# Pathogen and pest communities in food security crops across climate gradients: Anticipating future challenges in the Great Lakes region of Africa

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## Abstract

Natural and human-driven disasters are a significant challenge to the sustainable production of food security crops in the Great Lakes region of Africa. A relevant research gap is the effect of climate change on the distribution of pathogens and pests of food security crops in this region. We evaluated the current geographic risk of pathogens and pests in the production of four food security crops — banana, cassava, potato, and sweetpotato — in the region, and the potential future risk under climate change. First, cropland connectivity analysis identified locations likely important in the spread and establishment of crop-specific pathogens and pests for each crop, with locations in Rwanda and Burundi emerging as important across crops. Second, we surveyed 27 economically important pathogens and pests in Rwanda and Burundi, mapping their distribution across landscapes and quantifying patterns of association. Cropland density, cropland connectivity, altitude, and contemporary and long-term temperature and precipitation were strongly associated with disease severity and pest infestation. Among ten machine-learning algorithms evaluated, random forests and support vector machines generally performed best for predicting severity and infestation. Third, an increase in temperature across altitudes is projected under future climate change scenarios in this region. We found evidence that 44% of the pathogen and pest species we studied in banana, potato, and sweetpotato could become more common with warmer temperatures at higher altitudes, while 17% may become less common. Ongoing development of pathogen and pest forecasts can guide strategic surveillance, mitigation and adaptation to future epidemics and pest invasions in high-risk crop locations under climate change.

# 1 | INTRODUCTION

## 1.1 | Impact of climate and crop landscape structure on pathogen and pest damage

The Great Lakes region of Africa faces recurrent disasters, exacerbated by climate variability, fragile ecosystems, and societal dynamics including demographic pressures, socio-political instability, and resource-related conflicts (Ong'ayo, 2018, Ogot & Niane, 1984). The geographic structure of cropland in this region, including crop density, cropland connectivity, and crop diversity, is influenced by heterogeneous agricultural practices, creating local habitats that can support the spread of pathogens and pests. Suitable climate factors such as rainfall, temperature, and relative humidity are essential to achieving optimal plant growth and maximum crop yields. However, climate change is likely to affect agricultural productivity and exacerbate the proliferation of some pathogens and pests in this region (Okonya & Kroschel, 2013, Ebregt *et al.*, 2005, Ferdu & Solbreck, 2010, Gallego-Tévar *et al.*, 2024). It reshapes ecosystems by altering temperature and precipitation patterns, driving pathogens and pests into new locations (Cilas *et al.*, 2016, Garrett *et al.*, 2022a, Garrett *et al.*, 2022b, Sparks *et al.*, 2014). The interactions among climate variability, the geographic structure of cropland, and the biology of pathogens and pests in this region remain poorly understood and represent a major knowledge gap. Although research has examined how climate change affects the dynamics of specific pathogens and pests (Adhikari *et al.*, 2015, Blomme *et al.*, 2020, Kroschel *et al.*, 2014), little is known about how regional factors—such as the geographic structure of cropland of key food security crops in the Great Lakes region—exacerbate these risks, including the potential for altitudinal shifts of pathogen and pest communities under climate change.

Climate matching identifies which locations have similar climate conditions, which may be equally suitable for a species; ecological communities may move following changes in where suitable climate conditions are found in the future (Colwell *et al.*, 2008, Chevalier *et al.*, 2024, Singh *et al.*, 2023). For example, pathogen and pest communities now at hotter, lower altitudes may move to what are currently cooler, higher altitudes if there is warming due to climate change. The dynamics of pathogens and pests across climate gradients have been widely studied (Hodkinson, 2005, Mishra *et al.*, 2024, Juroszek *et al.*, 2022, Pautasso *et al.*, 2012). Higher altitudes are commonly associated with lower species richness, disease severity, and pest damage (Blomme et al., 2020, Hodkinson, 2005). Since altitude is typically negatively correlated with temperature (Poveda *et al.*, 2012), altitude can be a useful proxy when evaluating the effect of temperature on crop disease and pest damage. For example, previous studies in South America and East Africa predicted that rising temperatures due to climate change will modify the geographic distribution of pathogens and pests, increasing crop disease severity or pest damage at higher altitudes (Blomme et al., 2020, Poveda et al., 2012). New climate conditions favorable to certain pathogens and pests are likely to occur at higher altitudes, disrupting ecological balances and exposing high-altitude crops and ecosystems to new risks.

