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Ecology and Epidemiology

Disentangling the Factors Affecting the Dynamic of *Pseudocercospora fijiensis*: Quantification of Weather, Fungicide, and Landscape Effects

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Abstract

Quantifying the effect of landscape composition on disease dynamics remains challenging because it depends on many factors. In this study, we used a hybrid process-based/statistical modeling approach to separate the effect of the landscape composition on the epidemiology of banana leaf streak disease (BLSD) from weather and fungicide effects. We parameterized our model with a 5-year dataset, including weekly measures of BLSD on 83 plots in Martinique. After estimating the intrinsic growth parameters of the stage evolution of the disease (SED), we evaluated the dynamic effect of five fungicides. Then, we added the intra- and inter-annual effect on disease dynamics using a generalized linear model. Finally, the whole model was used to assess the annual effect of the landscape on the SED for 11 plots. We evaluated the significance of the landscape composition (proportions of landscape elements in 200-, 500-, 800-, 1,000-m-radius buffer zones) on the landscape effect evaluated with the model. The percentage of hedgerows in a 200-m-radius buffer zone was negatively correlated to the landscape effect, i.e., it acted as a constraint against BLSD spreading and development. The proportion of managed-banana-plants in a 1,000-m-radius buffer zone was negatively correlated to the landscape effect, probably due to a mass effect of fungicide treatments. Inversely, the proportions of forest and the proportion of unmanaged-banana-plants, both in 1,000-m-radius buffer zones, were positively correlated with the landscape effect. Our study provides a holistic approach of the role biotic and abiotic factors play on the dynamics of BLSD.

Keywords: black leaf streak disease, black Sigatoka, epidemiological model, French West Indies, *Musa* spp., suppressive landscape

Landscape composition is an important feature for agroecological management. It refers to the proportion of each landscape element around cultivated fields. There is a wide literature on the effect of landscape composition on natural enemies and on pest regulation (Aviron et al. 2016; Chaplin-Kramer et al. 2011; Lykouressis et al. 2008; Tscharntke et al. 2007). Pests' development is modulated by landscape elements that provide favorable or unfavorable habitats, facilitate their dispersal, and modify microclimate. The landscape composition can differentially be conducive or suppressive to the dynamics of a pathogen (Veres et al. 2013). For example, Condeso and Meentemeyer (2007) demonstrated that a large host area from 50 m around a disease spot increases severity of the disease (Condeso and Meentemeyer 2007). At the opposite, host density can also reduce disease severity (Finckh et al. 1999).

To date, few studies have been dedicated to a clear demonstration of landscape effects on plant diseases (Plantegenest et al. 2007). This is probably due to the complexity of disentangling landscape effects from other factors such as natural disease growth, cultural practices, and weather. Tools to partition these different effects in a standardized way are required to better assess the effect of landscape composition on diseases and ultimately to better use this lever in integrated agroecological strategies.

Modeling the spatial dynamics of crop diseases is increasingly used to understand the factors involved in pathogen dispersal and landscape effects, such as landscape structure, the relative position of each landscape element (Papaïx et al. 2014), or the effect of the presence of resistant plants (Pacilly et al. 2018). However, existing models often remain theoretical approaches that are scarcely based on biological or agricultural data. Moreover, most of these approaches neglect management practices (prophylaxis or pesticide treatment) unless they probably play an important role (Pacilly et al. 2018). On the other hand, purely statistical approaches including Bayesian computing (Martins et al. 2013) are appropriate for extracting climatic or environmental effects (Cendoya et al. 2020), but are limited in taking into account more complex cultural practices. Here, we propose an approach that combines dynamic modeling and statistical analysis in order to partition major effects involved in the dynamics of a fungal disease of bananas, including epidemiological traits of this disease, disease management practices, and the weather, in order to estimate landscape effects on an aerial tropical polycyclic disease.

Black leaf streak disease (BLSD), also called black Sigatoka, a foliar disease caused by the ascomycetous fungi *Pseudocercospora fijiensis*, is the main issue for banana production systems for exportation (de Lapeyre de Bellaire et al. 2009). This disease is an emerging disease whose intercontinental expansion can now be considered as almost complete (Guzmán et al. 2018). It was reported for the first time in Martinique in 2010 (Ioos et al. 2011). This foliar disease provokes yield losses but also a reduction of fruit green life, which is essential for their exportation (Churchill 2011). The main control methods are chemical treatments, which represent a significant economic production cost as well as environmental issues that are still largely unknown (de Lapeyre de Bellaire et al. 2009). Like most fungal diseases of plants, climatic factors (particularly temperature and humidity) influence the whole life cycle of the pathogen including infection, host colonization, sporulation but also dispersion and survival (Bebber 2019; Jacome et al. 1991). *P. fijiensis* can disperse by two types of propagules: ascospores resulting from

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sexual reproduction and conidia resulting from asexual reproduction (Meredith and Lawrence 1969). Conidia are produced at the youngest stages of the disease (1 to 4 on the 6 scale) (Fouré 1987) and can disperse over a distance of about 10 m, whereas ascospores are only produced in the oldest necrotic stage (stage 6) and can disperse over several hundred meters (Rieux et al. 2014). Landscape composition and structure are therefore likely to play multiple roles in this disease. Rieux et al. (2013) have shown using neutral clines markers that landscape composition did not affect genetic structure of pathogen populations at a local scale (50 × 80 km). However, this study does not preclude landscape effects on disease epidemics since this genetic structure was mostly influenced by historical fungal expansion in this area through long-distance dispersal events. At a plot scale, it has been shown that the presence of trees near banana plants (within 10 m) can reduce the inoculum of *P. fijiensis* available for new infections (Poeydebat et al. 2018), but no study has been conducted at a larger scale to determinate how landscape structure or composition (as the presence of hedgerows) participate to control disease.

There are currently very few models dealing with BLSD. In their model, Landry et al. (2017) simulated BLSD dynamics, taking into account the biology of the plant and its architecture as well as pathogen development (infection, lesion development, sporulation, and spore dispersal). This model simulates the disease development at plant scale and does not allow an integration of potential landscape effects nor the effect of chemical control practices. Our model aims to work at a larger scale and take into account these effects.

In this paper, we have developed a model that simulates the BLSD dynamics accounting for its exponential growth, the effects of weather, fungicide applications, and landscape. It simulates the stage of evolution of the disease (SED) that is a disease monitoring descriptor (Fouré and Ganry 2008). This model, combines (i) an exponential growth rate of the SED that is altered by the effects of weather and fungicide applications with (ii) a generalized linear model allowing to take into account the dynamics of the disease since its introduction in Martinique and the seasonality of BLSD in Martinique. After parameterization, we used the model to estimate landscape effect on SED. Finally, we investigated how landscape metrics influenced this landscape effect.

Materials and Methods

This study was conducted in Martinique (latitude, 14°36′32N; longitude, 61°4′24W), a Caribbean island characterized by a tropical climate with highly contrasted climatic conditions according to altitude and windward exposition (between 1,000 and 5,000 mm annual rainfall depending on area). Landscape structure and composition are contrasted in Martinique according to topography, proximity to the coast, prevalence of cultivated bananas (about 5,000 ha or 25% of the useful agricultural area of the island), human habitat, or natural forest areas. Almost all banana production is exported and cultivated with banana cultivars of the Cavendish subgroup (*Musa acuminata*, AAA group, Cavendish subgroup), which are highly susceptible to BLSD.

SED as a disease parameter

We have used a data set of regular weekly BLSD monitoring carried out in banana plantations over 83 banana plots representative of all island situations over a 5-year period from 2015 to 2019 (Fig. 1). The disease parameter measured weekly was the SED, which is an indicator of the speed of development of the disease in a field that is used for making the decision of the application of fungicides (Fouré and Ganry 2008). The SED is a quantitative evaluation of BLSD symptoms on the four youngest banana leaves where initial infections occur. For each leaf number/stage of the disease, a coefficient is attributed taking into account the speed of evolution of the disease and the density of infection (Table 1). Technically, the observation is made weekly on the same 10 banana plants and the SED is the sum of all the coefficients multiplied by the mean foliar emission rate (Fouré and Ganry 2008). Indeed, the SED reflects the presence of new infections detected in the youngest banana leaves taking into account their stage and their abundance. Since a banana plant has a regular weekly foliar emission and that new infections occur mainly on these young leaves, SED is a good indicator of new epidemic waves of this polycyclic tropical disease (de Lapeyre de Bellaire et al. 2010). This indicator is impacted by all the variables that alter disease progress and is continuous, 10 new banana plants being selected after flowering.

