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Simulating seasonal drivers of aphid dynamics to explore agronomic scenarios

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Abstract.   With the regulation of pesticides in European agricultural landscapes, it is important to understand how pest populations respond to climate and landscape variables in the absence of pesticides at different spatial–temporal scales. While models have described individual biological processes, few have simulated complete life cycles at such scales. We developed a spatially explicit simulation model of the dynamics of the bird cherry–oat aphid (*Rhopalosiphum padi*) in a pesticide-free simulated landscape using data from an agricultural landscape located in southwest France. Using GLMMs, we ran two statistical methods, one at the crop level, focusing on aphid densities within each crop individually (wheat and its regrowth, corn, and sorghum), and another at the landscape level where aphid densities were not differentiated by crops. For each season, we analyzed how temperature, immigration, and habitat availability impacted on aphid densities. Predictors of aphid densities varied between crops and between seasons, and models for each individual crop resulted in better predictions of aphid densities than landscape-level models. Aphid immigration and temperature were important predictors of aphid densities across models but varied in the directionality of their effects. Moreover, landscape composition was a significant predictor in only four of the nine seasonal crop models. This highlights the complexity of pest–landscape interactions and the necessity of considering fine spatial–temporal scales to identify key factors that influence aphid densities, essential for developing future regulation methods. We used our model to explore the potential effects of two agronomic scenarios on aphid densities: (1) replacement of corn with sorghum, where increases in available sorghum led to the dilution of aphid populations in sorghum in spring and their concentration in summer, and (2) abandonment of pastures for wheat fields, which had no significant effect on aphid densities at the landscape scale. By simulating potential future agronomic practices, we can identify the risks of such changes and inform policy and decision-makers to better anticipate pest dynamics in the absence of pesticides. This approach can be applied to other systems where agronomic and land cover data are available, and to other pest species for which biological processes are described in the literature.

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INTRODUCTION

Agriculture is highly impacted by the presence of pests (Deutsch et al. 2018). Aphids, in particular, affect a wide variety of crops and can be found worldwide (Van Emden and Harrington 2017). Climate drives many of the processes involved in the life cycle of these ectotherm organisms, such as survival (Pons et al. 1993), reproduction (Simon et al. 2002), and development (Campbell et al. 1974). Other than favorable climatic conditions, aphids also require different habitats to fulfill their biological cycles, which can be unevenly distributed through space and time (Schellhorn et al. 2015). Therefore, the composition and configuration of habitats within landscapes (Chaplin-Kramer et al. 2011) should be considered when studying aphid population dynamics. Recent meta-analyses have, however, highlighted that natural pest regulation exhibits inconsistent responses to surrounding landscape structure (Rusch et al. 2016, Karp et al. 2018). One hypothesis explaining this result is that agricultural landscapes are subject to frequent changes due to their strong anthropogenic nature, which leads to highly variable spatial–temporal dynamics (Urruty et al. 2016). Farm management shapes spatial–temporal variability of land cover through factors such as crop rotation (Wibberley 1996), crop variety (Asrat et al. 2010), or individual crops managed differently due to the experience and ideological beliefs of farmers (McGuire et al. 2015).

With agricultural practices changing rapidly due to economical (Van Vliet et al. 2012) and climatic (Rickards and Howden 2012) drivers, it is essential to develop a conceptual framework exploring how pests respond to these shifts. Such a framework would assist in anticipating undesired effects on pest dynamics and help identify new management methods. This tool should build upon the Integrated Pest Management framework (IPM; Elliott et al. 1995), which focuses on understanding the interactions between pests and landscapes. The aim of IPM strategies is not to eradicate pests, but to maintain populations below economically injurious levels (Stenberg 2017). The general IPM framework can be divided into two complementary approaches: a bottom-up approach regulating resource availability for the pest to minimize

population dynamics, and a top-down approach increasing resource availability for natural enemies, in order to increase their abundance and thus increase their predation pressure on pest dynamics. Both approaches aim at managing resources in space and time. Therefore, it is necessary to consider a wide range of spatial–temporal scales, ranging from the finest scale (the individual plant) to the broadest (the landscape on a pluriannual scale). Fine-scale control methods are relatively well-documented, such as delaying sowing dates to temporally avoid pest migration windows and thus limit colonization (McLeod et al. 1992), or push-pull strategies (Cook et al. 2007), which control pest movement behavior through the use of natural chemical signals produced by specific plants. Landscape-scale control involves looking at the spatial–temporal organization of crops and semi-natural habitats within the landscape and much is still to be learnt about how mobile organisms respond to these parameters. For example, the source–sink processes of aphid colonization in agricultural landscapes represent an important challenge for crop management (Vialatte et al. 2006, Bianchi et al. 2007).

Resource availability at the landscape level can have contrasting impacts on the abundance of pests. High abundance of host crops can decrease (e.g., through a dilution effect; Thies et al. 2008) or increase (e.g., through a concentration effect; Root 1973) the abundance of a pest in a given year at the field level. Agricultural practices conducted in the neighboring host crop fields are an important factor of these concentration or dilution effects (Monteiro et al. 2013). Interannual effects can also be observed, such as population explosions following a year where resource availability was high (Marrec et al. 2017). Finally, Batáry et al. (2011) have underlined that species respond differently to increases in landscape heterogeneity, with generalists responding positively and specialists negatively.

The top-down approach of pest regulation has been studied mostly through predator–prey interaction models (Liere et al. 2012, Thierry et al. 2015). On the contrary, fewer studies have focused on regulating pest populations through bottom-up approaches, with some examples on cereal aphids (Parry et al. 2006) and weevils (Vinatier et al. 2012). The dynamics of pests

represented in these models usually focus on fine spatial–temporal scales, modeling one process (i.e., dispersal) during a small time frame (mainly during spring colonization of crops). These models also tend to use a binary approach when modeling habitat, with all habitat types sharing the same properties. Kieckhefer and Gellner (1988) have shown that crop type and phenological stages can have different impacts on the reproductive success of cereal aphids. Thus, modeling habitat quality as a range of different values rather than a binary process should be considered.

