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Prevalence and spatial distribution of Fusarium wilt of banana in the Peruvian Amazon

Prevalencia y distribución espacial de la marchitez por Fusarium de bananos en la Amazonía peruana

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ABSTRACT

Fusarium wilt of banana (FWB), caused by *Fusarium oxysporum* f. sp. *cubense* (Foc), is a primary threat to *Musa* spp. Despite its impact, the intensity and potential drivers of the disease in the Peruvian Amazon remain poorly understood. This study assessed FWB prevalence, spatial distribution, and associated biophysical and management variables at the mesoscale. A census of 189 plots (213,005 mats) was conducted across six regions using visual inspection. Overall prevalence was 28.04%, with the highest value in Junín (55.56%). FWB was significantly associated with Isla (Iholena, AAB) and Seda (Gros Michel, AAA) cultivars. Spatial analysis revealed hierarchical aggregation with localized foci (radius = 13.8 km) and broader farm clustering at intermediate scales. Disease was more frequent in areas with higher altitudes (> 762.5 m a.s.l.) and annual precipitation (> 1481 mm). Higher flood risk zones, linked to pronounced rainfall seasonality, were identified as critical for pathogen movement via watercourses. FWB was identified as the main phytosanitary issue in affected areas, where the lack of intervention on symptomatic plants strongly correlated with disease presence.

Keywords: epidemiology; Foc; FWB; *Musa*; Panama Disease.

RESUMEN

La marchitez por Fusarium del banano (MFB), causada por *Fusarium oxysporum* f. sp. *cubense* (Foc), es una de las principales amenazas para *Musa* spp. A pesar de su impacto, la intensidad y los posibles factores determinantes de la enfermedad en la Amazonía peruana siguen siendo poco comprendidos. Este estudio evaluó la prevalencia de la MFB, su distribución espacial y las variables biofísicas y de manejo asociadas a nivel de mesoescala. Se censaron 189 parcelas (213005 plantas) en seis regiones mediante inspección visual. La prevalencia global fue del 28,04%, registrándose el valor más alto en Junín (55,56%). La MFB se asoció significativamente con los cultivares Isla (Iholena, AAB) y Seda (Gros Michel, AAA). El análisis espacial reveló una agregación jerárquica con focos localizados (radio = 13,8 km) y agrupamientos de fincas más amplios a escalas intermedias. La enfermedad fue más frecuente en áreas con mayores altitudes (> 762,5 m s.n.m.) y precipitación anual (> 1481 mm). Las zonas con mayor riesgo de inundación, vinculadas a una marcada estacionalidad de las lluvias, se identificaron como críticas para el movimiento del patógeno a través de cursos de agua. La MFB fue el principal problema fitosanitario en las zonas afectadas, donde la falta de intervención en las plantas sintomáticas se correlacionó fuertemente con la ocurrencia de la enfermedad.

Palabras clave: epidemiología; Foc; MFB; *Musa*; Mal de Panamá.

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1. Introduction

Fusarium wilt of banana (FWB), caused by soil-borne fungi known as *Fusarium oxysporum* f. sp. *cubense* (Foc), has historically represented one of the major threats to global banana and plantain production (Ploetz, 2006; Pegg et al., 2019). These *Musa* spp. crops are among the most widely produced, traded, and consumed fruits worldwide (FAO, 2025), serving as staple foods and continuous sources of income for countries in Asia, Africa and Latin America and the Caribbean (LAC) (Dita et al., 2013; Altendorf et al., 2017).

The pathogen is primarily disseminated through infected planting material (Pegg et al., 2019). Once established in the plant, it colonizes the xylem and causes a typical wilt disease that cannot be controlled by chemical or biological methods (Dita et al., 2018). Foc can persist for decades in infested soils, even in the absence of its primary hosts, by producing thick-walled asexual spores (chlamydospores) that act as survival structures and constitute the main primary inoculum (Ploetz, 2015). Foc also spreads through contaminated soil, irrigation water, tools, machinery, vehicles, wild animals, insects, and birds (Dita et al., 2018; Pegg et al., 2019), and may infect weeds asymptomatically (Hennessy et al., 2005). Consequently, effective management currently relies on the use of resistant cultivars or the planting of healthy, disease-free material in pathogen-free soils (Ploetz, 2015).

Within Foc, differences in pathogenicity to *Musa* spp. genotypes have led to the recognition of four races: Race 1 (R1), pathogenic to Gros Michel (AAA); Race 2 (R2), pathogenic to Bluggoe (ABB); subtropical Race 4 (SR4), affecting Cavendish (AAA) under subtropical or abiotic stress conditions; and tropical Race 4 (TR4), which infects Cavendish under both subtropical and tropical conditions (Ploetz, 2006). TR4 also affects a wide range of varieties susceptible to R1 and R2 (Munhoz et al., 2024)

In the 20th century, R1 devastated the banana industry dominated by Gros Michel and eliminated more than 50,000 ha in Central and South America; however, its impact was mitigated by the adoption of Cavendish cultivars resistant to R1 under tropical conditions (Ploetz, 2015). This shift reduced research efforts until the disease reemerged, and concern has recently increased in LAC due to the arrival of TR4, which affects all commercial banana cultivars (Munhoz et al., 2024). TR4 was first reported in Colombia in 2019 (García-Bastidas et al., 2019), followed by Peru in 2021 (Acuña et al., 2022), Venezuela in 2023 (Herrera et al., 2023), and Ecuador in 2025 (IPPC, 2025). In parallel, R1, R2, and SR4 continue to affect local cultivars, causing economic losses and threatening food security (Dita et al., 2018; Dita et al., 2020). In Peru, R1 was first reported in 1951 in Tingo María, a city located in the central high jungle and later spread to Piura and Tumbes along the northern coast (Pinchinat et al., 1986).

The epidemiology of FWB has been extensively reviewed (Dita et al., 2018; Pegg et al., 2019), as have the environmental and management factors associated with disease development (Olivares et al., 2021; Fernández-Ledesma et al., 2023; Heck et al., 2021). However, several biophysical factors remain poorly understood under *in situ* conditions (Staver et al., 2020; Munhoz et al., 2024). This information is essential to anticipate disease risk, even in areas where TR4 has not yet been detected, and to design locally adapted management strategies for diseases caused by other Foc populations.

In South America, Ibarra-Zapata et al. (2021) identified Peru as the fourth country at highest risk of Foc TR4 spread. The Peruvian Amazon, located on the eastern flank of the Andean Cordillera and extending from north to south, is highly dedicated to *Musa* cultivation and accounts for more than 70% of national production units (Rojas et al., 2022). These crops are essential for rural food security and local economies. The region's environmental heterogeneity, diverse landscapes, variable management practices, and wide cultivar diversity make it particularly relevant for studying disease features (Yuen & Mila, 2015; Rojas et al., 2022).

Understanding the spatial and temporal characteristics of FWB and the factors associated with its occurrence is essential for developing effective management strategies (Heck et al., 2021). Translating the existing general FWB epidemiology knowledge into context-specific interventions requires identifying environmental, edaphic, and agronomic variables linked to disease occurrence (Blomme et al., 2024; Munhoz et al., 2024). Accordingly, to address a knowledge gap in a poorly studied yet highly relevant *Musa*-producing region of Peru, this study addresses the following questions: What is the prevalence and spatial distribution of FWB in the Peruvian Amazon? How are cultivar use, environmental factors, and management practices associated with the occurrence of FWB at the mesoscale?

