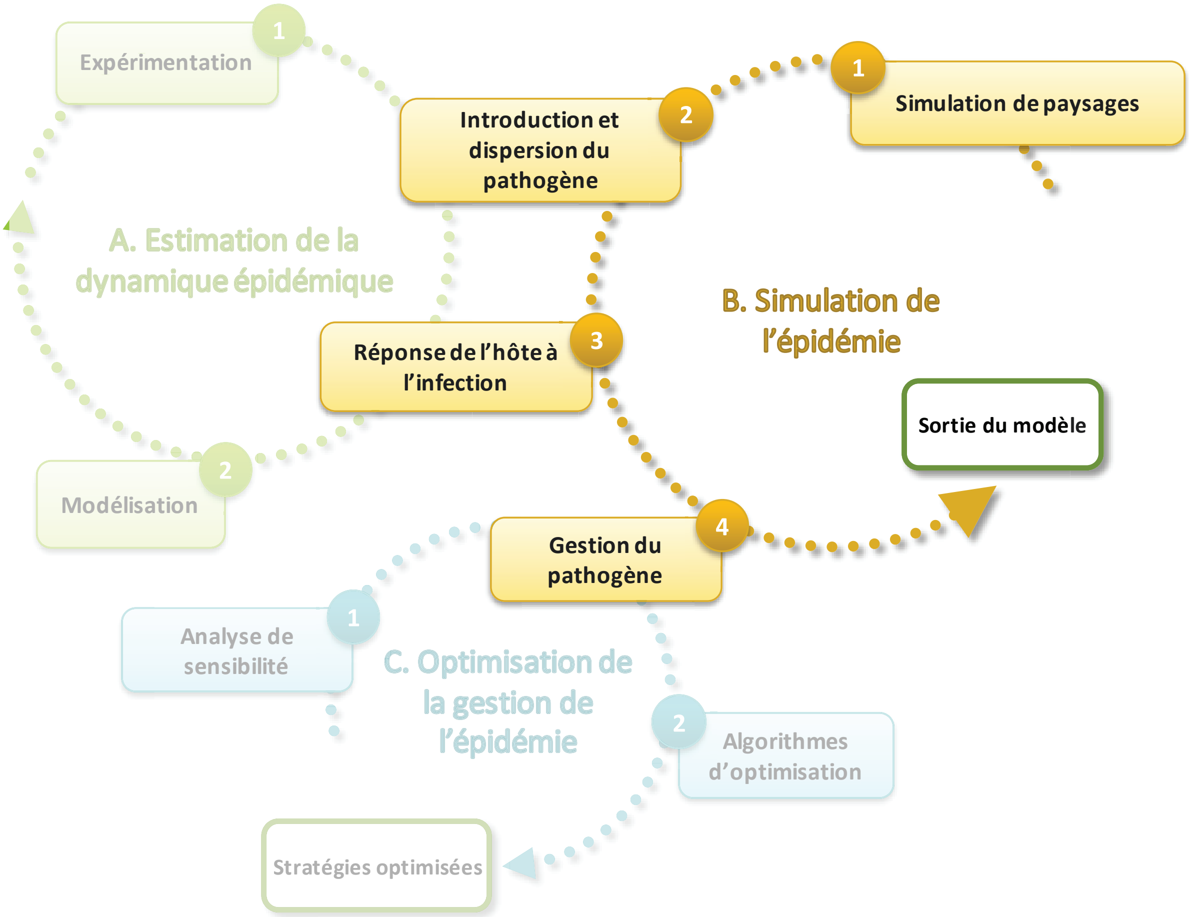
ETUDE DE L'INFLUENCE DU PAYSAGE SUR LES STATEGIES DE GESTION DES MALADIES



Lorsque des paramètres décrivant la dynamique d'une épidémie sont disponibles, des modèles de simulation permettent de tester différents scénarios épidémiques et/ou de gestion. Dans le cadre d'une gestion spatialisée de la maladie, ces modèles ont généralement besoin d'un paysage explicite et réaliste, d'un scénario d'introduction et de dispersion du pathogène, d'équations décrivant les changements de statut des hôtes et d'actions de gestion visant à réduire la propagation de la maladie.

Le paysage (caractérisé ici par la disposition spatiale et la forme des parcelles) n'est pris en compte que depuis peu dans les études de modélisation en épidémiologie, bien qu'il puisse avoir un fort impact. Ainsi, les études Pleydell et al. (2018) et Rimbaud et al. (2018a, 2018b) ont été réalisées sur un unique paysage. Elles ne permettent donc pas d'estimer des paramètres épidémiologiques et d'identifier des stratégies de gestion efficaces sur différents paysages. Afin d'étudier l'influence du paysage sur les stratégies de gestion de la sharka, j'ai tout d'abord modifié ce modèle pour permettre la simulation de l'épidémie dans des paysages variés.

Pour ce faire, j'ai modifié le paysage utilisé dans l'étude de Rimbaud et al. (2018a) afin d'obtenir des paysages de taille et de densité différentes. Dans cette approche, le paysage constitué de 553 parcelles a été dupliqué par 3 (avec un total de 1659 parcelles), puis par 7 (avec un total de 3871 parcelles). Des parcelles de ces paysages ont ensuite été retirées pour diminuer la densité. Des simulations de l'épidémie avec la stratégie de gestion française ont ensuite été réalisées pour évaluer l'impact des caractéristiques du paysage sur la dynamique épidémique et l'efficacité de la gestion. Plus précisément, l'influence de la taille du paysage et de la densité des parcelles cultivées a été étudiée sur deux critères : un critère agronomique et un critère économique. Le premier critère correspond au nombre moyen équivalent d'arbres pleinement productifs, et le deuxième à la valeur actuelle nette (VAN ; Rimbaud et al. 2018a).

Dans un deuxième temps, j'ai développé un algorithme simulant des paysages réalistes : il permet de définir les principales caractéristiques d'un paysage telles que le nombre de parcelles ou leur agrégation spatiale à partir d'une simulation de tessellation en T. Cet algorithme m'a permis de simuler 3 types de paysages variant par le niveau d'agrégation de leurs parcelles. Ces paysages contrastés ont été utilisés pour toutes les études présentées dans la suite de cette thèse. De même que précédemment, des simulations avec la stratégie de gestion française ont ensuite été réalisées. De plus, pour étudier l'influence du paysage sur les paramètres du modèle et identifier les paramètres clés de la propagation et de la gestion d'une épidémie, j'ai réalisé des analyses de sensibilité sur les 3 paysages définis. Ces analyses permettent de mieux comprendre les épidémies et d'identifier les paramètres de gestion les plus influents sur la VAN (ces paramètres peuvent alors être d’une importance capitale si l’on souhaite identifier des stratégies de gestion performantes). Elles permettent également d’analyser comment l’influence de ces paramètres varie en fonction du niveau d’agrégation des parcelles.

L’article 4 détaille en partie les résultats de ce chapitre. Il expose également des résultats concernant l’optimisation des paramètres de gestion qui seront abordés dans le chapitre suivant.

ARTICLE 4

Analyzing the influence of landscape aggregation on disease spread to improve management strategies

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ABSTRACT

Epidemiological models are increasingly used to predict epidemics and improve management strategies. However, they rarely consider landscape characteristics although they can influence the epidemic dynamics, and thus the effectiveness of disease management strategies. Here, we present a generic *in silico* approach which assesses the influence of landscape aggregation on the costs associated to an epidemic and on improved management strategies. We apply this approach to sharka, one of the most damaging diseases of *Prunus* trees, for which a management strategy is already applied in France. Epidemic simulations were carried out with a spatiotemporal stochastic model under various management strategies in landscapes differing in patch aggregation. Using sensitivity analyses, we highlight the impact of management parameters on the economic output of the model. We also show that the sensitivity analysis can be exploited to identify several strategies that are, according to the model more profitable than the current French strategy. Some of these strategies are specific to a given aggregation level, which shows that management strategies should generally be tailored to each specific landscape. However, we also identified a strategy that is efficient for all levels of landscape aggregation. This one-size-fits-all strategy has important practical implications because of its simple applicability at a large scale.

Keywords: landscape, management, optimization, SEIR, sharka, spatiotemporal model, virus

1. Introduction

Understanding epidemiological processes is crucial to anticipate outbreaks, to predict the spread of epidemics, and thus to propose optimized management strategies that aim to reduce or eliminate a disease (Ferguson et al. 2001). However, epidemics are the result of complex interactions between biological processes, human interventions and the spatial arrangement of patches in the landscape. Thus, understanding epidemics and assessing the effectiveness of disease management options is often a difficult task, especially as field trials are generally limited by regulatory, ethical and logistical constraints (particularly for large-scale experimental studies). To overcome these limitations, epidemiological models are an interesting approach because of their ability to test several epidemic and management scenarios using the best available knowledge (Cunniffe et al. 2015; Keeling and Rohani 2008; Keeling et al. 2003).

Spatially explicit models have been used to estimate epidemiological parameters such as dispersal functions (Parnell et al. 2011; Parry et al. 2014; Pleydell et al. 2018; Soubeyrand et al. 2008), infection rates (Cunniffe et al. 2014) and incubation durations (Cunniffe et al. 2014; Pleydell et al. 2018). This approach leads to disease-specific, data-calibrated models that can then be exploited to assess the efficacy of control measures, e.g., sampling frequency and intensity (Parnell et al. 2012, 2014; Soubeyrand et al. 2018), plantation density (Chan and Jeger 1994; Cunniffe et al. 2014; Cunniffe et al. 2015b; Jeger and Chan 1995), insecticide spraying frequency and location (Filipe et al. 2012), and zones and dates of removal (Cunniffe et al. 2014, 2015b; Filipe et al. 2012; Parnell et al. 2009, 2010; Sisterson and Stenger 2012).

However, these modeling studies mostly focused on only one or two management parameters, other parameters being set at their reference value. Rimbaud et al. (2018b) tried to optimize several parameters simultaneously however, like almost all previous studies, they performed simulations in a single landscape and did not consider landscape characteristics. Nevertheless, in order to study outbreaks and large-scale management strategies, considering landscape characteristics can be crucial. Indeed, they can influence epidemic dynamics, implying that the best management strategies may vary depending on the landscape (Papaïx et al. 2014). A review by Ostfeld et al. (2005) analyzed the few studies that demonstrate how spatial locations of crop patches can influence disease risk, suggesting that a true integration of the landscape within epidemiological studies would be fruitful. As a consequence, promising approaches have been developed to integrate landscape characteristics into epidemiological models. For example, it was shown that, for the purpose of eradication, the optimum radius of orchard removals increases with the level of patch aggregation and the host density in the landscape, both factors increasing epidemic spread (Parnell et al. 2009, 2010).

However, in these studies patch layout is summarized by patch centroid coordinates although plot size and shape play an important role in disease dispersal (Mikaberidze et al. 2016; Pleydell et al. 2018), and thus on the impact of disease management. Indeed, such simplification can introduce a bias in connectivity estimates when patches have different shapes and sizes, e.g., the connectivity between the centroids of two patches would erroneously be the same whatever their area. Here, we try to understand how landscape structure influences disease spread and the impact of control options thanks to simulations of disease spread and management on various landscapes.