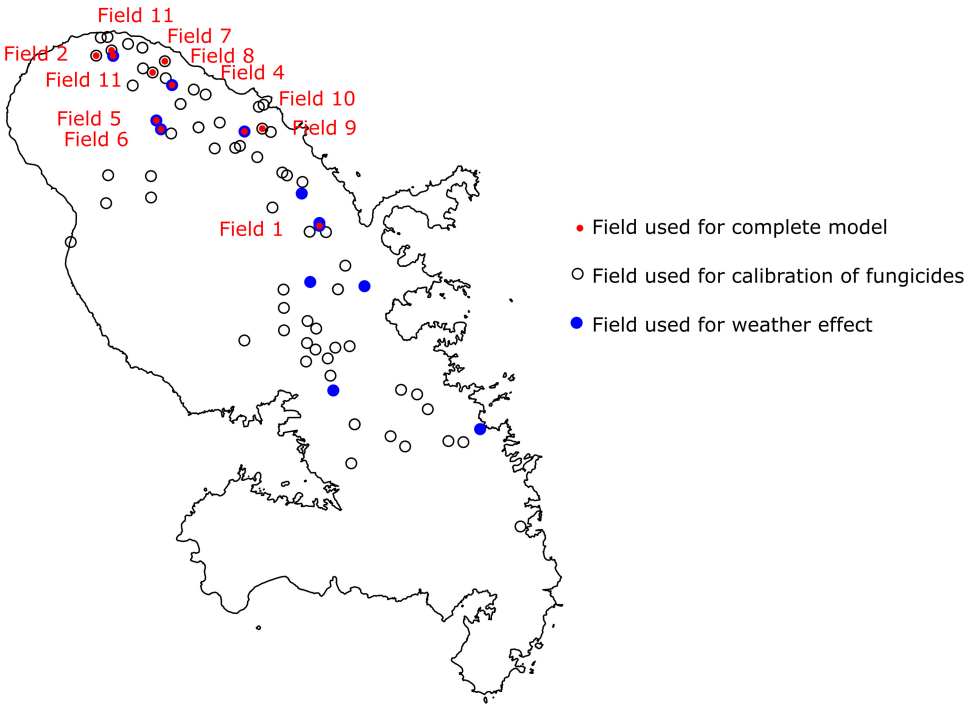

Fig. 1. Field locations used for the study. Black spots are fields where only SED where measured and were used for equations 2 and 4 calibration. Blue spots are fields where stage evolution of the disease and Piche evaporation were measured. Red spots are fields where equations 1b and 1c with the closest Piche evaporation data were measured.

We used data collected from 2015 to 2019; after 2015, it is possible to consider that BLSD had already invaded all banana plantations of Martinique and showed a significant level in all regions. In total, our database contains 17,628 rows (1 week of measure in one given field). All fungicide treatments were collected weekly on the various plots from 2017 to 2019, for a total of 2,020 treatments with five types of fungicides (SICO: Difenoconazole, 250 g liter^{-1}, SYNGENTA France SAS; CONSIST: Trifloxystrobin, 500 g kg^{-1}, BAYER SAS; LUNA: fluopyram, 250 g liter^{-1}, BAYER SAS; SERENADE: *Bacillus subtilis* str. QST 713, 15.67% m/m, BAYER SAS; and TILT: Propiconazole, 250 g liter^{-1}, SYNGENTA France SAS).

Weather data

Piche evaporation is a meteorological data that integrates various weather factors such as humidity, rainfall, wind, and temperature (Jacobs and Arriëns-Bekker 1983). Piche evaporation measured in a modified shelter is a very good indicator of hydric status at the leaf surface and is correlated with BLSD development and particularly SED (Ganry and Laville 1983; Ganry and Meyer 1972). Our dataset contains 12 Piche evaporation measurement sites on 12 plots (blue points in Fig. 1) where SED was assessed weekly from 2015 to 2019 (1,633 data in total for the 12 fields).

Landscape metrics

We described the landscape composition for several plots (red points in Fig. 1, selected in a high pressure area of BLSD with evaporation data closed to the plot) within 200-, 500-, 800-, and 1,000-m-radius buffer zones from the center of the plot (Fig. 2) because such areas are potentially influenced by ascospore dispersal (Rieux et al. 2014). As the landscape composition (especially the crops and their surfaces) is changing over the years, we mapped and established the proportion of each landscape element for each year between 2017 and 2019. The composition of landscape was established thanks to several geographic information system databases:

- The Graphic Land Registers edited by the French Ministry of Agriculture (DAAF, Direction de l'Agriculture, de l'Alimentation et de la Forêt) for 2017, 2018, and 2019) (contains data for all crops).
- Vegetation formations drawn by the French ministry of environment (DEAL, Direction de l'Environnement, de l'Aménagement et du Logement) (contains data for forest elements).
- Land use drawn by the DEAL also (contains data of all artificial structures).

Following this mapping, the landscape composition of each buffer zone was classified into five categories of landscape elements that may have an effect on the epidemiology of BLSD:

- Percentage of cultivated host crops (%Managed-banana-plants) including fields of Cavendish export bananas and plantain: maintained and treated for most of the surface (98.55% of this surface is regularly treated with fungicides).
- Percentage of forest (%Forest): it is an element of the landscape that can alter the microclimate, the dispersion of the pathogen with high strata vegetation, and that can also contain scarce untreated banana plants.
- Percentage of hedgerows (%Hedgerow): positioned around fields, of various width and height. Such features could potentially play a role of barrier limiting the dispersal of spores. We took into account the surface of hedgerows in order to take into account width and length and to compare with other landscape elements.
- Percentage of nonhost elements (%Non-banana-culture-and-artificial-structures) including (grassland, cane, road, and building) with assumed neutral effect on the epidemiology of the disease except through fragmentation of host areas among the landscape.
- Potential sources of inoculum (%Unmanaged-banana-plants): it includes fallows after banana plantation and home gardens that can both include banana plants without fungicide treatments.

TABLE 1. Coefficients used for calculating stage evolution of the disease for black leaf streak disease of bananas and plantains

Stages		Leaves II	Leaves III	Leaves IV
1	−	60	40	20
	+	100	80	60
2	−	100	80	60
	+	140	120	100
3	−	140	120	100
	+	180	160	140
4	−	180	160	140
	+	200	200	180
5	−	220	200	180
	+	260	240	220
6	−	260	240	220
	+	300	280	260

Model description

The whole model was coded with R 4.1.1 (R Core Team 2021). All variables and model parameters are presented in Tables 2 and 3. This model does not aim at predicting long-term disease levels but at partitioning biotic and abiotic factors influencing BLSD dynamics. This model was used at each weekly time step to simulate the SED from the measured value of SED at the previous time step by calculating each factor that could be quantified and isolate the part associated to landscape effect. The model was parameterized in three modeling steps (Fig. 3). First, we assumed that the variation in SED depended on the biological growth of the disease (exponential growth rate and weather effect) and the effect of fungicide applications. In a second step, we evaluated the intra- and inter-annual effect based on the residuals of the model of step 1. Finally, we assessed the effect of the landscape based on the residuals of the model of step 2. The three following sections present these modeling steps.

Modeling step 1: Biological growth and fungicide effect

In this first step, we used a dynamic model to simulate the evolution of SED thanks to a generalized linear model including the biological growth (BG_t) that was modelled according to a logistic growth that is altered by weather and by fungicide applications (Fig. 3; equation 1a).

$$\delta SED_t = BG_t \left(1 - \varepsilon fungicide_t\right) + Err1_t \tag{1a}$$

with δSED_t the simulated variation of SED at time step t, BG_t the biological growth of the SED at time step t, $\varepsilon fungicide_t$ the effect of fungicide application at time step t, and $Err1_t$ the residues of the model at time step t.

The biological growth of the SED (BG_t) is represented by a logistic equation (equation 2) (Donzelli and Churchill 2007). This formalism is suitable to simulate a growth that can be very fast (exponential growth).

$$BG_t = r \times SED_{t-1} \left(\frac{K_t - SED_{t-1}}{K_t}\right) \tag{2}$$

with r and K_t the exponential growth rate and the carrying capacity of the logistic growth of the SED at step t, respectively.

The exponential growth rate of SED (r), was evaluated on sequences of exponential growth over a period of at least 4 weeks and without fungicide treatment. The estimation of the exponential growth rate of SED was achieved on 372 sequences of exponential growth, selected from 71 plots and corresponding to 1,830 SED measurements (Fig. 4; Table 4). We standardized these data to the

first value of each sequence. Then, we determined the exponential growth r by fitting (with the nls function of R) an exponential model $y = e^{(r.x)}$, where y is the standardized SED and x is the number of weeks after the beginning of each selected sequence.

The weather is an important factor that alter the potential of development of the disease. Air humidity allows the disease to develop (Guzmán et al. 2018), and saturation of air humidity and the presence of free water on the leaf surface allows the germination and sporulation of ascospora and conidia (Meredith and Lawrence 1969). We assumed that K_t, the maximum value attainable by the SED at time step t, follows a logistic curve with the evaporation measured on the field (equation 3).

$$K_t = \frac{ka}{1 + e^{-kb \times (Evap_t - kc)}} \quad (3)$$

with $Evap_t$ the evaporation measured in the plot at step t. ka, kb, and kc are the parameters of the exponential function that links K_t and the evaporation, corresponding to asymptote of the function, i.e., the maximal value of K_t, the slope of the curve, and the value of $Evap_t$ at inflexion, respectively.