The geographic distribution of crop production can also influence geographic patterns of disease severity and pest damage. Crop landscape structure has been well documented to influence crop damage from diseases and pests (Poveda et al., 2012, Thies & Tscharntke, 1999). Analysis of the network structure of crop landscapes, such as cropland connectivity analysis, has been used to identify candidate priority locations for surveillance and management of crop-specific pathogens and pests (Xing *et al.*, 2020, Andersen Onofre *et al.*, 2021, Buddenhagen *et al.*, 2022). A general

assessment of cropland geographic structure helps us understand the potential introduction, establishment, and spread of pathogens and pests. Higher crop density increases the local risk of crop-specific pathogen and pest establishment, while greater cropland connectivity also increases the risk of spread and establishment.

### 1.2 | Disaster plant pathology: Vulnerabilities and solutions in the Great Lakes region

Many families living in the Great Lakes region rely on food security crops such as banana and plantain, cassava, potato, and sweetpotato. However, many households remain food insecure because of declining agricultural productivity, driven by frequent disasters in the region, including conflicts, health emergencies, and natural disasters that displace populations and disrupt agriculture (Ochieng *et al.*, 2015, Ochieng *et al.*, 2014, Ong'ayo, 2018). These challenges are compounded by the cascading effects of high prevalence of pests and diseases, low agricultural input use, loss of harvest and assets, dysfunctional or non-existent markets, high food prices, and socioeconomic conflicts (McEwan, 2016, Almekinders *et al.*, 2019, Kroschel et al., 2014). The Rwandese genocide in 1994, the civil war in Burundi from 1993 to 2005 and also in 2015, and the persistent conflicts in Eastern DR Congo are particularly important humanitarian disasters in the Great Lakes region, which have left an indelible mark (Ong'ayo, 2018). Health emergencies and natural disasters, such as severe droughts in Ethiopia, Kenya, and Uganda (2015-2016) and devastating floods in Rwanda, Uganda, and DR Congo (2020), have severely restricted agricultural practices such as effective surveillance and management of fields, causing considerable damage to infrastructure and cropland (Ochieng et al., 2015, Ochieng et al., 2014).

Disaster plant pathology, integrating concepts from plant pathology and disaster science,

114 addresses the risks and potential impact of plant diseases before, during, and after disaster
115 events that threaten agricultural systems and ecosystems (Etherton *et al.*, 2024, Mouafo-
116 Tchinda *et al.*, 2024). It focuses on disturbances that modify host-pathogen dynamics and
117 increase damage and the spread of pathogens, and the development of strategies for better
118 managing plant health. A combination of global and national research efforts has been adopted
119 to manage the impacts that these disasters, pathogens, and pests may have on agroecological
120 systems (RTB, 2013, Science Group Project on Accelerated Varietal Improvement and Seed
121 Systems in Africa, 2024). For example, disease control programs which encourage farmers to
122 recognize and destroy diseased plants, and disease-resistant crop breeding programs are
123 currently underway across the Great Lakes region.

124 When models of pathogen and pest responses to environmental variables are available,
125 decision-support tools can be developed to predict where specific disease- and pest-resistant
126 varieties will be needed in the long-run, and in the short-run whether likely economic injury
127 levels motivate management actions by growers (Fenu & Malloci, 2021, Kaundal *et al.*, 2006,
128 Carisse & Fall, 2021). Pest and disease forecasting can reduce production costs, pesticide use,
129 and environmental pollution, protecting the health of farmers and consumers. Machine learning
130 can analyze high volume datasets, and improve the predictive power, accuracy, and efficiency
131 for diseases and pests (Garrett et al., 2022a, Kaundal et al., 2006). Implementing decision
132 support systems in low-resource countries such as those in the Great Lakes region is challenging;
133 in addition to the often-limited availability of high-resolution local weather data as input to
134 models, field observations and georeferenced datasets for the many important pathogen and
135 pest species are often unavailable for constructing predictive models.

