is not
Syrphidae	Paragus sp.	Paragus sp.	possible
Syrphidae	P.pruinosomaculata	Pelecocera pruinosomaculata Strobl, 1906	
Syrphidae	P.tricincta	Pelecocera tricincta Meigen, 1822	
Syrphidae	P.austriaca	Pipiza austriaca Meigen, 1822	
Syrphidae	P.divicoi	Pipizella divicoi (Goeldlin), 1974	
Syrphidae	P.virens	Pipizella virens (Fabricius), 1805	
Syrphidae	P.zeneggenensis	Pipizella zeneggenensis (Goeldlin), 1974	
Syrphidae	Pipizella sp.	Pipizella sp.	
Syrphidae	P.albimanus	Platycheirus albimanus (Fabricius), 1781	
Syrphidae	P.albimanus.muelleri	Platycheirus albimanus (Fabricius), 1782 /	the identification is not possible, could be both
		Platycheirus muelleri (Marcuzzi), 1941	species
Syrphidae	P.clypeatus	Platycheirus clypeatus (Meigen), 1822	
Syrphidae	P.Platycheirus	Platycheirus sp.	the identification is not possible
Syrphidae	R.campestris	Rhingia campestris Meigen, 1822	
Syrphidae	S.dignota	<i>Scaeva dignota</i> (Rondani, 1857)	
Syrphidae	S.pyrastri	Scaeva pyrastri (L.), 1758	



Syrphidae	S.silentis	Sericomyia silentis (Harris), 1776
Syrphidae	S.scripta	Sphaerophoria scripta (L.), 1758
Syrphidae	S.taeniata	Sphaerophoria taeniata (Meigen), 1822
Syrphidae	S.Sphaerophoria	Sphaerophoria sp.
Syrphidae	S.pipiens	Syritta pipiens (L.), 1758
Syrphidae	S.ribesii	Syrphus ribesii (L.), 1758
Syrphidae	S.torvus	Syrphus torvus (Osten-Sacken), 1875
Syrphidae	S.vitripennis	Syrphus vitripennis (Meigen), 1822
Syrphidae	V.bombylans	Volucella bombylans (L.), 1758
Syrphidae	V.inanis	Volucella inanis (L.), 1758
Syrphidae	V.pellucens	Volucella pellucens (L.), 1758
Syrphidae	V.zonaria	<i>Volucella zonaria</i> (Poda), 1761
Syrphidae	X.citrofasciatum	Xanthogramma citrofasciatum (De Geer), 1776
Syrphidae	X.dives	Xanthogramma dives (Rondani), 1857
Plants	A.millefolium	Achillea millefolium
Plants	A.genevensis	Ajuga genevensis
Plants	A.sphaerocephalon	Allium sphaerocephalon
Plants	A.pyramidalis	Anacamptis pyramidalis
Plants	A.ramosum	Anthericum ramosum
Plants	A.montana	Anthyllis montana
Plants	A.vulneraria	Anthyllis vulneraria
Plants	A.monspeliensis	Aphyllanthes monspeliensis
Plants	A.aggregata	Arenaria aggregata
Plants	A.cynanchica	Asperula cynanchica
Plants	A.linosyris	Aster linosyris
Plants	B.perennis	Bellis perennis
Plants	B.laevigata	Biscutella laevigata
Plants	B.perfoliata	Blackstonia perfoliata
Plants	B.repanda	Brassica repanda
Plants	B.falcatum	Bupleurum falcatum
Plants	C.patula	Campanula patula
Plants	C.rapunculus	Campanula rapunculus
Plants	C.rotundifolia	Campanula rotundifolia
Plants	C.erythraea	Centaurium erythraea
Plants	C.jacea	Centaurea jacea
Plants	C.scabiosa	Centaurea scabiosa
Plants	C.acaule	Cirsium acaule
Plants	C.vulgare	Clinopodium vulgare
Plants	C.cantabrica	Convolvulus cantabrica
Plants	C.minima	Coronilla minima
Plants	C.capillaris	Crepis capillaris
Plants	C.foetida	Crepis foetida
Plants	C.planiflora	Cuscuta planiflora var. godronii
Plants	D.carota	Daucus carota
Plants	D.pentaphyllum	Dorycnium pentaphyllum
Plants	E.vulgare	Echium vulgare
Plants	E.ritro	Echinops ritro

the female identification is not possible



Plants	E.atrorubens	Epipactis atrorubens	
Plants	E.campestre	Eryngium campestre	
Plants	E.cyparissias	Euphorbia cyparissias	
Plants	E.esula	Euphorbia esula	
Plants	E.exigua	Euphorbia exigua	
Plants	E.nicaeensis	Euphorbia nicaeensis	
Plants	E.stricta	Euphrasia stricta	
Plants	F.ericoides	Fumana ericoides	
Plants	F.procumbens	Fumana procumbens	
Plants	G.corrudifolium	Galium corrudifolium	
Plants	G.mollugo	Galium mollugo	
Plants	G.pumilum	Galium pumilum	
Plants	G.amarella	Gentianella amarella	
Plants	G.vulgaris	Globularia vulgaris	
Plants	G.conopsea	Gymnadenia conopsea	
Plants	H.apenninum	Helianthemum apenninum	
Plants	H.nummularium	Helianthemum nummularium	
Plants	H.oelandicum	Helianthemum oelandicum	
Plants	H.stoechas	Helichrysum stoechas	
Plants	H.lachenalii	Hieracium lachenalii	
Plants	H.pilosella	Hieracium pilosella (synonyms)	Pilosella
-			(accepte
Plants	H.comosa	Hippocrepis comosa	
Plants	H.perforatum	Hypericum perforatum	
Plants	I.montana	Inula montana	
Plants	K.arvensis	Knautia arvensis	
Plants	L.angustifolia	Lavandula angustifolia	
Plants	L.hispidus	Leontodon hispidus	
Plants	L.graminifolium	Leucanthemum graminifolium	
Plants	L.vulgare	Leucanthemum vulgare	
Plants	L.catharticum	Linum catharticum	
Plants	L.narbonense	Linum narbonense	
Plants	L.tenuifolium	Linum tenuifolium	
Plants	L.corniculatus	Lotus corniculatus	
Plants	L.delortii	Lotus delortii	
Plants	M.lupulina	Medicago lupulina	
Plants	M.minima	Medicago minima	
Plants	M.capillacea	Minuartia capillacea	
Plants	M.rostrata	Minuartia rostrata	
Plants	M.arvensis	Myosotis arvensis	
Plants	O.verna	Odontites verna	
Plants	O.supina	Onobrychis supina	
Plants	O.natrix	Ononis natrix	
Plants	O.repens	Ononis repens	
Plants	O.vulgare	Origanum vulgare	
Plants	O.angustifolium	Ornithogalum angustifolium	
Plants	P.orbiculare	Phyteuma orbiculare	
Plants	P.hieracioides	Picris hieracioides	
Plants	P.saxifraga	Pimpinella saxifraga	