We calibrated the relationship between evaporation and maximum SED values using data from 12 plots (blue points in Fig. 1) for

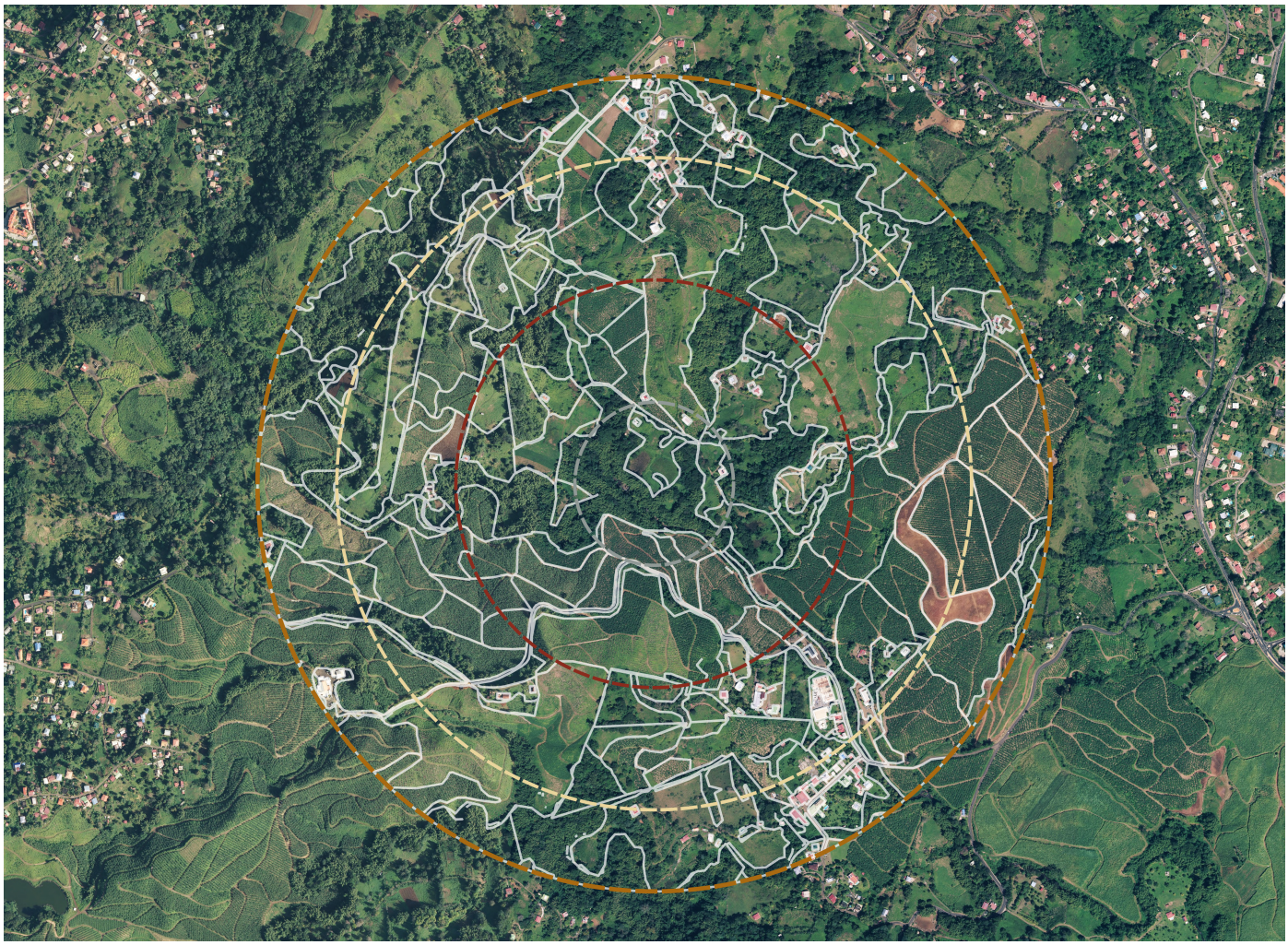

Fig. 2. Illustration of the four buffer zones (200, 500, 800, and 1,000 m) around the plot where stage evolution of the disease was measured.

TABLE 2. Description of the state and input variables of the model

Variables	Unit	Description
State variables		
SED_t	–	Stage of evolution of the disease at step t
$SEDst_t$	–	Standardized stage of evolution of the disease at step t
BG_t	–	Biological growth of the disease at step t
K_t	–	Carrying capacity of the disease (maximal value of SED achievable) at step t
$\varepsilon fungicide_t$	–	Effect of fungicides on the SED at step t
εiia_t	–	Intra- and inter-annual effect on the SED at step t
$\varepsilon landscape_t$	–	Effect of the landscape on the SED at step t
Input variables		
$Evap_t$	mm	Evaporation measured at step t
$tat_{p,t}$	week	Time after application of fungicide p at step t
tae_t	week	Time after the beginning of the measures at step t
woy_t	week	Week of the year at step t

which evaporation measurements were available (1,633 measurements in total; Table 4). We defined evaporation classes by 5 mm (and >10 mm because there was not enough data below 10 mm) and selected the SED values of the last quartile of each class. Next, we fitted equation 3 to these values, which we assumed to be the maximum achievable SED in each evaporation class.

Fungicides are clearly a major driver of the dynamic of plant diseases while it is rarely taken into account. Here, the effect of fungicides on SED was considered as a logistic function decreasing with time after application (equation 4) based on the whole dataset (all points in Fig. 1). We isolated 1,350 treatment sequences (Table 4) composed of the value of the SED each week from the week of the treatment and the following 5 weeks (beyond 5 weeks, too few data were available for the parameterization). The decay of this three-parameter logistic function (α, β, and γ) allows representing the maximum effect of fungicides and its decay after application.

$$\varepsilon\text{fungicide}_t = \frac{\alpha_f}{1 + e^{\left(\frac{\beta_f - \text{tat}_{f,t}}{\gamma_f}\right)}} \tag{4}$$

with f the fungicide and $\text{tat}_{f,t}$ the time (in weeks) after treatment of the fungicide f at step t. α_f, β_f, and γ_f are the parameters of the logistic function that link the effect of fungicide f and the $\text{tat}_{f,t}$, corresponding to the asymptote of the function, the value of $\text{tat}_{f,t}$ at inflexion, and the slope of the function, respectively.

Because $\varepsilon\text{fungicide}_t$ could be applied directly as the fraction of SED lost at time t because of pesticide application, we performed a standardization of the data to assess the effect of fungicides

TABLE 3. Description and calibrated values of the parameters of the model

Parameters	Calibrated values	Unit	Description
R	0.415	–	Exponential growth rate of SED
Ka	2,309.1666	–	Maximal value of Kt
Kb	−0.1250	–	Slope of the exponential function that link K_t and Evap_t
Kc	30.6787	mm	Value of Evap_t at inflexion in the exponential function that link K_t and Evap_t
α_f	0.8601	–	Asymptote values of the logistic function that link $\varepsilon\text{fungicide}_t$ and $\text{tat}_{p,t}$ for CONSIST, LUNA, SERENADE, SICO, and TILT, respectively
	1.4027		
	0.7480		
	0.8663		
	0.8103		
β_f	3.4585	week	The values of $\text{tat}_{p,t}$ at inflexion in the logistic function that link $\varepsilon\text{fungicide}_t$ and $\text{tat}_{p,t}$ for CONSIST, LUNA, SERENADE, SICO, and TILT, respectively
	1.2584		
	2.5512		
	3.4660		
	3.2769		
γ_f	−0.6109	–	Slopes of the logistic function that link $\varepsilon\text{fungicide}_t$ and $\text{tat}_{p,t}$ for CONSIST, LUNA, SERENADE, SICO, and TILT, respectively
	−1.8806		
	−0.4702		
	−1.2331		
	−0.7032		
$\text{int}_{\varepsilon\text{iia}}$	−54.1486	–	Intercept of the linear model that predict εiia_t
coef_{tae}	0.09978	–	Coefficient of the effect of tae_t on the prediction of εiia_t
coef_{woy}	4.1265	–	Coefficient of the effect of woy_t on the prediction of εiia_t

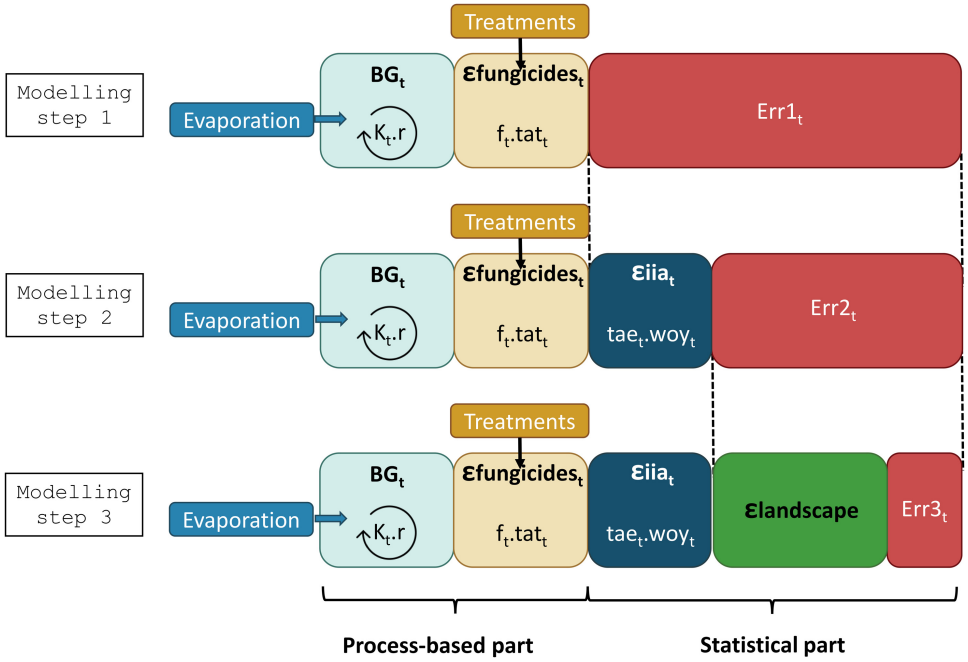

Fig. 3. Model diagram illustrating the partitioning of stage evolution of the disease at time step t (SED_t) as performed in the three modeling steps, including process-based and statistical parts. All variables are described in Table 1.

by subtracting the biological growth of the disease, following the formula:

$$SEDst_t = \frac{SED_t}{SED_{t-1}} - r - 1$$

with $SEDst_t$ the standardized value of SED at time step t and r the exponential growth. In this equation, the subtraction of 1 allowed the calculated ratio to be directly applicable in the model.

After calibration of equations 2, 3, and 4, the model described in equation 1a (with data from sites shown in red in Fig. 1) led to a prediction of the SED_t as illustrated by yellow points in Figure 5, and to residues $Err1_t$.