136 ## 1.3 | Objectives

137 In this study, we evaluated the geographic risk of pathogens and pests in the production of four
138 food security crops — banana (including plantain), cassava, potato, and sweetpotato — in the
139 Great Lakes region of Africa, including the potential future risk under climate change. The first
140 objective was to analyze the geographic risk of crop-specific pathogen and pest spread based on
141 crop landscape connectivity for these crops. The second objective was to characterize the
142 seasonal and geographic occurrence and associations of 27 economically important pathogens
143 and pests affecting these crops, through field surveys conducted in two key locations in the
144 region, Rwanda and Burundi. Part of this dataset has been used to characterize the prevalence of
145 potato viruses and vectors (Okonya *et al.*, 2021) and the occurrence of banana pests and
146 diseases across altitudes (Nakato *et al.*, 2023). The third objective was to predict pathogen and
147 pest severity/infestation based on climate variables and crop landscape structure using machine
148 learning, and to assess which pathogens and pests are likely to experience altitudinal range shifts
149 under projected changes in temperature. The field surveys were implemented along
150 environmental gradients to compare low- and high-altitude pathogen and pest communities,
151 where lower-altitude communities have the potential to move toward higher altitudes in the
152 future. These risk assessments can support decision-making by (i) national agricultural agencies
153 that plan geographic surveillance strategies for economically important pathogens and pests, (ii)
154 local agricultural research communities and international partners as they prioritize efforts to
155 improve current and future mitigation responses to pathogens and pests, and (iii) farmer
156 communities that need to be prepared for changes in pathogen and pest dynamics due to
157 natural or human-driven disasters or changing climates.

## 2 | METHODS

### 2.1 | Landscape structures influencing pathogen and pest risk

#### 2.1.1 | Identifying locations with high cropland connectivity

The spatial pattern of host availability is a key ecological trait that influences the spread of crop-specific pathogens and pests. We analyzed the connectivity of crop landscapes in the Great Lakes region to map the potential establishment and regional spread of crop-specific pathogens and pests, to identify candidate priority locations for spatially targeted surveillance in four food security crops — banana (including plantain), cassava, potato, and sweetpotato. This cropland connectivity analysis assesses how crop production is connected in a landscape, based on host availability and physical proximity in a gravity model (Jongejans *et al.*, 2015). Cropland connectivity analysis identifies potential habitat networks through which pests and pathogens can spread between croplands, a first approximation to epidemic or invasion networks, which can be improved as more data become available (Margosian *et al.*, 2009, Xing et al., 2020, Andersen Onofre et al., 2021).

For each crop, we used publicly available estimates of the cropland harvested area (or cropland density) across sub-Saharan Africa in 2017 (International Food Policy Research Institute, 2020) as a proxy for host availability to crop-specific pathogens and pests. Maps of cropland density, aggregated at a spatial resolution of 10-min (or grid cells of image 9.27 km × 9.27 km), were used to evaluate the potential epidemic or invasion network using a gravity model (Xing et al., 2020). Here the gravity model incorporated two pathogen or pest dispersal kernels: $c_i c_j d_{ij}^{-\beta}$ for the

178 inverse power law model, and $c_i c_j e^{-\gamma d_{ij}}$ for the negative exponential model. In each dispersal
179 model, $d_{ij}$ is the Vincenty ellipsoid distance between a pair of cropland nodes (locations) $i$ and $j$,
180 $c_i$ is the cropland density for node $i$, and $\beta$ and $\gamma$ are dispersal parameters describing the
181 relative likelihood of pathogen or pest movement across $d_{ij}$(Xing et al., 2020, Andersen Onofre
182 et al., 2021).