In this study, we used a spatially explicit simulation model to (1) determine how climate, pest immigration, and spatial–temporal variation in habitat availability influence seasonal variation of pest populations in both individual crops and at the landscape level, and (2) explore agronomic scenarios to identify potential effects of changes in practices on aphid populations and help inform future decision-making. To explore how these variables influence the entire life cycle of our pest, population dynamics were simulated in a theoretical environment with no pesticide applications to avoid chemically induced population crashes. To validate our approach, we focused on a specific case study of cereal aphid populations in France, the bird cherry–oat aphid, *Rhopalosiphum padi* (L.). This pest causes both direct damage to cereal crops and indirect damage through transmission of the barley yellow dwarf virus (Plumb 1983). Our theoretical landscape was based on the long-term ecological research site Vallées et Coteaux de Gascogne (part of the Zone Atelier Pygar) located in the southwest of France. We selected this site due to both availability of agronomic data and its high heterogeneity of natural elements, which studies have shown to be the ideal structure to reduce potential pest infestations in agricultural landscapes (Veres et al. 2013). Landscape dynamics were simulated using the Agricultural Landscape Simulator ATLAS (Thierry et al. 2017). We also explored two agronomic scenarios, based on changes in agricultural practices currently observed in our study region, to determine whether *R. padi* populations are likely to increase in the future with agricultural landscape changes.

MATERIALS AND METHODS

Simulating the agricultural landscape

The studied agricultural landscape is a 2 × 2 km landscape from the region of Vallées et Coteaux de Gascogne. This site is part of the Long Term Ecological Research (L LTER_-EU_FR_003) network located in the southwest of France, near the city of Toulouse (43°17′ N, 0°54′ E). The climate is semi-oceanic, including hot and dry summers and cool and humid winters. The landscape is composed of parallel hillsides and valleys in which water bodies, such as streams, can be found. The agricultural system is essentially composed of crop–livestock farming. The geographical distribution of fields and pastures is directly influenced by the topography, with pastures located along the hillsides, whereas crops are generally sowed in the bottom of the valleys (Choisis et al. 2012).

To simulate the spatial–temporal evolution of the agricultural landscape, we used the ATLAS simulator (Thierry et al. 2017). ATLAS simulates daily agricultural practices in a spatially explicit landscape. The advantage of this simulator is the possibility to reproduce realistic configuration and composition values for crops at the landscape level by considering user-defined crop rotations and crop phenological stages. Crop phenology and crop rotations used in this paper (see Appendix S1: Table S1) are the ones described in Thierry et al. (2017) with the addition of wheat volunteer, which is regrowth of wheat shortly after it is harvested. Wheat volunteer is common in our study system but is usually removed by farmers early November. In our model, wheat volunteer is simulated using the same properties as wheat seedlings and was removed at latest on 7 November, based on observed events in the study system.

Simulating aphid dynamics

A detailed description of the model can be found in the supplementary material (see Appendix S2) using the ODD (overview, design concepts, detail) protocol for describing models (Grimm et al. 2010). The aim of this model was to represent dynamics of *R. padi* throughout the year in relation to climate, immigration, and habitat quality and availability. Four potential host crops were included in the model: corn,

sorghum, wheat, and wheat volunteer. Habitat quality was represented by different reproduction rates of aphid depending on the host and its growth stage (Kieckhefer and Gellner 1988), and through different carrying capacities (crops vs volunteer). We did not consider pastures or other natural elements of the landscape as potential habitat in this model, in relation to evidence of habitat specialization of cereal aphids in French agricultural landscapes (Gilabert et al. 2014). To model the population dynamics, different submodels were put together simulating aphid development, reproduction, mortality, and dispersal. Populations were represented using a cellular automaton, with cells of 30 × 30 m, each possibly containing an aphid population composed of adults and nymphs and covering the entirety of the 2 × 2 km landscape (67 × 67 grid for a total of 4489 cells). For the sake of simplicity, plant density was not considered in the model to estimate populations. Aphid immigration was derived from 5 yr of suction trap collected in Montpellier, France, from the AGRAPHID network between 1997 and 2001. To avoid population explosions due to favorable conditions (no pesticide interventions), we considered a daily mortality rate due to natural enemies (a 30% potential daily mortality rate; Arrignon et al. 2007) in relation to daily mean temperature (see Appendix S2, mortality submodel).

Exploring agronomic scenarios

We explored the potential effects of two scenarios describing plausible changes in agricultural practices in the Vallées et Coteaux de Gascogne region on *R. padi* dynamics. In the first scenario, we simulated the effect of a change in crop type by replacing all corn with sorghum. Sorghum is much less demanding in terms of water needs than corn (Farré and Faci 2006) and is increasingly popular in local crop rotations where summers are getting dryer over time due to a decreasing time trend in rainfall (Juvanon Du Vachat 2014). In our second scenario, we simulated the effect of a drastic land-use change, through the abandonment of livestock farming. We replaced all temporary pastures with wheat in the crop rotations. This change has already been initiated in the early 2000s in this region (Choisis et al. 2010) mainly due to the intensity of

work needed for livestock farming and the low financial benefits of it compared with crop farming (Ryschawy et al. 2013).

