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Spatial dynamics and hidden spread of banana bunchy top disease in Benin

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Introduction: Banana Bunchy Top Disease (BBTD), caused by the Banana Bunchy Top Virus (BBTV) and transmitted by the aphid *Pentalonia nigronervosa*, poses a growing threat to banana production in West Africa, often resulting in 100% yield loss in infected plantations. Yet its epidemiological dynamics remain poorly known. Current management in Benin relies on visual symptom identification and informal seed networks, both of which are vulnerable to the pathogen's prolonged latency.

Methods: We conducted a structured cross-sectional survey of 176 banana farms across 12 departments of Benin between December 2024 and February 2025, complemented with archival surveillance data from 2018–2020. Apparent disease incidence was estimated from visual inspection and corrected for diagnostic error using a hierarchical Bayesian misclassification model.

Results and Discussion: Extreme gradient boosting (XGBoost) identified wind speed in April, sucker density, and September maximum temperature as the primary drivers of symptom expression (AUC = 0.913). Bayesian adjustment for imperfect sensitivity (Se ≈ 0.78) and specificity (Sp ≈ 0.92) revealed that true incidence exceeded field estimates by a median factor of 2.1 (95% CrI 1.6–2.8), exposing substantial under-detection of infection in southern agroecological zones. Integration of bias-adjusted posterior incidence across years reconstructed the epidemic wavefront, indicating a northward expansion from Akpro-Missérété (6.6° N) to ~ 9.8° N by 2025. Linear regression of front displacement on time yielded a mean spread rate of 37.8 km yr⁻¹, with residual patterns suggesting acceleration during 2020–2022, likely due to secondary introductions or intensification of local transmission. This study provides the first spatially explicit quantification of BBTD spread in Benin, demonstrating that visual field assessments substantially underestimate the true burden of the disease. The integration of Bayesian bias correction and wavefront modeling provides a robust framework for mapping and forecasting the spread of plant diseases under imperfect detection conditions.

KEYWORDS

Bayesian bias correction, BBTD, disease velocity, dispersal mechanism, symptoms drivers, wavefront modeling

1 Introduction

Musa species, including banana varieties and plantains, are essential foods that significantly alleviate poverty and hunger in numerous regions of sub-Saharan Africa. In Benin, at least 21 locally recognized varieties are consumed, utilized as traditional medicinal remedies, and, as a means of generating income for smallholder farmers (Chabi et al., 2018). Nevertheless, these crops face threats from pests and diseases, with banana bunchy top disease (BBTD) being the most significant. The pathogen responsible for BBTD, banana bunchy top virus (BBTV), belonging to the genus *Babuvirus*, family *Nanoviridae*, is transmitted by a sap-sucking aphid (*Pentalonia nigronervosa*) (Chen and Hu, 2013). Early symptoms of BBTD appear as irregular dark green streaks along the veins, midrib, and petiole. As the disease progresses, new leaves emerge smaller, narrower, and upright, forming a crowded “bunchy” appearance at the top, while the leaf tissues become stiff and brittle. Infected plants, especially those infected early, fail to produce fruit, while late infections may lead to deformed bunches; suckers from infected plants show severe dwarfing and never bear fruit (Myrianne-Flore et al., 2025).

Although certain initial symptoms, such as the emergence of dark green lines along the veins, can appear relatively quickly after infection, with reports suggesting that they may occur as early as around 25 days after infection, such instances typically reflect the earlier phase of the symptomatic range (Chabi et al., 2018). While enhanced training for farmers can indeed facilitate the quicker identification of these initial streaks, it does not resolve the significant number of infections that remain without symptoms long after this period. Currently, the only reliable means of detecting the presence of BBTV in its early stages is through molecular diagnostics. Indeed, despite the multitude of symptoms that allow for visual appraisal, it is noteworthy that infected *Musa* plants can remain asymptomatic for an extended latency period, often exceeding 60 days (Allen, 1987). This prolonged asymptomatic phase poses challenges for visual diagnosis, making it difficult for even experienced agricultural professionals to detect the disease in its early stages. During this latency window, the absence of symptoms can lead to an oversight in identifying the disease, resulting in a lag in appropriate management strategies. Thus, visual appraisal often leads to an underestimation of the actual incidence rates within crops. This underreporting not only hampers timely intervention but also skews decision-making processes regarding crop management and disease control. Therefore, there is an urgent need for the development of effective diagnostic methods embedded in a surveillance program that can address this inherent bias associated with visual assessments. Such innovations would enable more accurate and efficient detection of the disease, ultimately improving the overall health of crops and ensuring better yield outcomes. Moreover, once the disease takes hold in a farm, it can devastate entire harvests, leading to significant economic losses for farmers and exacerbating regional food insecurity (Retkute et al., 2025). The catastrophic impact of BBTD can be magnified through the intricate social networks of seed exchange that exist among farmers. During the planting season, many farmers often rely on seeds from their own

farms or seeds obtained from their neighbors, which may unknowingly harbor pathogens (Nduwimana et al., 2022). This practice not only facilitates the spread of the disease from one farm to another but can also lead to widespread outbreaks across an entire region.

BBTD was first identified in Benin in 2011 in the commune of Ouémé (Lokossou et al., 2012). Since then, investigations have been conducted to understand its spread and incidence, uncovering patterns that threaten the viability of *Musa* farming in Benin. Specifically, it was found that the majority of growers cultivating *Musa* spp for commercial reasons rely significantly on informal seed networks, and display a lack of awareness and poor BBTD symptom recognition (Retkute et al., 2025). The same study also mapped the disease across six administrative departments, identifying higher prevalence in the humid southern regions and highlighting the relative effectiveness of different management practices through simulation models (Retkute et al., 2025). Similarly, the implementation of spatial scan statistics and regression modeling proved instrumental in the identification of BBTD hotspots and the evaluation of environmental and managerial factors associated with disease prevalence, particularly in southern municipalities such as Dangbo, Houéyogbé, and Adjara (Dato et al., 2021). Together, these studies have highlighted the distribution of BBTD and its drivers within local production systems in Benin. However, these studies share important limitations: (1) a reliance on visual detection, which ignores the ‘asymptomatic gap,’ and (2) a static spatial approach that cannot quantify the rate of disease expansion. These gaps that restrict the comprehension of BBTD’s spatio-temporal dynamics. Their analyses covered limited geographic areas and single time points, which prevents tracking the spread and evolution of the disease over time. Reliance on farmer-reported symptoms and visual detection methods may also underestimate early or asymptomatic infections. Moreover, neither study integrates longitudinal or high-resolution surveillance data capable of capturing the temporal progression of BBTD foci and the role of dispersal agents across ecological zones; a limitation that contrasts with active surveillance progress made on other phytopathosystems where space and time-explicit modeling frameworks have been implemented. For example, in cucurbit, networks of sentinel plots coupled with hierarchical spatiotemporal models have been used to quantify uncertainty, track the wavefronts of cucurbit downy mildew, and connect early-season outbreak magnitude to final epidemic size at regional scales (Ojiambo et al., 2015).