The findings provide a baseline to support targeted interventions and policy decisions, enhancing the sustainability of banana and plantain production in the Peruvian rainforest amid the emerging threat of Foc TR4. Although currently confined to the northeastern coastal region (Piura), TR4 poses a serious risk to local varieties critical to Amazonian and broader Peruvian communities.

2. Methodology

2.1. Surveyed plots

A survey was conducted in 189 *Musa* spp. plots covering a total area of 199.47 ha and distributed across six regions of the Peruvian Amazon: Cajamarca (CAJ; n = 16; 17 ha), Amazonas (AMA; n = 37; 34.55 ha), Junín (JUN; n = 45; 45 ha), Cusco (CUS; n = 31; 33.75 ha), Madre de Dios (MDD; n = 16; 14.1 ha), and San Martín–Loreto (SML; n = 44; 55.07 ha). The fields were located between latitudes −13.035540 and 5.176995 and longitudes −78.916114 and −69.131548. Altitude ranged from 131 m a.s.l. in AMA to 1,836 m a.s.l. in CUS. Plantations were found either as monocultures or in association with other crops, occasionally with mixed cultivars (Figure 1). Plot sizes ranged from 0.25 to 4 ha, and plantation age varied between six and 130 months. The assessments included 13 cultivar categories belonging to 10 genomic groups, with some plots containing mixed cultivars (Table 1). Surveys were conducted between April and October 2022, and each plot was georeferenced using a handheld GPS device.

Figure 1. Plots evaluated for FWB across different regions, production systems, and landscapes. (a–d) In association with other crops; (e–h) under monoculture.

Table 1
Distribution of the number of plots and the evaluated area according to *Musa* spp. cultivar and its corresponding genomic group

Cultivar Subgroup	Genome	Local names of Cultivars	Number of Plots	Area (ha)
Gros Michel	AAA	Seda	56	51.8
Iholena	AAB	Isla	39	49
Plantain	AAB	Inguiri	37	41.85
		Bellaco Horn	21	21
		Bellaco Plantano	9	11
		Bellaco Plantano + Bellaco Horn	1	1
		Bellaco Plantano + Inguiri	2	1.5
Silk	AAB	Manzano	4	1.55
Bluggoe	ABB	Sapino	3	3.5
Maoli-Popoulu	AAB	Palillo	3	1.5
Cavendish	AAA	Williams	3	1.75
		Valery	1	1
Sucrier	AA	Bizcocho	3	3.5
Plantain + Silk	AAB	Bellaco Plantano + Manzano	2	2
		Inguiri + Manzano	1	1.27
Red	AAA	Rojo = Morado	1	1
Plantain + Iholena	AAB	Inguiri + Isla	1	0.25
FHIA	AAAA	FHIA-23	1	4
Sucrier + Iholena	AA + AAB	Bizcocho + Isla	1	1

According to data from Peru’s Ministerio de Desarrollo Agrario y Riego (MIDAGRI, 2025), the evaluated regions contributed the following shares of national banana and plantain production and cultivated area in 2022: CAJ, 1.89% and 3.6%; AMA, 4.89% and 6.74%; JUN, 9.12% and 10.64%; CUS, 1.19% and 1.94%; MDD, 1.5% and 1.7%; and SML, 20.09% and 21.8%. Collectively, these regions accounted for 38.68% of national production and 46.24% of the total cultivated area.

2.2. FWB assessment

All plants within each plot were visually inspected through a census to detect typical external and internal symptoms of FWB. External symptoms included yellowing of older leaves, basal petiole collapse, and hanging leaves forming a skirt-like appearance (Dita et al., 2021). Internal symptoms were confirmed by the presence of continuous necrosis or vascular discoloration, as well as gummy pockets within the vascular tissue observed in transverse sections (de Beer et al., 1999; Dita et al., 2021). For this purpose, a window cut (5 cm × 10 cm) was made in the pseudostem, and xylem tissue was extracted from three leaf sheaths (Dita et al., 2021). The collected tissue was blotted dry with absorbent paper, placed in paper envelopes, and stored under refrigeration. Subsequent isolations were performed on PDA medium, and morphology was examined using monosporic cultures (Leslie & Summerell, 2006).

2.3. Disease prevalence

Prevalence was calculated as the percentage of plots with at least one FWB-affected mat relative to the total number of farms evaluated per region (Campbell & Madden, 1990). Regional differences were assessed using contingency tables and chi-square goodness-of-fit tests at a 5% significance level. Associations between FWB occurrence, region, and cultivar were evaluated using Pearson’s chi-square test at a 5% significance level, and Cramér’s V coefficient was used to quantify the strength of associations. Standardized residuals (|residual| > 1.96) were used to identify variable levels contributing most to the observed associations. Statistical analyses were conducted in R version 4.3.3 using the *stats*, *DescTools*, and *tidyverse* packages.

2.4. Spatial analysis

Spatial dependence of disease occurrence at the regional scale was evaluated using Join Count analyses based on *k*-nearest neighbors (*k*-NN). The analysis was conducted on a georeferenced dataset comprising all assessed farms, with each unit classified according to disease presence (1) or absence (0). Latitude and longitude coordinates were converted into spatial objects using the *sf* package (Pebesma, 2018). Neighborhood matrices and spatial weights were constructed using the *spdep* package (Bivand et al., 2013), evaluating different *k*-values for each farm’s nearest neighbors. For each *k*, the Join Count statistic was calculated for the 1:1 combination, generating observed and expected counts, variances, and Z-values. The p-values were derived from the Z-statistic by Monte Carlo simulation (10,000 replicates), and subsequent adjusted using the Bonferroni method for global analyses (k = 1–189) and the Holm method for regional analyses (k = 1 to the regional maximum). The mean geodesic distance to the k nearest neighbors and the approximate cluster radius were also calculated using geodesic functions from the *sf* package. All analyses were performed in R version 4.3.3.

2.5. Edaphoclimatic characteristics

Bioclimatic variables related to temperature (BIO1–BIO11) and precipitation (BIO12–BIO19) were obtained from the WorldClim v2.1 database (Fick & Hijmans, 2017) at a spatial resolution of 5 arc-minutes (~9.2 km²) using the *geodata* package in R version 4.3.3 (Hijmans et al., 2023) (Table 2). Farm altitude was included in the analysis. For spatial visualization, raster layers were masked by province, and variables showing significant associations and sufficient variability were used to generate thematic maps with the *terra*, *sf*, *ggplot2*, and *ggspatial* packages. Soil properties were obtained from SoilGrids v2.0 at depths of 15–30 cm or 0–30 cm (Poggio et al., 2021). Analyzed variables included soil pH (water), clay, silt, and sand contents (%), bulk density (g cm^{-3}), organic carbon (%), and total nitrogen (%). Raster values were extracted at plot locations using the *terra* and *sf* packages. Crop age was also analyzed. The variables were categorized relative to their median values and evaluated in relation to disease presence or absence. Observations were classified as greater than or less than or equal to the median, and 2 × 2 contingency tables were constructed. Pearson's chi-square test of independence was applied at a 5% significance level, and Cramér's V and standardized residuals were analyzed.