Simulation planning

We explored six different versions of the simulation model (Table 1): (1) a reference model integrating habitat quality and a 30% potential daily mortality rate due to predation pressure, (2) a null model where phenological stages of all crops had the same effect of aphid dynamics, (3) a high predation model where predation pressure was increased (50% potential daily mortality rate), (4) a low predation model where predation pressure was decreased (10% potential daily mortality rate), (5) a pasture scenario where livestock was abandoned for wheat, and (6) a sorghum scenario where corn was replaced entirely with sorghum. Models (2), (3), and (4) were compared to the reference model (1) to explore the effects of habitat quality and predation pressure in the model. Models (5) and (6) were compared to the reference model (1) for scenario exploration.

Each model was simulated a total of ten times, and each simulation was set to last 10 yr. The 10-yr window was chosen since it allowed the longest crop rotation to be simulated once and others multiple times. The agricultural practices observed within a 10-yr window are usually relatively stable, and this period appears appropriate according to socioeconomical and global changes. To fit this 10-yr window, our 5 yr of suction data was repeated twice. With aphid immigration being highly correlated with climate (Klueken et al. 2009), we also repeated the corresponding 5 yr of weather data associated with the location of the trap twice. Details of both data sets are available in the supplementary material (see Appendix S1).

Statistical analysis

Using the R statistical software (Version 3.4.3, R Development Core Team 2016), we conducted the statistical analyses in two steps: (1) identification of the effects of climate, aphid immigration, habitat availability, and previous season aphid densities on seasonal aphid densities at both the crop scale and the landscape scale, and (2) comparison of seasonal aphid densities at the crop level between the reference scenario and the two theoretical agronomic scenarios. The simulation

Table 1. Description of the parameterization of the six versions of the model used in this study.

Model version	Habitat quality	Predation pressure	Daily potential mortality rate	Crop rotations	Use in study
(1) Reference model	Crop/stage-specific	Average	0.3	Current practices	Base model
(2) Null model	Constant	Average	0.3	Current practices	Model exploration
(3) High predation model	Crop/stage-specific	High	0.5	Current practices	Model exploration
(4) Low predation model	Crop/stage-specific	Low	0.1	Current practices	Model exploration
(5) Pasture scenario model	Crop/stage-specific	Average	0.3	Pasture scenario	Scenario exploration
(6) Sorghum scenario model	Crop/stage-specific	Average	0.3	Sorghum scenario	Scenario exploration

Notes: The parameters that could differ among versions were how habitat quality was considered (same across all crops/phenological stages or specific for each crop/phenological stage pair), the daily potential mortality rate by predation pressure (low, average, or high), and the crop rotations considered in the simulation (current practices, pasture scenario, or sorghum scenario).

model produced daily outputs for all parameters, and aphid densities were recorded at the cell level. To facilitate the analysis of our outputs, we divided the year into four 3-month periods (winter, January–March; spring, April–June; summer July–September; and fall, October–December), representing seasonality throughout the year. Temperature was summarized over the 3-month intervals by calculating cumulated degrees. Aphid immigration was transformed as the total sum of immigrating aphids over each season. Landscape composition was considered as the total area assigned to each crop at the seasonal level. Finally, aphid densities were summed up at the crop level daily as a density per square meter and were averaged across all days where the crop was available during the season. An example of the data used to analyze model outputs is available in the supplementary material (see Appendix S3: Table S1). While crop metrics and aphid densities are simulated, climate and immigration data are based on a 5-yr data set and thus are of a sample size of 20 unique values. Correlations between climate and landscape variables were tested using Pearson's correlation tests (see Appendix S3: Table S2). The variables retained in our analyses were chosen so that no pair showed strong correlations (>|0.5|) following Cohen's benchmark for large effect (Cohen 2013). Correlation between weather and crop metrics is bound to happen because of seasonality; thus, correlation between both was not used to select variables. Strong correlation between sorghum and corn, and wheat and wheat volunteer led us to consider only sorghum and wheat in our models, as they are the covers increasing in our scenarios.

To explore the effects of climatic and habitat availability parameters on simulated aphid densities, we ran two types of statistical methods, one at the crop level, focusing on aphid densities within each crop individually to see how well models could predict densities, and another at the landscape level where aphid densities were not differentiated by crops. We decided to compare these two methods since explanatory variables and seasonal availability varied across crops using the reference scenario outputs. The unit of observation for these statistical models was the seasonal average aphid density per square meter within fields. These were estimated by averaging model outputs (daily aphid densities) into a unique seasonal value. Since our simulation spanned over a 10-yr window, each replicate produced a total of ten data points per season, and we repeated the simulation ten times. The main difference among these two approaches was how the unit of observation (aphid densities) was estimated. For crop-level models, we only considered aphid densities within each crop individually, while for landscape-level models, aphid densities were averaged across all crops.

The models used were all general linear mixed models (GLMMs). Each explanatory variable was standardized between 0 and 1 using the range01 function from the modEvA package (Márcia Barbosa et al. 2013) to allow estimates to be comparable within and between models. All GLMMs were modeled using a Poisson distribution (see Appendix S3: Table S4) and an observation-level random intercept. An observation-level random intercept was added to the model to account for a possible overdispersion of the data (Lee and Nelder 2000). We used the Akaike information criterion for model selection through the dredge function in the MuMIn package (Bartón and Barton 2013). Marginal R^2 was calculated for the fixed effects using the r.squaredGLMM function (MuMIn package) and reported for every model to assess how well the model predicted our response variable (Nakagawa and Schielzeth 2013). Significance of fixed effects for each model was estimated using a type II ANOVA (car package; Fox et al. 2012). To compare seasonal aphid densities among the reference model and the two agronomic scenarios, we used the emmeans package (Lenth et al. 2018) with a general linear mixed model with a random intercept on crop type (see Appendix S3: Table S5).

