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Banana bunchy top disease in Africa—Predicting continent-wide disease risks by combining survey data and expert knowledge

Hein Bouwmeester[1] | Guy Blomme[2] | Aman Bonaventure Omondi[3] | Walter Ocimati[4]

[1]GeoSpace, Ede, Netherlands

[2]Bioversity International, c/o The International Livestock Research Institute, Addis Ababa, Ethiopia

[3]Bioversity International, Cotonou, Benin

[4]Bioversity International, Kampala, Uganda

Correspondence
Hein Bouwmeester, GeoSpace, Ede, Netherlands.
Email: hein@geospace.nl

Abstract

Across Africa, banana bunchy top disease (BBTD) severely impacts banana production and livelihoods of millions of smallholder farmers. Mapping vulnerability of landscapes to monitor BBTD establishment and spread is crucial for proactive measures of disease exclusion. To highlight current and future risks of BBTD in Africa, the relationship between 1160 field observations from 14 BBTD surveys and environmental covariate maps was determined using logistic regression. From these relationships, we inferred the environmental suitability of the African landscape for the possible wider spread of BBTD. Using this information and expert knowledge, we generated a map highlighting the main banana production areas at risk of BBTD entry and establishment. We combined these maps to create a priority map that highlights the areas that need most attention in combating BBTD through surveillance and measures to prevent its spread. Our analysis shows that BBTD is widespread across tropical Africa, with dispersal over several hotspots. Central and Western Africa are most favourable for the development of BBTD. Central, West and South-East Africa are most at risk of BBTD entry and initial establishment. Areas in West and Central Africa, in the Great Lakes Region in Eastern Africa and in South-East Africa, particularly in Malawi and Mozambique, score high on the prioritization index for surveillance and mitigation efforts. Recent reports of BBTD presence in north-western Uganda and western Tanzania support these risk predictions. For these and other not-yet-infected areas, measures for close surveillance and proactive management of the disease are needed.

KEYWORDS
banana bunchy top disease, infection risk, logistic regression, mapping diseases, spatial statistics

1 | INTRODUCTION

Banana bunchy top disease (BBTD), caused by the banana bunchy top virus (BBTV), is the most serious and destructive viral disease of banana and plantain (Dale, 1987). The disease was first observed in Fiji in 1879, in Egypt around 1900 and in Sri Lanka and Australia in 1913 (Magee, 1927). BBTD is currently widespread in South-East Asia, South Pacific, India and Africa. In Africa, a second entry

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of BBTD was reported in the 1950s in the Democratic Republic of Congo (Blomme et al., 2013; Wardlaw, 1961). BBTD has since spread to 19 countries within the African continent (Table 1) where it causes significant yield losses and is increasingly threatening unaffected banana production areas (Kumar et al., 2011, 2015).

The Invasive Species Specialist Group (ISSG) of the Species Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN) listed BBTV among the world's top 100 worst invasive species, thus requiring rigorous quarantine measures (Invasive Species Specialist Group, 2020).

BBTD symptoms include dark green discontinuous streaks on leaf lamina and midribs, chlorosis and drying of leaf margins, and, ultimately, rosetting or bunching of leaves (Food and Agricultural Organization, 2018a; Niyongere et al., 2011). Infected suckers (i.e., lateral shoots) are often severely stunted and bunchy in appearance. BBTD-affected plants produce no or inedible fruits (Food and Agricultural Organization, 2018a). The disease is reported to have nearly wiped out the banana industry in Australia between 1913 and 1920 (Magee, 1927). In Africa, the disease reduced the area under banana production from 3500 ha to 800 ha in the Malawi districts of Nkhatabay and Nkhotakota in the 1990s (Soko et al., 2009). Severe BBTD effects have also been reported in the central African region, with yield losses of up to 90% in banana cultivars such as Km5 (*Musa* AAA genome) and Cavendish (*Musa* AAA genome) (Niyongere et al., 2011).

BBTD is mainly spread from infected plants to other plants by the banana aphid, *Pentalonia nigronervosa* (Magee, 1927). The aphids are present in all banana-producing regions of the world, mainly living between outer banana leaf sheaths. The virus can also spread through infected bananas. Transmission of the virus through farming tools does not occur (Niyongere et al., 2015).

Controlling BBTD is extremely difficult due to the omnipresence of the aphid vector and the lack of easy-to-apply control measures to eliminate the disease effectively once the virus becomes established (Food and Agricultural Organization, 2018a; Omondi et al., 2020). The most effective control measure is roguing of diseased mats or diseased fields, and the use of clean planting materials (Omondi et al., 2020). Roguing of perennial banana mats is difficult and needs to be timely and consistently done. Total eradication of infested perennial fields is cumbersome and costly and so has been poorly adopted (Abiola et al., 2020; Lepoint et al., 2013). Early-stage symptoms are variable among varieties and difficult to detect, especially in older plants, thus hampering timely roguing. Roguing would be more effective if applied at landscape scale to reduce the general inoculum pressure. However, it is challenging to convince all smallholder farmers within a landscape to rogue their fields at the same time when apparently healthy plants still appear in their fields. Large-scale roguing can potentially also negatively affect the available banana germplasm diversity (Ocimati, Blomme, et al., 2013), the environment and other ecosystem services (Ocimati et al., 2018), so caution is required. Use of clean, preferably micropropagated (i.e., in vitro-derived) plantlets to establish new fields is recommended for disease management. However, access to clean planting materials is limited in most banana-producing areas in Africa, with farmers predominantly relying on suckers from their own and neighbouring farms (Djailo et al., 2016; Ocimati, Karamura, et al., 2013). Movement of micropropagated plantlets not certified to be virus-free has been demonstrated to transmit BBTV (Drew et al., 1989), further complicating access to clean seed in BBTD-affected areas. Given the extreme difficulty of eradicating BBTD once established, especially in small-scale farming settings, the most effective control strategy is the prevention of disease introduction. Such a proactive measure requires an in-depth knowledge of the current geographical spread of the disease, an estimation of the environmental suitability of landscapes to BBTD or the aphid vector, and an assessment of the vulnerability/risk of banana production areas to disease entry, initial establishment, and wider spread.

TABLE 1 Timeline of establishment of banana bunchy top disease in Africa.