183 We calculated a cropland connectivity risk index (CCRI) (Xing et al., 2020) for each location with
184 crop production in the region as a measure of its likely importance in epidemic or invasion
185 networks. The CCRI was the weighted mean of four network metrics (node centralities),
186 evaluated using the geohabnet package v2.0.0 (Keshav *et al.*, 2024) in R v4.4.0 (R Core Team,
187 2024), averaged across the results from a sensitivity analyses for a range of dispersal
188 parameters, as described by Mouafo-Tchinda et al. (2024). Two CCRI formulations were used to
189 capture key facets of node connectivity. The first CCRI considered ("CCRI-betweenness") was the
190 mean of betweenness centrality weighted by 1/2, node strength weighted by 1/6, eigenvector
191 centrality weighted by 1/6, and the sum of nearest neighbors' degrees weighted by 1/6. The
192 second, "CCRI-closeness", considered 1/2 closeness centrality instead of betweenness centrality,
193 with the same weights for the other metrics. We emphasized betweenness or closeness
194 centrality to account for, respectively, the importance of a node as a bridge between parts of the
195 network and the relative facility with which a location can be reached from all other locations in
196 the network.

197 Habitat connectivity analysis using the geohabnet package (Keshav et al., 2024) is part of the
198 R2M toolbox for rapid risk assessment supporting mitigation of pathogens and pests

199 (garrettlab.com/r2m). Other examples of applications of habitat connectivity and R2M tools, in
200 addition to those discussed elsewhere in this paper, illustrate how these tools can be used in an
201 integrated analysis (Mouafo-Tchinda et al., 2024, Andersen Onofre *et al.*, 2019, Etherton *et al.*,
202 2025, Etherton *et al.*, 2023, Garrett, 2021).

### 203 2.1.2 | Associations among altitude, crop landscape structure, and climate

204 We characterized associations among altitude, crop landscape structure, and climate in the
205 Great Lakes region. The map of altitudes was retrieved from the Shuttle Radar Topography
206 Mission (SRTM) database, using the geodata package v0.5-8 (Hijmans *et al.*, 2023) in R. We also
207 retrieved the 19 bioclimatic variables for the region from Worldclim database v2.1 (Fick &
208 Hijmans, 2017) using the geodata package version 0.5-8 (Hijmans et al., 2023) and the terra
209 package v1.8-0 (Hijmans, 2024) in R. For crop landscape structure variables, we used the raster
210 maps of cropland density and connectivity (CCRI-closeness) generated in section 2.1.1, using the
211 terra package (Hijmans *et al.*, 2022). We assessed the associations between altitude, bioclimatic
212 variables, and cropland structure by calculating the Pearson correlations between these
213 variables using the metan package v1.18.0 (Olivoto & Lúcio, 2020) in R.

## 214 2.2 | Pathogen and pest communities

### 215 2.2.1 | Field sampling and spatiotemporal structure of pathogen and pest communities

216 For each crop species, we identified fields for sampling along four survey transects in Rwanda
217 and Burundi, each transect representing an altitude gradient. In Burundi, the field surveys
218 included cropland around Lake Tanganyika in the Rusizi watershed, representing the Bubanza,

219 Bujumbura Rural, Cibitoke, and Muramvya provinces (Figure 1C). In Rwanda, the field surveys
220 were in major cropland around Lake Kivu in the Ruhengeri watershed, which includes part of the
221 Northern and Western provinces (Figure 1C). The survey locations represented major crop
222 landscapes in both countries, encompassing a mixture of cropping systems and a range in
223 altitude from 900 to 2800 m.a.s.l. (Figure 1a-b) (Kroschel et al., 2014). Fields for sampling were
224 selected at regular intervals along the transects regardless of whether diseases or pest damage
225 were apparent. The number of fields sampled in Burundi and Rwanda was 189 and 103 for
226 banana, 78 and 116 for potato, and 107 and 104 for sweetpotato, respectively. For cassava,
227 sampling was only carried out in 50 fields in Burundi, with the second Burundi survey not
228 conducted due to civil unrest, and Rwanda was not sampled because few farmers grew cassava
229 in the Rwanda study area.