2.6 Watercourses linked to disease occurrence

The minimum distance between each of the 189 georeferenced plots and the nearest watercourse was calculated. Hydrographic data was obtained from the HydroRIVERS database (Lehner & Grill, 2013), and administrative boundaries (regional, provincial, and/or district) from the GADM database using the *gadm* function from the *geodata* package. Plot coordinates were converted into spatial objects, the hydrographic network was clipped to Peru's boundaries, and the nearest river or stream was identified for each plot. Rivers and streams were ranked by the number of FWB-affected plots for which they were the nearest watercourse, and a 2 × n contingency table was constructed with disease occurrence as rows and watercourses as columns. A global association was tested using Fisher's exact test with Monte Carlo simulation (10,000 replicates). When significant ($p < 0.05$), post hoc pairwise comparisons were conducted between each watercourse and all others using 2 × 2 contingency tables and Fisher's exact test. The p-values were adjusted for multiple testing using the Bonferroni method. Watercourses with adjusted p-values < 0.05 were considered significantly associated with FWB occurrence among nearby plots. All spatial analyses were performed in RStudio using the *sf*, *geodata*, *dplyr*, and *ggplot2* packages.

Table 2
Bioclimatic variables from the WorldClim v2.1 database used in the study

Bioclimatic variable (BIO)	Description	Median
BIO1	Annual Mean Temperature	22.91 °C
BIO2	Mean Diurnal Range [Mean of monthly (max temp − min temp)]	11.40 °C
BIO3	Isothermality (BIO2/BIO7) × 100	84.99 %
BIO4	Temperature Seasonality (standard deviation ×100)	57.89 %
BIO5	Max Temperature of Warmest Month	29.62 °C
BIO6	Min Temperature of Coldest Month	16.02 °C
BIO7	Temperature Annual Range (BIO5 − BIO6)	13.42 °C
BIO8	Mean Temperature of Wettest Quarter	23.27 °C
BIO9	Mean Temperature of Driest Quarter	22.17 °C
BIO10	Mean Temperature of Warmest Quarter	23.47 °C
BIO11	Mean Temperature of Coldest Quarter	22.12 °C
BIO12	Annual Precipitation	1481 mm
BIO13	Precipitation of Wettest Month	214 mm
BIO14	Precipitation of Driest Month	55 mm
BIO15	Precipitation Seasonality (Coefficient of Variation)	31.58 %
BIO16	Precipitation of Wettest Quarter	619 mm
BIO17	Precipitation of Driest Quarter	180 mm
BIO18	Precipitation of Warmest Quarter	412 mm
BIO19	Precipitation of Coldest Quarter	201 mm

Note: The variables represent long-term climatic averages for the period 1970–2000 and were generated through interpolation of observed climate data from weather stations worldwide. Variables include annual trends, seasonality, and extreme or limiting environmental factors related to temperature and precipitation.

2.7. Farmer perception and management practices related to FWB

Associations between FWB occurrence and farmers’ responses were evaluated using data from structured surveys conducted with 189 producers at their respective farms. The surveys included questions on growers’ perception of FWB, management practices applied to diseased plants, and general crop management. For each variable, contingency tables were constructed, and Pearson’s chi-square test of independence was applied at a 5% significance level. The Cramér’s V coefficient and standardized residuals were analyzed.

3. Results and discussion

3.1 FWB assessment

FWB was observed only in Isla (Iholena, AAB), Seda (Gros Michel, AAA), Manzano (Silk, ABB), and Morado (Red, AAA), all of which exhibited continuous internal xylem discoloration. External symptoms varied slightly and were occasionally accompanied by soft rots (Figure 2a–f). Tissue samples with vascular necrosis yielded fungal isolates with cultural and morphological characteristics typical of *Fusarium* spp. (Figure 2g–k). Colonies grown on PDA displayed variable pigmentation, ranging from pink to reddish-purple, and microscopic examination revealed scattered microconidia or microconidia arranged in false heads on microconidiophores, foot-shaped macroconidia, and chlamydospores. These features are consistent with *Fusarium oxysporum*, which includes the causal agent of FWB (Leslie & Summerell, 2006).

3.2 Disease prevalence

This is the first study in Peru that involved an exhaustive assessment of FWB through visual inspection of all 213,005 banana and plantain mats across the evaluated fields, ensuring high accuracy in estimating disease occurrence and prevalence. Of the 189 farms surveyed, 53 contained diseased plants, resulting in an overall prevalence of 28.04%, attributable to R1/SR4 based on the affected cultivars and surveyed regions (Ploetz, 2015; Mostert et al., 2017; Martínez de la Parte et al., 2024). This prevalence was intermediate compared with reports from other regions. In southeastern Africa, using a census approach, the disease was reported in approximately 53.8% of farms, mainly due to Foc R1 and, to a lesser extent, R2 (Karangwa et al., 2016). In Ethiopia, a prevalence of 67.22% was recorded using subsampling based on 100 m^2 areas within 180 farms (Mengesha et al., 2018). Similar to the present study, FWB caused by SR4 was detected in 23% of 100 plots in the Canary Islands, using a 500 × 500 m quadrant subsampling approach (Perera et al., 2024).

Prevalence varied significantly among regions ($\chi^2 = 84.248$; df = 5; $p < 2.2 \times 10^{-16}$), with a non-uniform spatial distribution across the evaluated zones (Figures 3 and 4a). A strong association was observed between region and FWB occurrence (Cramér’s V = 0.43).

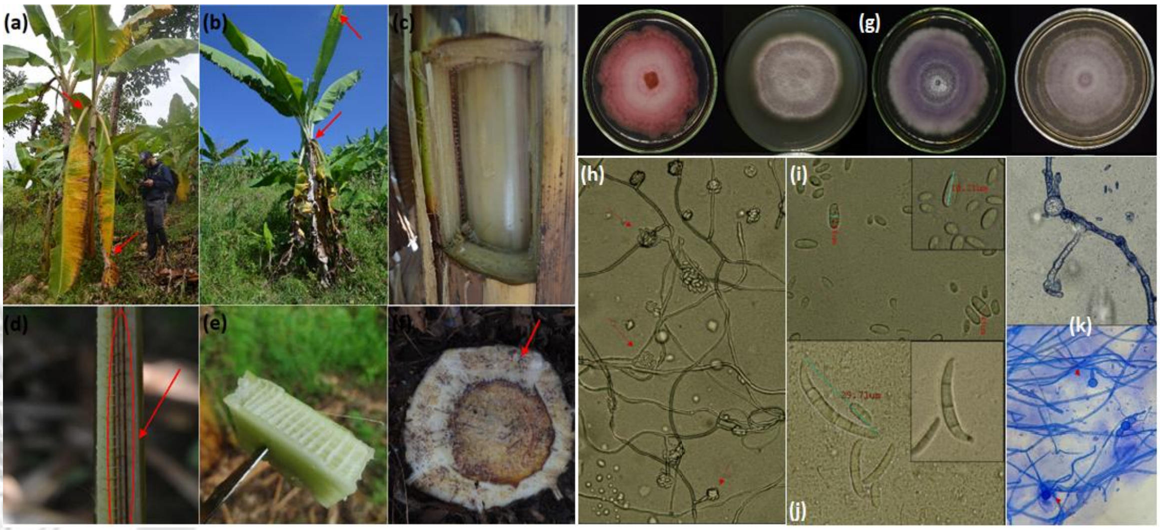

Figure 2. External and internal symptoms of FWB. (a, b) Wilt syndrome on Isla and Seda cultivars; (c) window cut to confirm internal symptoms; (d) continuous xylem necrosis from the pseudostem sample; (e) xylem view from a healthy plant; and (f) vascular necrosis and yellow discoloration at the corm level. (g) Cultural characteristics of selected isolates; (h) microconidia grouped in false heads or borne on microconidiophores; (i) solitary microconidium; (j) characteristic macroconidia of *Fusarium oxysporum*; and (k) chlamydospores.