We apply this approach to sharka, one of the most damaging diseases of trees belonging to the *Prunus* genus (e.g., peach, apricot and plum) (Cambra et al. 2006; Rimbaud et al. 2015). The causal agent of this disease, *Plum pox virus* (PPV, genus *Potyvirus*, family *Potyviridae*), is naturally transmitted by aphids in a nonpersistent manner. The presence of PPV symptoms (such as fruit deformation (Németh 1986), apparition of light green rings, mosaic, mottling, and distortions on the leaves (Rimbaud et al. 2015) reduces potential sales, occasioning a significant economic impact (Cambra et al. 2006), with yield losses up to 100% for the most sensitive cultivars. Different alternatives for sharka management strategies exist in the world (eradication, suppression, containment, or resilience) depending on the epidemic context (Rimbaud et al. 2015). In France, sharka management aims to reduce the number of PPV-infected trees to mitigate its impact (suppression); it is compulsory and defined by a national decree specifying a complex procedure based on nursery protection, frequent visual inspections of orchards and removal of symptomatic trees or, possibly, whole orchards, as well as plantation restrictions (JORF 2011; Fig. 1). In a previous study, key parameters of a sharka epidemic were identified, and an improved management strategy was highlighted for a single landscape (Rimbaud et al. 2018b). In the present article, we use the same model to analyze the influence of landscape characteristics on plant disease control. For that purpose, we first study the influence of landscape structure on *Prunus* productivity under the French management strategy (JORF 2011). Next, we use sensitivity analyses to assess the relative influence of model parameters on crop productivity depending on the level of patch aggregation in the landscape. Then, we exploit the results of these analyses to identify several efficient strategies and we study how the landscape influences their impact. This last point allows to asses if the management can be generic (i.e., if a unique management strategy is efficient for all landscapes), or should be specific to each landscape.

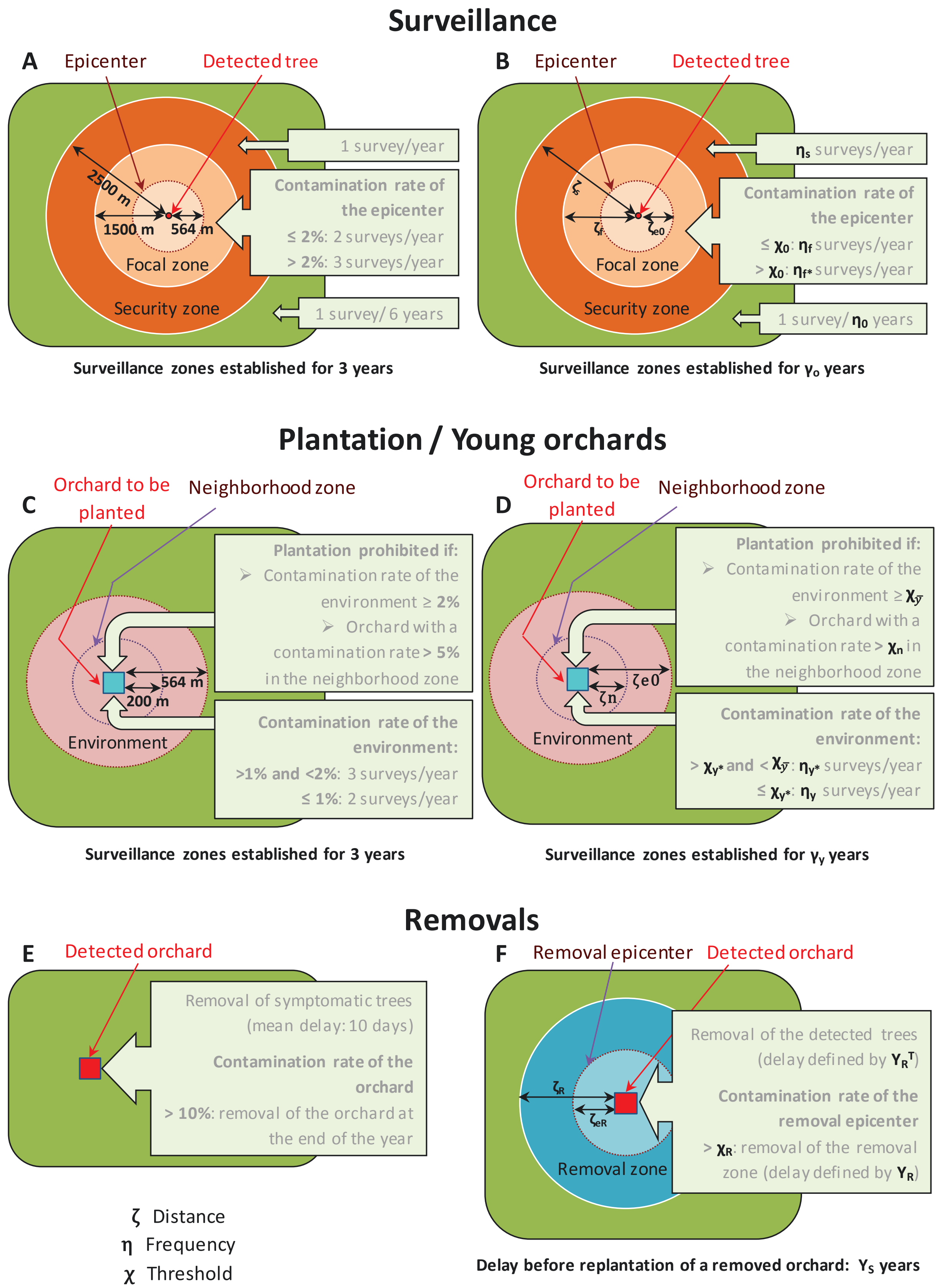

Figure 1: A, C and E, Management actions currently applied in France. B, D and F, Management actions implemented in the model. The detected orchards include at least one observed infected tree.

2. Materials and methods

2.1. Landscape generation

In this study, the landscape is considered as a set of cultivated patches (i.e., pieces of land) in a defined study area on which the pathogen may spread when trees are planted. Patches of different sizes and aggregation levels were simulated by (i) replicating real patches and (ii) simulating patches with a T-tessellation algorithm.

2.1.1. Replication of real patches

In a previous study, Pleydell et al. (2017) and Rimbaud et al. (2018a) developed a model allowing to simulate virus dispersal on a real landscape comprising 553 patches (524 ha of patches in a study area of 2730 ha). This landscape was generated from a database collected in a peach producing area in southeastern France. Here, artificial landscapes were constructed by replicating this real landscape 3 times to obtain a total of 1659 patches and 7 times to obtain 3871 patches (with the size of the study area increasing accordingly). In addition, to obtain landscapes with lower levels of patch aggregation, some of the patches were removed (subsampled) from the 2 replicated landscapes. For the landscape replicated three times, 40% and 70% of the patches were removed randomly from each of the original landscapes (with 553 patches). For the landscape replicated 7 times, 40% and 80% of the patches were removed randomly from each of the original landscapes. Three independent landscapes were generated for each subsampled landscape. An example of each landscape type is displayed in Supplementary Fig. S1. In this way we obtained three sizes of study area, with one aggregation level for the smaller one (corresponding to the real landscape) and three different aggregation levels for each of the larger study areas (and three different landscapes for each subsampled landscape).

2.1.2. Landscape simulations with T-tessellations

To avoid being dependent on a single real landscape, we also simulated new agricultural landscapes with various levels of patch aggregation and a realistic outlook (Fig. 2). Three landscapes comprising n=400 patches were simulated, thereafter called H, M and L based on the value of the aggregation parameter: d=1 (H: high aggregation), d=200 (M: medium aggregation) and d=400 (L: low aggregation) (Fig. 3; Supplementary Fig. S2). These values were chosen to represent diverse patch aggregation levels: with d=400, patches were scattered throughout the study window and with d=1, we obtained only neighboring patches in each cluster. The value of parameter p was chosen to ensure the simulation of on average 15 clusters: p=1-15/n=0.96. This parameter accounts for landscape irregularities due to the presence of features such as soil, topology, lakes, rivers, roads or towns, which require that patches are generally grouped. We simulated 30 landscapes with these parameter values for each aggregation level.

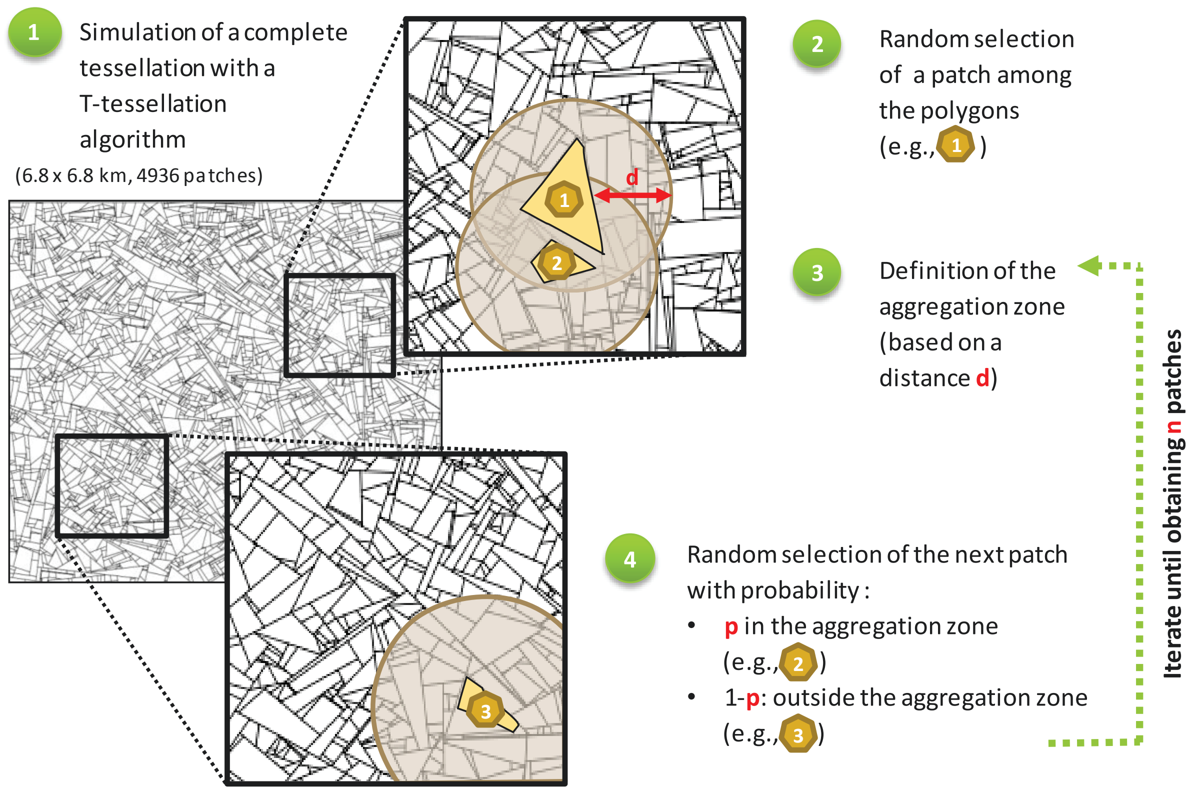

Figure 2: Algorithm for the simulation of landscapes with a specified aggregation level of patches of susceptible hosts. The aggregation level is defined by 3 parameters: n, p and d. Parameter d determines the size of an "aggregation zone" including all polygons located within d meters of a previously selected patch. In steps 2 and 4, patches are selected randomly and uniformly.