Consequently, a comparable dynamic, time-explicit modeling framework is still lacking for BBTD, limiting our understanding of how disease emerges in new locations, spreads, and persists under varying environmental and management conditions in Benin.

Understanding the dynamics of BBTD requires a grasp of the dispersal mechanisms of its pathogen and detecting the disease wavefront. This understanding would lay the groundwork for formulating effective strategies to control and prevent further spread of BBTD in the country. Research has shown that, beyond the traditional dispersal methods associated with plant reproduction (i.e., use of infected planting materials), disease propagules such as virions, infected plant tissues (e.g., suckers), or

infected vectors can facilitate the spread of BBTV between and within fields (Campbell, 1999). Understanding the speed and direction of disease spread helps analyze transmission patterns and develop effective containment strategies (Campbell, 1999; Ojiambo et al., 2015). Recent simulation-based work in other plant pathosystems illustrates how such dynamics can be quantified in practice; for example, a study on *Xylella fastidiosa* in Puglia, Italy, showed that existing containment measures reduced the rate of disease progression in olive trees by approximately 2 km per year (Chapman et al., 2025). Unfortunately, there is a notable scarcity of epidemiological studies focused on crop health that adequately tackle this question, that is, how BBTD spreads across space and time, and the mechanisms influencing its rate and direction of propagation. As a result, existing surveillance efforts for BBTV in Benin leave the true burden of the disease and the velocity of its spread across the landscape largely analytically invisible.

To address these gaps, we developed a data-driven spatial epidemiological framework for BBTD in Benin. We integrate large-scale, structured field surveys with climatic and agronomic covariates to produce bias-adjusted, spatially explicit quantification of BBTV incidence and epidemic wave dynamics. By coupling incidence correction with directional spread modeling, this approach enables early detection, accurate estimation of true infection rates, and visualization of epidemic progression across space and time. The resulting framework provides not only a robust understanding of BBTD dynamics in Benin but also a transferable methodology for studying vegetatively propagated crop diseases in other endemic regions.

2 Materials and methods

2.1 Study area

Benin is located in West Africa, positioned between the Atlantic Ocean to the south and the inland territories to the north. Benin shares a border with Togo to its west, Nigeria to its eastern side. Burkina Faso in the northwest and Niger to the northeast. Administratively, Benin is organized into twelve departments that encompass a total of 77 communes. The climate is tropical, with an average temperature of 26.3°C (WorldData.info, 2025). However, a significant temperature disparity exists between the southern and northern regions, with variations exceeding 1°C (The World Bank Group, 2025). The southern region, influenced by the coastal proximity, experiences a more temperate climate, while the northern areas, which are further inland, exhibit higher temperatures, particularly during the dry season. This climatic variation plays a significant role in shaping agricultural practices, especially banana production (Chabi et al., 2018; Retkute et al., 2025).

2.2 Data collection

We carried out a structured cross-sectional field survey of 176 banana and plantain farms throughout Benin from December 2024

to February 2025. Data collection at each farm required approximately 45 to 60 minutes, encompassing both the visual inspection of 20–30 plants and the recording of agronomic and climatic covariates. The survey followed a strategic south-to-north geographic sequence, beginning in the southern departments (e.g., Ouémé and Littoral). This starting point was chosen because these regions represent both the highest density of Musa production and the initial 2011 detection sites of BBTD; characterizing the established endemic core was essential before tracking the epidemic wavefront toward the northern ‘information frontier. The selection of subsequent farms was guided by a systematic-random approach designed to minimize local spatial autocorrelation. Specifically, we maintained a minimum distance of 1 km between any two sampled plots. Whenever practical, the next survey site was chosen by bypassing at least five intervening farms along the sampling transect. This ensured that the survey captured the broad-scale spatial transition of the disease rather than localized clusters of a single outbreak. For each farm, we documented GPS coordinates (latitude and longitude), inspection date, management type (commercial, smallholder, or home garden), and agronomic factors (cultivar, planting age, planting density). We recorded the visual health status of each plant, including the presence or absence of BBTD symptoms, a symptom severity score, the location of observed BBTD symptoms based on a standardized scale (Niyongere et al., 2011), and the count of observed aphids. The symptom severity score varied from 1 to 6 (Table 1).

All collected data were entered electronically and verified for completeness, including GPS accuracy, prior to analysis. The disease status of each plant was subsequently utilized to compute the observed incidence of BBTD. The estimated incidence was calculated at the field level and expressed as the ratio of diseased plants to the total plant count. The geolocation of each farm was adjusted using a regular expression and projected via the WGS84 georeferencing system. Climate information, which includes monthly statistics for lowest, average, and highest temperatures; rainfall; solar energy; wind velocity; water vapor tension; cumulative precipitation; and bioclimatic factors obtained from monthly temperature and rainfall records for an aggregate of 103 bioclimatic variables, was obtained from WorldClim 2.1 raster datasets (WorldClim, 2020) along with raster files concerning soil pH, soil water pH, and soil organic matter (ISRIC, 2015). These raster files were then aggregated, and the relevant value for each variable was extracted for every location. The previously mentioned

TABLE 1 Symptom severity scoring scale for banana bunchy top disease (BBTD).

Score	Symptom description
1	Healthy or symptom-free condition
2	Dark green streaks on the leaf lamina
3	Dark green streaks on the petiole
4	Presence of chlorosis on the leaf edges
5	Reduction in leaf size
6	Bunchy top appearance

field dataset was supplemented with additional records regarding farm visual inspections of BBTD in Benin from 2018 to 2020, which were sourced from previous studies (Lokossou et al., 2012; Bouwmeester et al., 2023; Vodounou et al., 2024).