Results

Application to the Vallées et Coteaux de Gascogne landscape

By coupling the aphid model with ATLAS, we simulated pluriannual population dynamics of *R. padi* in a dynamic agricultural landscape. We explored the effects of different predation rates by natural enemies in the model (Fig. 1). Higher predation pressure (0.5 mortality rate when natural enemies are active) caused extremely low population levels in late summer. Lower predation rates (0.1 mortality rate when natural enemies are active) created much higher population concentrations in spring compared with the other two scenarios. The reference scenario, with a predation pressure of 0.3 daily mortality rate when predators are active, produced in-field dynamics matching known patterns, with a period of colonization and settlement, followed by a strong population reduction (specifically in wheat fields) due to the intervention of natural enemies. We also explored the effect of

considering the quality of the successive host crops and their impact on aphid dynamics through different reproductive rates by comparing the reference model to the null model (Fig. 1). Considering stage-specific reproductive rates led to wheat housing higher densities of aphids at its late phenological stages, while summer crops were of lower habitat quality for aphids overall in comparison with the null model.

The relation between environmental parameters and aphid densities

In the crop-level models, the significance and directionality of the effect of explanatory variable varied greatly across crops and seasons (Table 2). We used marginal pseudo-R^2 to identify models where total variance was poorly explained by our fixed effects. The corn–spring, sorghum–spring, and volunteer–fall performed the poorest (marginal $r^2 \leq 0.1$) and are thus not further discussed. Temperature was a significant predictor of aphid densities across all wheat models (negative effect of higher temperature on aphid abundance in winter and spring, positive effect of higher temperature on aphid abundance in fall) and the volunteer–summer model (negative effect of higher temperature on aphid abundance). Aphid immigration was also a significant predictor across models, with higher aphid immigration leading to lower aphid densities in the wheat–spring and volunteer–summer models while leading to higher aphid densities in the wheat–fall and corn–summer models.

The two landscape composition variables (area assigned to wheat and area assigned to sorghum) had contrasting effects when significant, with wheat having a negative effect in the wheat–fall model, while sorghum had a positive effect in the volunteer–summer and corn–summer models (Table 2). Finally, aphid densities within crops in the previous season seemed to be a strong predictor of aphid densities across the six models that performed best. Directionality of the effects varied across crops and seasons, with a strong negative effect of aphid abundance in volunteers in the previous season on aphids in wheat during the winter.

In the landscape-level models where aphid densities were averaged at the landscape level, the spring, summer, and fall models performed
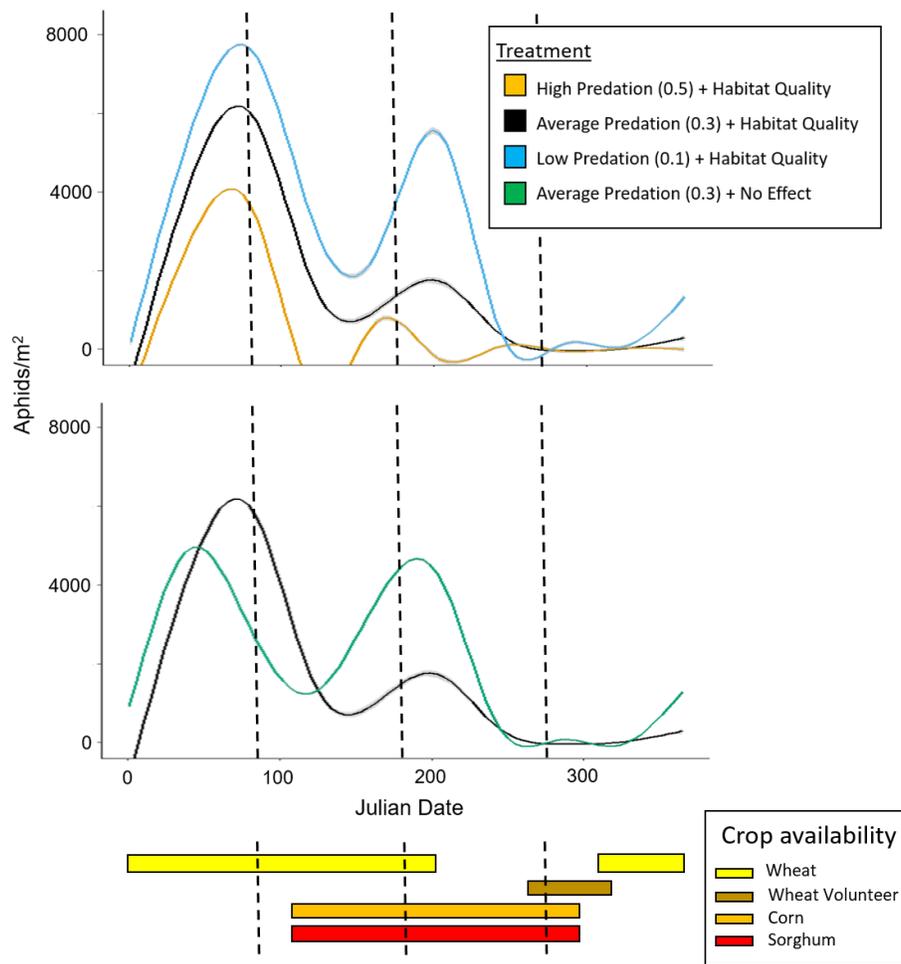
Fig. 1. Mean fitted aphid density per square meter of host crop in the landscape throughout a specific year (year 3) in a randomly chosen simulation for different predation pressure values and phenology models. Dashed lines separate the year into four different seasons. Crop availability throughout the year is indicated below the graph. Predation pressure is applied as a daily mortality rate when temperature values are high enough for natural enemy activity. The habitat quality model takes into account different reproduction values for aphids depending on the crop they are currently feeding on and its growth stage, in contrast to the null model, which uses a similar rate across all crops and stages. We explored three values of predation pressure with the habitat quality (top). We also explored the effects of habitat quality by comparing the null phenology model and the habitat quality phenology model (bottom), with a predation pressure fixed at the rate of 0.3. The mean values of aphids were fitted using a general additive model smoothing (GAM).

poorly (marginal $r^2 \leq 0.1$) and had no predictive power (Table 3). In winter, populations responded to the same drivers as wheat since it was the only available crop during that season.