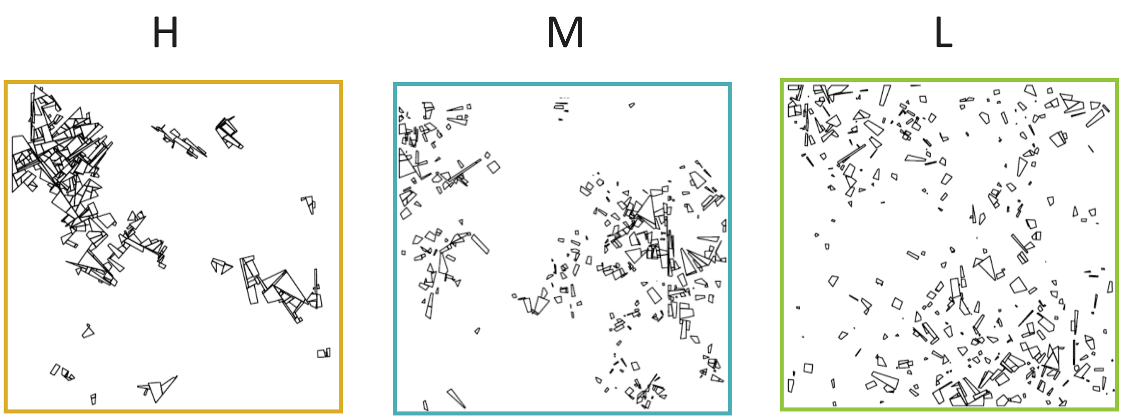

Figure 3: Examples of landscapes simulated using the process presented in Fig. 2 with parameters n=400, p=15. Three values of the aggregation parameter are used: H, d=1 (high aggregation); M, d=200 (medium aggregation); L, d=400 (low aggregation).

2.2. Epidemiological model

To simulate disease spread and management in landscapes, we used an existing stochastic, spatially explicit, SEIR (susceptible-exposed-infectious-removed) model (Pleydell et al. 2018; Rimbaud et al. 2018a, 2018b). The model is orchard-based, with a discrete time step of 1 week. At the beginning of the simulation, the trees in the patches are not infected: they are in the "susceptible" (i.e., healthy) state. The virus is introduced at the beginning of the first year of the simulation in one of the patches (defined by its connectivity quantile) and then spreads through orchards, causing changes in tree status: from "susceptible", they become "exposed" just after virus infection, "infectious hidden" (and symptomatic) after the end of the latent period, "infectious detected" after detection of the infected tree during surveys, and "removed" when the tree is removed from the patch. In addition, new introductions can also occur (with a specified probability) during the entire simulation at each patch plantation. Epidemic spread is governed by 6 epidemiological parameters (Table 1). Furthermore, a management strategy based on the French management of sharka in *Prunus* orchards is implemented as previously described (Rimbaud et al. 2018b). Briefly, a disease management strategy defined by 23 parameters (Fig. 1 and Supplementary Table S1) is applied after 5 years of epidemic to allow the spread of the virus. The model output is an economic criterion: the net present value (NPV), which corresponds to the sum of the gross margin (GM) calculated each year and updated by a discount rate (Rimbaud et al. 2018b). The GM represents the difference between the benefits generated by the cultivation of productive hosts and the costs induced by production and management actions (including surveillance, removal and replantation).

Table 1: Epidemiological parameters implemented in the model, and their variation ranges in simulations.

		Min	Max
q_κ	Quantile of the connectivity of the patch of first introduction	0	1
φ	Probability of introduction at plantation	0.0046	0.0107
p_{MI}	Relative probability of massive introduction	0	0.1
W_{exp}	Expected value of the dispersal weighting variable	0.469	0.504
β	Transmission coefficient	1.25	1.39
θ_{exp}	Expected duration of the latent period (years)	1.71	2.14

2.3. Epidemic simulations and sensitivity analyses

2.3.1. Simulations with the French management

To study the influence of the landscape on productivity under the French management strategy, we performed simulations for all the landscapes described above. A realistic turnover of peach orchards was simulated on patches using a mean cultivation duration of 15 years (Rimbaud et al. 2018b). Simulations were run for 35 years (5 years without management and 30 years with management), which is a reasonable duration to assess the long-term impact of an epidemic in cultivated perennial plants. For each simulation, the 6 epidemiological parameters were drawn from uniform distributions using the bounds corresponding to sharka pathosystem (as described in Rimbaud et al. (2018b) and in Table 1) and management parameters representing the French management strategy (Fig. 1, JORF 2011). On the replicated real landscapes, 10,000 simulations were carried out on the three landscapes without subsampled patches, and 3,334 simulations were performed on each of the three replicates of the subsampled landscapes (to obtain a total of 10,000 simulations for each aggregation level). Likewise, on landscapes simulated by the T-tessellation algorithm, 334 simulations were performed for each of the 30 replicates.

2.3.2. Sensitivity analyses

The relative influence of epidemic and management parameters on disease impact was assessed for simulated sharka epidemics. For this purpose, Sobol's method for sensitivity analysis was used, which consists of: (i) the definition of target parameters and of their respective variation ranges; (ii) the generation of a numerical experimental design to explore parameter space; (iii) simulation; and (iv) the computation of Sobol's sensitivity indices which quantify the influence of each target parameter on the output variable (Faivre et al. 2013; Saltelli et al. 2008; Sobol 1993). The first-order sensitivity index of a parameter, noted SI_1, measures the main effect of this parameter whereas the total sensitivity index, noted SI_{tot}, also accounts for its interactions with other parameters. These indices are bounded by 0 and 1, a total index close to 0 meaning that the parameter has a negligible effect on the output variable.

Here, to get results specific to each level of patch aggregation, three sensitivity analyses were performed independently for the three simulated landscapes. We targeted 23 control parameters defining the implemented management strategy and 6 epidemiological parameters. Variation ranges were defined as their respective definition domain, possibly restricted using expert's opinion when this domain was infinite (Table 1, Supplementary Table S1; Rimbaud et al. 2018b). For each of the 30 landscapes (for each aggregation level), simulations were performed with 310,155 parameter combinations generated with Sobol sequences (Sobol 1967, 1976). Then, Sobol's indices were calculated on the mean of the 30 replicates. First-order indices were estimated with the Sobol-Saltelli method (Saltelli et al. 2010; Sobol et al. 2007) whereas total indices were estimated with the Sobol-Jansen method (Jansen 1999; Saltelli et al. 2010).

2.3.3. Simulation of improved strategies

Using outputs of the sensitivity analyses we identified an improved strategy for each aggregation level. This improved strategy corresponds to the parameter combination leading to the highest NPV among the 310,155 combinations. We call these strategies "Best point H", "Best point M" and "Best point L" for each aggregation level (high, medium and low, respectively). Then, 10,000 simulations were performed with these three management strategies for the three aggregation levels as described in "Simulations with the French management" section.

We compared the mean NPV ($\overline{\mathrm{NPV}}$) and the lowest decile of the NPV (i.e., 10% of the NPV values are below the lowest decile, noted $\mathrm{NPV}_{10\%}$). This last criterion was chosen considering that farmers do not accept a management strategy which can too often lead to a low NPV. The purpose of this initial step was to assess whether a strategy that is efficient in a particular landscape remains efficient on landscapes with different characteristics. This provided an overview of the influence of landscapes features on management strategies.

2.4. Heuristic optimization of management strategies

The sensitivity analyses were carried out with 310,155 combinations of both epidemiological and management parameters. Thus, the three strategies "Best point H", "Best point M" and "Best point L" were selected because they were effective for one epidemic (characterized by the 6 epidemiological parameters). However, the other combinations of management parameter could have led to higher NPV with other epidemic parameters. Thus, we searched improved combinations of management parameters for various "epidemic cases". Each epidemic case corresponds to a set of different value ranges of the epidemiological parameters (example of one epidemic case: $q_\kappa \in [0,0.25]$, $\beta \in [1.25,1.29]$, $\varphi \in [0.0046,0.0108]$, $p_{MI} \in [0,0.05]$, $W_{exp} \in [0.469,0.0175]$, $\theta_{exp} \in [1.71,1.925]$). The level of subdivision of the value ranges was based on the results of the sensitivity analyses, with more subdivisions for more influential epidemiological parameters. Then, each of the 310,155 parameter combinations was allocated to the corresponding epidemic case. Finally, for each epidemic case and each aggregation level, we identified the combination of management parameters leading to the highest NPV, and we performed 10,000 simulations with these strategies on the corresponding landscape, while varying the epidemiological parameters within their respective variation ranges (Supplementary Table S1).

To finish, we selected the 10 parameter combinations corresponding to the highest $\mathrm{NPV}_{10\%}$ for each aggregation level and we performed 10,000 simulations of these strategies on the other landscapes. The strategies leading to the best $\mathrm{NPV}_{10\%}$ for each aggregation level are called respectively “Improved strategy H”, “Improved strategy M” and “Improved strategy L”.

3. RESULTS

3.1. Landscape organization influences the impact of management strategies

3.1.1. Landscape influence on productivity with the French management strategy

We performed simulations of epidemic spread on duplicated and simulated landscapes under the French management strategy (JORF 2011). In both cases, the NPV decreased for landscapes with increasing patch aggregation (Fig. 4).