2.3 Distribution of BBTD-infected fields in Benin and factors associated with the appearance of BBTD symptoms

To provide an overview of the distribution of infected fields in Benin, we undertook a mapping process, plotting points that indicated the presence of at least one infected *Musa* plant. Following this mapping, we compiled a detailed statistical summary categorized by administrative level 1 (department). This summary includes the number of infected fields relative to the total number of surveyed fields within each department, allowing us to calculate the incidence for each department. Additionally, we computed the square error, which provides insights into the variability and distribution of infections per area. This aggregated summary aims to provide a clear and informative overview of the BBTD distribution across Benin, facilitating our understanding of the disease's impact on local agriculture.

To ensure that the associations identified in our analysis were not driven by random variability, we applied a workflow involving dimension reduction, a structured machine-learning pipeline, cross-validation, and Partial Rank Correlation analysis. Specifically, we instituted a preprocessing pipeline wherein variables exhibiting pairwise correlations exceeding 60% (a level at which two variables begin to convey largely the same information) were systematically excluded. This approach ensured that only predictors that contributed largely unique information were preserved for the fitting of the model. Subsequently, we employed extreme gradient boosting (XGBoost) to quantify the relative significance of the retained variables as determinants of symptom manifestations in infected *Musa* plants. Model training was performed using an 80/20 split (80% training, 20% testing). Model performance was subsequently validated using k-fold cross-validation to assess stability across multiple training subsets and evaluated through the area under the receiver operating characteristic curve (AUC), providing a robust assessment of predictive accuracy and generalizability. Partial Rank Correlation Coefficient (PRCC) analysis revealed patterns that aligned with the machine-learning findings, further affirming that the observed relationships are reliable and not a result of random noise.

This assessment utilized a combination of field data collected by trained data collectors and relevant climate data, allowing us to identify potential environmental or climatic influences on the manifestation of BBTD symptoms.

2.4 Estimation of the bias-adjusted incidence of the BBTD in Benin

We calculated the BBTD incidence at the field level, which we referred to as the apparent incidence (the ratio of infected plants to the total number assessed through visual inspection, represented on a map for each of the 176 farms surveyed). The apparent BBTV incidence was adjusted for misclassification using a Bayesian

hierarchical measurement-error model. For each field i with N_i plants, we modeled the observed positives X_i

$$X_i \sim \text{Binomial}(N_i, \text{Se} \cdot p_i + (1 - \text{Sp}) \cdot (1 - p_i)),$$

and modeled prevalence on the logit scale with covariates

$$\text{logit}(p_i) = \alpha + x_i^T \beta + \mu_i$$

where μ_i is the region random effect, x_i the covariate vector for field i (e.g., the most important covariate previously highlighted), p_i is the latent true incidence. Field prevalences p_i were given informative priors and Se , Sp were assigned Beta priors informed by expert elicitation and prior surveillance literature (plausible ranges: Se sensitivity, i.e., ability to correctly identify individuals who have a specific disease or condition, 0.40–0.90; Sp specificity, i.e., the proportion of truly negative detections, 0.80–0.99) (Arndt et al., 2022; Combes et al., 2025). Posterior inference was obtained by Monte Carlo Markov Chain (MCMC) (Ref); we report posterior medians and 95% credible intervals for each p_i . Sensitivity to the Se/Sp prior was assessed using the Rogan-Gladen approach (Rogan and Gladen, 1978).

2.5 Estimation of the wavefront of BBTV in Benin

Data collected in 2025 were complemented with survey data from 2018–2020 on banana farms across Benin. The spatial and temporal propagation of BBTD was reconstructed using a Bayesian bias-adjusted incidence model, followed by spatial interpolation and epidemic front detection based on posterior infection probabilities. Bias-adjusted incidence values, represented by the posterior medians from the Bayesian misclassification model, were used as the observed estimates at each time point to derive true incidence at the administrative level (Commune). Detection errors can shift apparent arrival times of infection; therefore, adjusting for the estimated sensitivity (Se) and specificity (Sp) minimizes bias in estimating epidemic velocity.

The bias-adjusted true incidence (π_i , t) at each location i at each time t was computed (Rogan and Gladen, 1978) as

$$\pi_{i,t} = \frac{I_{i,t} + \text{Sp} - 1}{\text{Se} + \text{Sp} - 1}$$

where $I_{i,t}$ is the apparent (observed) incidence.

The posterior samples were drawn using a hierarchical Bayesian logistic misclassification model. The posterior uncertainty was propagated by sampling from the full posterior distribution (Pioz et al., 2011). The posterior probability of infection at each location and time was therefore defined as:

$$p_{i,t} = P(\text{infection at location } i, \text{ time } t | \text{data})$$

and summarized by posterior medians and 95% credible intervals.

To delineate the BBTD front, we considered all locations with non-zero posterior probability of infection or used adaptive quantiles of the posterior distribution to define regions of infection. Nonetheless, a location is classified as infected when the posterior probability of infection ($p_{i,t}$) was ≥ 0.5 .

Isocontour (i.e., boundary showing how far the disease has spread at a given time t) (C_t) corresponding to this threshold was computed to define the spatial boundary of infection (Gilg, 1973).

$C_t = \{(x, y) | p_{(x,y),t} = 0.5\}$ or, alternatively,

$C_t = \{(x, y) | p_{(x,y),t} > 0 \text{ or } p_{(x,y),t} \text{ exceeds a posterior quantile}\}$

Posterior median prevalence values were interpolated using the Akima bilinear interpolation method (Akima, 1978). Each contour delineated the epidemic front at time t . Contour geometries were clipped to administrative boundaries (Benin communes), projected to UTM Zone 31N, and used to compute polygonal areas (A_t , in km^2) and centroid locations ($\bar{x}_t$, $\bar{y}_t$).

The earliest detected focus (θ) was defined as the centroid of the highest posterior prevalence in the first observation year (2018). For each time interval, the spatial boundary of infection was represented by the contour polygons, and the front position was characterized by the mean great-circle distance of these polygons from θ :

$$D_t = \frac{1}{|C_t|} \sum_{(x,y) \in C_t} \text{dist}_H((x, y), \Theta)$$

where dist_H denotes the haversine distance function, and Θ is the origin.