Exploring agronomic scenarios

Daily areas assigned to each crop varied between the reference scenario (1) and the two

crop change scenarios (5 and 6; Fig. 2a). In the pasture scenario, all temporary pastures in the crop rotations were replaced by wheat (see Appendix S1: Table S1). This led to a 50% increase in the average area assigned to wheat and wheat volunteer throughout the seasons compared with the other two scenarios. This represents a change from wheat covering about 30%

Table 2. Summary of generalized linear mixed models (GLMMs) for the simulated mean aphid density per square meter in each habitat crop at the landscape scale throughout the seasons.

Fixed effect	Est	χ^2	df	P	Marginal R^2
Wheat					
Winter ($n = 100$)					0.68
Intercept	**8.45**	. . .	. . .	***	
Cumulated degrees	**−7.59**	**39.69**	1	***	
Total aphids immigrating	−0.90	1.36	1	ns	
Area wheat	0.09	0.10	1	ns	
Area sorghum					
Aphid density (prev season)					
Wheat	**9.37**	**25.36**	1	***	
Volunteer	**−98.81**	**62.10**	1	***	
Corn					
Sorghum					
Spring ($n = 100$)					0.35
Intercept	**12.79**	. . .	. . .	***	
Cumulated degrees	**−7.40**	**25.88**	1	***	
Total aphids immigrating	**−0.62**	**31.94**	1	***	
Area wheat	−0.16	0.86	1	ns	
Area sorghum	−0.07	0.15	1	ns	
Aphid density (prev season)					
Wheat	**0.72**	**24.46**	1	***	
Volunteer					
Corn					
Sorghum					
Fall ($n = 100$)					0.56
Intercept	**3.67**	. . .	. . .	***	
Cumulated degrees	**9.89**	**22.08**	1	***	
Total aphids immigrating	**15.06**	**28.21**	1	***	
Area wheat	**−3.64**	**9.92**	1	**	
Area sorghum					
Aphid density (prev season)					
Wheat					
Volunteer	**5.75**	**6.05**	1	*	
Corn	−1.17	0.55	1	ns	
Sorghum	**−7.61**	**19.96**	1	***	
Wheat volunteer					
Summer ($n = 100$)					0.75
Intercept	**6.87**	. . .	. . .	***	
Cumulated degrees	**−4.08**	**9.31**	1	**	
Total aphids immigrating	**−4.83**	**190.83**	1	***	
Area wheat					
Area sorghum	**0.36**	**3.25**	1	†	
Aphid density (prev season)					
Wheat	**0.77**	**10.10**	1	**	
Volunteer					
Corn					
Sorghum					
Fall ($n = 100$)					0.10
Intercept	**−9.86**	. . .	. . .	**	
Cumulated degrees					
Total aphids immigrating	**38.83**	**4.84**	1	*	
Area wheat					
Area sorghum					
Aphid density (prev season)					

(Table 2. Continued.)

Fixed effect	Est	χ^2	df	P	Marginal R^2
Wheat					
Volunteer	**25.62**	**5.82**	**1**	*	
Corn					
Sorghum	**−132.40**	**4.61**	**1**	*	
Corn					
Spring ($n = 100$)					0.10
Intercept	0.32	. . .	. . .	ns	
Cumulated degrees					
Total aphids immigrating	**1.06**	**12.65**	**1**	***	
Area wheat	**−1.07**	**3.00**	**1**	†	
Area sorghum					
Aphid density (prev season)					
Wheat					
Volunteer					
Corn					
Sorghum					
Summer ($n = 100$)					0.18
Intercept	**8.89**	. . .	. . .	***	
Cumulated degrees	−1.03	1.05	1	ns	
Total aphids immigrating	**1.85**	**40.96**	**1**	***	
Area wheat					
Area sorghum	**0.95**	**20.80**	**1**	***	
Aphid density (prev season)					
Wheat	**−0.67**	**12.55**	**1**	***	
Volunteer					
Corn	−47.93	0.06	1	ns	
Sorghum	**−0.25**	**3.62**	**1**	†	
Sorghum					
Spring ($n = 68$)					0.09
Intercept	**9.65**	. . .	. . .	***	
Cumulated degrees	**−2.35**	**5.14**	**1**	*	
Total aphids immigrating	**−0.14**	**6.76**	**1**	**	
Area wheat	0.20	1.32	1	ns	
Area sorghum	−0.06	0.33	1	ns	
Aphid density (prev season)					
Wheat	**0.24**	**2.93**	**1**	†	
Volunteer					
Corn					
Sorghum					
Summer ($n = 68$)					0.19
Intercept	1.14	. . .	. . .	ns	
Cumulated degrees	3.41	1.45	1	ns	
Total aphids immigrating					
Area wheat					
Area sorghum	−0.78	2.05	1	ns	
Aphid density (prev season)					
Wheat	**−0.95**	**5.80**	**1**	*	
Volunteer					
Corn					
Sorghum	**3.60**	**8.26**	**1**	**	

Notes: Each fixed effect is described by its coefficient value. Chi-square, degrees of freedom, and estimated significance (P value; ns = not significant, †$P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$) are obtained using a type II Wald chi-square test. For each model, we also report a marginal pseudo-R^2 representing the variance explained by fixed factors. Bold values are significant effects.