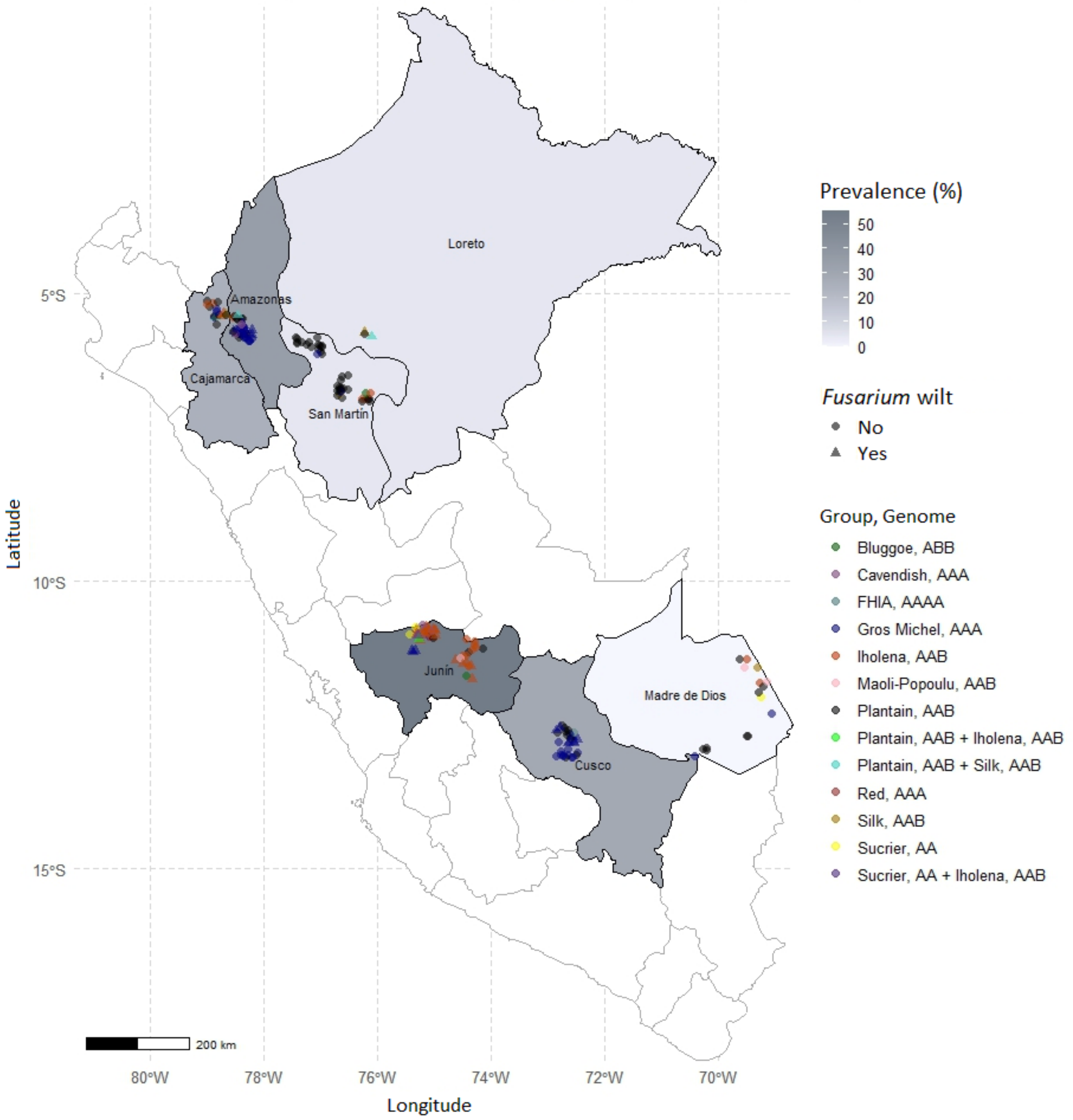

Figure 3. Spatial distribution of the 189 plots evaluated for FWB in different *Musa* spp. cultivars across six regions of the Peruvian Amazon. Regional prevalence is represented using grayscale shading. Each point corresponds to an evaluated plot. Symbols indicate the presence (▲) or absence (●) of the disease, while colours represent the associated cultivar subgroup(s).

The highest prevalence was found in JUN (25 of 45 plots; 55.56%), with a significantly greater number of affected plots than expected under independence ($\chi^2 = 35.000$; $p < 1.50 \times 10^{-6}$). In contrast, due to the higher proportion of Plantain (ABB), only 2 of 44 plots in SML (4.55%) showed FWB-affected plants, and no affected plots were recorded in MDD (16 plots), both values being significantly lower than expected.

A significant and very strong association was found between cultivar and disease occurrence ($\chi^2 = 68.047$; df = 12; $p = 7.42 \times 10^{-10}$; Cramér's V = 0.601) (Figures 3 and 4b). The Isla cultivar (Iholena, AAB) showed the strongest association, followed by Seda (Gros Michel, AAA). FWB also occurred more frequently than expected in plots with Manzano (Silk, AAB) mixed with Plantain subgroup cultivars (AAB). A significant association was observed between the evaluated region and the cultivar used ($\chi^2 = 196.15$; df = 60; $p = 2.31 \times 10^{-16}$), with a strong relationship (Cramér's V = 0.456). The Isla variety was overrepresented in JUN, and Seda in AMA and CUS (Figure 5a). The interaction between region and cultivar was also significantly and very strong associated with FWB occurrence ($\chi^2 = 90.16$; df = 34; $p = 5.60 \times 10^{-7}$; Cramér's V = 0.691). The use of Isla in JUN was associated with a much higher-than-expected disease occurrence (Figure 5b)