Pilosella officinarum (accepted name)



Plants	P.lanceolata	Plantago lanceolata
Plants	P.media	Plantago media
Plants	P.neumanniana	Potentilla neumanniana
Plants	P.reptans	Potentilla reptans
Plants	P.veris	Primula veris
Plants	P.grandiflora	Prunella grandiflora
Plants	R.bulbosus	Ranunculus bulbosus
Plants	R.gramineus	Ranunculus gramineus
Plants	R.lutea	Reseda lutea
Plants	R.pumilus	Rhinanthus pumilus
Plants	R.canina	Rosa canina
Plants	S.minor	Sanguisorba minor
Plants	S.columbaria	Scabiosa columbaria
Plants	S.triandra	Scabiosa triandra
Plants	S.autumnalis	Scilla autumnalis
Plants	S.acre	Sedum acre
Plants	S.album	Sedum album subsp. micranthum
Plants	S.jacobaea	Senecio jacobaea
Plants	S.libanotis	Seseli libanotis
Plants	S.montanum	Seseli montanum
Plants	S.spiralis	Spiranthes spiralis
Plants	S.recta	Stachys recta
Plants	Taraxacum sp.	Taraxacum sp.
Plants	T.montanum	Teucrium montanum
Plants	T.humifusum	Thesium humifusum
Plants	T.dolomiticus	Thymus dolomiticus
Plants	T.praecox	Thymus praecox
Plants	T.vulgaris	Thymus vulgaris
Plants	T.pratensis	Tragopogon pratensis
Plants	T.pratense	Trifolium pratense
Plants	T.glauca	Trinia glauca
Plants	V.persica	Veronica persica
Plants	V.tetrasperma	Vicia tetrasperma
Plants	V.hirundinaria	Vincetoxicum hirundinaria



**Table S3.** Table of model accuracy. The upper part of the table shows the results of the self-validation: in the region Occitanie the self-validation was tested for the site Bois de Fontaret (BF ~ BF) and the site of Fourches (F ~ F); in the region Normandie for the site of Château Gaillard (CG ~ CG) and the sites of Falaises (FAL ~ FAL); and in the region Hauts-de-France for the site of Larris (LAR ~ LAR) and for the site of Riez (R ~ R). The lower part of the table shows the results of the cross-validation only between each site of the same region: in the region Occitanie between Bois de Fontaret et Fourches (BF ~ F and vice versa F ~ BF); in the region Normandie between the site of Château Gaillard and Falaises (CG ~ FAL and vice versa FAL ~ CG); and in the region Hauts-de-France between the site of Larris and Riez (LAR ~ R and vice versa R ~ LAR).

Model type	Region	Sites	Threshold	AUC	Omission rate	Sensitivity	Specificity	Prop correct	Карра
Self-validation	Occitanie	BF ~ BF	0.15	0.78	0.20	0.80	0.75	0.75	0.22
	Occitanie	F ~ F	0.16	0.78	0.19	0.81	0.74	0.75	0.25
	Normandie	CG ~ CG	0.44	0.75	0.29	0.71	0.79	0.78	0.34
	Normandie	$FAL \sim FAL$	0.37	0.76	0.16	0.84	0.67	0.69	0.27
	Hauts-de-France	$LAR \sim LAR$	0.29	0.75	0.16	0.84	0.66	0.69	0.27
	Hauts-de-France	$R \sim R$	0.27	0.81	0.23	0.77	0.86	0.84	0.53
Cross-validation	Occitanie	BF ~ F	0.15	0.73	0.14	0.86	0.59	0.63	0.20
	Occitanie	F ~ BF	0.16	0.67	0.30	0.70	0.64	0.65	0.17
	Normandie	CG ~ FAL	0.44	0.62	0.45	0.55	0.70	0.67	0.21
	Normandie	FAL ~ CG	0.37	0.68	0.24	0.76	0.60	0.63	0.25
	Hauts-de-France	$LAR \sim R$	0.29	0.63	0.35	0.65	0.61	0.61	0.17
	Hauts-de-France	R ~ LAR	0.27	0.65	0.42	0.58	0.72	0.69	0.22

#### Appendix S1: Model Code

The model code (in JAGS language) given in this supplementary material refers to the "model Z0" which considers all four parameters (model effects, Table 2 in the main text). Overall, we estimated 16 models that included between 0 and 4 of the above-mentioned effects. To create the code for these other models, parameters should be removed following the order in the Tab. 2. The four parameters tested in the model are: (i) alpha: effect of the phenology overlap (cooc) on the probability of interaction; (ii) epsilon: effect of the phenology overlap on the intensity of visits; (iii) gamma: effect of the insect abundances (ab\_I) on the intensity of visits; and (iv) delta: effect of the plant abundances (ab\_P) on the intensity of visits.

```
model
{
 for( i in 1 : dim1 ) {
   for( p in 1 : dim2 ) {
    inter[i, p] ~ dbern(mu[i, p])
        logit(mu[i, p]) <- beta + alpha*cooc[i, p] + effet_l[i] + effet_P[p]</pre>
        lambda[i,p] <- exp(theta[i,p])</pre>
        theta[i,p] <- theta0 + gamma*ab_l[i] + delta*ab_P[p] + epsilon*log(1+cooc[i,p])</pre>
        visit[i,p] ~ dpois( inter[i,p]*lambda[i,p] )
        loglik[i,p] <- log(ifelse(visit[i,p]==0,1-mu[i,p]+mu[i, p]*dpois(visit[i,p],lambda[i,p]),mu[i,
p]*dpois(visit[i,p],lambda[i,p])))
   }
 }
 for( i in 1 : dim1 ) {
   effet_I[i] ~ dnorm( 0.0,tau_I)
 }
 for( p in 1 : dim2 ) {
   effet P[p] ~ dnorm( 0.0,tau P)
 }
        tau_l \sim dexp(10)
        tau_P ~ dexp( 10)
        alpha ~ dnorm(0,0.01)
        beta ~ dnorm(0,0.01)
        theta0 \sim dnorm(0,0.01)
        gamma ~ dnorm(0,0.01)
        delta ~ dnorm(0,0.01)
        epsilon ~ dnorm(0,0.01)
}
```

#### Appendix 2: Model script for the 16 models – LOO values

The following generic script was applied to all the study sites using all 16 models. The script is separated in three blocks which communicate among them: the script options, the model definitions and the execution (model inference). We defined three options to set (i) the name of the directory (-d), (ii) the site (-s) and (iii) the type of model (-m).

We used, as an example, the information for the site of Bois de Fontaret (BF).