Table 3. Summary of generalized linear mixed models (GLMMs) for the simulated mean aphid density per square meter in all cereal fields in the landscape throughout the seasons.

Fixed effect	Est	χ^2	df	P	Marginal R^2
Winter ($n = 100$)					0.68
Intercept	**8.45**	. . .	. . .	***	
Cumulated degrees	**−7.59**	**39.69**	1	***	
Total aphids immigrating	−0.90	1.36	1	ns	
Area wheat	0.09	0.10	1	ns	
Area sorghum					
Aphid density (prev season)					
Wheat	**9.37**	**25.36**	1	***	
Volunteer	**−98.81**	**62.10**	1	***	
Corn					
Sorghum					
Spring ($n = 268$)					0.01
Intercept	**8.39**	. . .	. . .	***	
Cumulated degrees	**−4.42**	**18.86**	1	***	
Total aphids immigrating	**−0.33**	**26.73**	1	***	
Area wheat	−0.32	0.90	1	ns	
Area sorghum					
Aphid density (prev season)					
Wheat	**0.40**	**15.28**	1	***	
Volunteer					
Corn					
Sorghum					
Summer ($n = 200$)					0.01
Intercept	**5.41**	. . .	. . .	***	
Cumulated degrees					
Total aphids immigrating	**−0.99**	**13.92**	1	***	
Area wheat					
Area sorghum					
Aphid density (prev season)					
Wheat					
Volunteer					
Corn					
Sorghum					
Fall ($n = 100$)					0.06
Intercept	−0.54	. . .	. . .	ns	
Cumulated degrees	**9.28**	**24.13**	1	***	
Total aphids immigrating	**14.39**	**33.37**	1	***	
Area wheat	**−3.42**	**10.82**	1	**	
Area sorghum					
Aphid density (prev season)					
Wheat					
Volunteer	**7.83**	**11.34**	1	***	
Corn	**−6.29**	**32.93**	1	***	
Sorghum					

Notes: Each fixed effect is described by its coefficient value. Chi-square, degrees of freedom, and estimated significance (P value; ns = not significant, **$P < 0.01$, ***$P < 0.001$) are obtained using a type II Wald chi-square test. For each model, we also report a marginal pseudo-R^2 representing the variance explained by fixed factors. Bold values are significant effects.

of the area assigned to fields each year to almost 45% on average. In the sorghum scenario, all corn in the crop rotations was replaced by sorghum (see Appendix S1: Table S1). This led to a 200% increase in the area assigned to sorghum yearly. This represents an increase from sorghum covering around 3.5% of the area assigned to fields to 10% on average. Overall, the pattern of
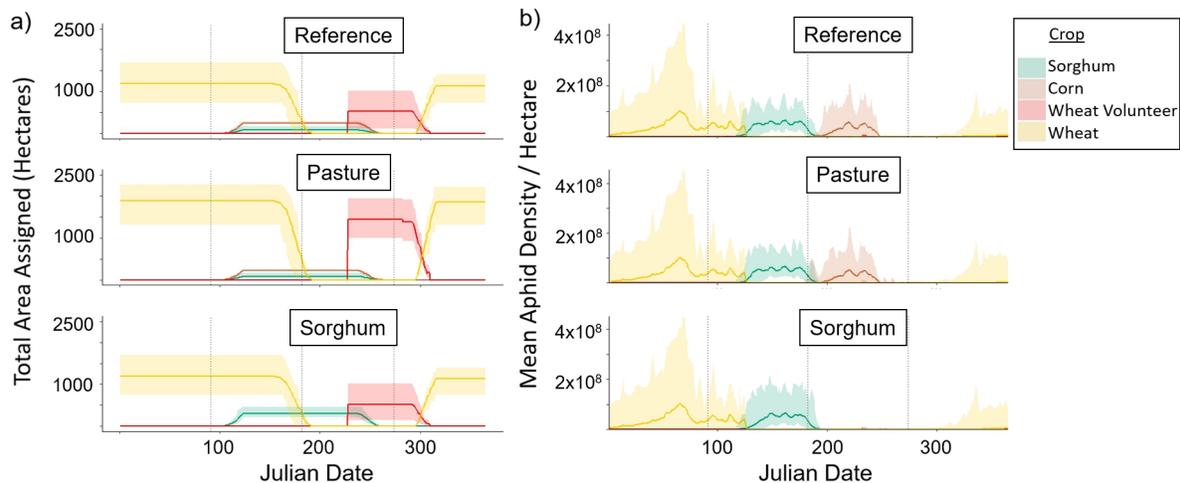
Fig. 2. Area assigned (a) and mean aphid density per hectare (b) throughout the year for each simulated crop type. Bold lines represent the mean values across all simulations, and the shaded areas represent minimum and maximum value ranges. Each plot represents a different scenario with the reference scenario on top, the pasture scenario where all pastures are replaced by wheat within the rotations in the middle, and the sorghum scenario where corn is replaced by sorghum within the rotations on the bottom.

simulated aphid dynamics remained consistent across all scenarios, except for the sorghum scenario where corn was no longer present as a possible habitat for aphids (Fig. 2b).

Mean aphid densities within wheat did not vary across scenarios (Figure 3). Aphid densities in wheat volunteer (summer and fall), corn (summer), and sorghum (spring and summer) significantly differed among scenarios. Aphid densities in wheat volunteer were higher in the pasture scenario during fall and lower during summer compared with the other two scenarios. Aphid densities in sorghum were lower in the sorghum scenario in spring and higher in summer compared with both other scenarios. Finally, aphid densities in corn in summer were lower in the pasture scenario compared with the reference scenario.