230 Sampling was conducted in each watershed during two cropping seasons, dry and rainy. In both
231 countries, two rainy seasons occur: one from March to May and the other from September to
232 December (WorldData.info, 2024). The dry seasons occur from June to August and January to
233 February (WorldData.info, 2024). For each field sampled, we evaluated crop-specific pest or
234 disease intensity (Table 2) based on prevalence in the region, disease severity, infestation rate
235 and intensity, and/or the number of pests, using methods as described by Nakato et al. (2023),
236 Okonya et al. (2021), and Legg *et al.* (2009). A total of 27 economically important pathogens and
237 pests in the region were included in this study, including 6 for banana, 6 for cassava, 7 for potato
238 and 8 for sweetpotato (Table 2). Here prevalence refers to the presence or absence of a pest or
239 disease in a field, while disease severity, pest infestation intensity or infestation rate is the
240 percentage of leaves or plants damaged by a disease or pest. For infestation rate, infestation

241 intensity, and severity, twenty plants per field, selected in a systematic pattern, were assessed
242 for visual symptoms of damage by pests and diseases. The percentage of plants infested was
243 noted as the infestation rate. The percentage of symptomatic leaves per plant was noted as
244 infestation intensity for pests and severity for diseases. For damage by some virus diseases and
245 pests such as cassava mosaic disease (CMD) and cassava green mite (CGM), crop damage was
246 scored from 1 (representing no symptoms) to 5 (the most severe) (Legg et al., 2009, Okonya et
247 al., 2021, Sseruwagi *et al.*, 2004). The disease or pest damage score measures the severity or
248 infestation intensity in a field, based on visual assessments and a predefined scale. Thirty plants
249 were randomly sampled at regular intervals along the season and damage was assessed by
250 scoring each plant on a scale of 1 to 5 as described by Legg et al. (2009).

251 For banana, fields were surveyed in Burundi in March 2015 (during the rainy season) and in July
252 2016 (dry season), while fields were surveyed in Rwanda in July 2015 (dry season) and in
253 November 2016 (rainy season). Cassava fields were surveyed only once in Burundi in March 2015