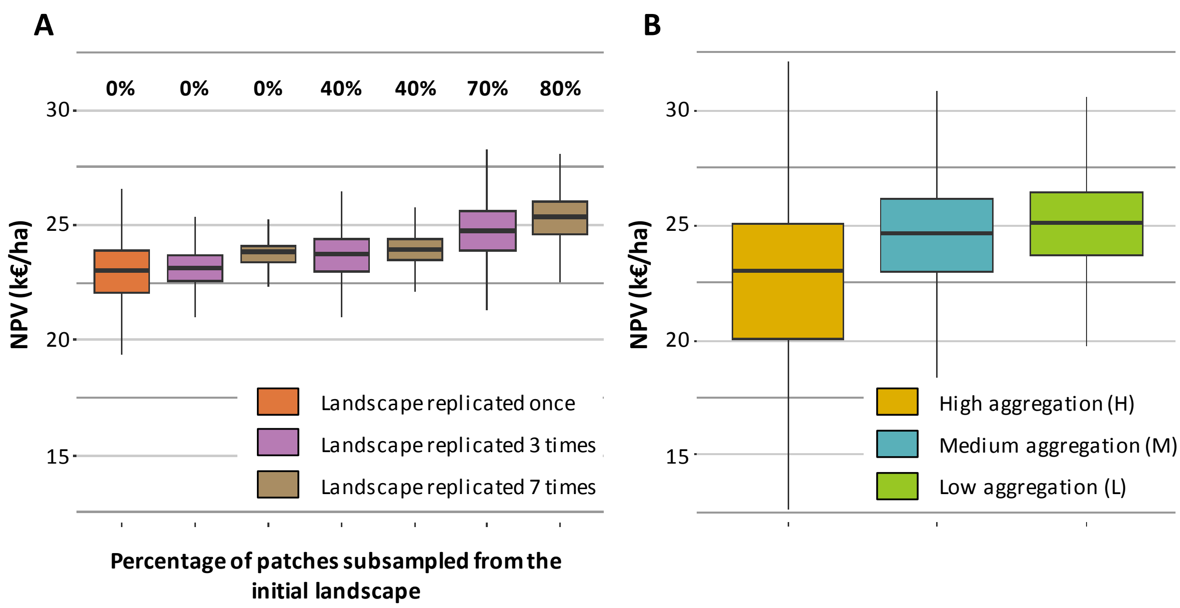

Figure 4: Distribution of the NPV for 10,000 simulations of sharka spread and management: A, on replicated landscapes; and B, on simulated landscapes.

In order to understand why the NPV is affected in landscapes with higher patch aggregation, we observed disease prevalence through time and studied the impact of patch aggregation on components of the economic criterion for simulated epidemics (Supplementary Fig. S3). During the early years of the epidemic, the virus spreads faster in landscape H than in landscapes M and L; prevalence and incidence are therefore slightly higher. Thus, surveillance is strengthened and increases costs (inducing a lower GM). In addition, the increased number of removals leads to a decrease in the number of productive trees (the average number of productive trees per ha per year is respectively 553, 557 and 559 for H, M and L landscapes over the 30 years of the epidemic), which entails yield losses.

3.1.2. Landscape influence on sensitivity to model parameters

Three sensitivity analyses were performed for the three levels of patch aggregation on 23 management parameters and 6 epidemiological parameters in order to identify the most influential input parameters on the NPV (Fig. 5). We showed that 2 parameters related to plantation (χ_n: contamination threshold for an orchard in the neighborhood, above which the plantation of orchards is forbidden) and removals (χ_R: contamination threshold in the removal epicenter, above which orchards inside the removal zone are removed) have a strong influence on the NPV and this result does not depend on patch aggregation. The high impact of these parameters was likely due to a loss of productivity when the contamination threshold for the plantation bans and removal was too low.

However, although the two most influential parameters are the same for the three landscapes, their relative influence depends on landscape aggregation. For landscape H, the most influential contributors to the NPV were first the plantation ban threshold (χ_n; SI_{tot}=0.62) and then the removal threshold (χ_R; SI_{tot}=0.29). Conversely, for landscape L, the most influential contributors to the NPV were first the removal threshold (χ_R; SI_{tot}=0.45) and then the plantation ban threshold (χ_n; SI_{tot}=0.42). Overall, when the landscape is highly aggregated much of the variance is explained by a few parameters; conversely, when the landscape is less aggregated a larger number of parameters explain the variance observed in the simulations (Fig. 5).

To summarize, management parameters do not have the same influence on the economic criterion depending on the landscape. Optimal management parameters can therefore depend on landscape features.

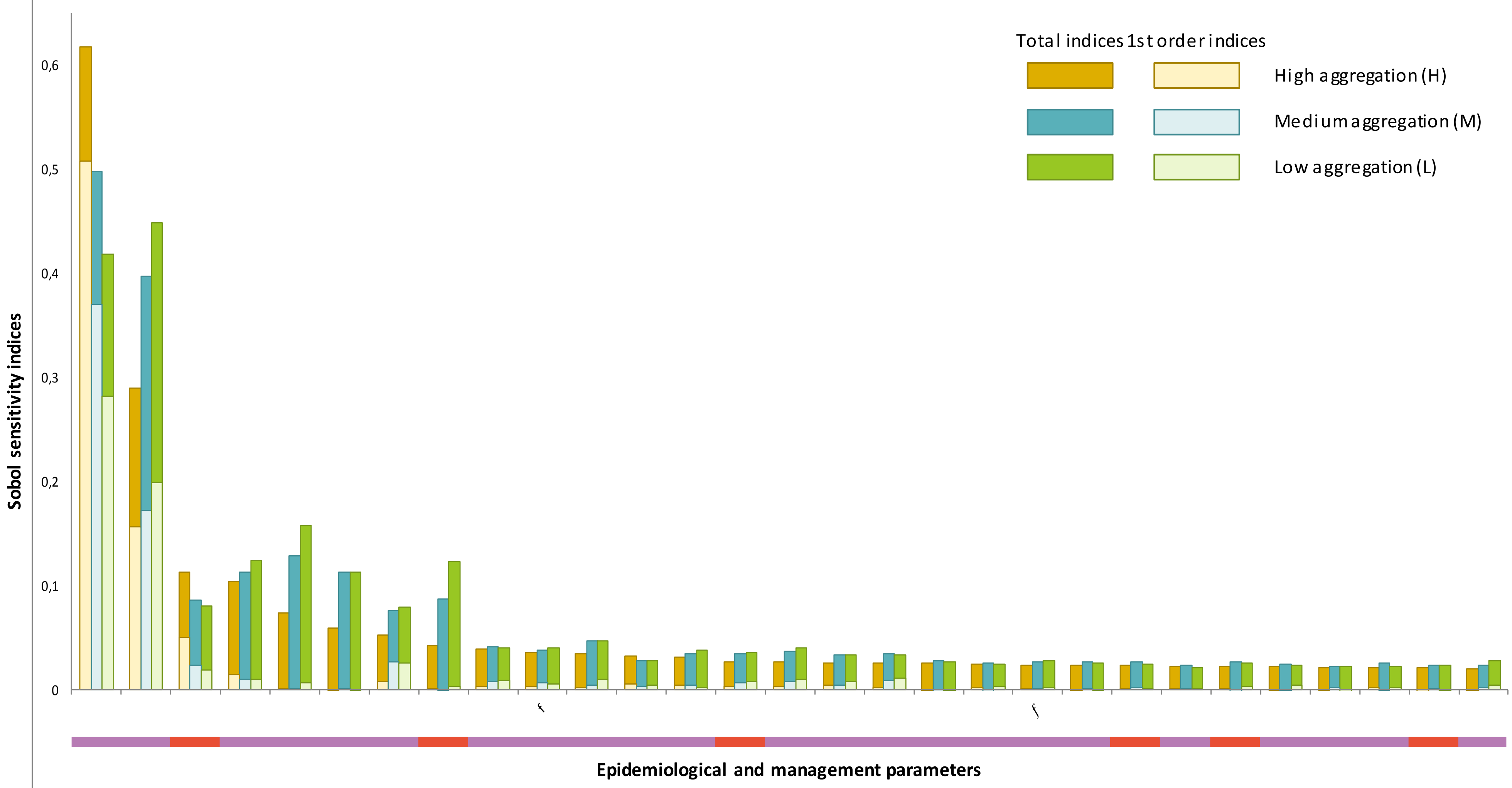

Figure 5: Sobol's sensitivity indices of 23 control parameters and 6 epidemiological parameters on the $\overline{\mathrm{NPV}}$, assessed for sharka epidemics in landscapes with 3 different aggregation levels (H, M and L). The line under the figure indicates the epidemiological parameters (red) and management parameters (purple).

3.1.3. Landscape influence on productivity for improved strategies

An improved strategy (i.e., the parameter combination resulting in the best NPV among the 310,155 tested combinations) was identified for each level of landscape aggregation, and named "Best point H", "Best point M" and "Best point L". For the three aggregation levels, these management strategies only very rarely involve orchard plantation bans, and only symptomatic trees are removed (and not entire orchards). In addition, surveillance zones (focal and security zones) are much smaller with these strategies than with the French management strategy (Supplementary Table S2), which reduces surveillance costs.

Then, simulations were carried out with these three strategies by varying epidemiological parameters on all the simulated landscapes (Fig. 6). Simulations performed on a landscape with the parameter combination identified for the same landscape lead to better $\overline{\mathrm{NPV}}$ and $\mathrm{NPV}_{10\%}$ than with the French management strategy. Besides, these analyses show that a management strategy that is efficient for a landscape is not necessarily efficient in another, and can be less profitable than the French strategy. Indeed, the "Best point H" strategy is more profitable than the French strategy when it is applied on landscapes M and L; however, the "Best point M" and "Best point L" strategies are less profitable than the French management strategy for landscape H: $\overline{\mathrm{NPV}}$ and $\mathrm{NPV}_{10\%}$ were largely lower (i.e., risk-taking is higher) than with the French strategy.

3.2. Landscape influence on improved management strategies

The sensitivity analyses show that 2 out of 6 epidemiological parameters have a high impact on the NPV (Fig. 5): $q_{\kappa,}$ the quantile of the connectivity of the patch of first introduction and β, the transmission coefficient. To define the epidemic cases (i.e., subsets of parameter values corresponding to similar epidemics), we divided the value ranges of these 2 parameters into four equal parts, and the 4 other epidemiological parameters (Φ, p_{MI}, W_{exp}, θ_{exp}) were divided into 2 equal parts. We obtained 4 x 4 x 2 x 2 x 2 x 2 = 256 epidemic cases for each level of landscape aggregation, and for each case we identified the combination of management parameters leading to the highest NPV. The majority of these strategies does not involve orchard plantation bans (in 85% of the cases for landscape H, and 89% for landscapes M and L) and does not impose removal of entire orchards (in 68% of the cases for landscape H, and 74% for landscapes M and L). In addition, surveillance zones are again much smaller for these strategies than for the French management.

For each aggregation level, (i) simulations were carried out with the corresponding 256 strategies, and (ii) the 10 parameter combinations resulting in the best $\mathrm{NPV}_{10\%}$ were retained. Simulations were then performed with these 30 combinations on all the landscapes (Supplementary Fig. S4). We observe that the impact of these management strategies is more important for landscape H than for landscapes M and L. Indeed, the $\mathrm{NPV}_{10\%}$ for landscape H varies between 15,945 €/ha and 22,987 €/ha with this 30 management strategies, between 23,110 €/ha and 24,202 €/ha for landscape M and between 23,111 €/ha and 24,616 €/ha for landscape L. The strategies leading to the best $\mathrm{NPV}_{10\%}$ ("Improved strategy H", "Improved strategy M" and "Improved strategy L") are detailed in Supplementary Table S2 and Supplementary Fig. S5. We note that the strategy leading to the best $\mathrm{NPV}_{10\%}$ is also the strategy leading to the best $\overline{\mathrm{NPV}}$ (for landscape L) or leading to a very close value to the best $\overline{\mathrm{NPV}}$ (for landscapes H and M).