Discussion

Our study highlights the complexity of interactions between climate, landscape, and population dynamics of aphids. Ecological predictors of aphid densities varied not only temporally (seasons) but also among crop types. Our framework offers an easy-to-apply method to inform integrated pest management while considering these

levels of complexity and exploring the consequences of potential changes in agricultural practices through the simulation of scenarios. Comparison between crop-level and landscape-level models indicates that crop-level models had better predicting accuracy for estimating aphid densities within the landscape, highlighting strong crop-specific dynamics. Our results highlight interesting key crop-specific seasonal processes that potentially play a role in regulating aphid densities at the landscape scale and help inform future decision-making.

Simulating seasonal aphid dynamics and understanding the effects of landscape parameters

In our simulations, there were no year–year dynamics of aphid densities due to a constant natural reset of aphid populations. Simulated *R. padi* dynamics were affected by a strong bottleneck during the end of summer and start of fall when wheat volunteer is the major remaining resource available within the landscape. The limited quality of this cover, which leads to low reproduction rates for aphids within this habitat due to poor nutritional quality, was not sufficient to maintain high densities of aphids within the landscape. This led to habitat discontinuity,
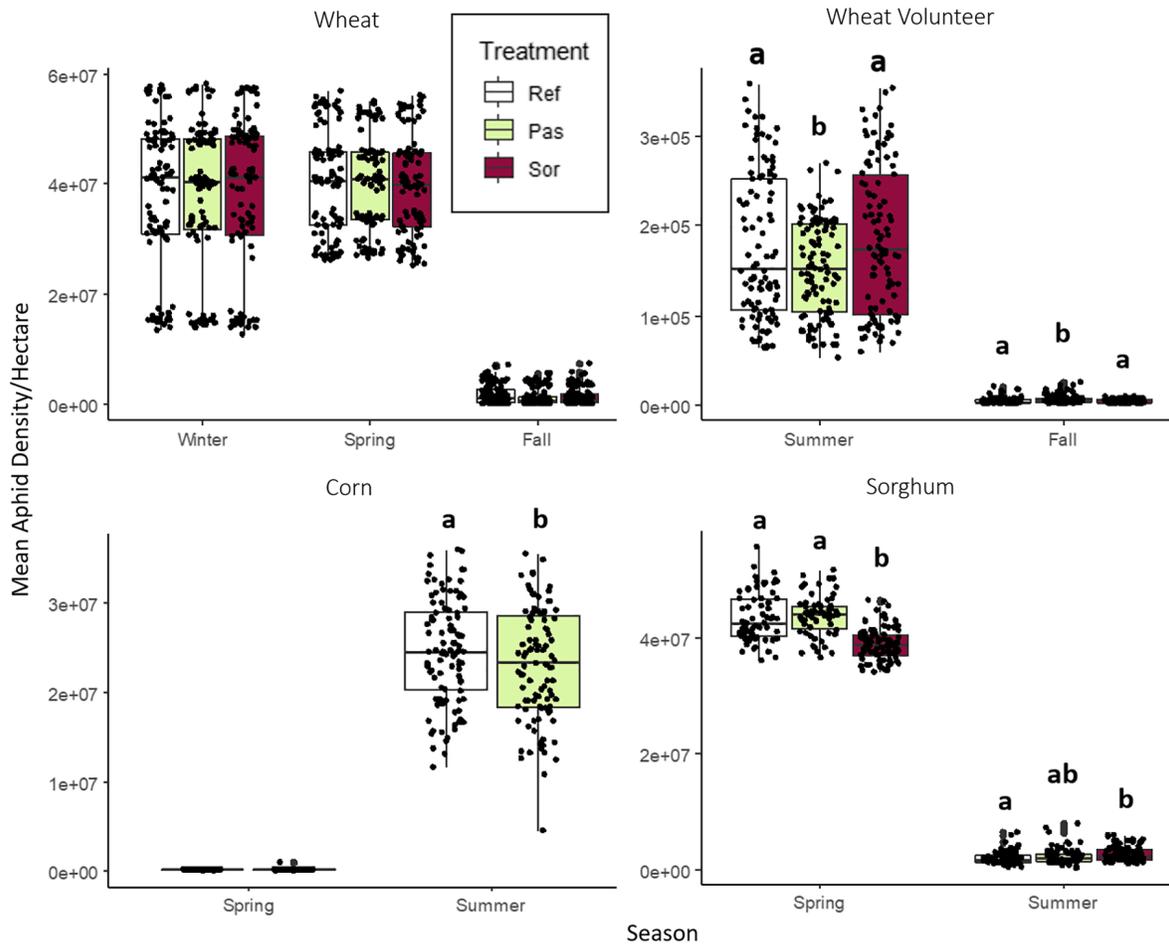
Fig. 3. Bar plots of mean aphid densities per hectare across all simulations for each crop. All data points are represented by black dots. Aphid densities are separated by season and by scenario (reference, pasture, sorghum). Statistical differences are represented using lowercase letters where different letters represent a statistically significant difference between two scenarios. The absence of letters represents no statistical difference among scenarios within the respective season.

which, coupled with high predation pressure during warmer periods, reduced aphid populations drastically. While it is difficult to compare this to field data due to the use of pesticides in situ, such population crashes have been commonly observed for arthropods in agricultural systems (Karley et al. 2003, Heiniger et al. 2014). Nevertheless, our proposed approach could be applied to systems where organic agriculture is predominant (Wyss et al. 2005). Krauss et al. (2011) discovered that pesticide applications might actually free aphid dynamics from predation pressure, which could easily be tested using our approach by adding a natural enemy

population model on top of our current submodels and introducing pesticide application scenarios.