Modeling step 2: Intra- and inter-annual effect

The second modeling step aimed at explaining the part of the residual variance from modeling step 1 ($Err1_t$) that can be attributed to the disease dynamics at the island scale taking into account the disease progress linked to progressive *P. fijiensis* expansion over the years and the seasonal variations (intra- and inter-annual effect, εiia). The equation of prediction of SED in the modeling step is presented in equation 1b.

$$\delta SED_t = BG_t\left(1 - \varepsilon fungicide_t\right) + \varepsilon iia_t + Err2_t \quad (1b)$$

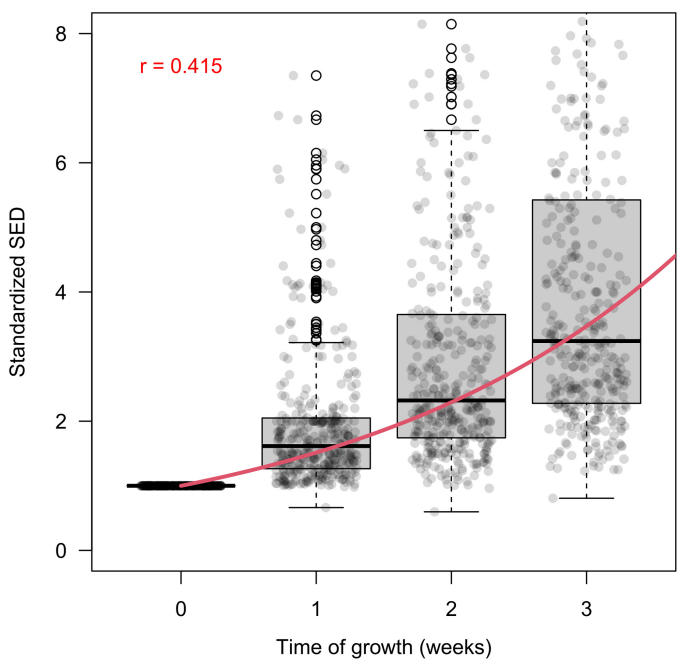

Fig. 4. Exponential growth modeling of stage evolution of the disease (SED) based on growth exponential sequences of SED data over 4-week periods without fungicide treatment from data from 2015 to 2019. The intrinsic growth rate r was calculated on standardized SED (1 as the value of SED on the first week from the sequences).

with εiia_t the intra- and inter-annual effect at time step t and $Err2_t$ the residues of the model at time step t.

The εiia_t was estimated with a linear model of the residuals from modeling step 1 ($Err1_t$) as response variable and with two predictors: (i) the time since the beginning of BLSD assessment in Martinique to take into account the progression of the disease since its introduction, and (ii) the week of the year to take into account the seasonality of inoculum levels that are clearly more important at the end the year (green line in Fig. 5). The calculation of εiia can thus be described as a function of tae_t, the time in weeks after the start of the measurements (01/01/2015), and woy_t the week of the year (equation 5).

$$\varepsilon iia_t = int_{\varepsilon iia} + coef_{tae} \times tae_t + coef_{woy} \times woy_t \quad (5)$$

with $int_{\varepsilon iia}$ the intercept of the model, $coef_{tae}$ the coefficient of increase of SED inter-annual, and $coef_{woy}$ the coefficient of increase of SED intra-annual.

After calibration of the linear model presented in equation 5, the model described in equation 1b (with data from the sites shown in red in Fig. 1) led to a prediction of the SED_t as illustrated by green points in Figure 5 and to residues $Err2_t$.

Modeling step 3: Landscape effect

The third modeling step aimed at explaining the part of the residual variance from modeling step 2 ($Err2_t$) that can be attributed to landscape effects. Finally, we used linear models to analyze how the previously described landscape metrics (hedgerow, forest, managed-banana-plants, non-banana-cultures-and-artificial-structures, and unmanaged-banana-plants) were good predictors of $Err2_t$. At the end, the model that partitions the variance of SEDt can be summarized in equation 1c.

$$\delta SED_t = BG_t\left(1 - \varepsilon fungicide_t\right) + \varepsilon iia_t + \varepsilon landscape_t + Err3_t \quad (1c)$$

with $\varepsilon landscape_t$ the landscape effects and $Err3_t$ the residuals of the model at step t, respectively.

Results

Estimation of the exponential growth rate of SED and the effect of weather

The estimation of the exponential growth rate of SED fitted is r = 0.415 (equation 2) (Fig. 4). Then, the calibration of weather effect on the growth of SED allowed us to estimate the parameters ka = 2,309.167, kb = −0.125, and kc = 30.679 of equation 3 using the 'nls' function of R (Fig. 6; Table 3).

Effect of fungicides

The calibration of fungicide effects on all SED data since 2017 provided the fit of α_f, β_f, and γ_f, which shows contrasting pesticide effects for each of the five fungicides used in the study (Fig. 7; Table 3). Time of effect and efficiency vary between the fungicides. Beyond the parameterization of the model, this approach provides a standardized comparison of the effect of each fungicide type.

TABLE 4. Datasets used for the parameterization of each part of the model

Use (parameters, equation)	Date/time	Number of data or sequences
Growth rate (r, equation 2)	2015–2019	372 sequences or 1,830 data selected manually on 83 plots
Weather effect (ka kb kc, equation 3)	2015–2019	1,633 data on 12 sites
Fungicides effect (α_p, β_p, γ_p, equation 4)	2017–2019	2,550 data from 1,350 sequences from 83 plots shared in • 329 data in 135 sequences for CONSIST • 332 data in 146 sequences for LUNA • 703 data in 322 sequences for SERENADE • 1019 data in 425 sequences for SICO • 767 data in 322 sequences for TILT
Intra- and inter-annual effect (εiia, equation 1b, 1c)	2017–2019	995 rows on 11 plots

The most effective fungicides 3 weeks after the application have the highest values of α_f and β_f (they were the systemic products CONSIST, SICO, and TILT). SERENADE efficiency decreased faster than the other fungicides after 2 weeks and had a negligible effect after 3 weeks. CONSIST has a better efficiency within 3 weeks, and SICO and LUNA remain the most effective after 4 weeks.

Intra- and inter-annual effects

The εiia_t was assessed by analyzing the model residuals of equation 1a (red points in Fig. 1) with a linear model including the time since measurements beginning (tae_t) and the week of the year (woy_t) as predictors (modeling step 2). These two predictors were significant ($P = 0.004$ and $P < 0.001$, respectively) with positive estimates ($coef_{tae}$ and $coef_{woy}$) 0.09 ± 0.03(SE) and 2.86 ± 0.75(SE), respectively. Both coefficients correspond to (i) an increase in disease pressure over time (explained by the fact that island colonization of the disease has been ongoing since its introduction in 2010), and (ii) the gradual increase of the disease over the year before a decrease at the beginning of the next year with the beginning of the dry season (Fig. 8).

Evaluation and analysis of the landscape effects

We have estimated the landscape effect and a residual variation in BLSD dynamics (εlandscape + Err) for each of the 11 plots selected (red points in Fig. 1) by analyzing the model residuals from equation 1b. The mean landscape effect on the disease of each plot and each year (εlandscape + Err) varied between −152.17 and 135.95 (Fig. 9). Next, we analyzed, for each field, for each year and in each buffer zone, how landscape metrics influenced εlandscape. We tested landscape metrics separately in each buffer zone in order to not suppress an effect because of the abundance of another element. For each landscape feature, we selected which buffer zone it was a better predictor of εlandscape (with the highest significance):

- The presence of managed-banana-plants with BLSD control had a depressive effect on BLSD at all distances (Fig. 10). However, the most significant effect was within the 1,000-m-radius buffer zone (Fig. 10). εlandscape values decreased with host crop area in a 1,000-m-radius buffer zone effect (−5.825, $P < 0.001$) and beyond 30% of managed banana area landscape effects values are nearly all negative (Fig. 11A).
- The presence of forest significantly promoted BLSD at all buffer zone sizes (Fig. 10), and stronger effects being at longer distances within the 1,000-m-radius buffer zone. At that distance, a positive linear coefficient (4.019, $P < 0.001$) indicates that εlandscape tends to increase with the amount of forest (Fig. 11B). When the percentage of forest exceeds 33.8 %, nearly all landscape effects are positive.
- Non-banana-cultures-and-artificial-structures characterized by the absence of host plants had a depressive effect on BLSD only significant for larger distances (800 and 1,000 m, Fig. 10). εlandscape values decreased when the percentage of such features increased with negative coefficients −4.105 ($P < 0.05$) and −5.384 ($P < 0.01$), for 800- and 1,000-m-radius buffer zones, respectively (Fig. 11C).
- The effect of Hedgerow was significant and maximal in the shorter radius buffer zone of 200 m (Fig. 10) and was depressive on BLSD (linear coefficients: −23.089, $P < 0.05$). Interestingly, when the percentage of hedgerows was just over zero, the landscape effect was always below (or near) zero (Fig. 11D). Largest

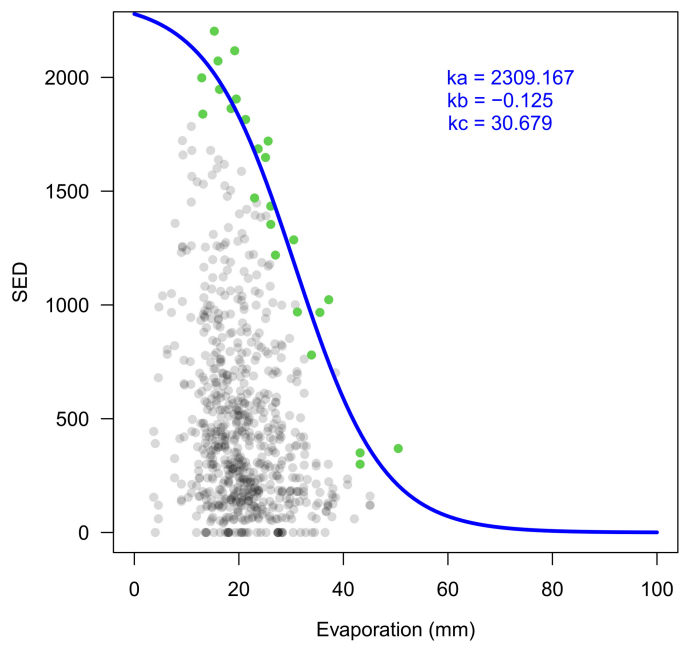

Fig. 6. Representation of stage evolution of the disease (SED) as a function of evaporation (millimeters). The blue curve represents the achievable SED (K) for each evaporation value (equation 2). Green points are the ones used to calibrate the line.