Finally, we compared the NPV from simulations without management, with the French management strategy, with the three "Best point" strategies, and with the three "Improved strategies" leading to the best $\mathrm{NPV}_{10\%}$ (Fig. 6). We could find substantially improved NPV for the three levels of patch aggregation. For instance, the $\mathrm{NPV}_{10\%}$ is 17,652 €/ha with the French management strategy, 20,474 €/ha with strategy "Best point H" and 22,987 €/ha with strategy "Improved strategy H". In addition, although each landscape has a specific improved strategy, the "Improved strategy H" could be, according to the model, an acceptable compromise for all landscapes (Fig. 7). Indeed, application of the "Improved strategy H" on landscapes M and L (instead of their respective "Improved strategies") leads to a reduction of only 184 €/ha and 640 €/ha in $\mathrm{NPV}_{10\%}$ over 30 years.

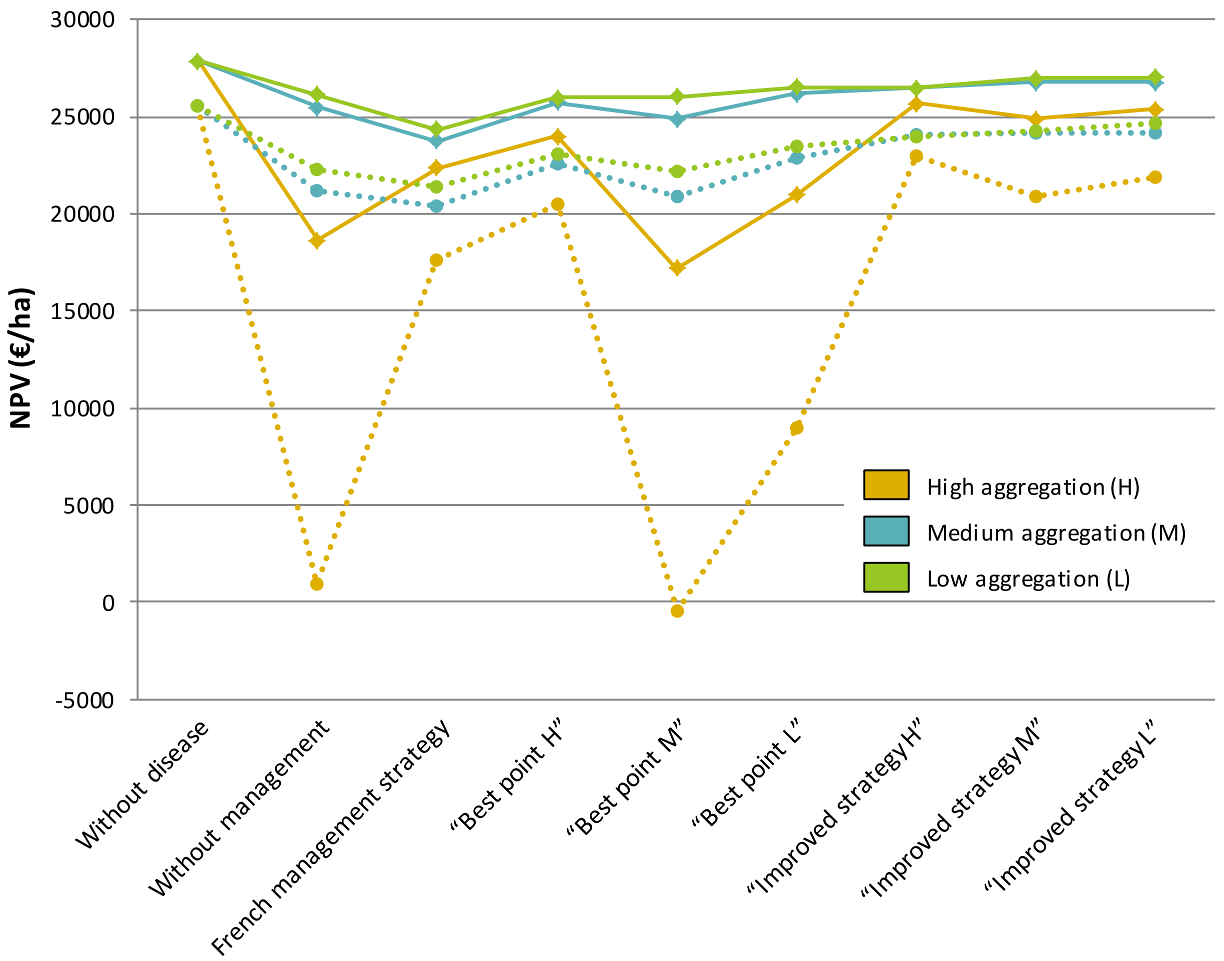

Figure 6: $\overline{\mathrm{NPV}}$ (solid lines) and $\mathrm{NPV}_{10\%}$ (dotted lines) obtained after simulations of PPV dispersal and management.

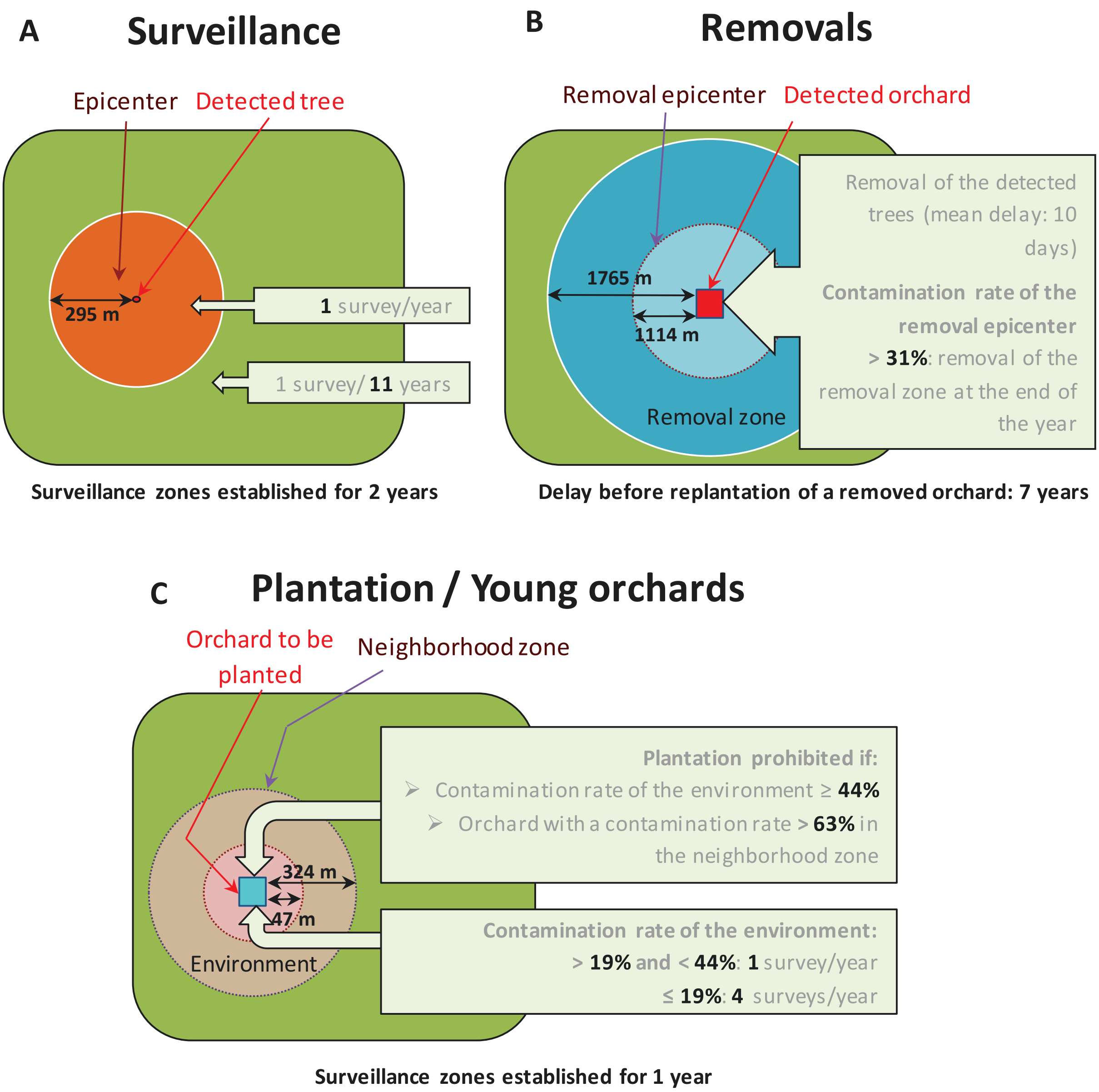

Figure 7: Management actions for the “Improved strategy H” (leading to the best lowest decile for the most aggregated landscape).

4. Discussion

This work aimed to understand how patch aggregation influences disease spread and the impact of control options. Simulations of disease spread and management within a sensitivity analysis framework showed that the landscape influences the profitability of different strategies for sharka control in peach orchards. In addition, the results of these sensitivity analyses were exploited to identify efficient strategies (more profitable than the present French management of sharka). These strategies are efficient for a specific aggregation level, but we also identified a generic strategy, namely the "Improved strategy H", that is efficient for various levels of landscape aggregation.

4.1. Influence of landscape in modeling studies

Our study shows the importance of taking landscape characteristics into account in the design and optimization of disease management strategies. First, we show that landscape aggregation influences sharka dispersal: in our simulations, profitability (NPV) increases with the distance between patches, both without sharka management or under the French management strategy (Fig. 6). In addition, we show that landscape aggregation influences the impact of management strategies, both because the relative influence of the management parameters on the NPV depends on landscape aggregation (Fig. 5), and because a management strategy which is efficient for a landscape is not necessarily efficient for the other landscapes (Fig. 6). This demonstration that the efficiency of a disease management strategy depends on landscape aggregation has important consequences for the improvement of management strategies (or, maybe less realistically, for the optimization of the landscape itself).

This result also means that such studies must be based on either real or realistic landscapes. However, as pointed out in the Introduction, generic realistic landscapes are rarely considered in epidemiological modeling studies. Because generic conclusions cannot be drawn on a single real landscape, it was important to simulate landscapes with a specified level of aggregation. Thus, we devised an algorithm based on T-tessellations to generate landscapes composed of various patches (with realistic enough shapes and sizes) that are more or less aggregated. Disease dispersal and the impact of control options might also be influenced by other landscape structures such as mountains, lakes, rivers, forests or roads (Brunker et al. 2018), species composition or proportion of suitable habitat (Ostfeld et al. 2005), including the proportion of resistant *vs*. susceptible hosts (Papaïx et al. 2014). Here we chose to focus on patch aggregation, but other landscape features might enter such models in the future if their epidemiological and economic impact is properly estimated.