Year of first observation	Country	References
1900	Egypt	Magee (1927)
1958	Democratic Republic of Congo	Wardlaw (1961)
1981	Equatorial Guinea, Eritrea, Gabon	Manser (1982), Saverio (1964)
1987	Congo-Brazzaville, Burundi, Rwanda	Sebasigari and Stover (1988)
1994	Central African Republic, Malawi	Diekmann and Putter (1996), Kenyon et al. (1997)
2007	Mozambique, Zambia	Gondwe et al. (2007), International Plant Protection Convention (2016)
2008	Angola, Cameroon	Oben et al. (2009), Pillay et al. (2005)
2011	Benin	Lokossou et al. (2012)
2012	Nigeria	Adegbola et al. (2013)
2015	South Africa	Jooste et al. (2016)
2017	Togo	Kolombia et al. (2021)
2020	Tanzania, Uganda	Ocimati et al. (2021), Shimwela et al. (2022)

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BBTD establishment and spread within a landscape is influenced by environmental variables such as temperature and rainfall that affect both the aphid vector and the virus (Raymundo & Pangga, 2011). A negative correlation has been reported between aphid populations and rainfall intensity, with the highest aphid populations observed in the dry season (Niyongere et al., 2013; Young & Wright, 2005). This has been mainly attributed to the direct impact of rain drops and runoff. Thus, banana production areas that have high precipitation will have a lower build-up of aphid populations, whereas drier areas will experience a higher aphid population and a greater risk of BBTD establishment and spread. Temperature has been reported to affect vector biology, BBTD symptom development, spread, and BBTV transmission efficiency (Allen, 1978; Anhalt & Almeida, 2008; Robson et al., 2007; Wu & Su, 1990). Aphid intrinsic growth rate and population growth have been reported to be highest at 25°C, declining at lower and higher temperatures (Robson et al., 2007). Allen (1978) reported a reduction in BBTD incubation period with increasing temperature. Wu and Su (1990) observed no BBTV transmission at 16°C and a maximum transmission efficiency at 27°C. Anhalt and Almeida (2008) observed a higher efficiency in BBTV transmission at 25 and 30°C than at 20°C. Simulations by Raymundo and Pangga (2011), showed that an increase in monthly mean temperature of 1–2°C resulted in a reduction in the number of viruliferous aphids. Thus, banana production zones with temperature extremes will experience a reduction in the reproduction of the aphid vector population and the efficiency of BBTV transmission, thus leading to slow BBTD spread (Anhalt & Almeida, 2008). In Burundi, for example, BBTD has been observed to dominate at the low- and mid-altitude sites (below 1300 m a.s.l.), having a conducive temperature (Walangululu et al., 2010). Nevertheless, aphid vectors have also been observed to acquire the virus at mid- and high-altitude areas, with lower temperatures (Niyongere et al., 2013). Niyongere et al. (2013) reported lower transmission rates with longer incubation periods at the high-altitude sites, possibly due to lower temperature conditions. For example, they observed a 21-day incubation period at an altitude of 780 m a.s.l. compared with 84 days at 2090 m a.s.l.

This paper describes the current geographical distribution of BBTD in Africa, the environmental suitability for possible wider spread and the risk to disease entry within rain-fed African *Musa* production systems. Suitability and vulnerability are spatially and explicitly predicted by combining point-based observations with auxiliary environmental datasets and expert knowledge. The developed insights translate into priority areas for surveys and/or interventions in *Musa* systems.

2 | MATERIALS AND METHODS

2.1 | Area of interest

The area of interest is the entire African continent, although the field observations were limited to the tropical regions of Africa. The area covers about 7600 km from west to east and 8000 km from north to south. Madagascar is included, but other African islands are not.

2.2 | Datasets

This study used 14 datasets/field surveys describing the presence or absence of BBTD on smallholder banana farms throughout Africa (Table 2). The datasets were collected from various sources, and none was specifically designed for this study. All 14 surveys were carried out between 2010 and 2020 and were different in design; some only recorded observations where BBTD was present, some recorded presence and absence, and still others recorded the on-farm incidence or severity of BBTD. In four datasets, no coordinates were available and therefore the BBTD observations were georeferenced from published maps. All datasets were subjected to several preprocessing and cleaning operations using R software (R Core Team, 2021), ArcGIS (Environmental Systems Research Institute, 2015) and Microsoft Excel, where (1) all observations were converted into the World Geodetic System 1984 (WGS84) coordinate system, (2) when observations had identical coordinates, only the first observation was kept, and (3) observations without coordinates were deleted. We explicitly focused on rain-fed *Musa* systems and therefore, eight of the field survey observations that were in areas unable to sustain bananas without additional irrigation (assuming precipitation of more than 800 mm per year was required) were deleted. The datasets were combined and plotted in Figure 1, which clearly illustrates BBTD to be widely spread in most sampled regions.

2.3 | Auxiliary environmental datasets

Eleven publicly available environmental datasets that were thought to have a plausible and significant relationship with BBTD or its aphid vector were selected as auxiliary covariates in a logistic regression model. The covariates were available in the public domain as spatially exhaustive maps for the entire African continent (Table 3). The first covariate was a digital elevation model that described altitude. Six covariates described temperature and precipitation in the period 1970 to 2000 (Fick & Hijmans, 2017). One covariate was the normalized differential vegetation index, which is a measure of the "greenness" of each cell over the period 1999 to 2017. Three covariates related to banana and plantain production (International Food Policy Research Institute, 2019). All covariate raster datasets were transformed into the WGS84 projection, and the cell size was converted to 30 arcseconds, which equals approximately 1 km, using R software (R Core Team, 2021). The raster datasets related to banana and plantain production contained cells with no values, which were reclassified to the value 0. The final covariate delineated the *Musa* areas in Africa and was the result of an undocumented banana mapping project undertaken by the International Institute of Tropical Agriculture (IITA) and Bioversity International and aided by regional banana experts. Spearman's rank correlation was calculated between the binominal disease variable and the covariates.

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TABLE 2 Number of field observations of banana bunchy top disease (BBTD) and average level of BBTD presence (%) for all 14 field surveys.

Dataset	Year	Source	No. of observations	Average BBTD presence (%)
Burundi (BXW/BBTD survey)	2015/2018	ISABU, Burundi (data)	205	100
Burundi (PRA)	2015	CGIAR RTB cluster CC3.1 (data)	93	80
Rwanda (PRA)	2015	CGIAR RTB cluster CC3.1 (data)	50	0
Burundi, Democratic Republic of Congo (PRA)	2015	CGIAR RTB cluster CC3.1 (data)	26	100
Democratic Republic of Congo	2014	Boloy et al. (2014)	129	100
Democratic Republic of Congo (FAO-IITA-UCG)	2010	Anonymous (2010)	13	100
Benin, Burundi, Democratic Republic of Congo, Kenya, Nigeria, Rwanda, Tanzania, Uganda, Zambia (maps in publication)	2013	Beed (2013)	115	38
Democratic Republic of Congo (maps in publication)	2014	Mukwa et al. (2014)	81	56
Angola, Cameroon, Democratic Republic of Congo, Gabon, Malawi (maps in publication)	2011	Kumar et al. (2011)	158	46
Benin	2018/2019	CGIAR RTB cluster CC3.4 (data)	71	70
Burundi	2016/2019	CGIAR RTB cluster CC3.4 (data)	76	99
Cameroon, Congo, Equatorial Guinea, Gabon	2015	Food and Agricultural Organization (2018b)	67	100
Togo	2018	Kolombia et al. (2021)	20	10
Uganda	2020	CGIAR RTB cluster CC3.4 (data)	56	30
Total			1160	70.6

2.4 | Environmental suitability for initial BBTD establishment and possible wider spread

The environmental suitability for BBTD establishment and spread (International Plant Protection Convention, 2023) within African landscapes was calculated with a generalized linear regression model, using the 'glm' function in R. The covariates were not preprocessed prior to analysis. Regression models predicted possible BBTD occurrence at unobserved locations using the relationship between the observed locations and environmental auxiliary datasets, here named covariates (Table 3). A spatial overlay resulted in a database of the field observations with values for BBTD presence and each of the 11 covariates, which served as input for fitting the regression model. Logistic regression was applied because the dependent variable (BBTD presence) was binary, either 1 for the presence of the disease or 0 for absence.