A linear regression model of the form:

$$D_t = \beta_0 + \beta_1 t + \epsilon_t$$

was fitted to estimate the mean rate of spread, with the slope (β_1) representing the average velocity (Cliff and Haggett, 1982) of BBTD (km per unit time). Uncertainty in velocity was quantified by the 95% confidence interval of β_1 :

$$v = \beta_1; 95\% \text{ CI}(v) = [\beta_{1L}, \beta_{1U}]$$

3 Results

3.1 Distribution of banana bunchy top disease in Benin and drivers associated with the disease symptoms

A total of 3541 banana plants in 176 fields were examined within the 12 departments of Benin (Figure 1). Figure 1 depicts the geographical distribution of surveyed fields. The geographical distribution of these fields, represented as infected (red) or healthy (green) markers in Figure 1 provides the high-resolution spatial data from which the departmental incidence rates in Table 2

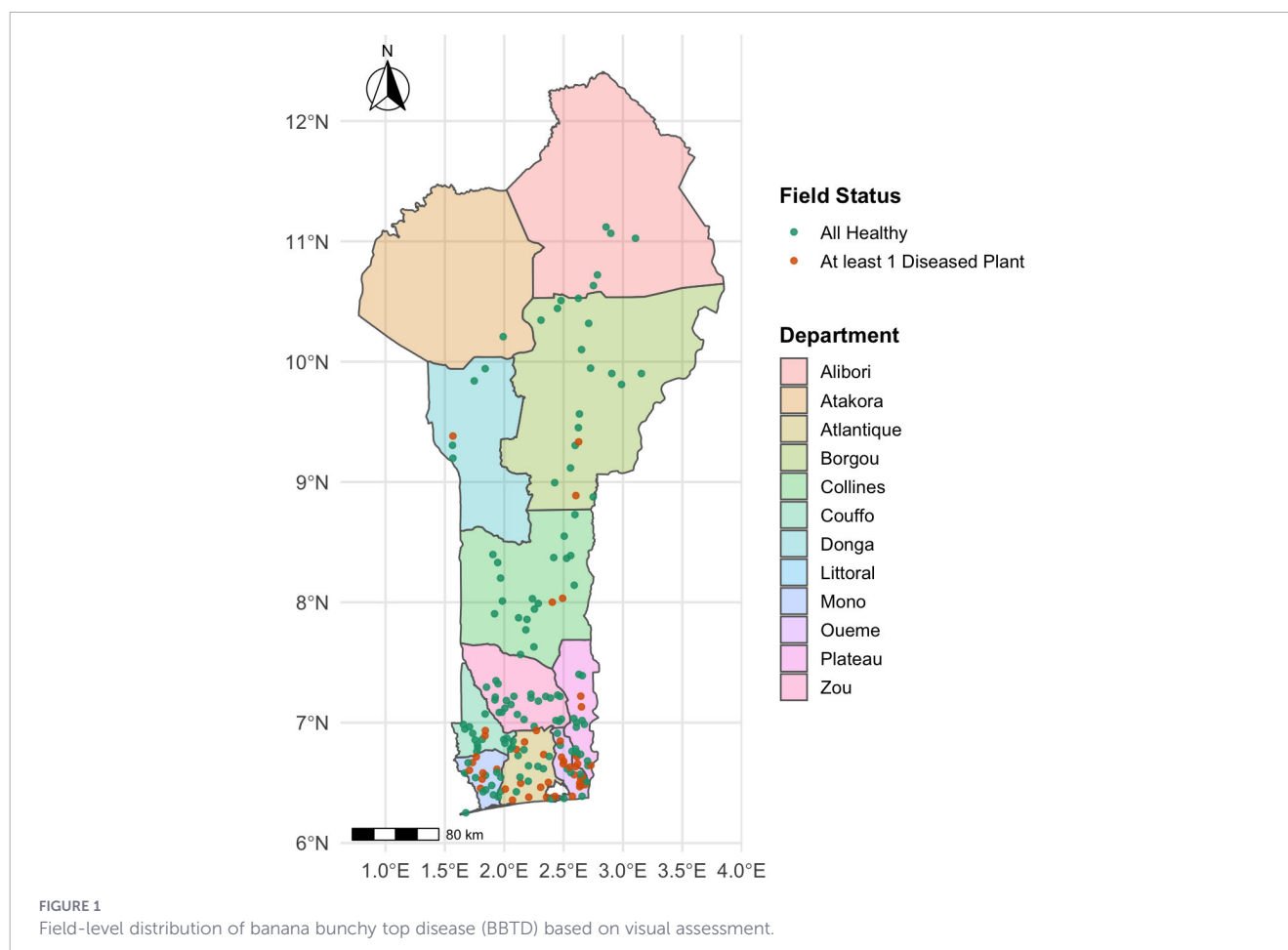


TABLE 2 Summary of BBTD incidence across the 12 departments of Benin.

Department	Total of fields	Infected fields	Incidence	SE
Ouémé	25	14	0.560	0.101
Littoral	2	1	0.500	0.500
Atlantique	25	11	0.440	0.101
Mono	17	7	0.412	0.123
Plateau	18	6	0.333	0.114
Donga	5	1	0.200	0.200
Couffo	15	2	0.133	0.091
Borgou	18	2	0.111	0.076
Collines	21	2	0.096	0.066
Alibori	5	0	0	0
Atakora	1	0	0	0
Zou	24	0	0	0
Overall	176	46	0.262	–

are derived. While Figure 1 illustrates the exact coordinates and clustering of the sampling effort, Table 2 provides the corresponding incidence of infection at the department level across 12 departments. Ouémé had the highest incidence at 0.56 (SE = 0.101), with 14 out of 25 fields being infected, followed closely by Littoral (0.50) and Atlantique (0.44). A moderate incidence was noted in Mono (0.41) and Plateau (0.33), whereas Donga (0.20), Couffo (0.13), Borgou (0.11), and Collines (0.095) exhibited relatively low incidence. No infected fields were observed in Alibori, Atakora, and Zou during the survey period. Overall, the cumulative incidence across all departments was 0.26, suggesting that about one-quarter of the surveyed fields were infected. Standard errors were higher in departments with very few sampled fields (e.g., Littoral and Donga), highlighting the greater uncertainty in these estimates. In summary, the presence of symptomatic plants varied significantly across different administrative regions.

The results of XGBoost based on the 16 retained predictors showed that the wind speed in April, the number of suckers, and the maximum temperature in September as the most influential drivers of disease symptoms (Figure 2). The PRCC analysis further revealed that wind speed and sucker density were positively associated with BBTD symptom expression, whereas higher September temperatures and greater field distance were protective (Figure 2). These specific months represent critical bioclimatic ‘windows’ for BBTD development in Benin; wind speeds in April likely facilitate the primary dispersal of the aphid vector (*P. nigronervosa*) during the onset of the rainy season, whereas maximum temperatures in September appear to govern the rate of symptom manifestation during the secondary peak of the vegetative growth cycle. For management practices, intercropping and field management (e.g., irregular weeding, poor sanitation, or lack of removal of infected plants) showed negative associations, suggesting potential leverage points for disease control. Precisely, improper field management and the absence of intercrops increase the risk of the appearance of BBTD symptoms.