4.2. *In silico* improvement of disease management

In the second part of the present study, for each level of landscape aggregation we searched improved management strategies. This was challenging since we attempted to improve a complex strategy including 23 management parameters (epidemiological modeling studies generally optimize one or two parameters at a time). To succeed, we used the results of sensitivity analyses for which numerous parameter combinations were tested. In addition, contrary to previous studies that pursued the same goal using an epidemiological criterion (Cunniffe et al. 2014, 2015b; Filipe et al. 2012; Parnell et al. 2009, 2010, 2012, 2104; Sisterson and Stenger 2012; Chan and Jeger 1994; Jeger and Chan 1995), here we balanced all costs and benefits of disease management strategies within an economic criterion (Rimbaud et al. 2018b), which is important when several parameters expressed in different units are co-optimized. Furthermore, modeling studies generally aim to improve the mean of the criterion to optimize and do not take into account the level of risk aversion of decision-makers. However, as shown by Cunniffe et al. (2015b, 2016), the optimal strategy can depend on which percentile of a criterion is optimized. Because decision-makers generally tend to minimize the risk of devastating scenarios, here we searched efficient strategies on the basis of the lowest decile of the NPV (i.e., $\mathrm{NPV}_{10\%}$). Improving this criterion allows to select management strategies that limit the proportion of epidemics causing substantial economic damage.

For different levels of patch aggregation, we identified with our simulations different improved management strategies ("Improved strategy H", "Improved strategy M" and "Improved strategy L"). Applying these strategies on the respective landscapes, we obtain better $\overline{\mathrm{NPV}}$ (as well as $\mathrm{NPV}_{10\%}$) than with previously improved strategies (Rimbaud et al. 2018b) (Supplementary Fig. S6). It may be due to the fact that these previous strategies were improved for a unique landscape and lacked robustness to changes in landscape aggregation. In addition, the number of simulations performed for each strategy may influence the results. Here, we selected 256 candidate management strategies for which we carried out 10,000 simulations where the epidemiological parameters vary, and we selected the strategy associated with an accurate estimate of the best $\mathrm{NPV}_{10\%}$. In their study, Rimbaud et al. (2018b) performed only 30 simulations for each of 310,155 random management strategies and (i) they isolated the parameter combination associated with the highest estimated $\overline{\mathrm{NPV}}$ ("Best-value strategy") and (ii) they performed a marginal optimization using the mode of the distribution of each parameter for the combinations associated with the best 1% values of NPV ("Best-percent strategy"). Our own attempt to perform such marginal optimization (not shown) failed to produce good NPV values, probably because the substantial interactions between management parameters (Fig. 5) are ignored by this approach.

The results of our heuristic optimization mean that, in theory, management could be tailored to each landscape. However, in practice, stakeholders may struggle to delineate zones that differ by their level of landscape aggregation, and to apply different strategies within the territory where they are involved. In addition, landscapes change through time, which means that strategies that are too specific to a given level of aggregation may become obsolete. Thus, such landscape-specific strategies may only be applicable when production areas with very different levels of landscape aggregation are distant enough. A practically useful alternative to such landscape-specific strategies is the identification of a robust, one-size-fits-all, strategy which could be an efficient compromise for all the landscapes. This is the case for the "Improved strategy H", which may thus be applied at a wide scale. This strategy could be interesting for stakeholders because it is both more profitable and simpler to implement than the present French management strategy. Indeed, it requires surveillance of small areas around each detected tree, very rarely involves orchard plantation bans, and almost never imposes the removal of entire orchards (we note that the last two points correspond to the most influential parameters in the sensitivity analyses).

This work is relevant to stakeholders because it shows that both landscape-specific and landscape-generic disease management strategies can be identified and improved *in silico*. Indeed, the current strategy applied in France on 11,045 ha of peach orchard (Agreste 2013) reduces economic losses in case of severe sharka epidemics, but according to our simulations on average 36 million euros could be saved by using the "Improved strategy H" over a period of 30 years for landscape H (24 million euros for landscape L), and 59 million euros for the lowest decile of the NPV (29 million for landscape L).

However, as previously mentioned (Rimbaud et al. 2018b) our results can be affected by some model assumptions (for instance, the detection probability may be overestimated). In addition, we used here a Sobol-type sensitivity analysis to improve management strategies. Although this analysis has good space-filling properties that enabled to test a huge number of parameter combinations well spread throughout the parameter space (Sobol 1976), this one is so vast that better strategies can be found between the sampled points. The main goal of the present study was to explore the impact of landscape aggregation on improved disease management strategies, but if interest lies in approaching more closely the actual optimum, one option may be to iteratively explore the parameter space as previously done (Rimbaud et al. 2018b). However, this approach involves some arbitrary choices at each iteration and inefficiencies in the use of computing resources; thus, dedicated optimization algorithms may be more efficient for future work.

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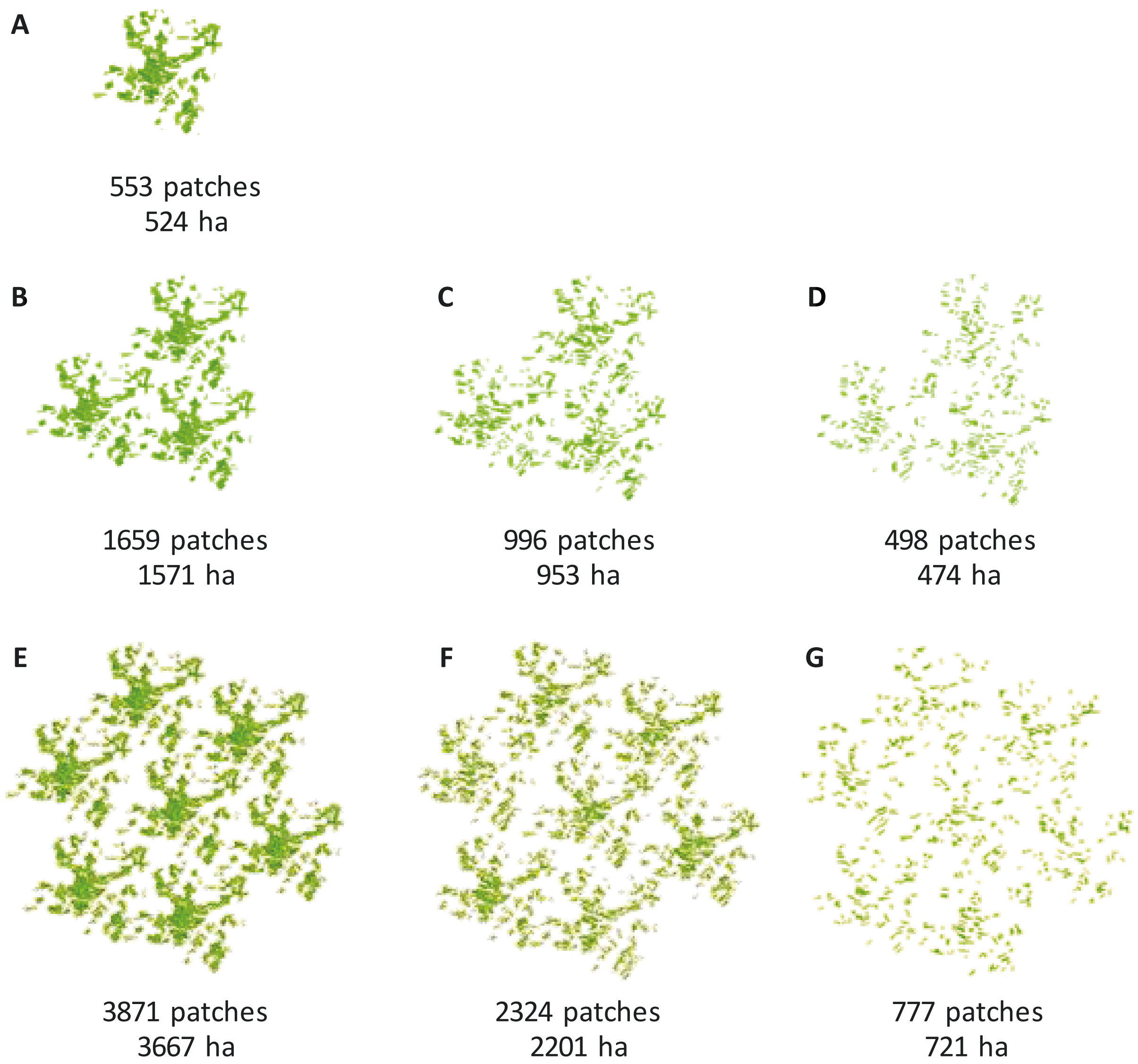
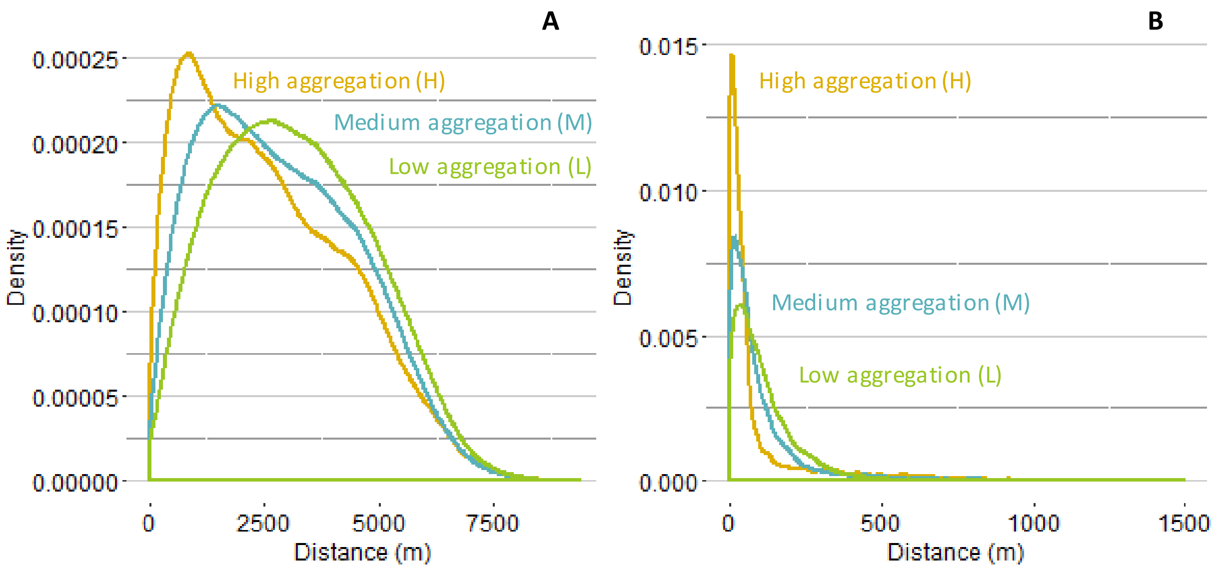
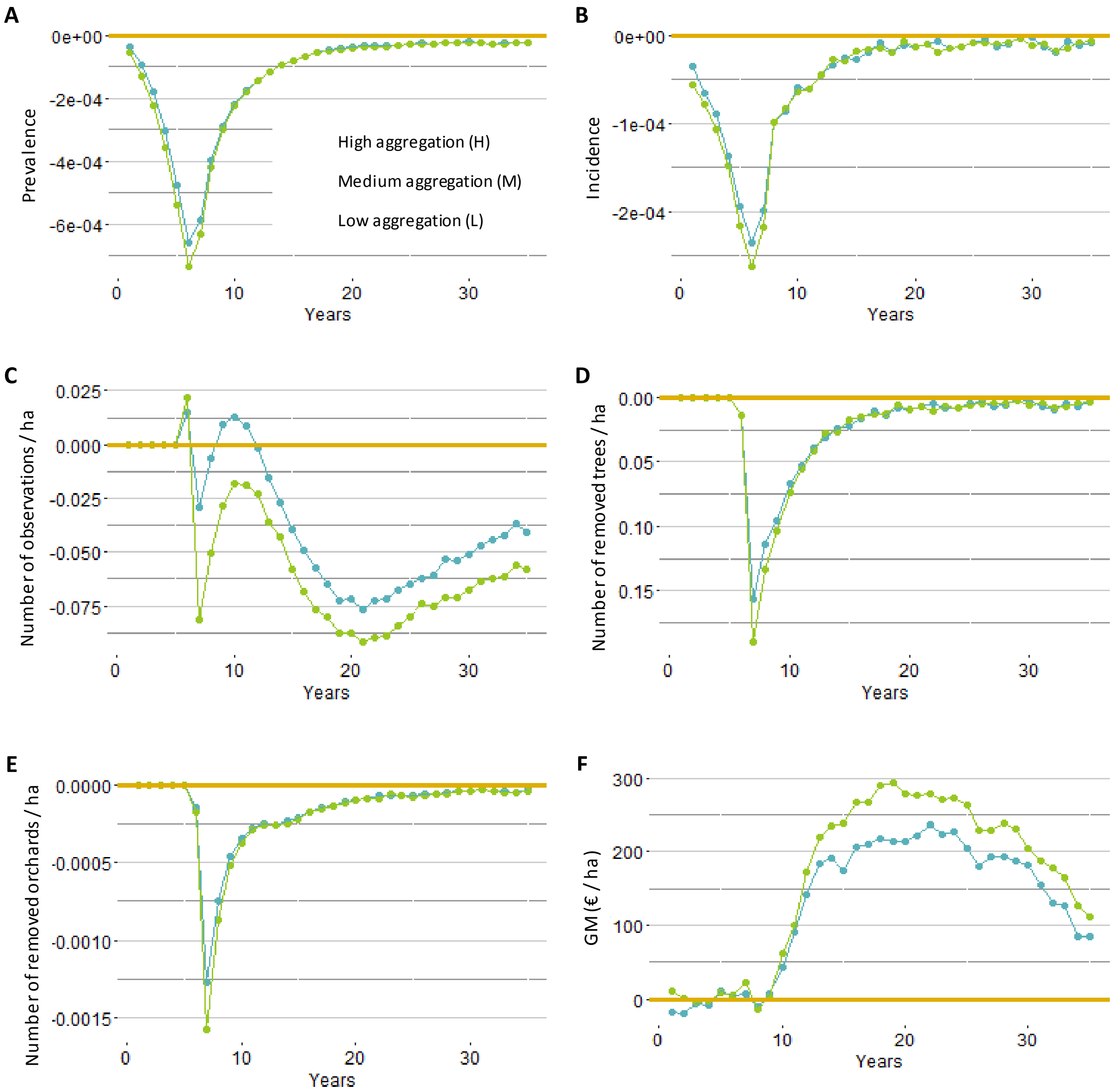
SUPPORTING INFORMATION