The theory and practical application of logistic regression are explained in research by Bouwmeester et al. (2012, 2016) and, therefore, only briefly described here. First, all covariates were entered into a univariate logistic regression model. The covariates with a significance level of $p < 0.25$ were entered into a multivariate logistic regression model. Then, using backward stepwise regression, the covariates that were not significant at the $p = 0.05$ level or did not contribute enough to lowering the deviance of the model were removed, one at a time. The goodness-of-fit of the model was assessed in terms of deviance and compared to the null model (i.e., the model without covariates) using the likelihood ratio test. Finally, the derived logistic regression model was applied to the remaining covariate maps to predict the environmental suitability of the African landscapes for BBTD establishment and wider spread.

2.5 | Risk of disease entry and initial establishment

The risk of disease entry and initial establishment (International Plant Protection Convention, 2023) depends on traffic (trade and connectivity of landscapes) and environmental and topographic covariates. The methodology to assign a risk of disease entry and initial establishment level for areas growing *Musa* is largely based on previous work by Ocimati et al. (2019). Instead of calculating the relationships for the entire African continent, as was done in the previous section, we only focused on the *Musa*-growing areas in Africa. These areas were delineated in a joint mapping exercise of the International Institute of Tropical Agriculture (IITA) and Bioversity International, and further detailed on the basis of the banana- and plantain-producing areas as defined by the International Food Policy Research Institute (IFPRI), that combines local crop production statistics and environmental data to map the world's main food crops (International Food Policy Research Institute, 2019). For Africa, with the help of regional and international experts, the areas were simplified and converted to distinct areas divided by country boundaries and dominant production systems in what we refer to as *Musa* areas (Figure 2). Note that on the map the '*Musa* areas' do not exactly coincide with the *Musa* production areas assigned by IFPRI because, in our opinion, the IFPRI marked areas are not always accurate/correct (e.g., in Ethiopia, Angola, South Africa, Kenya, Benin). We claim that our *Musa* areas

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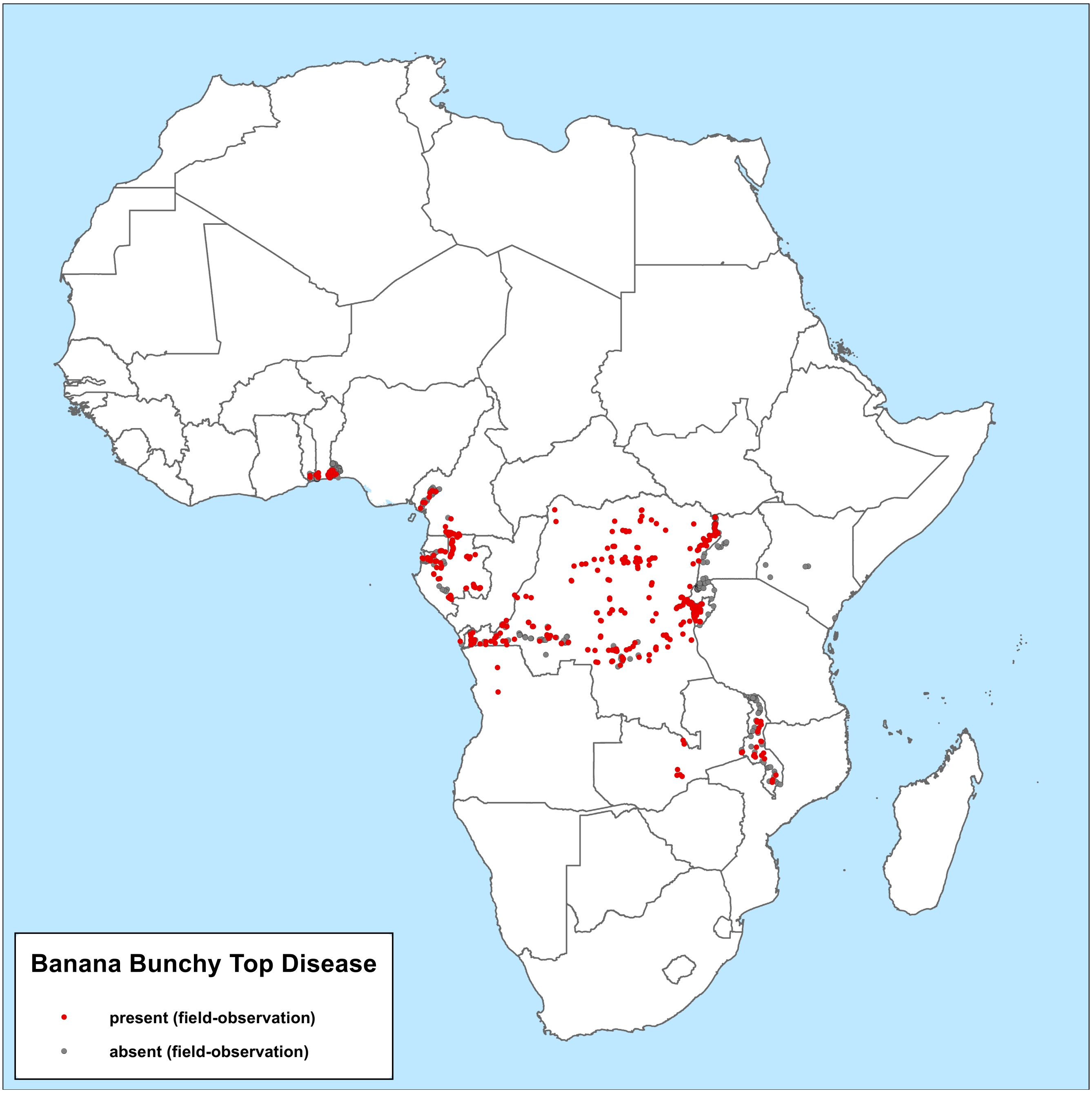

FIGURE 1 Distribution of field observations for banana bunchy top disease presence or absence in *Musa*-growing areas across Africa.

cover at least 95% of the major production areas in Africa. Additional highlighted regions (IFPRI map), outside of our marked *Musa* areas cover banana production areas of minor importance.