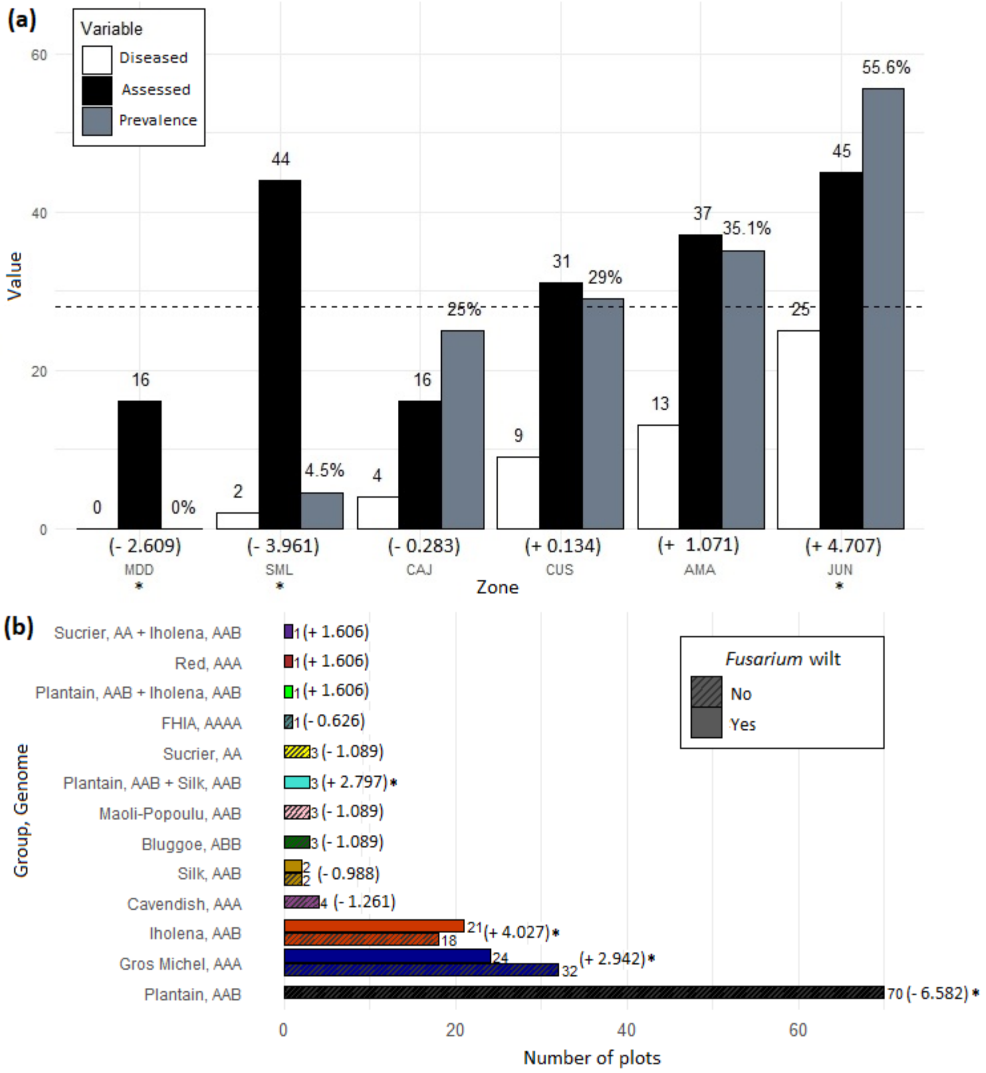

Figure 4. (a) Distribution of evaluated plots, FWB affected plots, and disease prevalence (%) across study zones; the dashed line indicates the overall prevalence. (b) Number of plots with and without disease by genomic group. In both panels, values in parentheses represent standardized residuals from χ² tests of independence for disease occurrence. Asterisks (*) indicate statistically significant associations (|residual| > 1.96), based on deviations from expected frequencies under the null hypothesis.

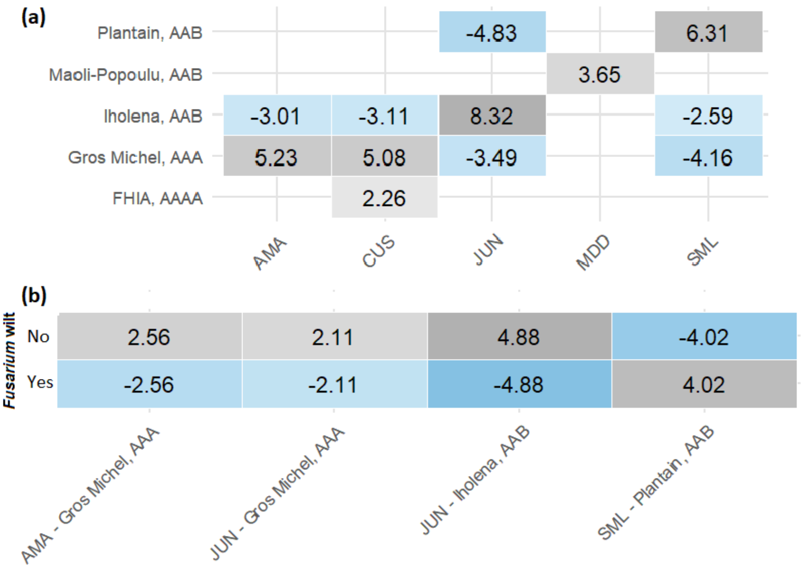

Figure 5. Significant associations between (a) *Musa* spp. cultivars and evaluated regions, and (b) specific cultivar–region combinations and disease occurrence. Values represent significant standardized residuals from χ² tests of independence (|residual| > 1.96), indicating deviation from expected frequencies under the null hypothesis.

Plantains (AAB) play a critical role in food security in the Peruvian Amazon and across LAC, primarily due to their resistance to R1 and SR4 (Munhoz et al., 2024). In this study, these cultivars were widely distributed, accounting for 40.26% of the total area and 39.25% of the plots evaluated, directly contributing to the lower regional prevalence and occurrence of FWB. However, their potential response to TR4 should be carefully considered, as field infections have been reported in Venezuela (INSAI, 2023), and variable responses among genotypes in China (Zhan et al., 2022b). This highlights the importance of including these cultivars in future, more detailed studies in Peru.

3.3 Spatial analysis

Global Join Count analysis using *k*-nearest neighbors (*k*-NN) revealed significant spatial clustering of FWB occurrence across multiple neighborhood orders, indicating a hierarchical spatial structure (Z-value > 1.96; adjusted p-values < 0.05) (Figure 6a). The first aggregation peak was detected at k = 8 nearest farms (Z = 11.96; radius = 13.8 km), suggesting localized infection foci. As the neighborhood size increased (k = 8–26), clustering slightly weakened but remained significant, with a second peak at 44.5 km (Z = 12.8), indicating disease aggregation at an intermediate spatial scale. Beyond k = 87 (Z = 4.74; radius = 131.6 km), clustering significance declined, reflecting a dilution of spatial aggregation at broader distances.

Regional analyses revealed variability in spatial aggregation among and within regions, with significant clustering detected for at least at one neighborhood order in CUS, SML, and JUN (Z-value > 1.96; adjusted p-values < 0.05). In CUS, the strongest aggregation occurred at k = 6 (Z = 7.82; radius = 5 km), indicating a high concentration of affected plots at small spatial scales (Figure 6d). Additional peaks were observed at k = 16 (Z = 4.34; radius = 14.1 km) and k = 18 (Z = 4.55; radius = 15.7 km), suggesting intermediate sub-clusters. In SML, clustering was highly localized, with a peak at k = 1 (Z = 7.29; radius = 1.64 km), followed by a rapid decline of significance beyond k = 4, indicating limited spatial spread (Figure 6f). In JUN, major aggregation peaks were identified at k = 8 (Z = 5; radius = 13 km) and k = 26 (Z = 4.95; radius = 34 km), suggesting local and intra-regional disease foci and broader spatial dispersion (Figure 6e). Although no significant aggregation was detected in AMA and CAJ, similar patterns of initial aggregation followed by dispersion and sub-cluster formation at larger scales were observed (Figures 6b and 6c).

Comparisons based on Z-values highlighted differences between JUN and CUS. In the first, lower aggregation despite a higher number of FWB-affected plots and weaker clustering intensity indicated a more dispersed disease pattern. This suggests that local factors, such as environmental conditions and inter-farm connectivity, may contribute to wider Foc dispersion. All surveyed farmers used plantlets or corms as planting material; however, no information exists on planting material or seed system networks in Peru, despite their relevance for monitoring, surveillance, and the potential diffusion of *Musa* spp. germplasm (Nduwimana et al., 2022).

Regional differences were evident since JUN producers more often sourced material from distant farms, whereas in CUS, most selected plantlets from their own or neighboring plots, potentially providing them with greater knowledge of the phytosanitary status of their planting material. The higher prevalence observed in JUN, together with planting material sources may have favored wider and more diffuse FWB distribution.

This aligns with previous reports emphasizing the role of infected plant propagules and farm-to-farm dissemination in regional pathogen spread, especially in areas with many affected farms (Karangwa et al., 2016; Bekeko et al., 2025; Ploetz, 2015). It highlights the necessity of a national *Musa* spp. planting material program, currently non-existent in the country, to improve disease surveillance.