Exemple: Rscript (name) "script-SEMLOO\_generique.R" "-d o-BFs-2016" "-s BFs"

In order to calculate the standardised coefficients for each parameters used, at the end of the third block, we added the functions to get the parameter values for each site and each model.

```
####BLOCK 1 - SCRIPT OPTION ####
library(optparse)
option_list = list(
    make_option(c("-d", "--dir"), type="character", default=NULL, help="directory",
metavar="character"),
    make_option(c("-s", "--site"), type="character", default=NULL, help="site name",
metavar="character"),
    make_option(c("-m", "--modele"), type="character", default="all", help="modele name",
metavar="character"))
opt_parser = OptionParser(option_list=option_list);
opt = parse_args(opt_parser);
site<-opt$site
dossier<-opt$dir</pre>
```

#### 

library(bipartite) library(vegan) library(igraph) library(magrittr) library(dummies) library(dumMln) library(muMln) library(rjags) library(boot) library(boot) library(coda) library(lattice) library(ggplot2) library(loo) library(matrixStats)

#### ########Function to record the LOO values #######

```
write_values<-function(x, f, app)</pre>
```

```
{
```

write.table(x, append=app, file=f, sep="\t", row.names=T, col.names=T, quote=F)

}

####BLOCK 2 – MODEL FUNCTIONS #####

```
#Model function and model initialization: one function for each model from model Z15, with 0
parameters, to Z00 with all the parameters#
### MODEL Z015
mZ015<-function(){
       init.funZ015 <-function(){</pre>
         list("tau_I" = rexp(1,10), "tau_P" = rexp(1,10), "beta" = rnorm(1,0,1), "theta0" =
rnorm(1,0,1), "effet I"=rnorm(dim1,0,1),"effet P"=rnorm(dim2,0,1), "inter"=inter0)
       }
        mod.Z015<<-jags(inits=init.funZ015,model.file = "modelZ015 code.txt",data =
list("visit","dim1","dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","beta","theta0", "loglik"),n.chains = 1, n.iter=1000000,
n.burnin = 250000, n.thin = 250)
       mod.Z015.mcmc<-as.mcmc(mod.Z015)</pre>
        mZ015<-mod.Z015$BUGSoutput$sims.list
        mZ015.deviance<-mZ015$deviance
       mZ015.loglik<-mZ015$loglik
        dimSEM<-dim(mZ015.loglik)[1]
       list.mZ015<-sapply(1:dimSEM,function(x) matrix(mZ015.loglik[x,,],nrow=dim1*dim2))
       list.tmZ015<-(t(list.mZ015))
       mZ015.loo<-loo(list.tmZ015)
       loo file<-paste(dossier, "/", site, " Z015 loo.txt", sep="")</pre>
       write_values("mZ015", app=F, loo_file)
        mZ015_loo_pointwise<-mZ015.loo$pointwise
        mZ015_loo_pareto_k<-mZ015.loo$pareto_k
        mZ015.loo$pareto k<-NULL
       mZ015.loo$pointwise<-NULL
       write values(as.matrix(mZ015.loo), app=T, loo file)
       save.image(paste(dossier, "/", site, "_Z015.RData", sep=""))
}
### MODEL Z014
mZ014<-function(){
       init.funZ014 <-function(){</pre>
         list("tau_l" = rexp(1,10), "tau_P" = rexp(1,10), "beta" = rnorm(1,0,1), "delta" = rnorm(1,0,1),
"theta0" = rnorm(1,0,1), "effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1), "inter"=inter0)
       }
        mod.Z014<<-jags(inits=init.funZ014,model.file = "modelZ014 code.txt",data =
list("visit","ab P","dim1","dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","delta","beta","theta0","loglik"),n.chains = 1,
n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z014.mcmc<-as.mcmc(mod.Z014)
        mZ014<-mod.Z014$BUGSoutput$sims.list
        mZ014.deviance<-mZ014$deviance
        mZ014.loglik<-mZ014$loglik
       dimSEM<-dim(mZ014.loglik)[1]
       list.mZ014<-sapply(1:dimSEM,function(x) matrix(mZ014.loglik[x,,],nrow=dim1*dim2))
        list.tmZ014<-(t(list.mZ014))</pre>
```

```
mZ014.loo<-loo(list.tmZ014)
        mZ014.loo
       loo_file<-paste(dossier, "/", site, "_Z014_loo.txt", sep="")</pre>
       write_values("mZ014", app=T, loo_file)
        mZ014 loo pointwise<-mZ014.loo$pointwise
        mZ014_loo_pareto_k<-mZ014.loo$pareto_k
        mZ014.loo$pareto k<-NULL
       mZ014.loo$pointwise<-NULL
       write values(as.matrix(mZ014.loo), app=T, loo file)
        save.image(paste(dossier, "/", site, "_Z014.RData", sep=""))
}
### MODEL Z013
mZ013<-function(){
       init.funZ013 <-function(){</pre>
         list("tau I" = rexp(1,10), "tau P" = rexp(1,10), "beta" = rnorm(1,0,1), "gamma" =
rnorm(1,0,1), "theta0" = rnorm(1,0,1), "effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1),
"inter"=inter0)
       }
        mod.Z013<<-jags(inits=init.funZ013,model.file = "modelZ013 code.txt",data =
list("visit","ab I","dim1","dim2"),parameters.to.save =
c("mu","effet I","effet P","tau I","tau P","gamma","beta","theta0","loglik"),n.chains = 1,
n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z013.mcmc<-as.mcmc(mod.Z013)
        mZ013<-mod.Z013$BUGSoutput$sims.list
        mZ013.deviance<-mZ013$deviance
       mZ013.loglik<-mZ013$loglik
        dimSEM<-dim(mZ013.loglik)[1]
       list.mZ013<-sapply(1:dimSEM,function(x) matrix(mZ013.loglik[x,,],nrow=dim1*dim2))
       list.tmZ013<-(t(list.mZ013))
       mZ013.loo<-loo(list.tmZ013)
        mZ013.loo
       loo_file<-paste(dossier, "/", site, "_Z013_loo.txt", sep="")</pre>
       write_values("mZ013", app=T, loo_file)
        mZ013 loo pointwise<-mZ013.loo$pointwise
        mZ013 loo pareto k<-mZ013.loo$pareto k
        mZ013.loo$pareto k<-NULL
       mZ013.loo$pointwise<-NULL
       write values(as.matrix(mZ013.loo), app=T, loo_file)
        save.image(paste(dossier, "/", site, "_Z013.RData", sep=""))
}
### MODEL Z012
mZ012<-function(){
       init.funZ012 <-function(){</pre>
         list("tau_I" = rexp(1,10), "tau_P" = rexp(1,10), "beta" = rnorm(1,0,1), "theta0" =
rnorm(1,0,1), "epsilon" = rnorm(1,0,1), "effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1),
"inter"=inter0)
```