We selected six covariates that were deemed important in determining the risk of disease entry and assigned vulnerability scores to each (Table S1). The first covariate is the dominant *Musa* genotype within each area. Certain genotypes are more susceptible to BBTV than others, as reflected by the assigned vulnerability scores. The dominant genotype and the score were supplied by international experts from Bioversity, who based their judgement on available literature and insights into current disease epidemiology. In each area 'other' genotypes were assumed to be minor in terms of total *Musa* production and disregarded when assigning the scores. Altitude negatively influences vector activity (Niyongere et al., 2013) and temperature affects the aphid vector that transmits the disease. Instead of the actual temperature, we used the variability in temperature as it was more correlated to BBTD presence. For each area, we calculated the mean temperature variability using the covariate map from Table 3 and divided the values into five classes, to which we assigned vulnerability scores. Precipitation affects plant growth rates, which in turn affect aphid multiplication and transmission rates. We used precipitation itself, rather than its variability in time, as it was more correlated to BBTD. The mean annual precipitation of each area was calculated using the precipitation covariate (Table 3). A vulnerability

Description	Resolution	Website	Dataset
Altitude (m.a.s.l.)	30 arcsec	http://srtm.csi.cgiar.org	SRTM v4.0
Annual precipitation (mm)	30 arcsec	http://worldclim.org	WorldClim v2.0
Precipitation driest month (mm)	30 arcsec	http://worldclim.org	WorldClim v2.0
Precipitation variation	30 arcsec	http://worldclim.org	WorldClim v2.0
Mean annual temperature (°C)	30 arcsec	http://worldclim.org	WorldClim v2.0
Mean temperature coldest month (°C)	30 arcsec	http://worldclim.org	WorldClim v2.0
Temperature variability	30 arcsec	http://worldclim.org	WorldClim v2.0
Normalized differential vegetation index 1997–2017 (%)	30 arcsec	http://open.esa.int	c_gls_NDVI-LTS_1999-2017-1121_GLOBE_VGT-PROBAV_V221
Physical area under *Musa* (m^2)	5 arcmin	http://mapspam.info	SPAM 2010 v1.1
Musa production (kg)	5 arcmin	http://mapspam.info	SPAM 2010 v1.1
Musa yield (kg/ha)	5 arcmin	http://mapspam.info	SPAM 2010 v1.1
Musa areas in Africa	Vector		

TABLE 3 Covariates used for the regression analysis, having a plausible or significant relationship with banana bunchy top disease or its aphid vector.

score was assigned to the precipitation ranges based on available literature and insights into disease epidemiology. The optimal average precipitation range is between 1000 and 1500 mm/year, with vulnerability decreasing above and below this range. Geographical connectivity plays a role, as BBTD is mainly transmitted by winged aphids and planting materials transported by humans. The connectivity was assessed using the field observations where BBTD was present (Figure 1). The vulnerability score indicates whether the *Musa* area is geographically connected to another area that has positive BBTD observations. Similarly, geographical distance from infected areas influences the risk of pathogen entry, which decreases with increasing distance from infected areas. The distance is determined by calculating the geographical central point of each *Musa* area and measuring its distance from the nearest positive observation on the map (Figure 1). The areas in which positive observations were located received a distance value of zero kilometres. The six covariate maps were standardized (mean value of 0 with a standard deviation of 1) and combined to determine the overall risk of BBTD entry and initial establishment of BBTD in each area.

The risk of BBTD entry and the initial establishment was calculated as the sum of the values of the six standardized covariates, where, for each covariate, a weighting factor was assigned by two international experts of our group with good knowledge of the epidemiology of banana diseases, who based the ranking on available literature and insights in disease epidemiology (Table 4).

2.6 | Priority areas for interventions

Ultimately, the priority areas for interventions, such as surveillance, quarantine measures and extended monitoring, were calculated by simply adding the environmental suitability for possible wider spread and the risk of entry and initial establishment within each area, where the suitability and the risk of entry were both standardized before summation to ensure equal weight. The logic behind this methodology was that interventions (such as surveillance and spread prevention) should be prioritized in areas that have a high environmental suitability to possible wider spread and a high risk of entry and initial establishment.

2.7 | Validation

To validate the model that predicts the environmental suitability to initial BBTD establishment, we used 10-fold cross-validation. The 1160 observations were randomly split into 10 folds, each containing 116 observations. Each of the 10 folds was used in turn to define a validation dataset (10% of observations), while the other nine folds defined the training dataset (90% of observations). Using the training dataset only, a logistic generalized linear regression model was fitted, using the same methodology as described earlier, to predict the environmental suitability for initial BBTD establishment. With this model, predictions were made for the validation dataset. After doing this 10 times, the validation results were combined, resulting in a dataset that included the binominal observed BBTD incidence value (0 or 1) and the continuous predicted value (between 0 and 1) for all 1160 cases. Note that the observation itself was not included to calculate its own predicted value. From the observed and predicted values, the mean absolute error was calculated, which characterizes the systematic error. As, in our case, the observed value was binary, either 0 or 1, and the predicted value was numerical, in between 0 and 1 the Brier score was calculated, which is a statistical validation metric for probabilistic predictions of binary events (Spiegelhalter, 2019).

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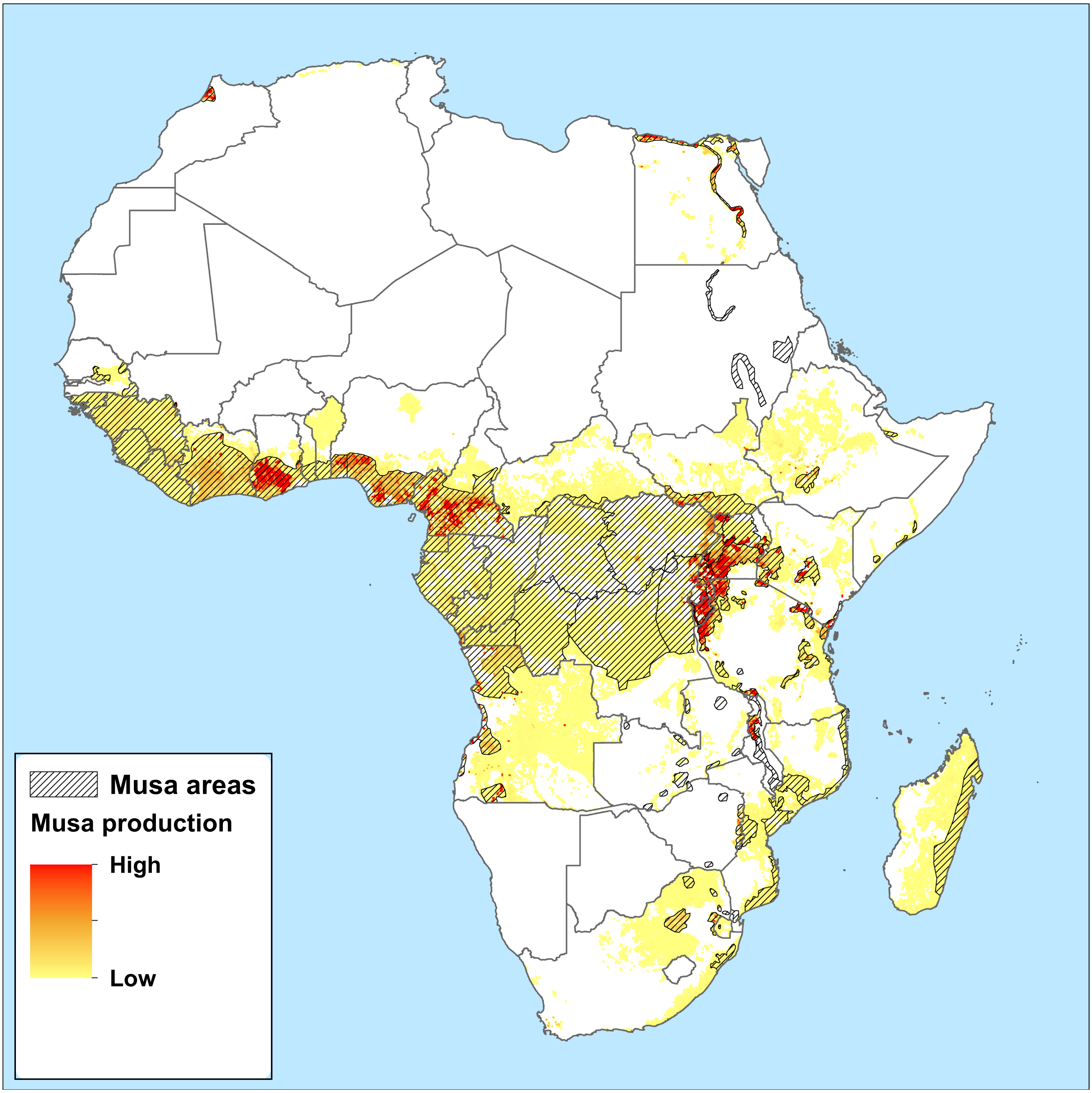