3.4 Edaphoclimatic associations

Bioclimatic variables related to temperature, precipitation, and altitude were significantly associated with FWB occurrence ($p < 0.05$) (Figures 7 a – g). Temperature-related variables showed the strongest associations, reflected by higher Cramér's V values. The disease was less frequent in areas with annual mean temperatures (BIO1) above the median (22.91 °C). Variables describing temperature periodicity showed moderate associations; higher temperature seasonality (BIO4; median = 57.89%) was linked to increased FWB occurrence. Disease presence was also more common at higher altitudes (> 762.5 m a.s.l.). Conversely, areas with values above the median for annual precipitation (BIO12: 1481 mm), precipitation of the wettest month (BIO13: 214 mm), warmest quarter precipitation (BIO18: 412 mm), and precipitation seasonality (BIO15: 31.58%) exhibited higher-than-expected FWB occurrence.

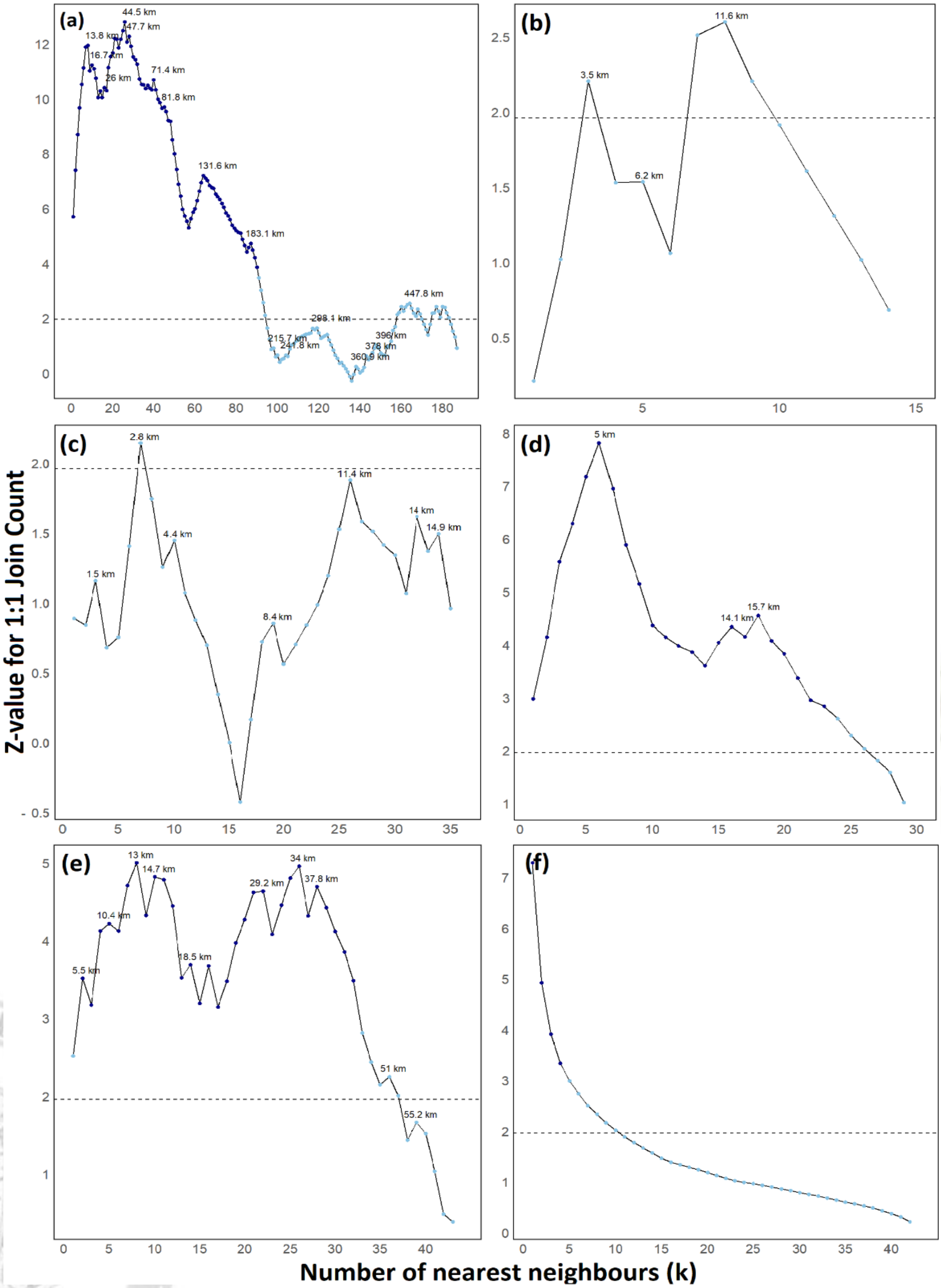

Figure 6. Analysis of spatial aggregation for the Join Count test using *k*-nearest neighbors (*k*-NN) of FWB-affected farms. (a) Global analysis; regional analysis for (b) AMA; (c) CAJ; (d) CUS; (e) JUN; and (f) SML. The mean radius for each corresponding k-nearest neighbor order is presented in kilometers. Points in dark blue indicate significant aggregation, with Z-values > 1.96 and adjusted p-values < 0.05.