The XGBoost model shows good ability in predicting disease state among Musa plants. With an AUC of 0.913 (Supplementary Figure S1), the model can correctly distinguish between symptomatic and non-symptomatic plants more than 91% of the time, making it highly reliable for practical applications.

3.2 Estimation of the true incidence of BBTD in Benin

Panel A (Figure 3) displays the field-observed incidence of BBTD, which ranged from 0–45% across fields, with densely clustered hotspots between 6°–7.5° N in southern Benin. After accounting for diagnostic misclassification ($Se \approx 0.78$, $Sp \approx 0.92$) through a hierarchical Bayesian correction, the posterior median of true incidence (Panel B, Figure 3) increased to 10–85%, with 95% credible intervals spanning ± 15 –20 percentage points at the field level.

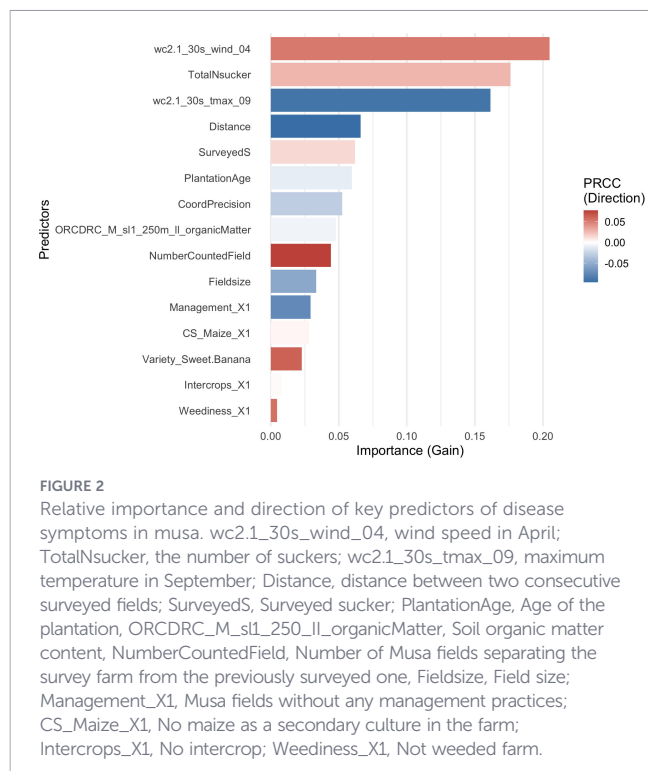
The adjustment reveals that the estimated true incidence in ~62% of sites exceeded the observed values, with a median correction factor of $2.1 \times$ (95% Credibility Interval: 1.6–2.8). The largest corrections were found in the southern regions, where visual assessments underestimated the infection burden by 40–60%. In contrast, farms in the central and northern regions, where infections were less frequent or sporadic, showed smaller upward adjustments. This pattern reflects lower posterior uncertainty (<10%) in the well-sampled southern areas and broader uncertainty ranges (up to 25%) in the more sparsely sampled northern zones.

Together, Figure 3 highlights the systematic under-detection bias inherent to visual appraisal and demonstrates the added value of Bayesian bias correction for mapping bias-adjusted infection intensity and uncertainty in field-based plant disease surveillance (Supplementary Table S1). This adjustment uncovers the hidden burden of infection that field appraisal alone underestimates.

3.3 Estimation of the wavefront of BBTV in Benin

The spatial progression of BBTD from 2018 to 2025 revealed a clear northward propagation pattern across Benin (Figure 4). The epidemic originated near the southern region ($\theta = 2.580^\circ$ E, 6.575° N) in the commune of Akpro-Misserete (Department of Ouémé) and progressively expanded toward central Benin reaching the department of Borgou (2.6166° E, 9.35° N) and Donga (1.666° E, 9.71666° N) (Figure 4). The colored isocontour represents posterior median bias-adjusted incidence at the 85th percentile threshold, delineating zones of high infection probability for each survey year.

Between 2018 and 2025, the epidemic front shifted from its southern origin toward approximately 9.8° N latitude, indicating a cumulative displacement of approximately 270 km. The black arrow (Figure 4) represents the dominant propagation vector (aphids) estimated from the displacement of the epidemic centroid across years. The estimated bearing of the spread was approximately 356° (north–northwest), consistent with short-distance, stepwise dissemination of the (*Pentalonia nigronervosa*) or infected banana material along banana-growing corridors.



The mean front distance (D_t) increased approximately 50-fold between 2018 and 2025, suggesting active northward diffusion over seven years. The number of contour polygons increased from 3 to 7, indicating fragmentation of high-incidence zones possibly due to multiple local foci (Table 3).

The results of the linear regression of front distance on time yielded an average epidemic velocity of 0.264 km yr^{-1} (95% CI: 0.04–0.49 km yr^{-1} ; $p = 0.033$, $R^2 = 0.935$, Supplementary Table S2).