FIGURE 2 Main *Musa* production areas in Africa. The hatched '*Musa* areas' were obtained from the 'banana mapper project', a joint mapping exercise of the International Institute of Tropical Agriculture and Bioversity International, while the coloured zones are derived from the Global Spatially Disaggregated Crop Production mapping project (International Food Policy Research Institute, 2019).

3 | RESULTS

3.1 | Correlations

Correlation coefficients between BBTD presence and covariates at field locations are low (Table 5). However, most of the correlations, with the exceptions of altitude, *Musa* yield, mean annual temperature and mean temperature of the coldest month, were very significant. The negative correlations with annual precipitation may suggest the development of BBTD is hindered by high rainfall levels. Variability of both temperature and precipitation seems unfavourable for the development of BBTD. The positive coefficients between BBTD and *Musa* production may suggest that BBTD benefits from increased production or density of the crop. The negative correlation with yields may be explained by better farm management. The positive correlation with the normalized differential vegetation index suggests that the greener an area, the more BBTD, which is logical as both bananas and aphids thrive in environments suitable for vegetation.

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TABLE 4 Weighting factors of covariates used for assigning risk of entry and initial establishment of banana bunchy top disease in Africa.

Covariate	Weighting factor	Weighting factor ratio
Dominant *Musa* genotype within area	70	0.17
Mean altitude of area (m a.s.l.)	65	0.16
Temperature variability	60	0.14
Precipitation (mm/year)	60	0.14
Connectivity to infected area	90	0.22
Distance to infected area (km)	70	0.17
Total		1.00

TABLE 5 Spearman rank correlation coefficients and *p* value between banana bunchy top disease presence of field observations and covariates.

Covariate	Correlation coefficient	*p*
Altitude above sea level (m)	−0.03	0.26
Musa areas	0.11	0.00
Physical area under *Musa* (m^2)	0.19	0.00
Musa production (kg)	0.18	0.00
Musa yield (kg/ha)	−0.01	0.68
Normalized differential vegetation index (%)	0.11	0.00
Annual precipitation (mm)	−0.07	0.01
Precipitation driest month (mm)	−0.13	0.00
Precipitation variation	−0.11	0.00
Mean annual temperature (°C)	0.00	0.90
Temperature variability	−0.19	0.00
Mean temperature coldest month (°C)	0.05	0.68

3.2 | Logistic regression model

A univariate logistic regression model was fitted between the BBTD incidence and all covariates. Not all covariates were significant but, nevertheless, they were included in the multivariate logistic regression model because these apparently contribute to lowering the deviance. In the stepwise regression procedure, the covariates temperature and precipitation were removed because these covariates did not contribute enough to lowering the deviance of the model or were not significant at the $p = 0.05$ level. The deviance of the logistic regression model (1154) is 17.9% smaller than for the null model (1405), which indicates that the covariates (Table 6) explain a larger part of the variation than the null model.

3.3 | Environmental suitability to possible wider spread of BBTD across African landscapes

The map that shows the environmental suitability for possible wider spread of BBTD across African landscapes (Figure 3) was calculated by applying the logistic regression model (Table 6) on the covariate maps. The map can be interpreted as the geographical expansion potential of BBTD, where the values reflect the probability of occurrence of BBTD. A high probability means the location is environmentally suitable for BBTD and a low occurrence probability means the location is not suitable. The occurrence probability for BBTD is clearly highest in tropical central and western Africa. Some *Musa* areas in southern Africa and Egypt represent production systems under irrigation and hence do not appear as suitable for BBTD infection, as all calculations are based on rain-fed systems. Parts of the Sahel and southern Africa have values of less than 1%, most probably due to the absence of rain-fed *Musa* production and unfavourable climatic conditions.

TABLE 6 Estimates and standard errors of covariates in logistic regression model between incidence of banana bunchy top disease and all covariates.

Covariate	Estimate	*SE*	*p*
Intercept	4.06×10^{0}	2.37×10^{0}	8.67×10^{-2}
Altitude (m a.s.l.)	-2.72×10^{-3}	5.04×10^{-4}	6.40×10^{-8}
Precipitation driest month (mm)	2.63×10^{-2}	7.72×10^{-3}	6.69×10^{-4}
Precipitation variability	1.85×10^{-2}	1.13×10^{-2}	1.03×10^{-1}
Mean temperature coldest month (°C)	-2.82×10^{-1}	8.52×10^{-2}	9.43×10^{-4}
Temperature variability	-1.19×10^{-2}	2.61×10^{-3}	4.97×10^{-6}
Normalized differential vegetation index (%)	2.04×10^{0}	7.09×10^{-1}	4.02×10^{-3}
Physical area under *Musa* (m^2)	6.55×10^{-4}	3.45×10^{-4}	5.77×10^{-2}
Musa production (kg)	1.16×10^{-4}	4.35×10^{-5}	7.85×10^{-3}
Musa yield (kg/ha)	-1.30×10^{-4}	2.75×10^{-5}	2.07×10^{-6}
Musa areas	2.11×10^{0}	7.65×10^{-1}	5.90×10^{-3}

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3.4 | Risk of entry and initial establishment of BBTD across African landscapes

The risk of entry and initial establishment of BBTD across rain-fed African *Musa* production systems is illustrated in Figure 4. The numerical thresholds that define the five categories on the map (very low to very high) were chosen such that each category displayed about a fifth of the total. The map can be interpreted as the ease of BBTD entry into a landscape and its ability to perpetuate within an area after entry. The map suggests that the most vulnerable areas are in Central, West and South-East Africa. In some cases, this is irrelevant, as BBTD is already present in these areas (Figure 1). However, this map showing the risk of BBTD entry and initial establishment has noticeable differences when compared to the map showing environmental suitability for possible wider spread (Figure 3). Most conspicuous are the many areas that are environmentally suitable but have a low risk of disease establishment, such as the coastal areas in south-western and northern Africa, large parts of the Sahel region and interior south-western Africa. This can be explained by the fact that there are no or very few bananas grown in these areas; therefore, they are not included in the *Musa* areas map (Figure 2). Another difference is the areas that are highly suitable for wider spread but not at risk of entry, such as western Africa and Madagascar. This can be explained by the fact that BBTD has, so far, not been observed in production zones close to these areas, resulting in a large geographical distance to infected areas and a low connectivity to these areas.