}

```
mod.Z012<<-jags(inits=init.funZ012,model.file = "modelZ012 code.txt",data =
list("cooc","visit","dim1","dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","beta","theta0","epsilon","loglik"),n.chains = 1,
n.iter=1000000, n.burnin = 250000, n.thin = 250)
       mod.Z012.mcmc<-as.mcmc(mod.Z012)
       mZ012<-mod.Z012$BUGSoutput$sims.list
       mZ012.deviance<-mZ012$deviance
       mZ012.loglik<-mZ012$loglik
       dimSEM<-dim(mZ012.loglik)[1]
       list.mZ012<-sapply(1:dimSEM,function(x) matrix(mZ012.loglik[x,,],nrow=dim1*dim2))
       list.tmZ012<-(t(list.mZ012))
       mZ012.loo<-loo(list.tmZ012)
       mZ012.loo
       loo_file<-paste(dossier, "/", site, "_Z012_loo.txt", sep="")</pre>
       write_values("mZ012", app=T, loo_file)
       mZ012 loo pointwise<-mZ012.loo$pointwise
       mZ012_loo_pareto_k<-mZ012.loo$pareto_k
       mZ012.loo$pareto k<-NULL
       mZ012.loo$pointwise<-NULL
       write values(as.matrix(mZ012.loo), app=T, loo file)
       save.image(paste(dossier, "/", site, "_Z012.RData", sep=""))
}
### MODEL Z011
mZ011<-function(){
       init.funZ011 <-function(){</pre>
        list("tau I" = rexp(1,10), "tau P" = rexp(1,10), "alpha" = 0.1, "beta" = rnorm(1,0,1), "theta0"
= rnorm(1,0,1), "effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1), "inter"=inter0)
       }
       mod.Z011<<-jags(inits=init.funZ011,model.file = "modelZ011_code.txt",data =
list("cooc", "visit", "dim1", "dim2"), parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","alpha","beta","theta0","loglik"),n.chains = 1,
n.iter=1000000, n.burnin = 250000, n.thin = 250)
       mod.Z011.mcmc<-as.mcmc(mod.Z011)
       mZ011<-mod.Z011$BUGSoutput$sims.list
       mZ011.deviance<-mZ011$deviance
       mZ011.loglik<-mZ011$loglik
       dimSEM<-dim(mZ011.loglik)[1]
       list.mZ011<-sapply(1:dimSEM,function(x) matrix(mZ011.loglik[x,,],nrow=dim1*dim2))
       list.tmZ011<-(t(list.mZ011))
       mZ011.loo<-loo(list.tmZ011)
       mZ011.loo
       loo_file<-paste(dossier, "/", site, "_Z011_loo.txt", sep="")</pre>
       write_values("mZ011", app=T, loo_file)
       mZ011 loo pointwise<-mZ011.loo$pointwise
       mZ011_loo_pareto_k<-mZ011.loo$pareto_k
```

```
mZ011.loo$pareto_k<-NULL
        mZ011.loo$pointwise<-NULL
       write_values(as.matrix(mZ011.loo), app=T, loo_file)
       save.image(paste(dossier, "/", site, "_Z011.RData", sep=""))
}
### MODEL Z010
mZ010<-function(){
       init.funZ010 <-function(){</pre>
         list("tau I" = rexp(1,10), "tau P" = rexp(1,10), "beta" = rnorm(1,0,1), "gamma" =
rnorm(1,0,1), "delta" = rnorm(1,0,1), "theta0" = rnorm(1,0,1),
"effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1), "inter"=inter0)
       }
       mod.Z010<<-jags(inits=init.funZ010,model.file = "modelZ010_code.txt",data =
list("visit","ab_I","ab_P","dim1","dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","gamma","delta","beta","theta0","loglik"),n.chains = 1,
n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z010.mcmc<-as.mcmc(mod.Z010)
       mZ010<-mod.Z010$BUGSoutput$sims.list
        mZ010.deviance<-mZ010$deviance
       mZ010.loglik<-mZ010$loglik
       dimSEM<-dim(mZ010.loglik)[1]
       list.mZ010<-sapply(1:dimSEM,function(x) matrix(mZ010.loglik[x,,],nrow=dim1*dim2))
       list.tmZ010<-(t(list.mZ010))</pre>
       mZ010.loo<-loo(list.tmZ010)
        mZ010.loo
       loo_file<-paste(dossier, "/", site, "_Z010_loo.txt", sep="")</pre>
        write values("mZ010", app=T, loo file)
        mZ010_loo_pointwise<-mZ010.loo$pointwise
        mZ010 loo pareto k<-mZ010.loo$pareto k
       mZ010.loo$pareto_k<-NULL
        mZ010.loo$pointwise<-NULL
       write_values(as.matrix(mZ010.loo), app=T, loo_file)
       save.image(paste(dossier, "/", site, "_Z010.RData", sep=""))
}
### MODEL Z09
mZ09<-function(){
       init.funZ09 <-function(){</pre>
         list("tau_l" = rexp(1,10), "tau_P" = rexp(1,10), "beta" = rnorm(1,0,1), "delta" = rnorm(1,0,1),
"theta0" = rnorm(1,0,1), "epsilon" = rnorm(1,0,1),
"effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1), "inter"=inter0)
       }
        mod.Z09<<-jags(inits=init.funZ09,model.file = "modelZ09_code.txt",data =
list("cooc", "visit", "ab P", "dim1", "dim2"), parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","delta","beta","theta0","epsilon","loglik"),n.chains = 1,
n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z09.mcmc<-as.mcmc(mod.Z09)</pre>
```

```
mZ09<-mod.Z09$BUGSoutput$sims.list
       mZ09.deviance<-mZ09$deviance
       mZ09.loglik<-mZ09$loglik
       dimSEM<-dim(mZ09.loglik)[1]
       list.mZ09<-sapply(1:dimSEM,function(x) matrix(mZ09.loglik[x,,],nrow=dim1*dim2))
       list.tmZ09<-(t(list.mZ09))</pre>
       mZ09.loo<-loo(list.tmZ09)
       mZ09.loo
       loo file<-paste(dossier, "/", site, " Z09 loo.txt", sep="")
       write_values("mZ09", app=T, loo_file)
       mZ09_loo_pointwise<-mZ09.loo$pointwise
       mZ09 loo pareto k<-mZ09.loo$pareto k
       mZ09.loo$pareto_k<-NULL
       mZ09.loo$pointwise<-NULL
       write values(as.matrix(mZ09.loo), app=T, loo file)
       save.image(paste(dossier, "/", site, "_Z09.RData", sep=""))
}
### MODEL Z08
mZ08<-function(){
       init.funZ08 <-function(){</pre>
        list("tau I" = rexp(1,10), "tau P" = rexp(1,10), "beta" = rnorm(1,0,1), "gamma" =
rnorm(1,0,1), "theta0" = rnorm(1,0,1), "epsilon" = rnorm(1,0,1),
"effet_l"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1), "inter"=inter0)
       }
       mod.Z08<<-jags(inits=init.funZ08,model.file = "modelZ08 code.txt",data =
list("cooc","visit","ab_l","dim1","dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","gamma","beta","theta0","epsilon","loglik"),n.chains = 1,
n.iter=1000000, n.burnin = 250000, n.thin = 250)
       mod.Z08.mcmc<-as.mcmc(mod.Z08)
       mZ08<-mod.Z08$BUGSoutput$sims.list
       mZ08.deviance<-mZ08$deviance
       mZ08.loglik<-mZ08$loglik
       dimSEM<-dim(mZ08.loglik)[1]
       list.mZ08<-sapply(1:dimSEM,function(x) matrix(mZ08.loglik[x,,],nrow=dim1*dim2))
       list.tmZ08<-(t(list.mZ08))
       mZ08.loo<-loo(list.tmZ08)
       mZ08.loo
       loo_file<-paste(dossier, "/", site, "_Z08_loo.txt", sep="")</pre>
       write values("mZ08", app=T, loo file)
       mZ08_loo_pointwise<-mZ08.loo$pointwise
       mZ08 loo pareto k<-mZ08.loo$pareto k
       mZ08.loo$pareto k<-NULL
       mZ08.loo$pointwise<-NULL