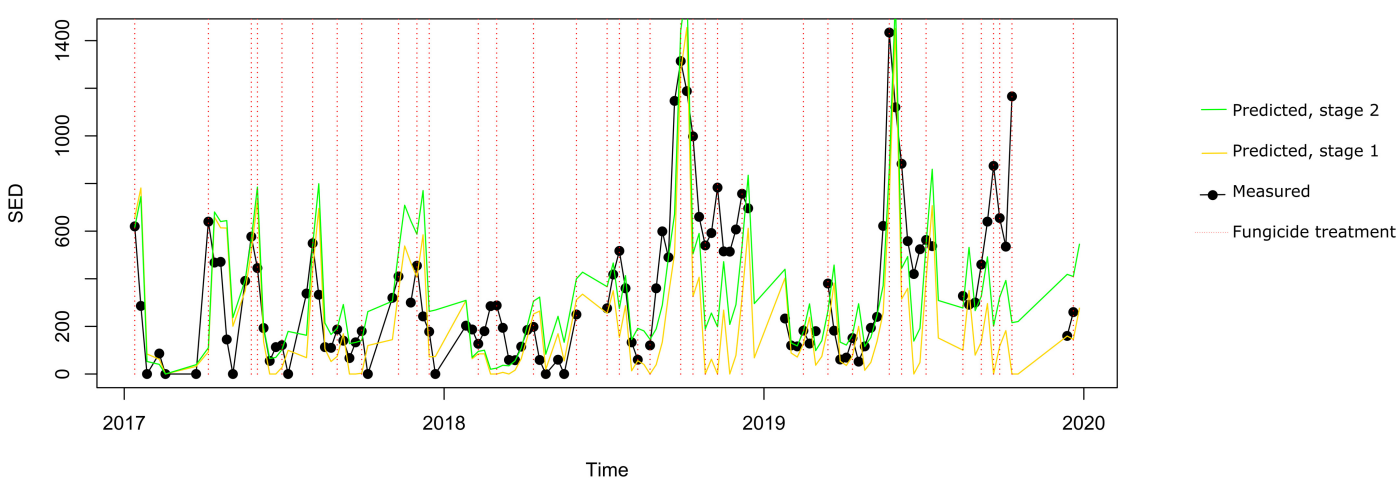

Fig. 5. Illustration of the weekly dynamic of stage evolution of the disease (SED) (field 6) between 2017 and 2019, measures are in black, predicted SED in modeling step 1 with equation 1a in yellow (SED prediction with weather and fungicide effect), and predicted SED in modeling step 2 with equation 1b in green (SED prediction with weather, fungicide, and intra- and inter-annual effects). Vertical red dotted lines show the fungicide applications.

effects were observed for percentage of hedgerows between 1 and 3%.

- The presence of unmanaged-banana-plants and therefore potential sources of inoculum had promoted BLSD only at the longest distance within the 1,000-m-radius buffer zone (Fig. 10) and has a positive coefficient that increases the εlandscape (6.704) (Fig. 11E).

Discussion

Our approach proposes a method that aims at disentangling, in the most process-based way possible, main factors influencing the epidemiological dynamics of an aerial foliar disease, at different spatiotemporal scales (from local fungicide application on banana plots to seasonal dynamics of the disease and landscape effects at different scales). The originality of the approach is to have a dynamic model, with a process-based part and a statistical part. In the process-based part, we took into account the exponential growth rate of the disease and the direct effects of weather and fungicide applications, and in the statistical approaches, we took into account the effects linked to larger temporal scales (colonization of the disease), to finally deduce the effect of the landscape. This strategy allowed a parsimonious approach in terms of the number of parameters and a biological significance of most of these parameters.

Modeling the dynamic of BLSD

Our model allowed estimating factors that were never quantified before and can be used in other modeling studies. As we studied

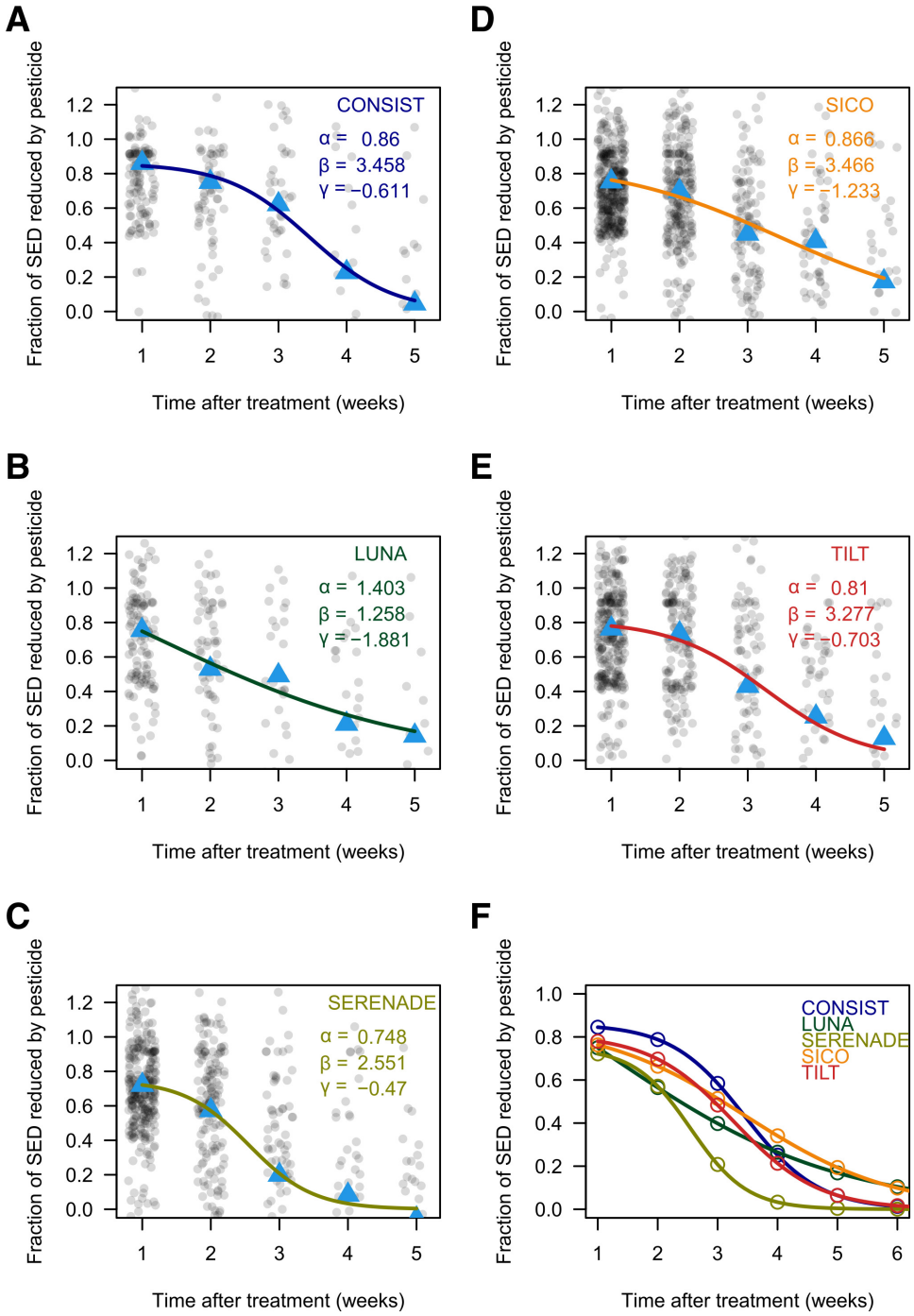

Fig. 7. Estimation of the pesticide effects fitted on the standardized stage evolution of the disease (SEDst) as a function of time after treatment (tat_t) following equation 4 for the five pesticides used in our study (**A,** CONSIST, **B,** LUNA, **C,** SERENADE, **D,** SICO, and **E,** TILT). **F,** Comparison of the fitted curves for the five pesticides. Parameters for each pesticide are presented in Table 2.

them separately, we have a good biologic appreciation of the contribution of each factor. The exponential growth rate (r) of the logistic growth (equation 2) is consistent with the fast growth of the disease (about 30% per week) under favorable conditions. In our model, the effect of weather is taken into account through the carrying capacity K of the logistic growth. The Piche evaporation is an integrative measure of weather that simulates leaf wetness and aggregates the temperature, wind speed, air humidity, and solar radiation (Ganry and Laville 1983). Our data set cover well most conditions typical of humid tropic climate. The calibration of K as a response to Piche evaporation shows that it strongly decreased for evaporation above 20 mm and was extremely low for evaporation above 40 mm (Fig. 6). These conclusions are in-line with Piche evaporation relationship with Sigatoka disease, another leaf spot disease of bananas (Ganry and Laville 1983). A maximal potential of growth of the disease for evaporation below 20 mm is consistent with existing literature that established an optimum growth for high humidity and air temperature between 25 to 28°C (Jacome and Schuh 1992). Moreover, sporulation of conidia and ascospores are initiated by humidity (92 to 100%) or free water, respectively (Jacome et al. 1991).