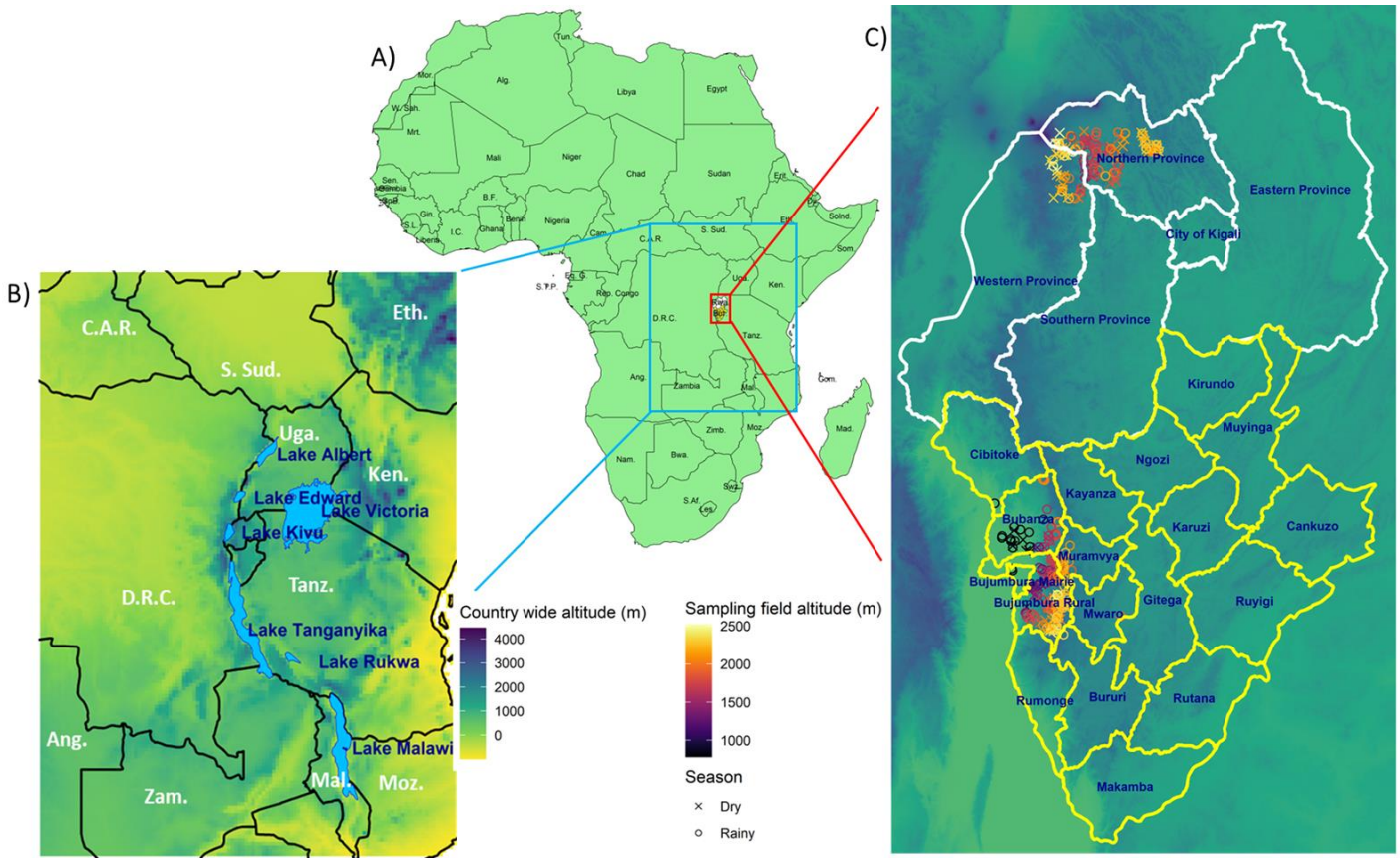


FIGURE 1| Location of fields of banana, cassava, potato, and sweetpotato where pathogen and pest surveys were carried out in Africa (A), in the Great Lakes region (B), in transects across altitude gradients, in Rwanda and Burundi (C). White lines in (C) indicate the province boundaries of Rwanda and yellow lines indicate the province boundaries of Burundi. Crosses and circles represent locations surveyed during the dry and rainy season, respectively. The complete surveillance effort included 412 crop fields.

(rainy season), for reasons described above. For potato, field sampling was conducted in Burundi in July 2016 (dry season) and December 2017 (rainy season), and in Rwanda in June-July 2015 (dry season) and November-December 2017 (rainy season). For sweetpotato, the field surveys took place in Burundi in November-December 2015 (rainy season) and August 2016 (dry season), and in Rwanda in July 2015 (dry season) and November 2017 (rainy season). The irregular dates for these crop-field surveys were due in part to the civil unrest prevailing in the region at the time the study was conducted.

261 2.2.2 | Quantifying patterns of field-scale association of crop pathogens and pests

262 We evaluated the patterns of association of pathogens and pests based on prevalence and
263 severity/infestation using non-metric multidimensional scaling (NMDS) (Kruskal, 1964) and
264 heatmaps (Pryke *et al.*, 2007) for visualization. We initially calculated five measures of
265 dissimilarity (Bray, Manhattan, Jaccard, Chao, and robust-Aitchison) in the NMDS analysis using
266 the ggvegan package v0.1.999 (Simpson, 2020) in R. We selected the Bray distance in the final
267 analysis due to its highest goodness of fit. A heatmap was prepared using the metan package
268 v1.18.0 (Olivoto & Lúcio, 2020) in R to map the association of pathogens and pests based on
269 prevalence and severity/infestation rates.