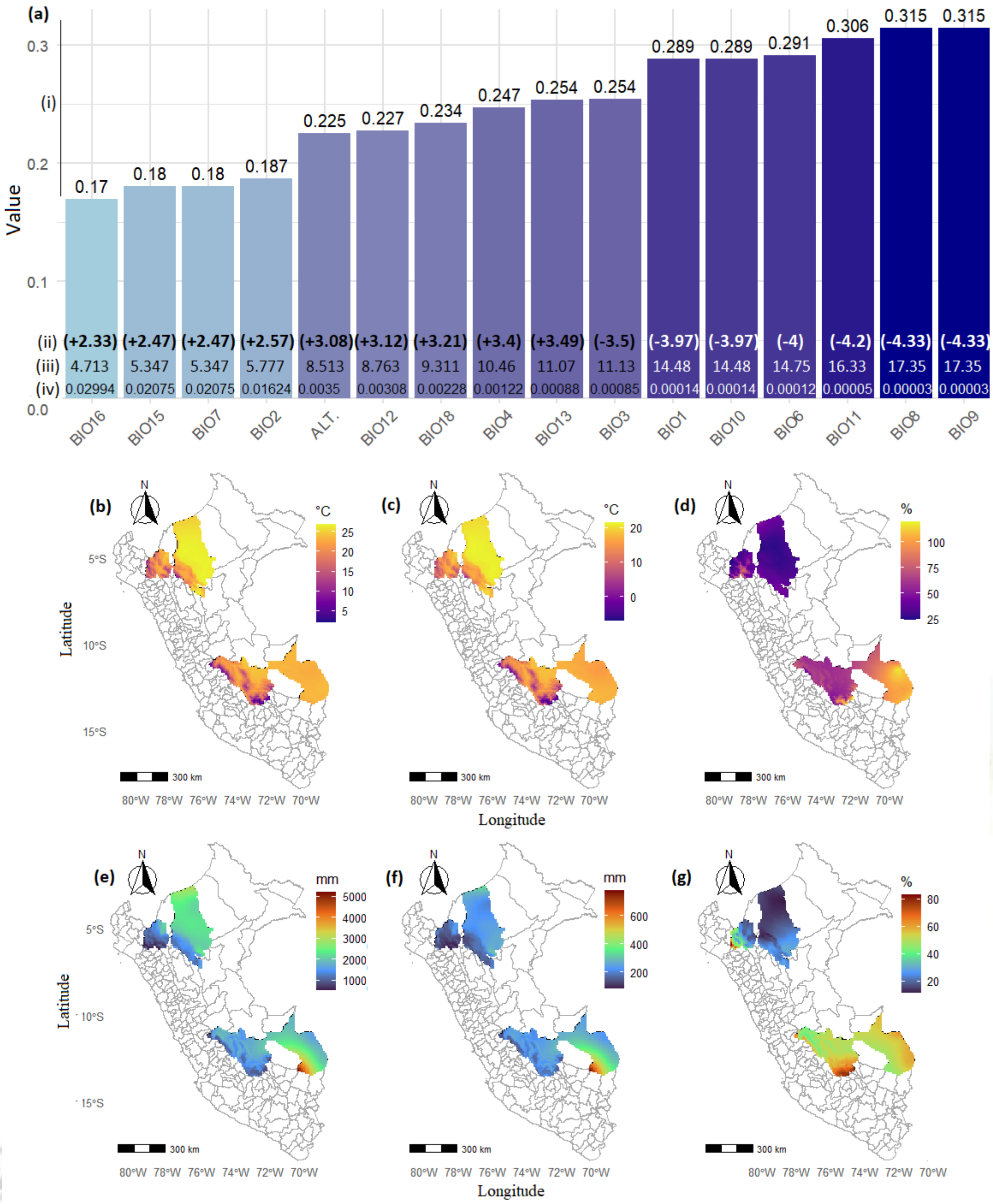

Figure 7. (a) Significant associations ($p < 0.05$) between values above the respective medians for bioclimatic variables and plot altitude, and the occurrence of FWB. Shown are: (i) Cramér's V coefficients; (ii) standardized residuals; (iii) χ^2 values; and (iv) p-values corresponding to each association. Climatic maps of the evaluated provinces for: (b) mean temperature of the coldest quarter (BIO11); (c) minimum temperature in the coldest month (BIO6); (d) temperature seasonality (BIO4); (e) annual precipitation (BIO12); (f) precipitation of the wettest month (BIO13); and (g) precipitation seasonality (BIO15).

The findings suggest that regions with greater rainfall variability and flood risk may experience increased inoculum dispersal and disease development at large scales. All evaluated plots were rainfed, as is typical of agriculture in the Peruvian Amazon. Areas with higher flood risk, associated with greater rainfall and pronounced seasonality, particularly in parts of JUN and AMA (Figures 7 e – g), may provide favorable conditions for FWB by affecting plant physiology and facilitating the movement of infested soil, plant parts, or entire infected plants along rivers and streams (Olivares et al., 2021). Although disease risk was not modeled in this study, Ibarra-Zapata et al. (2021), using similar bioclimatic variables, reported comparable precipitation-related patterns for Foc TR4 risk across the Pantropical Americas, while observing opposite trends for temperature. Similar rainfall-related patterns were reported in Colombia (Rodríguez-Yzquierdo et al., 2023), and extreme rainfall events, such as Cyclone Yaku in Piura, were associated with the spread of Foc TR4 in northern Peru (Munhoz et al., 2024). The association between disease occurrence and lower temperatures observed here may reflect local adaptation of Foc genotypes to cooler environments, differing from patterns reported for TR4 risk.

Significant associations were found between FWB occurrence and higher levels of total nitrogen, organic carbon stocks, and organic carbon density ($p < 0.05$) (Table 3). The strongest, though still weak, association was observed for total nitrogen (Cramér's V = 0.2094). This pattern may reflect the characteristics of the SoilGrids database, which includes agricultural soils whose baseline values are influenced by land use and management practices. In JUN, where the Isla cultivar predominates, farms are often managed by itinerant producers applying intensive practices and urea-based fertilizers, potentially contributing to elevated nitrogen levels. Similar associations between nitrogen-enriched soils and FWB have been reported in Africa, particularly in areas where organic banana residues were incorporated into the soil (Bekeko et al., 2025). Orr et al. (2022) demonstrated that, under controlled conditions, higher nitrogen application rates favored disease development in FWB-affected plants, likely increasing inoculum production and facilitating Foc spread, especially when compounded by anthropogenic and environmental factors in Peruvian regions.

3.5 Watercourses linked to disease occurrence

When individual watercourses were analyzed, a significant association with FWB occurrence was detected for one stream within the Perené basin in Chanchamayo Province, JUN ($p < 0.05$). Affected plots were predominantly located along this watercourse, suggesting that hydrographic connectivity within the basin may be associated with the local spatial distribution (Figure 8).

The role of watercourses in the dissemination of Foc is a key factor to consider (Dita et al., 2018). In certain areas of northern Vietnam, their influence on pathogen spread has been described as nearly uncontrollable (Chittarath et al., 2022; Nguyen et al., 2025). This is particularly relevant in zones with a high risk of flooding, including areas distant from major rivers due to the presence of low-order streams (Lima et al., 2025), such as those found in the Perené basin in Chanchamayo Province, where 21 of the 28 FWB-affected plots in JUN were located. The findings suggested that low-order streams could be an overlooked dispersal factor in specific regions in Peru, representing a mandatory consideration.

3.6 Farmer perception and management practices related to FWB

A significant association was observed between FWB occurrence and its farmers' perceptions, at both the individual and neighborhood levels, as well as with the management of diseased plants ($p < 0.05$) (Table 4). FWB was more frequent where producers considered it the main phytosanitary issue, noted its recent increase, were aware of nearby affected or abandoned plots, had eliminated or abandoned their own fields due to its impact, and did not intervene on diseased plants. This finding occurred within the common context of the Peruvian Amazon, characterized by scarce biosecurity measures, as reported in other studies in the Central Jungle of Peru (Staver et al., 2023). The findings, alongside the higher occurrence of FWB at greater altitudes, suggest potential farm-to-farm transmission favored by agroclimatic conditions.

Table 3
Association between soil properties and the occurrence of FWB

Soil property	χ^2_{cal}	χ^2_{tab}	df	p-value	Std. Residual [a]	Cramér's V
[b] Total nitrogen * (median = 1.58 g x kg^{-1})	7.2046	3.8415	1	0.0073	+ 2.847746	0.2094
[c] Organic carbon stocks * (median = 6.6 kg x m^{-2})	6.4666	3.8415	1	0.0110	+ 2.706691	0.1990
[b] Organic carbon density * (median = 25.2 kg x m^{-3})	6.2465	3.8415	1	0.0124	+ 2.662858	0.1958

Note: The values correspond to Pearson's chi-square (χ^2) test of independence using 2 × 2 contingency tables based on plot-level disease presence and whether soil property values were above or below the median. Values with an asterisk (*) indicate statistically significant associations ($p < 0.05$). (a) Standardized residuals refer to the association between disease presence and values above the respective medians for each soil property. Soil property data were obtained from SoilGrids v2.0 at a depth of 15–30 cm (b) or 0–30 cm (c).