Habitat quality played an important role in the spatial–temporal distribution of *R. padi* populations. *R. padi* population dynamics within both simultaneously available summer crops were highly contrasted with clear temporal discrepancies between aphid dynamics within sorghum and corn. Aphid populations tended to develop in sorghum in spring and reach very low levels in summer, while the opposite occurred in corn, due to different quality values of these crops and their growth stages (Kieckhefer and Gellner

1988). We found the same patterns in the literature, where sorghum infestations usually occur as soon as the crop appears (Chantereau et al. 2013), whereas corn infestations occur at the flowering stages (Brown et al. 1984).

Drivers of aphid densities varied greatly among seasons and among crops. Overall, crop-level models performed better in predicting aphid densities compared with landscape-level models, highlighting the importance of considering inter-habitat variability. Temperature, which plays a key role in regulating ectotherm population dynamics (Huey and Berrigan 2001), was a significant predictor of aphid densities in wheat across all seasons in which the crop is present. Temperature not only regulated population dynamics through development and mortality but also influenced predation pressure by natural enemies, an important driver of aphid mortality at the end of winter and start of spring. This echoed empirical studies that highlighted early predation as a strong regulator of pest population dynamics during spring and summer (Raymond et al. 2014). Habitat availability was not a consistent predictor of aphid densities across seasons and crops. This could be related to *R. padi*'s dispersal behavior that allows for rapid colonization of agricultural landscapes in favorable conditions (Parry 2013), thus leading to individuals always finding a suitable habitat within the landscape.

Immigration was a strong predictor of aphid densities throughout the year and landscape. During fall, a season particularly sensitive to aphid infestations within wheat (Pike and Schaffner 1985), we observed a significant effect of the number of aphids immigrating into the landscape on aphid densities within wheat. In relation to *R. padi* dynamics, fall is the season during which a part of the population will produce sexual, winged aphids. In the western and southern parts of France, where the primary host is rather rare, most of the population is anholocyclic (Simon et al. 1991) and can survive within crops during winter if conditions are not too extreme. A minor percentage of the population migrate to their primary host (*Prunus padus*) as sexual individuals where they produce their offspring by oviposition to anticipate unfavorable winter weather conditions (Leather and Dixon 1981). This hypothesis should be evaluated by

gathering precise data on the proportion of sexual aphids caught in suction traps in fall in our region. In more temperate areas, such as Brittany in France, the main source of aphids colonizing wheat in fall is corn (Vialatte et al. 2006). In our case study region, there was no overlap between summer and winter crops, and such transfers were impossible. On the other hand, wheat volunteer is known as an alternative source of aphid colonizers (Hawkes and Jones 2005, Vialatte et al. 2007). Aphid densities in volunteer in fall had a strong negative impact on densities in wheat during the next season. Competition and density-dependent mortality in late fall could make it difficult for *R. padi* populations to survive within the landscape until wheat emerges later in the winter.

Studying the potential effects of agronomic scenarios

Changing agricultural practices led to variation in aphid densities among both crops and seasons. The pasture scenario, which strongly increased the area assigned to wheat and thus wheat volunteer, presented lower aphid densities in wheat volunteer in summer but higher densities in fall. In the sorghum scenario, increasing the area assigned to sorghum within the landscape (in place of corn) led to reduced densities in sorghum in spring and increased densities in summer. These observations in both volunteer and sorghum can be associated with the theory of concentration/dilution exposed by Tscharntke et al. (2012). They state that increasing the surface of a resource can lead to increasing the density of a specialist herbivore until a threshold is reached at which a dilution effect occurs, given that it is impossible for the population to forage the whole area available. This hypothesis was illustrated on coffee-pollinating bees (Veddeler et al. 2006) where increasing the concentration of flowers at a field scale leads to a concentration effect of bee densities, while doing the same at the landscape scale leads to a dilution effect. This opposes Root's concentration hypothesis (Root 1973), which states that the more a resource is present within the landscape, the higher the chances are for detection and successful colonization by herbivores. Such effects can also be partly explained by reproductive behavior, where bees reproduce in limited amounts while aphid

continuous reproduction favors population accumulations. Sorghum is a favorable habitat during spring and summer, where local dispersal is favored. Hambäck and Englund (2005) have highlighted the importance of considering dispersal and immigration as one of the key drivers of the resource concentration hypothesis. Thus, increasing sorghum in spring led to the dilution of aphid populations, unavailable to forage the whole area, while increasing sorghum in summer led to a concentration effect, due to the limited number of other cereal habitats in the landscape.

Concentration of *R. padi* populations in sorghum could be problematic in regard to agricultural changes. Increasing the relative abundance of sorghum within crop rotations could lead to sorghum fields potentially acting as local reservoirs for aphid dispersal and recolonization in other crops after pesticide treatments. This could be particularly true in ecosystems where local transfers of aphids from crop to crop play an important role, such as in Brittany (Vialatte et al. 2007). Thus, land managers should be aware of this potential risk if integrating sorghum within their crop rotations and act accordingly to prevent any potential outbreaks of *R. padi* during spring and summer. The abandonment of pastures for winter crops, explored in the pasture scenario, does not seem to influence *R. padi* densities, and thus, no recommendations can be made for land managers in regard to this agronomic change.

Conclusion

Our model is a first attempt at modeling the spatial–temporal dynamics of both an agricultural landscape and cereal aphid population dynamics to better comprehend the main drivers of seasonal aphid densities. We recognize that this is an application focused on a unique species of aphids, in a unique agricultural landscape of the southwest of France. While many assumptions behind model calibration, such as the choice of landscape simulator, crop rotations, and pest species, affect directly the model outputs, our study highlights the importance of considering individual crops as unique habitats to better comprehend the interactions between landscape and pest dynamics. With the

integration of future empirical studies to validate the hypotheses emerging from model simulations, our scenario exploring framework could help identify key processes for designing future agricultural landscapes allowing for low pest densities.

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