The effect of fungicides is a major limit to understanding how the landscape structure and composition is involved in ecological processes because it hides ecological regulations and it is often difficult to disentangle ecological and pesticide effects (Ricci et al. 2019).

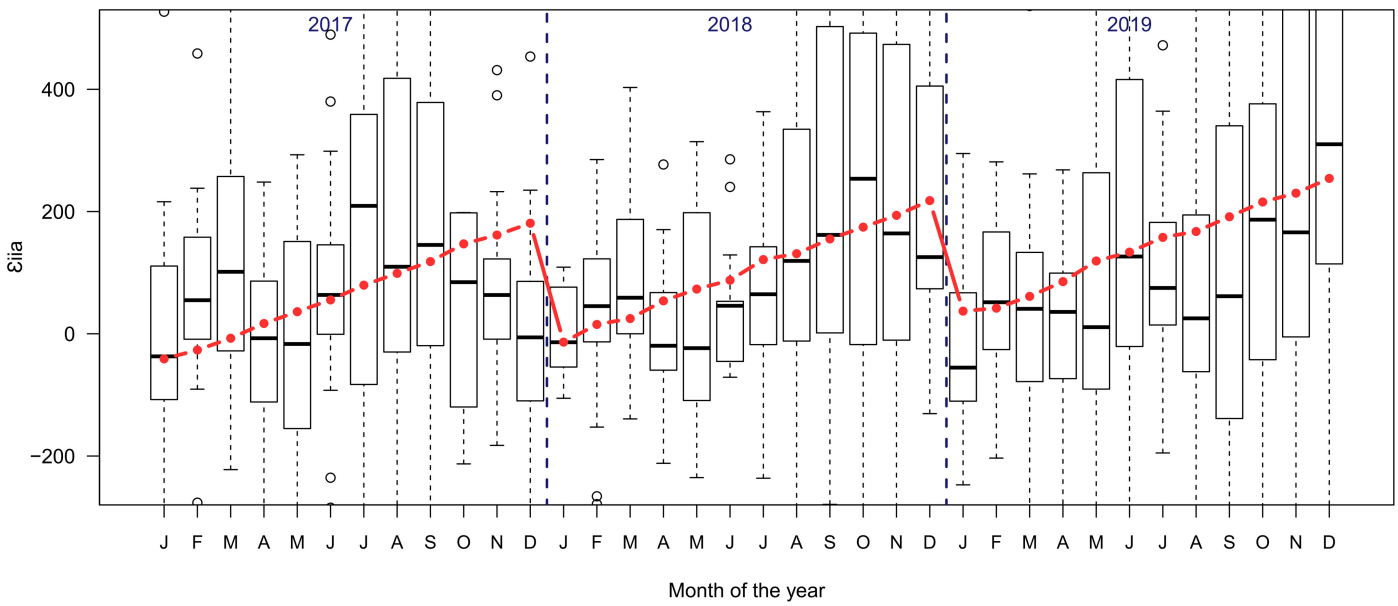

Fig. 8. Variability of the intra- and inter-annual effect (εiia) weekly estimated, based on the residual of the model (equation 1a) between 2017 and 2019. Each box shows the first and third quartiles, and black lines in the middle of each box show the median of the εiia. The dotted line shows the fit of the linear model with number of the week of the year and the time since the first measurement as predictors (equation 5).

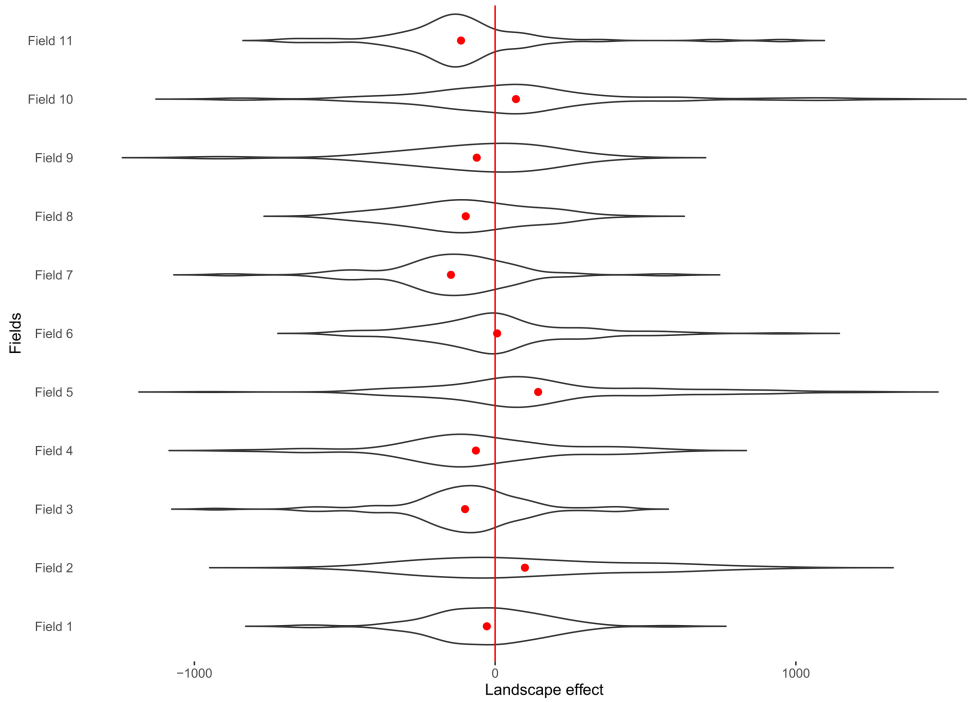

Fig. 9. Distribution of landscape effects estimated weekly on the 11 fields studied. Landscape effects are the residues of the model (equation 1b). Each distribution of landscape effects corresponds to data analyzed of a given field (33 to 135 weeks). Points show the mean value the landscape effect for a given field. Negative and positive landscape effects correspond to suppressive and conductive landscapes, respectively.

While crucial, this effect is rarely addressed since it requires having dynamic data of the disease and the exact information on the date and nature of pesticide applications. Other experiments determined the global efficiency of fungicides on the disease (Samuelian et al. 2016; Vawdrey et al. 2005) but not their dynamic effect in field conditions. Our approach allowed the estimation of the effect of each fungicide on the reduction of the SED during the 5 weeks after their application. Our estimation of this effectiveness was consistent with former knowledge of experimental evaluation of the efficiency of these products and with the appreciation of farmers on their farms. Specifically, the three systemic products with the strongest curative effect (CONSIST, SICO, and TILT) showed a stronger and a more persistent effect than other products. This is the first time that such a precise and dynamical estimation of fungicide effect was achieved on BLSD and was possible thanks to the precise dataset and to the modeling approach.

Estimation of the effect of landscape

Taking into account the effects of the landscape in the control of crop pests is increasingly mentioned as a lever to be mobilized in alternative strategies to chemical treatments (Delaune et al. 2021; Fabre et al. 2015), but few studies are available for fungal diseases. The quantification and modeling of the landscape effect on a disease progress remains rare and difficult because this effect is associated with many other factors. Our approach allowed an estimation of this effect by subtracting, in the most process-based way possible, factors related to the exponential growth rate of the disease, the effect of weather, pesticides, and seasonal dynamics. For each plot studied, we estimated an annual average landscape effect that covered values corresponding to different levels of suppressiveness or conduciveness of the disease (Fig. 11).

At short distance (200-m-radius buffer zone), the presence of hedgerow showed a significant suppressive effect on BLSD. This suggests that the effect of hedgerows might be effective once a hedgerow is present and only at short distances to the plot. This seems consistent with the potential effect of hedgerows in limiting the dispersal of diseases, i.e., a barrier effect including the interception of spores, the modification of airflow patterns and potentially of microclimate (Forman and Baudry 1984). Overall, presence of hedgerow increases the suppressiveness of the landscape, even at small percentages of hedgerow area. In future studies, it could be interesting to evaluate experimentally the effect of different types of hedgerows (size, width, and maturity) on inoculum dispersal.

As expected, landscape features without host plants (%non-banana-cultures-and-artificial-structures) were suppressive (forest excluded), confirming that the fragmentation of landscape with non-host area limit the epidemic progression of BLSD through two potential ways: (i) a reduction of inoculum level per unit area and (ii) an increase of distance between susceptible hosts (Mundt 2002). This effect was observed at all distances but significant and maximal for 800- and 1,000-m-radius buffer zones. Beyond 15% of nonhost plants in 800-m-radius buffer zone, εlandscape values were all negative and landscape effect always suppressive. These discontinuity areas did not have significant effect at small scale because the distance between host areas was not large enough to reduce dispersion (Condeso and Meentemeyer 2007). A similar effect was expected for forest features, but surprisingly forests promoted BLSD at all radius buffer zone sizes (most significant and higher effect in the 1,000-m-radius buffer zone). Forests might alter the epidemiology of BLSD through contrasted effects: (i) increasing host discontinuity that should be suppressive, and (ii) modifying microclimate that should be conducive. Indeed, forests tend to increase the air relative humidity, which is favorable to most fungal diseases