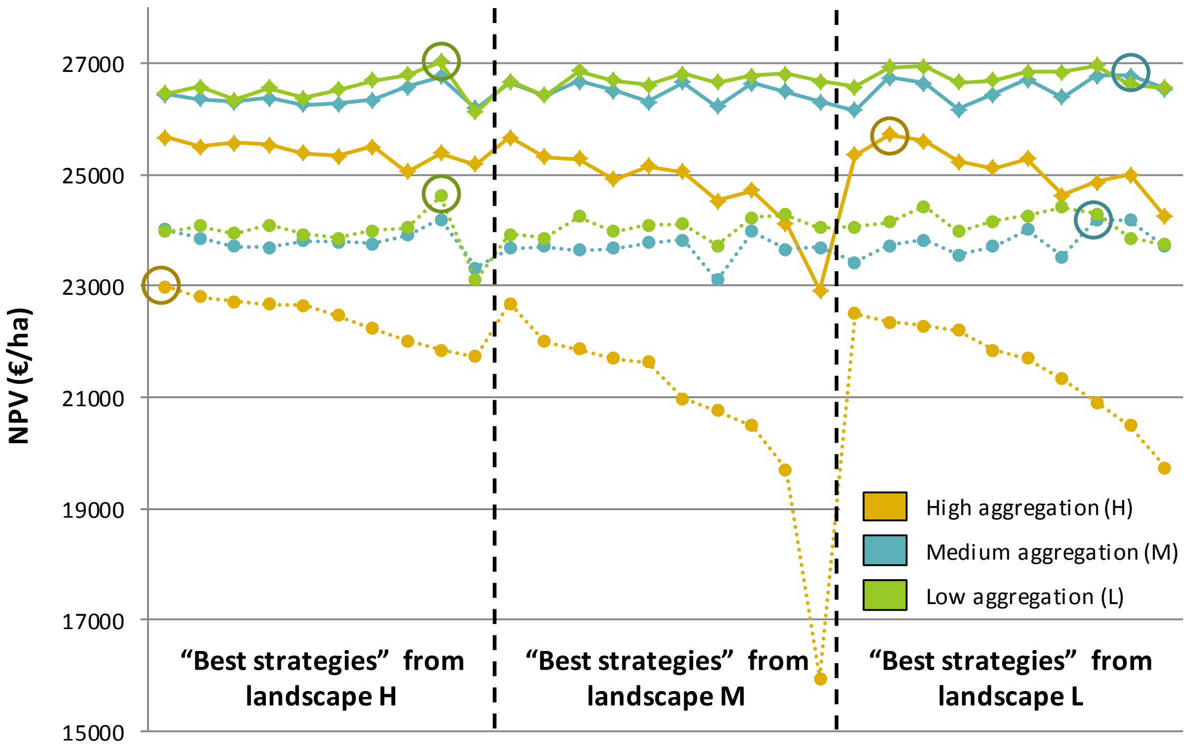
Supplementary Fig. S1: Duplicated and subsampled landscapes. A, real landscape of 553 peach patches (green polygons). B, real landscape duplicated 3 times. C and D, examples of landscapes obtained after the random removal of 40% and 70% of the patches from landscape B, respectively. E, real landscape duplicated 7 times. F and G, examples of landscapes obtained after the random removal of 40% and 80% of the patches from landscape E, respectively.



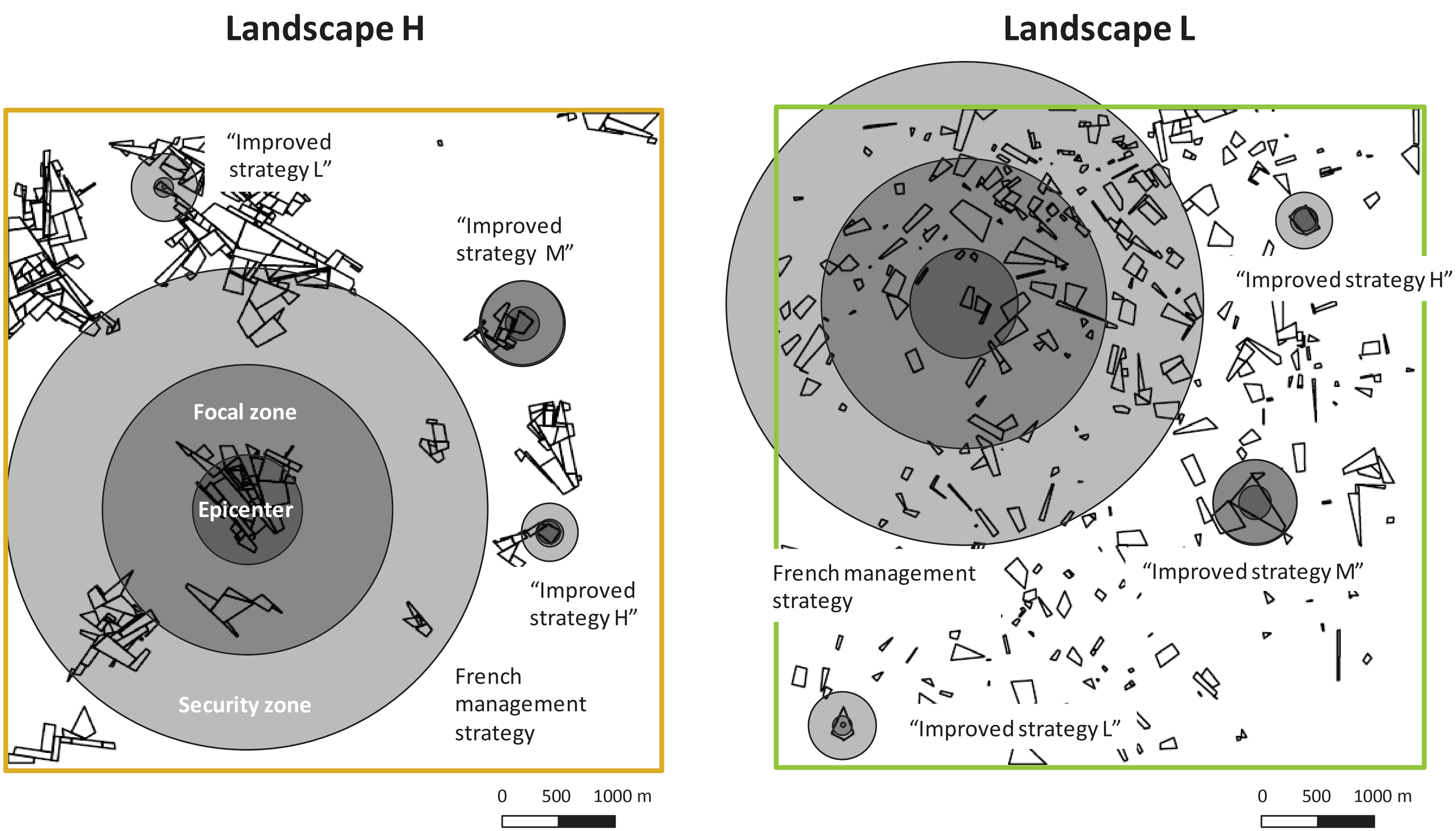
Supplementary Fig. S2: Probability densities of the distances for landscapes H, M and L between the centroids of: A, all the patches and B, all nearest neighbor patches.