       write values(as.matrix(mZ08.loo), app=T, loo file)
       save.image(paste(dossier, "/", site, "_Z08.RData", sep=""))
```

```
}
```

```
### MODEL Z07
mZ07<-function(){
       init.funZ07 <-function(){</pre>
         list("tau_I" = rexp(1,10), "tau_P" = rexp(1,10), "alpha" = 0.1,"beta" = rnorm(1,0,1), "delta" =
rnorm(1,0,1), "theta0" = rnorm(1,0,1), "effet I"=rnorm(dim1,0,1),"effet P"=rnorm(dim2,0,1),
"inter"=inter0)
       }
        mod.Z07<<-jags(inits=init.funZ07,model.file = "modelZ07_code.txt",data =
list("cooc", "visit", "ab P", "dim1", "dim2"), parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","alpha","delta","beta","theta0","loglik"),n.chains = 1,
n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z07.mcmc<-as.mcmc(mod.Z07)
       mZ07<-mod.Z07$BUGSoutput$sims.list
        mZ07.deviance<-mZ07$deviance
        mZ07.loglik<-mZ07$loglik
       dimSEM<-dim(mZ07.loglik)[1]
       list.mZ07<-sapply(1:dimSEM,function(x) matrix(mZ07.loglik[x,,],nrow=dim1*dim2))
       list.tmZ07<-(t(list.mZ07))
       mZ07.loo<-loo(list.tmZ07)
       mZ07.loo
       loo file<-paste(dossier, "/", site, " Z07 loo.txt", sep="")
       write_values("mZ07", app=T, loo_file)
        mZ07_loo_pointwise<-mZ07.loo$pointwise
        mZ07_loo_pareto_k<-mZ07.loo$pareto_k
        mZ07.loo$pareto k<-NULL
       mZ07.loo$pointwise<-NULL
       write values(as.matrix(mZ07.loo), app=T, loo file)
       save.image(paste(dossier, "/", site, "_Z07.RData", sep=""))
}
### MODEL Z06
mZ06<-function(){
       init.funZ06 <-function(){</pre>
         list("tau_l" = rexp(1,10), "tau_P" = rexp(1,10), "alpha" = 0.1, "beta" = rnorm(1,0,1), "gamma"
= rnorm(1,0,1), "theta0" = rnorm(1,0,1), "effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1),
"inter"=inter0)
       }
        mod.Z06<<-jags(inits=init.funZ06,model.file = "modelZ06 code.txt",data =
list("cooc","visit","ab_l","dim1","dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","alpha","gamma","beta","theta0","loglik"),n.chains = 1,
n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z06.mcmc<-as.mcmc(mod.Z06)
       mZ06<-mod.Z06$BUGSoutput$sims.list
        mZ06.deviance<-mZ06$deviance
       mZ06.loglik<-mZ06$loglik
       dimSEM<-dim(mZ06.loglik)[1]
        list.mZ06<-sapply(1:dimSEM,function(x) matrix(mZ06.loglik[x,,],nrow=dim1*dim2))
```

```
list.tmZ06<-(t(list.mZ06))</pre>
        mZ06.loo<-loo(list.tmZ06)
        mZ06.loo
       loo_file<-paste(dossier, "/", site, "_Z06_loo.txt", sep="")</pre>
       write values("mZ06", app=T, loo file)
        mZ06_loo_pointwise<-mZ06.loo$pointwise
        mZ06 loo pareto k<-mZ06.loo$pareto k
       mZ06.loo$pareto_k<-NULL
       mZ06.loo$pointwise<-NULL
       write_values(as.matrix(mZ06.loo), app=T, loo_file)
       save.image(paste(dossier, "/", site, "_Z06.RData", sep=""))
}
### MODEL Z05
mZ05<-function(){
       init.funZ05 <-function(){</pre>
         list("tau_I" = rexp(1,10), "tau_P" = rexp(1,10), "alpha" = 0.1,"beta" = rnorm(1,0,1), "theta0"
= rnorm(1,0,1), "epsilon" = rnorm(1,0,1), "effet I"=rnorm(dim1,0,1),"effet P"=rnorm(dim2,0,1),
"inter"=inter0)
       }
        mod.Z05<<-jags(inits=init.funZ05,model.file = "modelZ05 code.txt",data =
list("cooc","visit","dim1","dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","alpha","beta","theta0","epsilon","loglik"),n.chains = 1,
n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z05.mcmc<-as.mcmc(mod.Z05)
        mZ05<-mod.Z05$BUGSoutput$sims.list
        mZ05.deviance<-mZ05$deviance
        mZ05.loglik<-mZ05$loglik
       dimSEM<-dim(mZ05.loglik)[1]
       list.mZ05<-sapply(1:dimSEM,function(x) matrix(mZ05.loglik[x,,],nrow=dim1*dim2))
       list.tmZ05<-(t(list.mZ05))
       mZ05.loo<-loo(list.tmZ05)
       mZ05.loo
       loo_file<-paste(dossier, "/", site, "_Z05_loo.txt", sep="")</pre>
       write_values("mZ05", app=T, loo_file)
        mZ05 loo pointwise<-mZ05.loo$pointwise
        mZ05_loo_pareto_k<-mZ05.loo$pareto_k
       mZ05.loo$pareto k<-NULL
       mZ05.loo$pointwise<-NULL
       write values(as.matrix(mZ05.loo), app=T, loo file)
       save.image(paste(dossier, "/", site, "_Z05.RData", sep=""))
}
### MODEL Z04
mZ04<-function(){
       init.funZ04 <-function(){</pre>
```

```
list("tau_l" = rexp(1,10), "tau_P" = rexp(1,10), "beta" = rnorm(1,0,1), "gamma" =
rnorm(1,0,1), "delta" = rnorm(1,0,1), "theta0" = rnorm(1,0,1), "epsilon" = rnorm(1,0,1),
"effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1), "inter"=inter0)
       }
        mod.Z04<<-jags(inits=init.funZ04,model.file = "modelZ04 code.txt",data =
list("cooc","visit","ab_l","ab_P","dim1","dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","gamma","delta","beta","theta0","epsilon","loglik"),n.chai
ns = 1, n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z04.mcmc<-as.mcmc(mod.Z04)
       mZ04<-mod.Z04$BUGSoutput$sims.list
        mZ04.deviance<-mZ04$deviance
        mZ04.loglik<-mZ04$loglik
       dimSEM<-dim(mZ04.loglik)[1]
       list.mZ04<-sapply(1:dimSEM,function(x) matrix(mZ04.loglik[x,,],nrow=dim1*dim2))
       list.tmZ04<-(t(list.mZ04))
       mZ04.loo<-loo(list.tmZ04)
       mZ04.loo
       loo_file<-paste(dossier, "/", site, "_Z04_loo.txt", sep="")</pre>
       write values("mZ04", app=T, loo file)
        mZ04 loo pointwise<-mZ04.loo$pointwise
        mZ04 loo pareto k<-mZ04.loo$pareto k
        mZ04.loo$pareto k<-NULL
        mZ04.loo$pointwise<-NULL
       write values(as.matrix(mZ04.loo), app=T, loo file)
        save.image(paste(dossier, "/", site, " Z04.RData", sep=""))
}
### MODEL Z03
mZ03<-function(){
       init.funZ03 <-function(){</pre>
         list("tau_I" = rexp(1,10), "tau_P" = rexp(1,10), "alpha" = 0.1,"beta" = rnorm(1,0,1), "gamma"
= rnorm(1,0,1), "theta0" = rnorm(1,0,1), "epsilon" = rnorm(1,0,1),
"effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1), "inter"=inter0)
       }
        mod.Z03<<-jags(inits=init.funZ03,model.file = "modelZ03 code.txt",data =
list("cooc", "visit", "ab I", "dim1", "dim2"), parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","alpha","gamma","beta","theta0","epsilon","loglik"),n.cha
ins = 1, n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z03.mcmc<-as.mcmc(mod.Z03)
        mZ03<-mod.Z03$BUGSoutput$sims.list
       mZ03.deviance<-mZ03$deviance
        mZ03.loglik<-mZ03$loglik
       dimSEM<-dim(mZ03.loglik)[1]