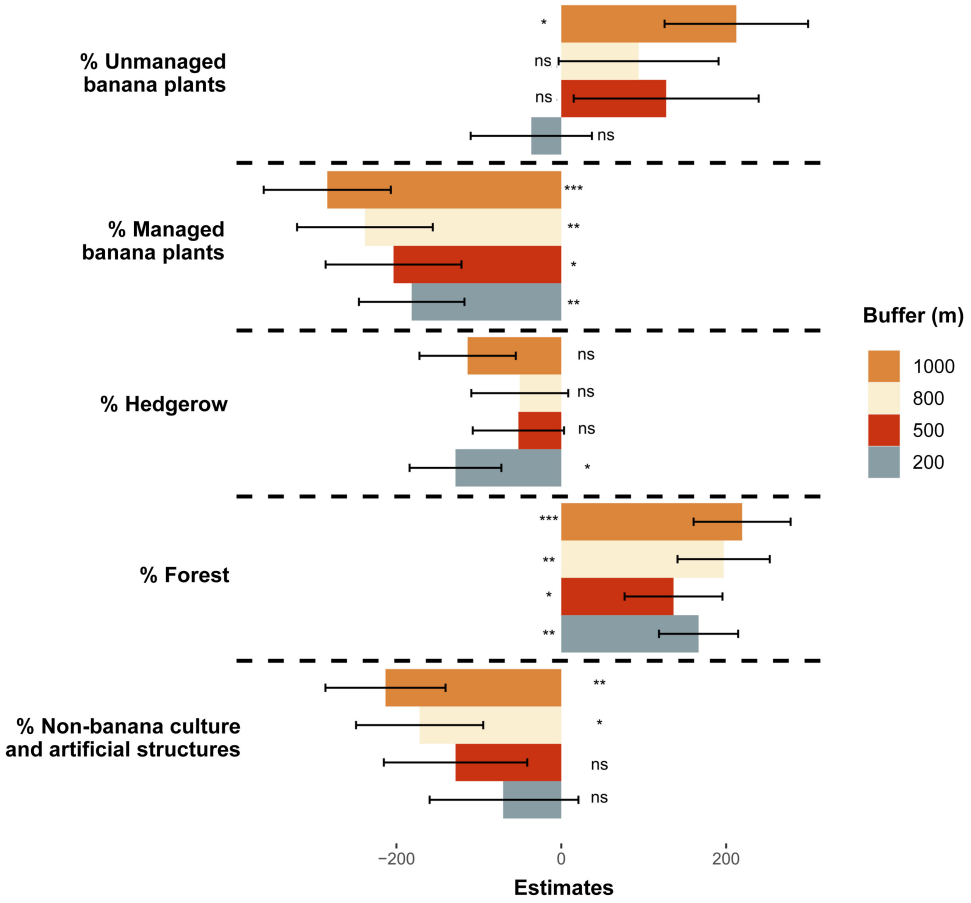

Fig. 10. Estimates (on the x-axis) and significance of the estimates (on each bar) of the standardized landscape metrics (in the four defined buffer zones) (on the y-axis) on the landscape effect. The symbols (on the side of each bar) ns, *, **, and ***, represent the level of significance of the *P* value: nonsignificant, <0.05, <0.01, and <0.001, respectively.

(Condeso and Meentemeyer 2007). Here we cannot exclude that banana plants could be present in forest as commonly observed in various occasions (personal observations). At small values of %forest, fragmentation effect compensates potential inoculum sources and are not able to modify microclimate. On the contrary, when %forest exceeds 30%, the risk of inoculum source and the negative effect on the microclimate is probably more important than the benefit of fragmentation.

The managed-banana-plants area had a significant suppressive effect on BLSD at all distances, with a stronger significance at 1,000 m. The managed-banana-plants area and the suppressive effect increased proportionally. Beyond 31% of managed-banana-plants area, landscape effects assessed were always suppressive. This result is counterintuitive because we expected a conducive effect of this landscape feature. However, this suppressive effect might traduce that BLSD control is more efficient in large banana plantations than in small banana plantations. Indeed, the suppressive effect increased with the percentage of host crop area. In most commercial banana plantations, because of fungicide applications and regular deleafing of necrotic areas, ascospores, that are dispersed at large distance, are generally absent and epidemics are only driven by conidia that disperse at very short distance. Rieux et al. (2013),

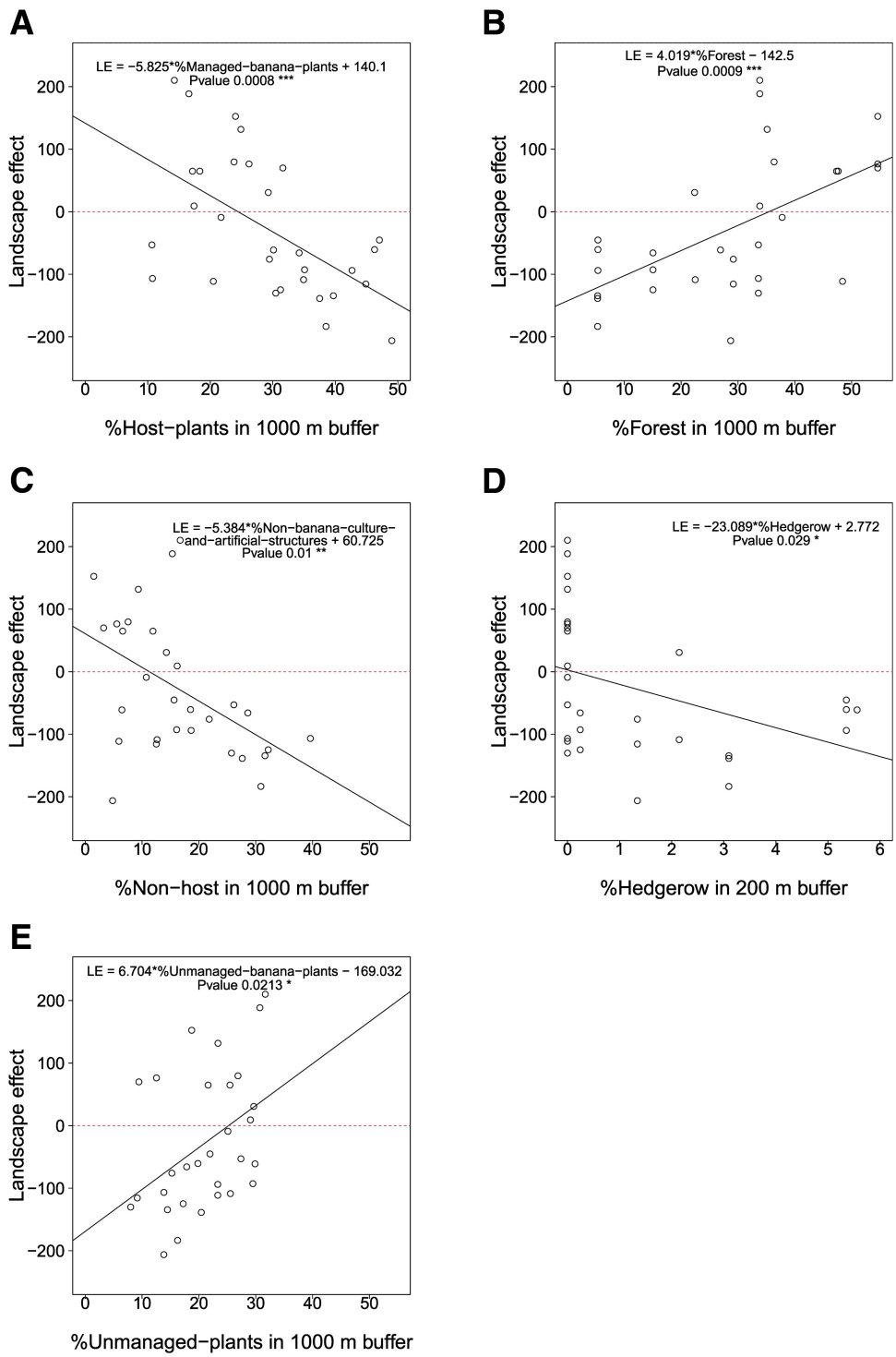

Fig. 11. Relationships between the landscape effect (mean of residues of equation 1b per field) and landscape metrics: **A,** percentage of hedgerow in 200-m radius buffer zone, **B,** percentage of forest in 1,000-m-radius buffer zone, **C,** percentage of managed-banana-plants in 1,000-m-radius buffer zone, **D,** percentage of unmanaged-banana-plants in 1,000-m-radius buffer zone, and **E,** percentage of non-banana-cultures-and-artificial-structures in 1,000-m-radius buffer zone. Black solid lines show the fit of the linear model. Dotted lines show the limit between conductive (positive values) and suppressive (negative values) landscapes.

on the other hand, showed that BLSD control is more efficient in bigger farms than in small farms (de Lapeyre de Bellaire, *personal communication*), which could explain the greatest significance of this feature at the largest scale.

The presence of potential inoculum sources (unmanaged banana plants) in a 1,000-m-radius buffer zone promoted BLSD, suggesting that these features could be important sources of BLSD ascospores. While this relation is poorly significant, it suggests that a better management of these areas would help decrease the sources of BLSD inoculum (especially in fallows after banana production and home gardens where untreated bananas might be present).

We have tried to explain the landscape effect via its composition. However, the landscape effect can also come from the organization of the landscape around the plot and the connectivity between the host areas. Although hedgerows are a significant constraint to disease dispersion, their arrangement may be a key solution to spore interception around plots. The distance between the plot and the hedge, the height of the hedge, and the angle to the prevailing winds are characteristics that we did not take into account and that may interfere with the amount of spore interception. The importance of the orientation of the barrier further to the wind has been shown in the study of Bouws and Finckh (2008) on potato blight, where the alternation of host and nonhost zones perpendicular to the wind shows a barrier effect.

Conclusion

In this study, we modeled step by step each factor that has an impact on the SED and used the residuals to quantify landscape effect on SED. This modeling approach has enabled the acquisition of new knowledge on the evolution of BLSD in Martinique on the growth parameters, the effect of meteorological conditions (Piche evaporation), the effects of fungicides, and finally on the effects of landscape elements. Our model separates effects and allows a better understanding of disease dynamics and the factors that affect this dynamic. This knowledge can be used as a basis for future disease management studies through levers related to the organization of the landscape, such as the presence of hedgerows close to the plot, in order to achieve collective management and a more reasoned use of pesticides. The efficiency of each fungicide over time could lead to better use of such fungicides. Interestingly, the hedgerow effect seems to be important, and it will be necessary to carry out field experiments to better understand their effect on the dispersal of spores.