3.5 | Priority areas

The priority areas (Figure 5) were calculated by summing the map of environmental suitability for possible wider spread (Figure 3) and the map that depicts the risk of entry and initial establishment (Figure 4). The numerical thresholds that define the five categories on the map were chosen such that each category displayed about a fifth of the total. The priority area map could be used as a prioritization tool to target areas in which surveillance and mitigation efforts are most needed. Areas in West and Central Africa, in the Great Lakes region of Eastern Africa, particularly Uganda and north-western Tanzania and the south-east of Africa, particularly in Malawi and Mozambique, score high on the prioritization index.

3.6 | Validation

The mean absolute error (predicted minus observed values) was −0.001, which means that the predictions were on average almost equal to the observed values and that the systematic error was negligible. The Brier score was 0.16, which means that the predicted probabilities were, on average, close to the observed outcomes.

4 | DISCUSSION

The high negative correlation of BBTD presence with precipitation and temperature variability suggests that a high climate variability is unfavourable for BBTD establishment and spread. This is supported by studies that have reported both extremes of rainfall and temperature to negatively impact either the survival of the BBTV aphid vectors and/or the transmission efficiency and development of the virus. Heavy rainfall and run-off have been reported to mechanically dislodge exposed aphid colonies, leading to a reduction in overall aphid populations (Kaakeh & Dutcher, 1993). In contrast, exceptionally low rainfall has also been associated with a quick decline in aphid population (Bakhetia & Sindhu, 1983).

Moderate temperatures between 25 and 30°C have been reported to be conducive for aphid population build-up and BBTV transmission, with extreme temperatures on either side reducing aphid populations and BBTV transmission efficiency. For example, the intrinsic growth rate of aphids and population build-up has been reported to be highest at 25°C, declining at lower and higher temperatures (Robson et al., 2007). Anhalt and Almeida (2008) observed a higher efficiency in BBTV transmission at 25 and 30°C than at 20°C while Wu and Su (1990) observed no BBTV transmission at 16°C and a maximum transmission efficiency at 27°C.

The high positive BBTD presence correlations with 'area under *Musa*', '*Musa* production areas' and '*Musa* yields' are not surprising as a high production density of the banana crop creates an environment for the build-up of the BBTV aphid vector and, thus, a higher chance for BBTD presence and spread. The high positive correlation with the normalized differential vegetation index can be attributed to the fact that environments that support an abundance of vegetation are also suitable for banana production.

Despite being small, altitude had a negative correlation with BBTD presence possibly due to temperature being negatively correlated with altitude. This negative correlation supports earlier studies (Niyongere et al., 2013; Walangululu et al., 2010) that reported a higher BBTD prevalence at low altitude sites characterized by warm and humid conditions, and vice versa. Spread to higher altitude sites (e.g., in Burundi and eastern Democratic Republic of Congo) has been primarily attributed to the movement of banana planting materials from infected lower altitude production areas. Furthermore, the previously colder high-altitude sites are gradually warming up and are thus becoming more suitable for aphid vector population build-up and virus transmission efficiency. In addition, *Musa* can grow in hot and humid lowland sites (e.g., plantains in West and Central Africa) as well as highland locations (up to 2200 m a.s.l.) along the Albertine rift valley where the East African Highland bananas (AAA-EAH) thrive. Given the findings of this study, expected future increases in temperature will make the high-altitude regions more suitable for the survival and population build-up of the aphids and enhance virus transmission efficiency and disease severity. This is especially crucial for the highland production areas of the East African region that are currently predominantly free of the disease. Thus, understanding the potential risks associated with

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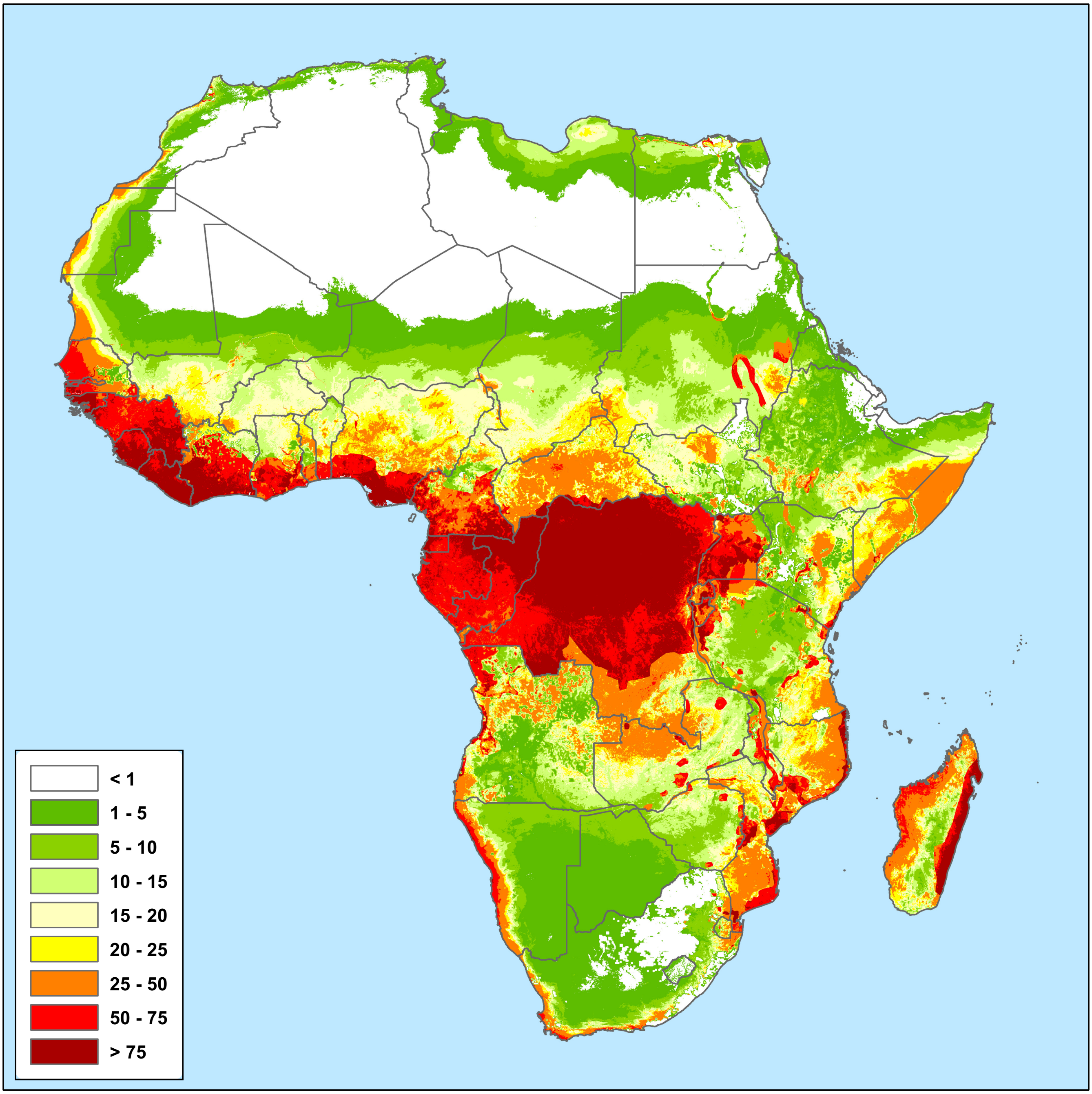