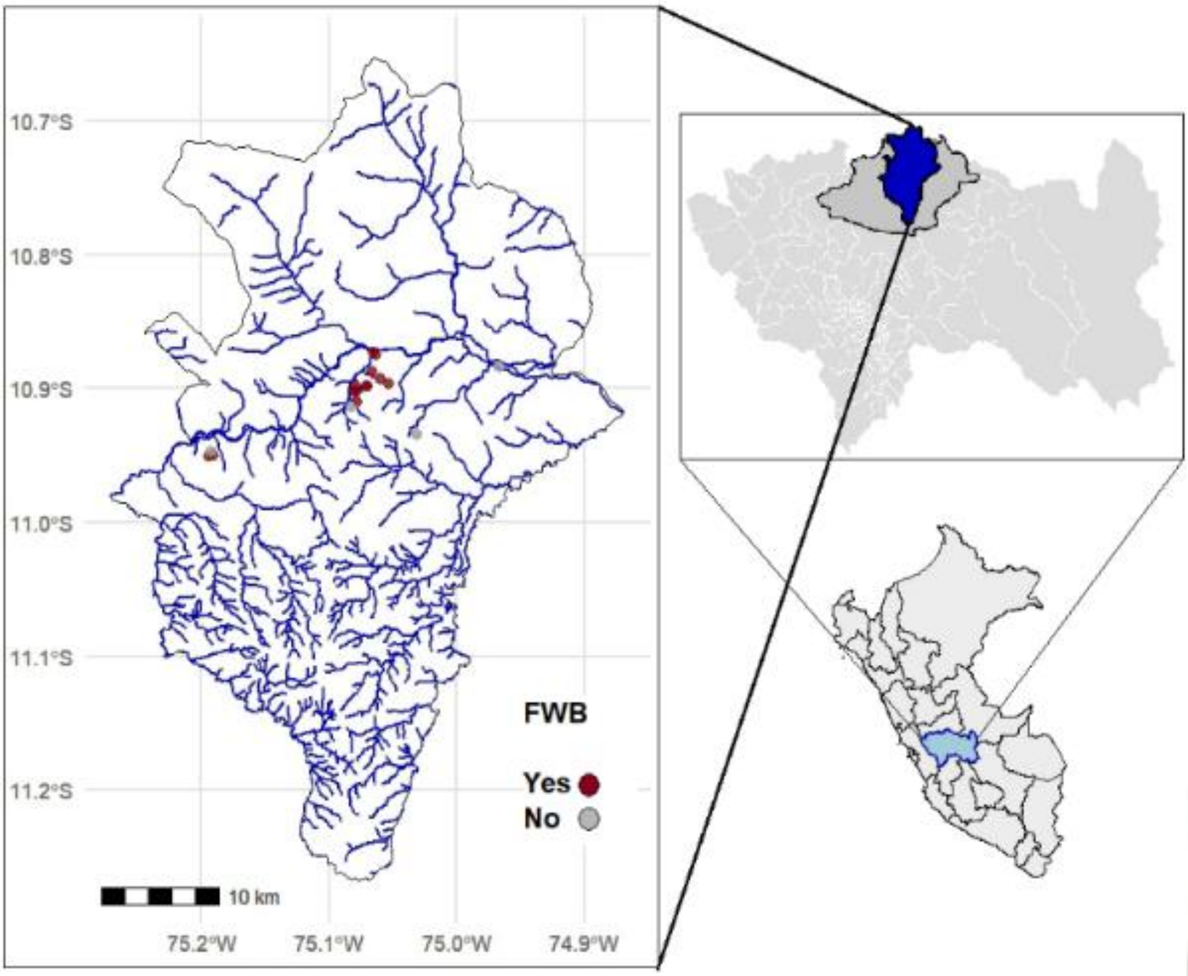

Figure 8. Spatial distribution of plots according to FWB occurrence along the Perené Basin, highlighting the watercourse significantly associated with the disease in Perené District, Chanchamayo Province, Junín Region.

Table 4
Significative associations between farmer's responses and FWB

Soil property	χ^2_{cal}	χ^2_{tab}	df	p-value	Std. Residual [a]	Cramér's V
Main Disease (FWB*)	69.9896	12.5916	6	4.10e-13	+ 6.209068	0.6085
Farms affected by FWB in the neighborhood (Yes*)	46.6804	5.9915	2	7.30e-11	+ 5.159749	0.4969
Farms abandoned due to FWB in the neighborhood (Yes*)	24.5536	5.9915	2	4.65e-06	+ 3.398838	0.3614
Perception of FWB in the neighborhood (Increase*)	39.0427	7.8147	3	1.69e-08	+ 3.680899	0.4545
Reason for eliminating the plantation (FWB*)	50.7245	38.8851	26	0.002573	+ 4.166604	0.5181
Measures against FWB affected plants (Nothing*)	53.3067	33.9244	22	0.000206	+ 1.981515	0.5311

Note: The values correspond to Pearson's chi-square (χ^2) test of independence using contingency tables based on plot-level disease presence and the farmer's answers to surveys about perception and management. (*) Terms in parentheses and marked with an asterisk represent variable categories with positive standardized residuals, suggesting a higher-than-expected number of cases in plots with FWB occurrence. (a) Standardized residuals refer to the association between disease presence and farmer's responses.

The spread of Foc may be facilitated by infected plant residues, as sporulation and aerial or rain-splashed dispersal of this and other *formae speciales* have been documented (Scarlett et al., 2015; Warman & Aitken, 2018). Potential aerial dispersal of Foc from abandoned infected residues may promote spread over longer distances among nearby plots; considering that Peruvian farms are often small, this could influence cluster size and spatial aggregation, as observed in JUN. Additionally, transmission can occur via watercourses, animals, and human activity (Dita et al., 2018). Plots surrounding the Perené basin associated with FWB occurrence were located at geodesic distances ranging from 105 to 1070 m, with over half within 307 m. This underscores the importance of properly removing inoculum by eliminating infected plants (Munhoz et al., 2024); however, a critical gap remains regarding the appropriate area to be eradicated for effective FWB management.

4. Conclusions

Based on a census of 189 banana and plantain plots across six regions of the Peruvian Amazon, the prevalence of FWB was 28.04%, with Junín showing the highest value at 55.56%. The use of the Isla cultivar (Iholena, AAB) was associated with increased disease occurrence. FWB exhibited hierarchical spatial aggregation into major foci and subclusters; in Junín, these were more geographically dispersed and covered broader areas. Disease occurrence was more frequent in areas with lower temperatures, higher altitude, and greater annual and seasonal precipitation. As the primary phytosanitary problem, FWB led to field abandonment or elimination in heavily affected areas, where a lack of intervention on symptomatic plants was strongly associated with disease presence. This landscape-scale epidemiological approach addressed key questions regarding the spread of TR4 raised by Munhoz et al. (2024). These findings benefit the agricultural sector by identifying biophysical variables that define high-risk zones, such as the Perené basin, and provide a baseline to refine regional strategies grounded in local biophysical and management characteristics. Surveillance in high-altitude zones and educational programs are recommended. Furthermore, the necessity of a national *Musa* spp. planting material program, currently non-existent in the country, is highlighted to improve disease surveillance.

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Conflicts of Interest

The authors declare that there are no conflicts of interest.

Authors’ contribution

D.S. Marín-Gil: Conceptualization, Methodology, Collecting field data. Formal analysis, Software, Data curation, Investigation, Writing – original draft. **J. Marín-Horna:** Collecting field data, Supervision, Writing – review & editing, Project administration. **M. Dita:** Conceptualization, Resources, Supervision, Validation, Writing – review & editing, Funding acquisition, Project administration.

Ethical statement

This research was conducted in compliance with ethical standards. All participating farmers provided informed consent for the collection of field data and samples.

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