       list.mZ03<-sapply(1:dimSEM,function(x) matrix(mZ03.loglik[x,,],nrow=dim1*dim2))
       list.tmZ03<-(t(list.mZ03))
        mZ03.loo<-loo(list.tmZ03)
        mZ03.loo
```

```
loo_file<-paste(dossier, "/", site, "_Z03_loo.txt", sep="")</pre>
       write_values("mZ03", app=T, loo_file)
        mZ03_loo_pointwise<-mZ03.loo$pointwise
        mZ03_loo_pareto_k<-mZ03.loo$pareto_k
        mZ03.loo$pareto k<-NULL
        mZ03.loo$pointwise<-NULL
       write values(as.matrix(mZ03.loo), app=T, loo file)
       save.image(paste(dossier, "/", site, "_Z03.RData", sep=""))
}
### MODEL Z02
mZ02<-function(){
       init.funZ02 <-function(){</pre>
         list("tau_l" = rexp(1,10), "tau_P" = rexp(1,10), "alpha" = 0.1, "beta" = rnorm(1,0,1), "delta" =
rnorm(1,0,1), "theta0" = rnorm(1,0,1), "epsilon" = rnorm(1,0,1),
"effet I"=rnorm(dim1,0,1),"effet P"=rnorm(dim2,0,1), "inter"=inter0)
       }
        mod.Z02<<-jags(inits=init.funZ02,model.file = "modelZ02 code.txt",data =
list("cooc","visit","ab_P","dim1","dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","alpha","delta","beta","theta0","epsilon","loglik"),n.chain
s = 1, n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z02.mcmc<-as.mcmc(mod.Z02)</pre>
        mZ02<-mod.Z02$BUGSoutput$sims.list
        mZ02.deviance<-mZ02$deviance
       mZ02.loglik<-mZ02$loglik
        dimSEM<-dim(mZ02.loglik)[1]
       list.mZ02<-sapply(1:dimSEM,function(x) matrix(mZ02.loglik[x,,],nrow=dim1*dim2))
       list.tmZ02<-(t(list.mZ02))</pre>
       mZ02.loo<-loo(list.tmZ02)
       mZ02.loo
       loo_file<-paste(dossier, "/", site, "_Z02_loo.txt", sep="")</pre>
       write_values("mZ02", app=T, loo_file)
        mZ02_loo_pointwise<-mZ02.loo$pointwise
        mZ02_loo_pareto_k<-mZ02.loo$pareto_k
       mZ02.loo$pareto_k<-NULL
        mZ02.loo$pointwise<-NULL
       write values(as.matrix(mZ02.loo), app=T, loo file)
        save.image(paste(dossier, "/", site, "_Z02.RData", sep=""))
}
### MODEL Z01
mZ01<-function(){
       init.funZ01 <-function(){</pre>
         list("tau_I" = rexp(1,10), "tau_P" = rexp(1,10), "alpha" = 0.1,"beta" = rnorm(1,0,1), "gamma"
= rnorm(1,0,1), "delta" = rnorm(1,0,1), "theta0" = rnorm(1,0,1),
"effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1), "inter"=inter0)
       }
```

```
mod.Z01<<-jags(inits=init.funZ01,model.file = "modelZ01_code.txt",data =
list("cooc","visit","ab_I","ab_P", "dim1", "dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","alpha","gamma","delta","beta","theta0","loglik"),n.chain
s = 1, n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z01.mcmc<-as.mcmc(mod.Z01)</pre>
        mZ01<-mod.Z01$BUGSoutput$sims.list
        mZ01.deviance<-mZ01$deviance
       mZ01.loglik<-mZ01$loglik
        dimSEM<-dim(mZ01.loglik)[1]
       list.mZ01<-sapply(1:dimSEM,function(x) matrix(mZ01.loglik[x,,],nrow=dim1*dim2))
       list.tmZ01<-(t(list.mZ01))</pre>
        mZ01.loo<-loo(list.tmZ01)
       mZ01.loo
       loo_file<-paste(dossier, "/", site, "_Z01_loo.txt", sep="")</pre>
       write_values("mZ01", app=T, loo_file)
        mZ01_loo_pointwise<-mZ01.loo$pointwise
        mZ01 loo pareto k<-mZ01.loo$pareto k
       mZ01.loo$pareto_k<-NULL
        mZ01.loo$pointwise<-NULL
       write_values(as.matrix(mZ01.loo), app=T, loo_file)
        save.image(paste(dossier, "/", site, " Z01.RData", sep=""))
}
### MODEL Z00
mZ00<-function(){
       init.funZ00 <-function(){
         list("tau_l" = rexp(1,10), "tau_P" = rexp(1,10), "alpha" = 0.1, "beta" = rnorm(1,0,1), "gamma"
= rnorm(1,0,1), "delta" = rnorm(1,0,1), "theta0" = rnorm(1,0,1), "epsilon" = rnorm(1,0,1),
"effet_I"=rnorm(dim1,0,1),"effet_P"=rnorm(dim2,0,1), "inter"=inter0)
       }
        mod.Z00<<-jags(inits=init.funZ00,model.file = "modelZ00_code.txt",data =
list("cooc","visit","ab I","ab P","dim1","dim2"),parameters.to.save =
c("mu","effet_I","effet_P","tau_I","tau_P","alpha","gamma","delta","beta","theta0","epsilon","loglik
"),n.chains = 1, n.iter=1000000, n.burnin = 250000, n.thin = 250)
        mod.Z00.mcmc<-as.mcmc(mod.Z00)
        mZ00<-mod.Z00$BUGSoutput$sims.list
        mZ00.deviance<-mZ00$deviance
        mZ00.loglik<-mZ00$loglik
       dimSEM<-dim(mZ00.loglik)[1]
       list.mZ00<-sapply(1:dimSEM,function(x) matrix(mZ00.loglik[x,,],nrow=dim1*dim2))
       list.tmZ00<-(t(list.mZ00))
        mZ00.loo<-loo(list.tmZ00)
       mZ00.loo
       loo_file<-paste(dossier, "/", site, "_Z00_loo.txt", sep="")</pre>
       write_values("mZ00", app=T, loo_file)
        mZ00 loo pointwise<-mZ00.loo$pointwise
        mZ00_loo_pareto_k<-mZ00.loo$pareto_k
```

```
mZ00.loo$pareto_k<-NULL
       mZ00.loo$pointwise<-NULL
       write_values(as.matrix(mZ00.loo), app=T, loo_file)
       save.image(paste(dossier, "/", site, "_Z00.RData", sep=""))
}
###### end model functions
print("JOB DONE")
###
       Network information (do not change) ###
###BLOCK 3 - MODEL EXECUTION ###
#launch_modele<-function(){</pre>
       ntw<-read.table(paste(dossier, "/", site, "_ntw.txt", sep=""),
sep="\t",header=T,row.names=1)
       dim1<-dim(ntw)[1]
       dim2<-dim(ntw)[2]
       web<-as.matrix(ntw,dim1,dim2)</pre>
       interO<-dget(paste(dossier, "/", site, " web i.txt", sep=""))</pre>
       cooc<-dget(paste(dossier, "/", site, "_co.txt", sep=""))</pre>
       visit<-read.table(paste(dossier, "/", site, "_ntw.txt", sep=""),sep="\t",header=T)</pre>
       visit<-as.matrix(visit)
       abundancel<-read.table(paste(dossier, "/", site, " abl.txt", sep=""), sep="\t", header=T)
       ab I <- log(abundanceI[,2])
       abundanceP<-read.table(paste(dossier, "/", site, "_abP.txt", sep=""), sep="\t", header=T)
       ab P <- log(abundanceP[,2])
       if(opt$modele == "all")
       {
               print("modele: all")
               for(i in 0:15)
               {
                       print(paste("COMPUTING MODELE ", i, "\n", sep=""))
                       mod<-eval(parse(text=paste("mZ0", i, sep="")))</pre>
                       mod()
               }
       }else{
               print(paste("modele: ", opt$modele), sep="")
               mod<-eval(parse(text=paste("m", opt$modele, sep="")))</pre>
                                                                            #recupération de la
fonction du modele
               mod()
       }
#### end model execution
#launch_modele()
### PARAMETER VALUES ###
library(optparse)
option_list = list(
```