FIGURE 3 Map of the predicted environmental suitability for possible wider spread of banana bunchy top disease (BBTD), derived from regression of covariates. The values shown reflect the probability of occurrence of BBTD.

projected changes under future climatic conditions is crucial for the implementation of proactive measures in managing BBTD across banana-producing landscapes.

The environmental suitability for possible wider spread of BBTD suggests that all banana-producing landscapes are suitable for the establishment and subsequent spread of the virus. A large swathe of areas covering mainly Central Africa, parts of West Africa, and regions within East Africa are highly suitable. Environmental conditions suitable for the banana crop also support the survival of the banana aphid, which is the sole vector for the virus. BBTD is increasingly observed at cooler, higher altitude sites (up to 1800 m a.s.l.). The disease mainly arrives at these sites through the movement of planting materials. Although aphid vector-mediated spread at these higher altitude sites is limited, it shows that the disease can be present and impact yields across most altitude ranges where banana is cultivated. Finally, the low-temperature variability observed within most of the rain-fed banana production areas of Africa favour BBTD.

The map showing the risk of entry and initial establishment of BBTD shows a high infection risk in the Central and West African regions because of favourable environmental and topographic conditions, and because many positive field observations have been in these areas. The map shows large swathes of production areas in

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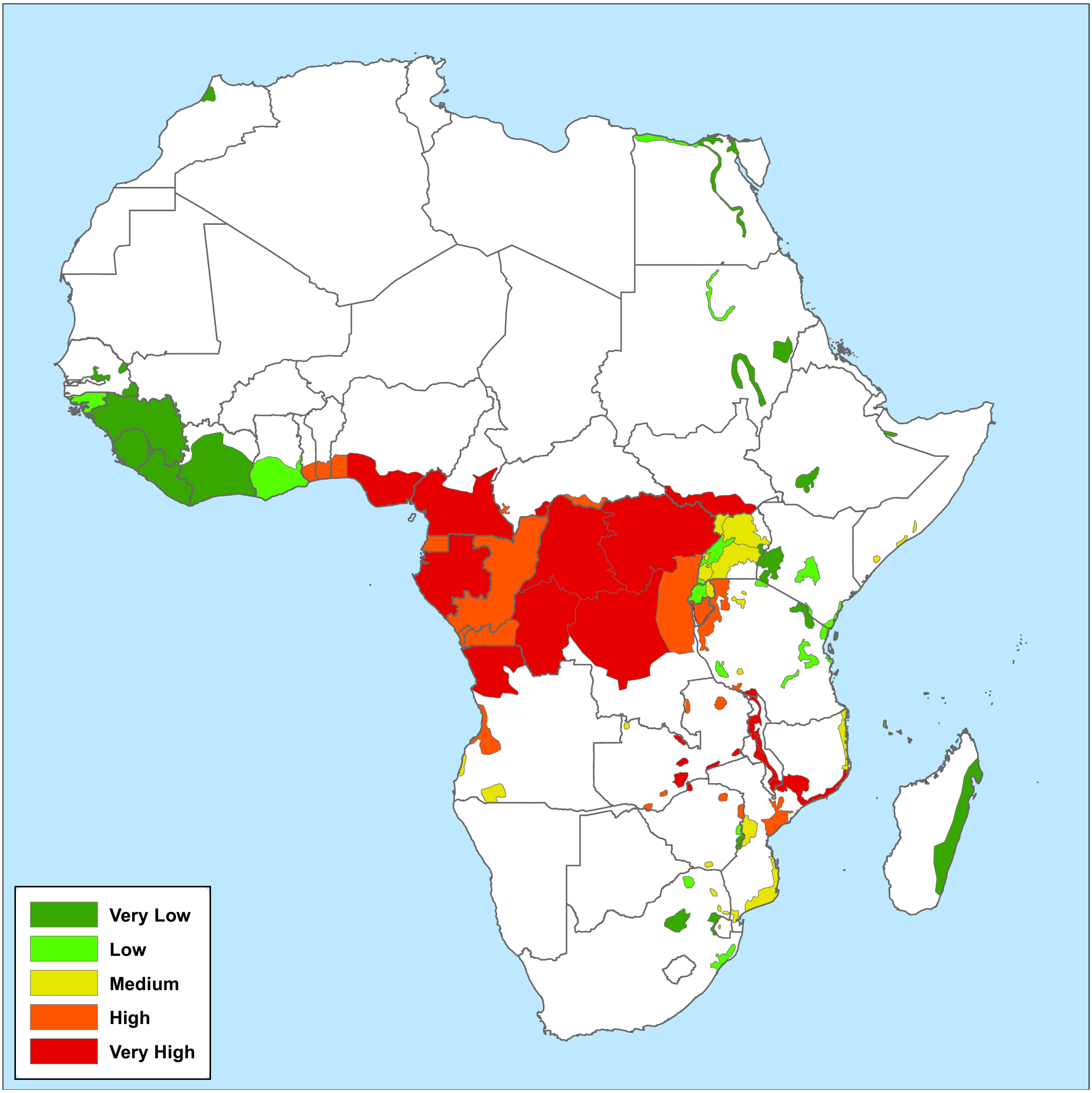

FIGURE 4 Map showing the risk of entry and initial establishment of banana bunchy top disease (BBTD). The vulnerability scores of six covariates: altitude, dominant *Musa* genotype, temperature variability, precipitation variability, connectivity with and distance to an infected *Musa* area, were based on the available literature and insights into disease epidemiology by international experts work on banana diseases. Maps of vulnerability scores for each of the covariates were standardized and combined to produce this map of overall risk of entry and initial establishment of BBTD.

Uganda and other parts of eastern Africa to be vulnerable to the disease. This can be attributed to their closeness and connection to infected areas in central and southern Africa. The risk of infection declines northwards, southwards and eastwards towards the Indian Ocean from the epicentres in the west and central Africa. This can be attributed to the reduced connection of these areas and unfavourable climatic conditions for both the banana crop and the aphid vectors.

The *Musa* production areas in central and west Africa, including countries of Nigeria, Benin and Togo, Malawi, and Mozambique, are ranked highest in the priority score. Most of these already have the disease and efforts here need to focus on disease mitigation and preventing further local spread.