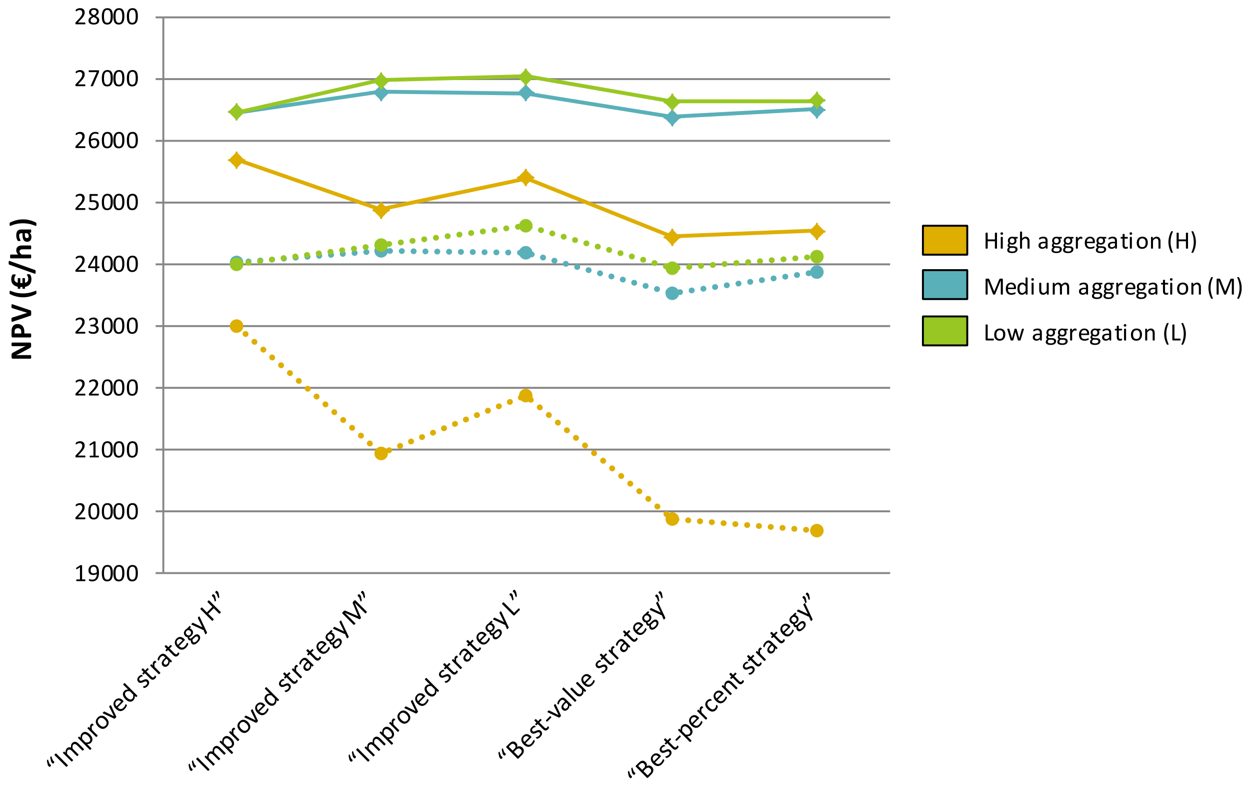
Supplementary Fig. S3: Evolution of NPV components on simulated landscapes with the French management strategy. These components are: A, prevalence; B, incidence; C, number of observations per ha; D, number of removed trees per ha; E, number of removed orchards per ha; F, gross margin (€/ha). For each component, the blue (resp. green) line represents the difference between landscape M (resp. L) and landscape H. Note, these lines are above the yellow line when the NPV component is higher than for landscape H (and vice versa).



Supplementary Fig. S4: $\overline{\mathrm{NPV}}$ (solid lines) and $\mathrm{NPV}_{10\%}$ (dotted lines) obtained after simulation of PPV dispersal and its management. Simulations were performed with the 30 improved combinations of management parameters (10 strategies leading to the best $\mathrm{NPV}_{10\%}$ among 256 strategies identified for the 3 aggregation levels), on the 3 levels of landscape aggregation. The circled points represent the best values of $\overline{\mathrm{NPV}}$ and $\mathrm{NPV}_{10\%}$ for each aggregation level. The strategies corresponding to the best $\mathrm{NPV}_{10\%}$ are called "Improved strategy H" (high aggregation level), "Improved strategy M" (medium aggregation level) and "Improved strategy L" (low aggregation level).



Supplementary Fig. S5: Schematic representation of the surveillance zones on landscapes H (high aggregation level) and L (low aggregation level). Four management strategies are represented : the French strategy and the 3 "Improved strategies".



Supplementary Fig. S6: $\overline{\mathrm{NPV}}$ (solid lines) and $\mathrm{NPV}_{10\%}$ (dotted lines) obtained after simulations of PPV dispersal and management. Simulations are carried out with the 3 "Improved strategies" and with the strategies improved by Rimbaud et al. (2018b). Simulations are performed for 3 levels of landscape aggregation.

Supplementary Table S1: Epidemiological and management parameters implemented in the previously developed model with minimum and maximum values corresponding to the variation range of each parameter in the sensitivity analysis.

		Min	Max
	Epidemiological parameters		
q_κ	Quantile of the connectivity of the patch of first introduction	0	1
φ	Probability of introduction at plantation	0.0046	0.017
p_{MI}	Relative probability of massive introduction	0	0.1
W_{exp}	Expected value of the dispersal weighting variable	0.469	0.504
β	Transmission coefficient	1.25	1.39
θ_{exp}	Expected duration of the latent period (years)	1.71	2.14
	Management parameters		
ρ	Probability of detection of a symptomatic tree	0	0.66
δ	Mean delay before removal of a detected tree (days)	-	-
γ_R^T	(Boolean) Individual trees are removed: 0: after a mean delay of 10 days 1: at the end of the year	0	1
γ_R	(Boolean) Whole orchards are removed: 0: after a mean delay of 10 days 1: at the end of the year	0	1
γ_S	Delay before replantation of a removed orchard (years)	0	10
γ_O	Duration of observation zones (years)	0	10
γ_Y	Duration of young orchards (years)	0	10
ζ_S	Radius of security zones (m)	0	5800
$r\zeta_f$	Ratio of the focal area over the security area	0	1
$r\zeta_{e0}$	Ratio of the observation epicenter area over the focal area	0	1
ζ_n	Radius of the close neighborhood (m)	0	5475
ζ_R	Radius of the removal zone (m)	0	5800
$r\zeta_{eR}$	Ratio of the removal epicenter area over the removal area	0	1
$1/\eta_0$	Maximal period between 2 observations (years)	1	15
η_s	Observation frequency in security zones (year^{-1})	0	8
η_f	Observation frequency in focal zones (year^{-1})	0	8
η_{f*}	Modified observation frequency in focal zones (year^{-1})	0	8
η_y	Observation frequency in young orchards (year^{-1})	0	8
η_{y*}	Modified observation frequency in young orchards (year^{-1})	0	8
χ_o	Contamination threshold in the observation epicenter, above which the observation frequency in focal zone is modified	0	1
$\chi_{\bar{y}}$	Contamination threshold in the environment around young orchards, above which the plantation of orchards is forbidden	0	1
$r\chi_{y*}$	Ratio (over $\chi\bar{y}$) of the contamination threshold in the environment, above which the observation frequency in young orchards is modified	0	1
χ_n	Contamination threshold on an orchard in the neighborhood, above which the plantation of orchards is forbidden	0	1
χ_R	Contamination threshold in the removal epicenter, above which orchards inside the removal zone are removed	0	0.34

Supplementary Table S2: Parameter combinations for the main management strategies.

Management parameters	French management strategy	"Best point strategies"			"Improved strategies"		
		High aggregation (H)	Medium aggregation (M)	Low aggregation (L)	High aggregation (H)	Medium aggregation (M)	Low aggregation (L)
ρ	0.66	0.47	0.06	0.53	0.65	0.30	0.48
γ_R^T	0	0	0	0	0	0	0
γ_R	1	1	0	1	1	1	0
γ_S	0	8	4	3	7	6	5
γ_o	3	10	0	0	2	9	1
γ_y	3	5	1	8	1	6	0
ζ_s	2500	252	461	3941	295	442	349
$r\zeta_f$	0.38	0.25	0.06	0.54	0.23	0.97	0.08
$r\zeta_{e0}$	0.60	0.51	0.83	0.49	0.68	0.06	0.16
ζ_n	200	4316	1437	4645	324	1592	2974
ζ_R	0	1309	2322	3372	1765	51	974
$r\zeta_{eR}$	0	0.91	0.03	0.87	0.63	0.88	0.89
$1/\eta_0$	6	8	15	10	11	9	7
η_s	1	2	4	3	1	0	0
η_f	2	6	4	2	0	1	3
η_{f*}	3	8	7	1	1	0	7
η_y	2	0	2	0	4	0	5
η_{y*}	3	5	5	6	1	4	8
χ_o	0.02	0.81	0.14	0.35	0.60	0.95	0.59
χ_y	0.02	0.75	0.15	0.56	0.44	0.29	0.25
$r\chi_{y*}$	0.50	0.15	0.18	0.80	0.44	0.56	0.17
χ_n	0.05	0.99	0.26	0.76	0.63	0.60	0.79
χ_R	0.10	0.14	0.27	0.26	0.31	0.30	0.32

Résultats clés de l'Article 4 (parties 2.1, 2.2, 2.3 et 3.1)

ANALYSE DE L'INFLUENCE DE L'AGREGATION DU PAYSAGE SUR LA PROPAGATION DES MALADIES POUR AMELIORER LES STRATEGIES DE GESTION

- **Une méthode pour étudier l'influence du paysage sur les stratégies de gestion**
    - Des paysages de taille et de densité différentes ont été simulés à partir de données géographiques associées à un parcellaire réel, ainsi que des paysages avec différents niveaux d'agrégation à partir d'un algorithme de tessellation en T.
    - Sur ces différents paysages, des épidémies de sharka et la gestion française de cette maladie ont été simulées.
    - Une analyse de sensibilité a été réalisée sur des paysages correspondant à 3 niveaux d'agrégation différents.

- **Le paysage influence les stratégies de gestion de la sharka**
    - Les simulations montrent que quelle que soit la taille du paysage, plus les parcelles sont agrégées, plus l'épidémie se répand vite, et plus les pertes économiques sont conséquentes (que ce soit avec ou sans gestion). L'organisation des parcelles cultivées dans un paysage a donc de l'influence sur les bénéfices de la production de pêches.
    - Deux paramètres de gestion avec une forte influence sur la VAN ont été mis en évidence grâce à l'analyse de sensibilité : ils concernent les interdictions de planter des vergers ainsi que les arrachages de vergers appartenant à une même zone géographique. Une attention particulière devra donc leur être portée dans l'optique d'optimiser les paramètres de gestion des épidémies de sharka.