make\_option(c("-d", "--dir"), type="character", default=NULL, help="model directory", metavar="character"),

```
make_option(c("-s", "--site"), type="character", default=NULL, help="site name",
```

```
metavar="character"))
```

opt\_parser = OptionParser(option\_list=option\_list);

opt = parse\_args(opt\_parser);

```
rdata<-list.files(opt$dir, pattern="*_Z015.RData")</pre>
```

load(paste(opt\$dir, "/", rdata, sep="")) #chargement du RData qui contient tous les modèles pour un site donné

print(paste("RData ", rdata, " loaded", sep=""))

for(mod in ls(pattern="mod.Z0\*"))

{

print(paste("getting values from ", mod, sep=""))

model<-eval(parse(text=mod))</pre>

if(is.null(model\$BUGSoutput\$mean\$alpha)){model\$BUGSoutput\$mean\$alpha<-NA} if(is.null(model\$BUGSoutput\$mean\$beta)){model\$BUGSoutput\$mean\$beta<-NA} if(is.null(model\$BUGSoutput\$mean\$delta)){model\$BUGSoutput\$mean\$delta<-NA} if(is.null(model\$BUGSoutput\$mean\$epsilon)){model\$BUGSoutput\$mean\$epsilon<-NA} if(is.null(model\$BUGSoutput\$mean\$gamma)){model\$BUGSoutput\$mean\$gamma<-NA}

val<-matrix(c(model\$BUGSoutput\$mean\$alpha, model\$BUGSoutput\$mean\$beta, model\$BUGSoutput\$mean\$delta, model\$BUGSoutput\$mean\$epsilon, model\$BUGSoutput\$mean\$gamma), 1, 5, dimnames=list("values", c("alpha", "beta", "delta", "epsilon", "gamma")))

write.table(val, file=paste(opt\$dir, "/", opt\$site, "\_", mod, "\_values.txt", sep=""), quote=F, sep="\t", row.names=F, col.names=T)
}

#### Appendix S3: Modularity and latent block model analysis

We calculated the modularity of the network using the cluster\_leading\_eigen method for modularity optimization implemented in the igraph package (Csardi and Nepusz 2006, Newman 2006). We then performed latent block models (LBM) using the BM\_poisson method for quantitative network data implemented in the blockmodels package (Leger et al. 2015). Blocks are calculated separately for the two groups (insect and plant) based on the number of visits (*i.e.* a weighted network). The algorithm finds the best divisions of insects and plants through fitting one Poisson parameter in each block of the visit matrix, thus essentially maximizing the ICL (Integrated Completed Likelihood; Biernacki et al. 2000, Daudin et al. 2007).