Production areas in Uganda, adjacent to the Democratic Republic of Congo border and around Lake Victoria rate high on the priority score, possibly due to their relative closeness/connectivity to infected

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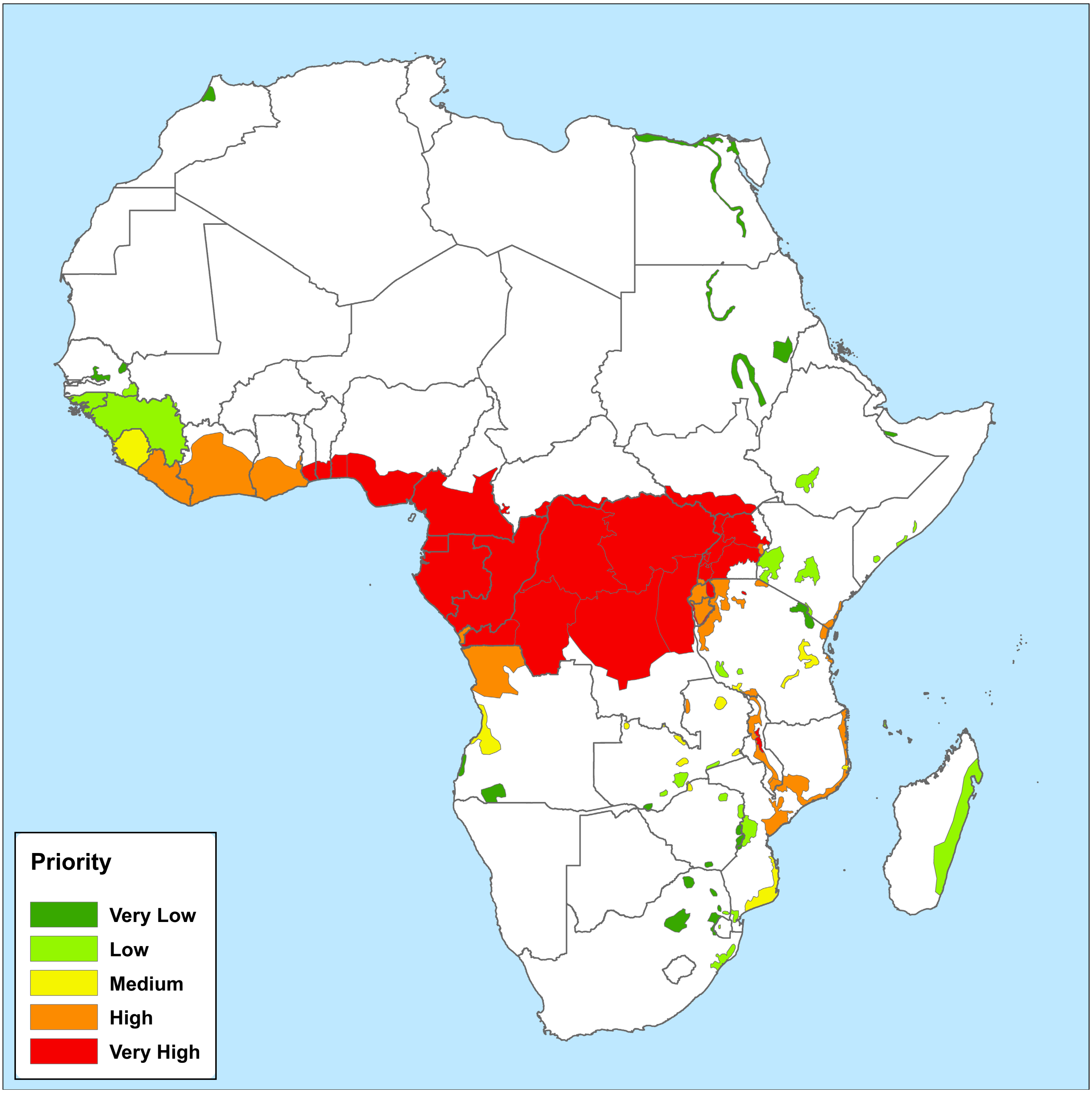

FIGURE 5 Map of priority areas for future surveillance and mitigation efforts against banana bunchy top disease (BBTD) of *Musa*. Areas were calculated as the sum of the environmental suitability for possible wider spread of BBTD and the risk of entry and initial establishment of BBTD.

areas in eastern Democratic Republic of Congo and favourable climatic conditions for BBTD establishment and spread. Recent reports on the presence of BBTD in the north-western region of Uganda (Ocimati et al., 2021) and north-western Tanzania (Shimwela et al., 2022) support these risk predictions. For these and other priority areas not yet infected, measures for close surveillance, quarantines and proactive management of the disease are needed.

The accuracy of the environmental suitability map is limited as the deviance of the logistic regression model is only 17.9% smaller than the null model. Reasons for the limited accuracy could be attributed to the sampling design of the surveys (i.e., low sampling density of the surveys in relation to the large area of interest and high variation of measurements at close range). In general, increasing the sampling density and/or applying a more uniform distribution of the observation sites could improve the accuracy of the prediction maps (Stein & Ettema, 2003). However, in this case, a more systematic survey design would be hindered by the large size of the study area and the practical difficulties that this raises. The observations of BBTD were made using different designs. The graded scale (i.e., severity on farmer fields) used in some of the

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surveys is probably better suited for predicting BBTD than the binary scale. The surveys are biased towards positivity because 70.6% of the observations were from surveys that only recorded the presence of BBTD. It is likely that the occurrence probability would generally have been lower if the surveys had also recorded the absence of BBTD. Field observations at larger spatial supports (averages over larger areas) may be a more adequate solution to tackle this problem because such averaging would lead to measurements from which local variability has partly been removed (Goovaerts, 1997). Hence, these measurements would probably be correlated more strongly with the coarse covariate maps (i.e., improved regression results). However, this would require tailored surveys and it was not possible to do this with the available surveys. Measurement errors may be reduced by harmonizing protocols and improved training of assessors. It is difficult to quantify the accuracy and confidence of the observations without doing additional validation surveys. Although BBTD symptoms are conspicuous, detectability of BBTD within banana fields by the assessors is not always very straightforward and may have affected the quality of the dataset used in this study.

The model of environmental suitability for initial BBTD establishment was validated using 10-fold cross-validation, with which the numerical (mean absolute error) and categorial (Brier) statistical metrics were calculated. Conventional cross-validation, as used in this study, may lead to overoptimistic results in datasets that are spatially clustered. It would be interesting to explore validation techniques that take account of these issues, such as spatial and weighted cross-validation (de Bruin et al., 2022).

The map of environmental suitability for initial BBTD establishment shows predictions for the entire African continent, while the actual observations are limited to clusters of observations in mainly Central and Eastern tropical Africa. In a conservative approach, we would not have shown the suitability predictions of unsampled areas outside the tropical Africa in Figure 3 because of extrapolation issues and because it is not possible to validate the predictions. Nonetheless, we opted to include predictions in these areas as results were generally deemed realistic by the authors.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Hein Bouwmeester https://orcid.org/0000-0001-6242-0295
Aman Bonaventure Omondi https://orcid.org/0000-0001-9711-5645
Walter Ocimati https://orcid.org/0000-0001-6177-7073

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