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Literature Cited

Aviron, S., Poggi, S., Varennes, Y. D., and Lefèvre, A. 2016. Local landscape heterogeneity affects crop colonization by natural enemies of pests in protected horticultural cropping systems. Agric. Ecosyst. Environ. 227:1-10.

Bebber, D. P. 2019. Climate change effects on Black sigatoka disease of banana. Philos. Trans. R. Soc. B Biol. Sci. 374:20180269.

Bouws, H., and Finckh, M. R. 2008. Effects of strip intercropping of potatoes with non-hosts on late blight severity and tuber yield in organic production. Plant Pathol. 57:916-927.

Cendoya, M., Martínez-Minaya, J., Dalmau, V., Ferrer, A., Saponari, M., Conesa, D., López-Quílez, A., and Vicent, A. 2020. Spatial bayesian modeling applied to the surveys of *Xylella fastidiosa* in Alicante (Spain) and Apulia (Italy). Front. Plant Sci. 11:1204.

Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J., and Kremen, C. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol. Lett. 14:922-932.

Churchill, A. C. L. 2011. *Mycosphaerella fijiensis*, the black leaf streak pathogen of banana: Progress towards understanding pathogen biology and detection, disease development, and the challenges of control. Mol. Plant Pathol. 12: 307-328.

Condeso, T. E., and Meentemeyer, R. K. 2007. Effects of landscape heterogeneity on the emerging forest disease sudden oak death. J. Ecol. 95:364-375.

de Lapeyre de Bellaire, L., Fouré, E., Abadie, C., and Carlier, J. 2010. Black leaf streak disease is challenging the banana industry. Fruits 65:327-342.

de Lapeyre de Bellaire, L., Ngando Essoh, J., Abadie, C., Chabrier, C., Blanco, R., Lescot, T., Carlier, J., and Côte, F. 2009. Is chemical control of Mycosphaerella foliar diseases of banana sustainable? Acta Hortic. 828: 161-170.

Delaune, T., Ouattara, M. S., Ballot, R., Sausse, C., Felix, I., Maupas, F., Chen, M., Morison, M., Makowski, D., and Barbu, C. 2021. Landscape drivers of pests and pathogens abundance in arable crops. Ecography 44:1429-1442.

Donzelli, B. G. G., and Churchill, A. C. L. 2007. A quantitative assay using mycelial fragments to assess virulence of *Mycosphaerella fijiensis*. Phytopathology 97:916-929.

Fabre, F., Rousseau, E., Mailleret, L., and Moury, B. 2015. Epidemiological and evolutionary management of plant resistance: Optimizing the deployment of cultivar mixtures in time and space in agricultural landscapes. Evol. Appl. 8:919-932.

Finckh, M. R., Gacek, E. S., Czembor, H. J., and Wolfe, M. S. 1999. Host frequency and density effects on powdery mildew and yield in mixtures of barley cultivars. Plant Pathol. 48:807-816.

Forman, R. T. T., and Baudry, J. 1984. Hedgerows and hedgerow networks in landscape ecology. Environ. Manage. 8:495-510.

Fouré, E. 1987. La cercosporiose noire des bananiers et des plantains au Gabon. Sélection de nouvelles molécules fongicides—Techniques d'avertissement. Pages 167-170 in: Reunion ACORBAT. F. R. A. Cirad-Irfa and C. R. I. Catie, eds. CATIE, San José, Costa Rica.

Fouré, É., and Ganry, J. 2008. A biological forecasting system to control black leaf streak disease of bananas and plantains. Fruits 63:311-317.

Ganry, J., and Laville, E. 1983. Cercospora diseases of banana and their treatments. Evolution of methods of treatment. 1. Fungicide treatments. 2. Forecasting. Fruits 38:3-20.

Ganry, J., and Meyer, J.-P. 1972. La lutte contrôlée contre le Cercospora aux Antilles. Bases climatiques de l'avertissement technique d'observation et de numération de la maladie. Fruits 27:665-676.

Guzmán, M., Pérez-Vicente, L., Carlier, J., Abadie, C., de Lapeyre de Bellaire, L., Carreel, F., Marin, D. H., Romero, R. A., Gaulh, F., Pasberg-Gauhl, C., and Jones, D. R. 2018. Black leaf streak. in: Handbook of Diseases of Banana, Abacá and Enset. D. R. Jones, ed. CABI, Boston, MA.

Ioos, R., Hubert, J., Abadie, C., Duféal, D., Opdebeeck, G., and Iotti, J. 2011. First report of black Sigatoka disease in banana caused by *Mycosphaerella fijiensis* on Martinique Island. Plant Dis. 95:359.

Jacobs, A. F. G., and Arriëns-Bekker, E. E. L. 1983. Evaporation data from a Piche evaporimeter. J. Hydrol. 60:367-380.

Jacome, L. H., and Schuh, W. 1992. Effects of Leaf wetness duration and temperature on development of black Sigatoka disease on banana infected by *Mycosphaerella fijiensis* var. *difformis*. Phytopathology 82:515-520.

Jacome, L. H., Schuh, W., and Stevenson, R. E. 1991. Effect of temperature and relative humidity on germination and germ tube development of *Mycosphaerella fijiensis* var. *difformis*. Phytopathology 81:1480-1485.

Landry, C., Bonnot, F., Ravigné, V., Carlier, J., Rengifo, D., Vaillant, J., and Abadie, C. 2017. A foliar disease simulation model to assist the design of new control methods against black leaf streak disease of banana. Ecol. Modell. 359:383-397.

Lykouressis, D., Giatropoulos, A., Perdikis, D., and Favas, C. 2008. Assessing the suitability of noncultivated plants and associated insect prey as food sources for the omnivorous predator *Macrolophus pygmaeus* (Hemiptera: Miridae). Biol. Control 44:142-148.

Martins, T. G., Simpson, D., Lindgren, F., and Rue, H. 2013. Bayesian computing with INLA: New features. Comput. Stat. Data Anal. 67:68-83.

Meredith, D. S., and Lawrence, J. S. 1969. Black leaf streak disease of bananas (*Mycosphaerella fijiensis*): Symptoms of disease in Hawaii, and notes on the conidial state of the causal fungus. Trans. Brit. Mycol. Soc. 52:459-IN16.

Mundt, C. C. 2002. Use of multiline cultivars and cultivar mixtures for disease management. Annu. Rev. Phytopathol. 40:381-410.

Pacilly, F. C. A., Hofstede, G. J., Lammerts van Bueren, E. T., Kessel, G. J. T., and Groot, J. C. J. 2018. Simulating crop-disease interactions in agricultural landscapes to analyse the effectiveness of host resistance in disease control: The case of potato late blight. Ecol. Modell. 378:1-12.

Papaïx, J., Touzeau, S., Monod, H., and Lannou, C. 2014. Can epidemic control be achieved by altering landscape connectivity in agricultural systems? Ecol. Modell. 284:35-47.

Plantegenest, M., Le May, C., and Fabre, F. 2007. Landscape epidemiology of plant diseases. J. R. Soc. Interface 4:963-972.

Poeydebat, C., Carval, D., Tixier, P., Daribo, M. O., and De Bellaire, L. D. L. 2018. Ecological regulation of black leaf streak disease driven by plant richness in banana agroecosystems. Phytopathology 108:1184-1195.

R Core Team. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria.

Ricci, B., Lavigne, C., Alignier, A., Aviron, S., Biju-Duval, L., Bouvier, J. C., Choisis, J. P., Franck, P., Joannon, A., Ladet, S., Mezerette, F., Plantegenest, M., Savary, G., Thomas, C., Vialatte, A., and Petit, S. 2019. Local pesticide use intensity conditions landscape effects on biological pest control. Proc. R. Soc. B Biol. Sci. 286:20182898.

Rieux, A., de Lapeyre de Bellaire, L., Zapater, M. F., Ravigne, V., and Carlier, J. 2013. Recent range expansion and agricultural landscape heterogeneity have only minimal effect on the spatial genetic structure of the plant pathogenic fungus *Mycosphaerella fijiensis*. Heredity 110:29-38.

Rieux, A., Soubeyrand, S., Bonnot, F., Klein, E. K., Ngando, J. E., Mehl, A., Ravigne, V., Carlier, J., and de Lapeyre de Bellaire, L. 2014. Long-distance wind-dispersal of spores in a fungal plant pathogen: Estimation of anisotropic dispersal kernels from an extensive field experiment. PLoS One 9:e103225.

Samuelian, S., Wright, C., and Vawdrey, L. L. 2016. Evaluation of chlorothalonil and paraffinic oil alone and in combinations with registered fungicides for the control of yellow Sigatoka (*Mycosphaerella musicola*) of bananas in Northern Queensland, Australia. Crop Prot. 82:45-50.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., Tylianakis, J. M., Nouhuys, S. V., and Vidal, S. 2007. Conservation biological control and enemy diversity on a landscape scale. Biol. Control 43: 294-309.

Vawdrey, L. L., Peterson, R. A., and Grice, K. R. E. 2005. Evaluation of strobilurins, acibenzolar and other chemicals, alone and in spray programs for the control of yellow Sigatoka leaf spot (*Mycosphaerella musicola*) of bananas in far northern Queensland, Australia. Int. J. Pest Manag. 51:245-251.

Veres, A., Petit, S., Conord, C., and Lavigne, C. 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. Agric. Ecosyst. Environ. 166:110-117.