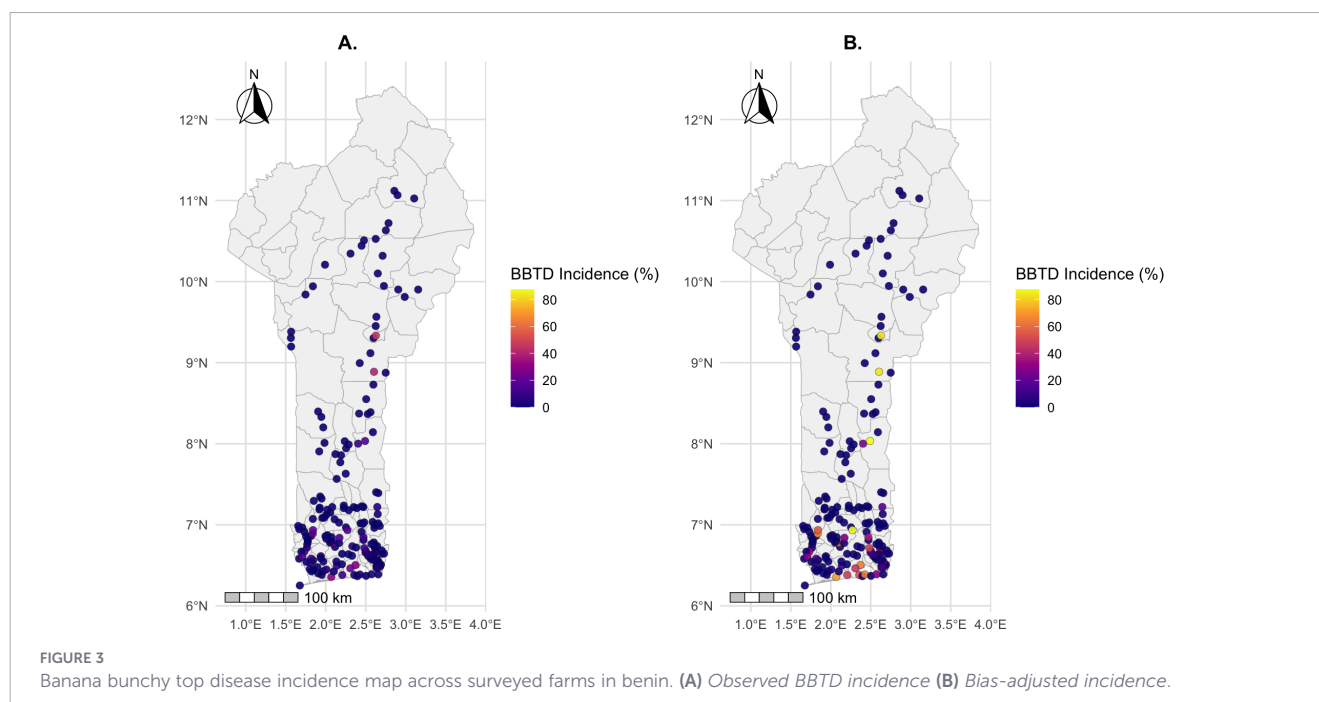
However, this estimate is not biologically interpretable because the model was fitted using raw calendar years (2018, 2020, 2025), and the coefficient therefore reflects the numerical scaling of the predictor rather than the actual rate of spatial spread. In this formulation, the slope describes the change in front distance per one-unit increase in the raw year, not the biological displacement of the epidemic. After properly re-scaling time as the number of years since the first detection. Thus, refitting the model with $t = \{0, 2, 7\}$, the estimated mean epidemic velocity is 37.8 km yr^{-1} . This re-scaled estimate is consistent with the observed 2018–2025 displacement and with the slow, short-range spread expected from local aphid movement and the exchange of infected planting material between farms.

Temporal heterogeneity in the regression residuals suggested a possible acceleration phase around 2020–2022 (Supplementary Table S2). This pattern likely reflects either secondary introductions of the pathogen into new areas or an intensification of local transmission dynamics, particularly in the central region, contributing to a faster spread and increased incidence during this period.

4 Discussion

4.1 Unveiling the hidden landscape of BBTD: spatial heterogeneity and diagnostic bias across Benin

Banana Bunchy Top Disease poses a threat to large-scale banana production and to the livelihoods of smallholder farmers, primarily because it is untreatable once established within a farm. The consequences of this disease can be devastating, often resulting in total crop loss. Research conducted in Benin has revealed a complex and varied distribution of BBTD, with certain regions



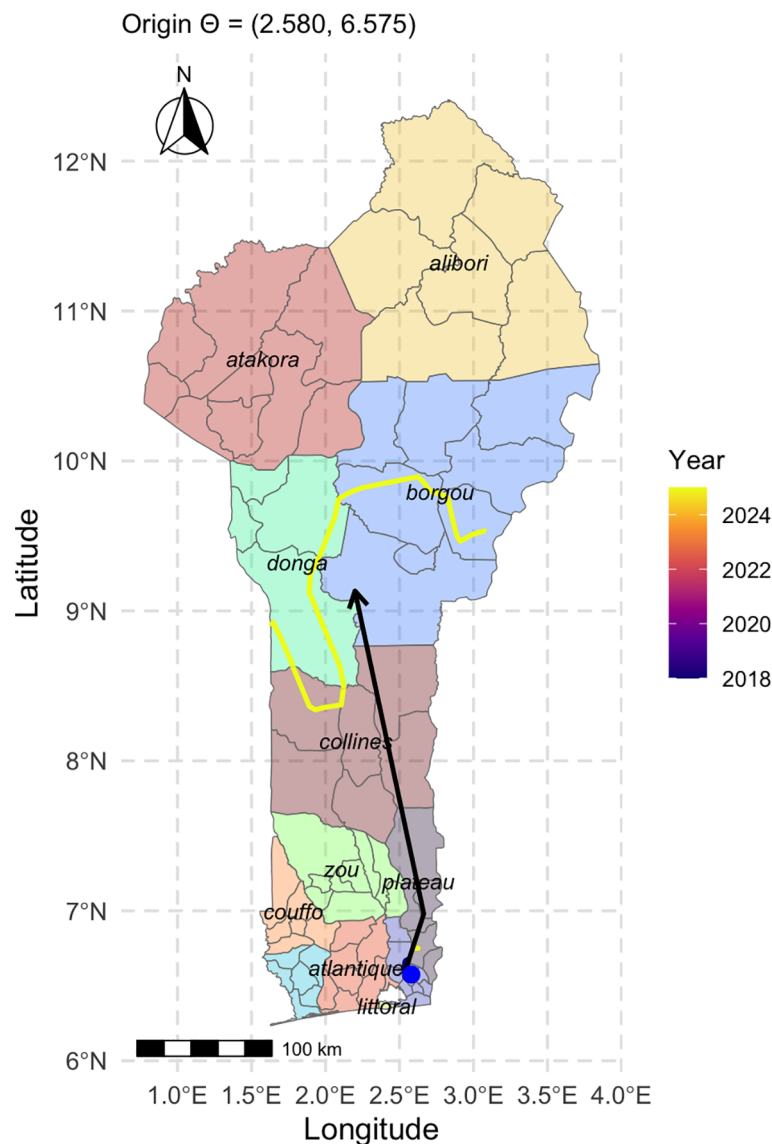


FIGURE 4

Wavefront estimation of banana bunchy top disease in Benin. The blue dot indicates the original focus where the posterior incidence of BBTD exceeded 50%; the arrow illustrates the progression of the wavefront from 2018 to 2025; the Isocontour is yellow-colored.

showing higher incidence rates, while the overall prevalence remains relatively low at the national level. Our findings highlight a clear spatial heterogeneity in BBTD occurrence, especially with most infections concentrated in the southern regions of Benin, which is the country's main banana-growing area. This geographic pattern aligns with earlier studies that identified higher incidence rates in four specific localities within southern Benin (Retkute et al., 2025). Conversely, the lower incidence rates observed in the northern departments are likely due to under-detection, possibly caused by the lower density of banana plants in those areas. Although the model indicated under-detection across the country, the northern regions, characterized by lower banana density and fewer surveyed fields, had sparser sampling coverage, which reduces the likelihood of detecting infections when they occur. Additionally, the spread of BBTD across the host landscape is influenced by temperature (Raymundo and Pangga, 2011). Each additional degree rise above the threshold of 25 °C decreases aphid (*Pentalonia*

nigronevosa) infectiousness by reducing their population density and gut viral load. This trend is especially noticeable when moving from the primary production zones to areas with the lowest incidence, where there is roughly a 1°C temperature rise (The World Bank Group, 2025).