library(bipartite) library(vegan) library(igraph) library(dummies) library(blockmodels) library(ade4) library(fields)

```
#site data (ex: Bois de Fontaret, BFs)
BFs<-read.table("ntwBFs.txt",header=T,sep="\t")
webBFs <- as.matrix(BFs)
BFs.graph.bin<-graph_from_incidence_matrix(webBFs,multiple=F) #binary
BFs.bin.cle<-cluster leading eigen(BFs.graph.bin)
BFs.bin.cle
#get phenology overlap matrix
coBF<-dget("coBFs.txt")
bmi BFs<-BM poisson('LBM', webBFs)
bmi_BFs$estimate()
numi BFs<-which.max(bmi BFs$ICL)
densi_BFs<-sum(webBFs)/(nrow(webBFs)*ncol(webBFs))
probi BFs<-bmi BFs$model parameters[[numi BFs]]$lambda
row.nb.gpi<-nrow(probi_BFs)</pre>
col.nb.gpi<-ncol(probi BFs)
prob.rowi<-bmi_BFs$memberships[[numi_BFs]]$Z1
hh.namei<-rownames(webBFs)
mbrshp.hhi<-apply(prob.rowi,1,which.max)
ls.freq.rowi<-rowSums(webBFs)</pre>
res.hhi<-cbind.data.frame(hh.namei=hh.namei, mbrshp.hhi=mbrshp.hhi, freg.hhi=ls.freg.rowi)
res.hh.ordi<-res.hhi[order(res.hhi$freq.hhi),]
cpt=0
for(k in 1: (nrow(res.hh.ordi)-1))
{
 if (res.hh.ordi$mbrshp.hhi[k] !=res.hh.ordi$mbrshp.hhi[k+1]) cpt=cpt+1
}
nb.diff.hhi=cpt-(length(levels(as.factor(res.hh.ordi$mbrshp.hhi)))-1)
#write tables
write.table(res.hh.ordi,sep="\t",row.names=FALSE)
prob.coli<-bmi_BFs$memberships[[numi_BFs]]$Z2
sp.namei<-colnames(webBFs)</pre>
mbrshp.spi<-apply(prob.coli,1,which.max)
ls.freq.coli<-colSums(webBFs)</pre>
res.spi<-cbind.data.frame(sp.namei=sp.namei, mbrshp.spi=mbrshp.spi, freq.spi=ls.freq.coli)
res.sp.ordi<-res.spi[order(res.spi$freq.spi),]
cpt=0
for (k in 1: (nrow(res.sp.ordi)-1))
{
 if(res.sp.ordi$mbrshp.spi[k] !=res.sp.ordi$mbrshp.spi[k+1]) cpt=cpt+1
}
```

```
nb.diff.spi=cpt-(length(levels(as.factor(res.sp.ordi$mbrshp.spi)))-1)
res.sp.ord2i=res.spi[order(res.spi$mbrshp.spi),]
write.table(res.sp.ordi,sep="\t",row.names=FALSE)
write.table(probi_BFs,file="_prob_BFs",sep="\t",row.names=FALSE)
```

#### 

```
par(mfrow=c(1,1))
webBFs2<-webBFs
webBFs[which(webBFs>1)]=1
nb.row=nrow(webBFs)
nb.col=ncol(webBFs)
nds=webBFs
nps=coBF
res.prob=read.table("_prob_BFs",sep="\t",h=TRUE)
ls.ord.col.prob=order(colSums(res.prob),decreasing=TRUE)
ls.ord.row.prob=order(rowSums(res.prob),decreasing=TRUE)
Is.ord.hhi=sapply(res.hhi$mbrshp.hhi,function(x) which (x==ls.ord.row.prob))
res.hh.ord2i=res.hhi[order(ls.ord.hhi),]
row.nb.gpi=length(levels(as.factor(res.hhi$mbrshp.hhi)))
res.hh.ord3i=NULL
for (h in ls.ord.row.prob)
{
 part=res.hh.ord2i[res.hh.ord2i$mbrshp.hhi==h,]
 part.ord=part[order(part$freq.hhi,decreasing=TRUE),]
 res.hh.ord3i=rbind.data.frame(res.hh.ord3i,part.ord)
}
ls.ord.sp=sapply(res.spi$mbrshp.spi,function(x) which (x==ls.ord.col.prob))
res.sp.ord2i=res.spi[order(ls.ord.sp),]
col.nb.gb=length(levels(as.factor(res.spi$mbrshp.spi)))
res.sp.ord3i=NULL
for (h in ls.ord.col.prob)
{
 part=res.sp.ord2i[res.sp.ord2i$mbrshp.spi==h,]
 part.ord=part[order(part$freq.spi,decreasing=TRUE),]
 res.sp.ord3i=rbind.data.frame(res.sp.ord3i,part.ord)
}
nds=nds[as.character(res.hh.ord3i$hh.namei),as.character(res.sp.ord3i$sp.namei)]
nps=nps[as.character(res.hh.ord3i$hh.namei),as.character(res.sp.ord3i$sp.namei)]
webBFs2=webBFs2[as.character(res.hh.ord3i$hh.namei),as.character(res.sp.ord3i$sp.namei)]
####### Plot matrix with heatcolors and the number of visits #######
visits<-matrix(webBFs2,nrow=dim(webBFs2)[1]*dim(webBFs2)[2],ncol=1)
visits<-visits[which(visits>0)] #without the zeros
coord.function<-function(x,nI,nP){</pre>
 c(((x-1)%%nl)+1,((x-1)%/%nl)+1)
}
```

```
func.plot.matrix<-function(x,y){</pre>
 indices<-which(x==1)
 min < -min(y)
 max < -max(y)
 yLabels<-rownames(x)
 xLabels<-colnames(x)
 title<-c("Bois de Fontaret")
 if(is.null(xLabels)){
  xLabels<-c(1:ncol(x))
 }
 if(is.null(yLabels)){
  yLabels<-c(1:nrow(x))
 }
 reverse<-nrow(x):1
 yLabels<-yLabels[reverse]
 y<-y[reverse,]
 image.plot(1:length(xLabels),1:length(yLabels),t(y),col=c("white",heat.colors(12)[12:1]), xlab="",
ylab="",axes=FALSE,zlim=c(min,max))
 if(!is.null(title)){
  title(ylab="Insects", line=8, cex.lab=1)
  title(xlab="Plants", line=6, cex.lab=1.2)
  title("Bois de Fontaret")
 }
 axis(BELOW<-1,at=1:length(xLabels),labels=as.factor(as.character(xLabels)),las =2, cex.axis=0.6)
 axis(LEFT<-2,at=1:length(yLabels), labels=as.factor(as.character(yLabels)),las= 2,cex.axis=0.6)
 axis(BELOW<-1,at=1:length(xLabels),labels=rep("",length(xLabels)),las =2,cex.axis=0.6)
 axis(LEFT<-2,at=1:length(yLabels),labels=rep("",length(yLabels)),las=2,cex.axis<-0.6)
 coo<-t(rbind(sapply(indices,function(xx) coord.function(xx,nrow(x),ncol(x)))))
 text(coo[,2],nrow(webBFs)+1-coo[,1],labels=visits, cex=0.6)
}
func.plot.matrix(nds,nps)
####### Black lines to delimit blocks in the plot ######
if (row.nb.gpi>1)
{
 ls.class=as.numeric(as.data.frame(table(res.hh.ord2i$mbrshp.hhi))[ls.ord.row.prob,2])
 ls.cum=sum(ls.class)-cumsum(ls.class)
 abline(h=ls.cum+0.5,col="grey20", lwd=2)
}
if (col.nb.gpi>1)
{
 ls.class=as.numeric(as.data.frame(table(res.sp.ord2i$mbrshp.spi))[ls.ord.col.prob,2])
 ls.cum=cumsum(ls.class)
 abline(v=ls.cum+0.5,col="grey20", lwd=2)
```