The results of the bias-adjusted analysis revealed a significant discrepancy in the visual assessments of BBTD conducted by trained field agents. These assessments frequently underestimated the actual incidence of the disease, highlighting the inherent limitations associated with symptom-based surveillance methods. The imperfections in both sensitivity and specificity of these visual evaluations compound the potential for underestimating the incidence of BBTV. In the Ouémé region, for instance, while the observed incidence of BBTD was approximately 56%, our corrected estimates indicate that the true incidence could be as high as 83% (Supplementary Table S1). This contrast underscores the critical nature of accurate diagnostics in understanding disease prevalence.

TABLE 3 Mean distance progression and area covered by BBTV in Benin from 2018 to 2025.

Year	Threshold	No. of contours	Mean distance from origin (km)	Max distance (km)	Area covered (km ²)
2018	0.85	3	5.45	9.85	4.19
2020	0.85	1	45.8	45.8	0.04
2025	0.85	7	270.0	361.0	81.2

Furthermore, our findings were corroborated by polymerase chain reaction (PCR) testing, which revealed that the incidence was as high as 60% in the samples collected in 2012 (Lokossou et al., 2012), and the risk in these areas was predicted to be above 75% in 2021 (Bouwmeester et al., 2023). This discrepancy can be further explained by the fact that only plants exhibiting severe infections, characterized by a significant viral load, tend to show visible symptoms beyond the latency period (Allen, 1987; Chabi et al., 2018). In contrast, newly infected plants often remain asymptomatic, complicating the detection of the disease during early stages of infection (Tanuja et al., 2019). Furthermore, the authors stated that the late appearance of symptoms in the asymptomatic plants could be associated with changes in the effectiveness of aphid transmission throughout the different stages of infection. This variability in transmission dynamics underscores the complexity of plant-vector-virus interactions and the challenges in accurately assessing infection prevalence within populations. Besides, these results not only illustrate the pressing need to identify and address hidden infection hotspots that conventional surveillance methods might miss, but they also emphasize the importance of integrating quantitative assessments of diagnostic uncertainty into the mapping of plant diseases in the field. By implementing this approach, we can substantially improve the precision of surveillance data for the effective management of BBTD. This enhancement in data accuracy will not only facilitate more informed decision-making but also contribute to the overall health of agricultural practices. As a result, we can expect to see improved crop yields and resilience, fostering a more sustainable agricultural environment and ensuring the long-term viability of banana cultivation. Ultimately, this proactive strategy will lead to better outcomes for farmers, consumers, and the agricultural ecosystem as a whole.

4.2 Ecological and agronomic drivers of symptom expression and spread of banana bunchy top disease

The manifestation of symptoms in plants infected with BBTV is mainly determined by an elevated viral load (Tanuja et al., 2019); however, our study has revealed that certain environmental factors significantly contribute to symptom appearance. Through the results of the extreme gradient boosting analysis, we identified wind speed in April as a prominent environmental driver of BBTD symptom expression, while sucker density emerged as a factor influencing the potential spread within fields. High sucker density likely increases the probability of secondary infections by providing more susceptible tissues and facilitating aphid movement between closely spaced plants, thereby enhancing local transmission dynamics. This finding suggests that both the mobility of aphid vectors and the

density of vegetative propagation play critical roles in the spread of BBTD. We hypothesize that increased wind activity in April may facilitate the dispersal of viruliferous winged aphids, thereby enhancing local transmission during this period. This assumption is based on seasonal patterns rather than direct observation, as the emergence of winged aphids from densely populated colonies during April has not been specifically investigated in this study. Nonetheless, this possible correspondence between early-season wind dynamics and aphid dispersal warrants further entomological monitoring to validate the mechanism. The emergence of wings occurs because, as aphid populations grow, they begin to face limitations imposed by overcrowding and competition for resources (Zhang et al., 2000). In response to the space unavailability, winged aphids emerge primarily in areas where host plants, such as bananas, are abundant and readily accessible. This strategic emergence allows them to exploit new niches and resources, thereby alleviating the strain on their original population. The development of wings is not merely a physical transformation; it may represent a significant adaptive strategy that enables these aphids to disperse more effectively and colonize diverse habitats. By taking to the air, these winged individuals can traverse greater distances in search of optimal feeding sites, which increases their chances of survival and reproduction. This adaptation not only aids in the distribution of the aphid population but also enhances the potential for virus transmission, as viruliferous aphids encounter new host plants and interact with other aphid populations. Conversely, we observed that higher maximum temperatures recorded in September and increased inter-field distances were negatively correlated with symptom expression. This indicates that climatic conditions and spatial arrangements may impose constraints on aphid activity and/or virus replication, thereby limiting the spread of the disease. These results are consistent with established theories in vector ecology, which propose that wind-assisted dispersal and the presence of dense vegetative stands can enhance local epidemic amplification (Allen, 1978, 1987; Raymundo and Pangga, 2011; Bouwmeester et al., 2023). This interplay between environmental factors and biological vectors emphasizes the multifaceted nature of disease dynamics within agricultural ecosystems. This complexity necessitates the implementation of integrated management strategies that take into account both biological, ecological, and climatic influences. Our research demonstrates that proactive management techniques, such as intercropping (Figure 2), can significantly alleviate disease symptoms. This finding suggests that adopting certain farm-level practices improves crop health and plays a crucial role in reducing the risk of local disease transmission. By fostering a more holistic approach to farm management, we can enhance resilience against diseases while promoting sustainable farming practices.

The reconstructed disease wave front revealed a northward progression extending over 270 km over a span of seven years,

corresponding to an average adjusted velocity of 37.8 km. yr⁻¹; a rate consistent with previous reports of BBTD spread. For example, a study in Cameroon documented a front displacement of nearly 30 km over a single year in previously unaffected farms during the 2016–2017 surveys (Ngatat et al., 2024). Building on this velocity-based comparison, the inferred origin of the epidemic in Benin aligns with the Ouémé region, where prevalence exceeds 50%, reinforcing earlier reports identifying this area as the initial focus of BBTV introduction. In 2012, the virus was first documented in various communes within Ouémé, specifically in Avrankou, Dangbo, Akpro-Missérété, and Porto-Novo (Lokossou et al., 2012). The trajectory of this epidemic suggests a potential pattern of spread that is linked to local agricultural practices. It has been observed that farmers typically source their banana seeds from their own or neighboring farms, creating a localized network of seed distribution. This phenomenon can be interpreted as a social banana seed network, where the proximity of farmers to one another plays a crucial role in the dissemination of both agricultural practices and, unfortunately, viral pathogens (Retkute et al., 2025). This underscores the interconnectedness of farming communities and the risk of rapid disease spread, such as BBTV, through seed exchanges. Understanding this social network is pivotal for creating effective strategies to manage and mitigate the impact of BBTD in the region. The current position of the wavefront is prominently located in the central regions of Benin, particularly within the Borgou and Donga departments. While these areas are not typically recognized for high production of banana, the presence of this wavefront signals an ecological shift: it suggests that aphid vectors, which are known to transmit various plant diseases, might have acquired the ability to adapt to more challenging environments characterized by a scarcity of densely populated host plants. This potential adaptation highlights the resilience of these aphid populations and underscores the critical need for proactive measures to contain them. The ability of these vectors to thrive in less favorable conditions implies that controlling their populations could be an effective strategy to mitigate the spread of BBTD. This is further validated by the experiment conducted in Assam, a northeastern state of India, where it was shown that four applications of Imidacloprid at 0.1% protect plants from infection (Kakati and Nath, 2019). Alternatively, although this study did not specifically assess the seed transfer network, the observed southward progression of the disease wavefront raises relevant implications for its role in disease dissemination. Given that the seed transfer network is largely concentrated within the Borgou and Donga departments (Figure 4), restricting the movement of banana planting material southward of this geographical latitude could represent a strategic approach to containing the spread of BBTD throughout Benin. By implementing such containment measures alongside targeted vector management, a dual approach could be established to more effectively manage the ongoing threat of BBTD in the country.

We found that the rate of dispersal aligns with short-range dispersal typical of *Pentalonia nigronervosa* (Allen, 1987). This reinforces the role of local vector diffusion and human-mediated planting material exchange. Such insights highlight the complex interplay between natural dispersal processes and anthropogenic

factors in the epidemiology of this disease. Moreover, the fluctuations observed in regression residuals over the time span from 2020 to 2022 (Supplementary Table S2) could suggest the presence of secondary introductions of pathogens or an accelerated phase of transmission that is potentially associated with a surge in banana trade or a significant rise in vector populations. This hypothesis opens up avenues for deeper exploration, as it implies that external factors such as trade dynamics and ecological changes may be influencing disease spread in ways not fully captured by the current study. To understand these interactions, it is imperative to conduct further research that delves into the intricacies of social seed network exchanges, as these may play a critical role in the dissemination of both agricultural practices and pest populations. Besides, the increase in the number of high-incidence contours (from 3 to 7) suggests progressive fragmentation of the epidemic into multiple localized foci (Table 2). This shift indicates that each potential foci exhibits unique transmission dynamics and epidemiological characteristics. Such fragmentation could complicate containment efforts and necessitate tailored interventions to address the specific needs of these challenges.

Although the study embedded within the bias-corrected process used the sensitivity and specificity from other species, the combined use of hierarchical Bayesian adjustment and wavefront analysis provides a replicable model for handling other perennial crop epidemics that involve imperfect detection. Additionally, incorporating posterior uncertainty maps is essential for directing focused monitoring efforts, thus prioritizing areas with a high likelihood of infection for proactive and early action. Furthermore, regional collaboration is critical to effectively restrict the movement of infected planting materials between countries and carefully regulate aphid vector transfer. Lastly, future surveys that incorporate advanced molecular diagnostics could greatly enhance the sensitivity and specificity priors, thereby significantly increasing the accuracy of true prevalence estimation.

5 Conclusion

This research demonstrates that accounting for observation bias is critical for analyzing BBTD dynamics in Benin. Our Bayesian framework reveals that visual assessments alone underestimate the true infection burden by more than half, potentially leading to inadequate control strategies. By integrating misclassification techniques with spatial wavefront estimation, we provide a dynamic model that bridges the gap between theoretical epidemiology and field surveillance. This approach empowers decision-makers to implement proactive, risk-based management and accurately predict the disease's northward expansion. While our framework establishes a robust baseline, several avenues for future research remain critical to enhancing the predictive power of these models. First, moving beyond Euclidean distance to incorporate 'Network Distance', specifically focusing on the informal trade routes and sucker exchange markets, would improve the delineation of the 'Information Frontier' where human activity accelerates natural dispersal. Second, future

studies should pair this Bayesian framework with longitudinal molecular diagnostics to empirically quantify the transition rates from asymptomatic to symptomatic states across different agroecological zones. Finally, expanding this surveillance architecture to a regional, cross-border scale is essential for monitoring the transboundary movement of the BBTD wavefront into neighboring West African countries. Such efforts will ensure that the ‘centralized regional firewall’ proposed in this study can be effectively operationalized at a scale matching the pathogen’s dispersal potential. Ultimately, adopting bias-adjusted spatial modeling into routine monitoring will allow national programs to anticipate disease movement and foster agricultural resilience in the face of changing climatic conditions.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: https://github.com/SaviKoissi/Wavefront_BBTV/tree/main.

Author contributions

MS: Visualization, Conceptualization, Investigation, Validation, Formal analysis, Supervision, Methodology, Data curation, Software, Writing – review & editing, Writing – original draft. CA: Validation, Writing – review & editing, Supervision. FT: Project administration, Writing – review & editing, Resources, Software, Supervision, Funding acquisition. AE: Project administration, Supervision, Writing – review & editing, Resources, Funding acquisition. JP: Project administration, Supervision, Resources, Writing – review & editing, Funding acquisition.

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Conflict of interest

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fagro.2026.1754220/full#supplementary-material>

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