270 2.3 | Prediction of pathogen and pest damage and geographic range shifts

271 2.3.1 | Machine learning to predict pathogen and pest levels

272 Weather, climate, and geographic variables were used to predict severity or infestation
273 rates/intensity, comparing machine learning algorithms. We retrieved weather variables
274 (monthly, quarterly, and annual temperature, precipitation, and relative humidity) from the
275 NASAPOWER database using the nasapower package v4.0.10 (Sparks, 2018) in R. The climate
276 variables included the 19 bioclimatic variables, solar radiation (kJ m-2 day-1), wind speed (m s-1),
277 and water vapor pressure (kPa) described, along with the altitude variable, in section 2.1.2. The
278 CCRIs and cropland density were assembled as described in section 2.1.1.

279 Data were preprocessed to exclude collinearity between variables. A stratified split was then
280 used to divide the data into training and test sets in an 8:2 ratio. We then trained ten machine-

281 learning algorithms: logistic regression (GLM and GLMNET), support vector machine (SVM, with
282 linear and radial basis function), neural network (NN), k-nearest neighbors (KNN), stochastic
283 gradient boosting (GBM, generalized boosted modeling), bagged trees, classification and
284 regression trees (CART), and random forest (RF). We compared the performance of these
285 algorithms to predict the severity or infestation of each pathogen and pest using the caret
286 package v6.0-94 (Kuhn, 2008) in R. We selected SVM (with radial basis function) and RF for
287 further analyses based on their having the highest performance in terms of MAE (mean absolute
288 error), RMSE (root mean squared error) and R-squared (Kaundal et al., 2006).

289 In the next stage using the SVM and RF models, we executed a 10-fold cross-validation with ten
290 repetitions to prevent overfitting the training model and used a grid search for hyperparameter
291 tuning. The tuning process was driven by trainControl, with RMSE-based model evaluation to
292 prioritize accuracy. Hyperparameter tuning for SVM included C (regularization parameter) and
293 Gamma (kernel coefficient), both with a tuneLength of 10. Hyperparameter tuning for RF
294 included mtry (the number of predictors randomly selected at each division) with a tuneLength
295 of 10. We trained the model using the train function in the caret package and estimated the
296 performance parameters MAE, RMSE, and R-squared. We used the resulting model to predict
297 severity or infestation rate/intensity for the test data and estimated the performance
298 parameters (RMSE and R-squared).

299 2.3.2 | Pathogen and pest communities across altitudinal gradients

300 To study the geographic range of pathogen and pest communities associated with the four crops
301 in the sample transects in Rwanda and Burundi, we evaluated how pathogen and pest levels

302 (prevalence, disease severity or infestation rate/intensity) changed with altitude across the
303 sampling locations. We also evaluated the pathogen and pest richness (number of pathogens
304 and pests present from those included in the sampling) in communities during the dry and rainy
305 seasons, across the altitude gradients. The associations between prevalence, infestation/severity
306 and richness of pathogens and pests across altitude gradients were evaluated based on
307 Pearson's correlation.

308 2.3.3 | Climate change: impact on regional temperature patterns

309 We assessed potential climate shifts along the altitude gradients in the Great Lakes region, using
310 current and future temperature data from WorldClim database v2.1 (Fick & Hijmans, 2017). We
311 used future climatic variables from three global circulation models (GCMs: GISS-E2-1-G, MIROC6
312 and CNRM-CM6-1), two Shared Socioeconomic Pathways (SSP1-2.6 and SSP5-8.5), and four
313 future time-periods: 2021-2040, 2041-2060, 2061-2080, and 2081-2100. We selected these
314 GCM modeling groups because of their equilibrium climate sensitivity (ECS) (Hausfather, 2019).
315 ECS indicates the severity of future warming impacts. CNRM-CM6-1 assumes a high value of ECS,
316 4.9 C, while GISS-E2-1-G and MIROC6 assumes low values of ECS, 2.7 and 2.6 respectively
317 (Hausfather, 2019). The two SSPs used in this study represent different emission pathways by
318 the year 2100: sustainability (SSP1-2.6) and fossil-fuel development (SSP5-8.5) emission
319 scenarios featured by the radiation forcing of 2.6 and 8.5 W/m², respectively (Pinnegar *et al.*,
320 2021). We calculated the average annual temperature across the three selected GCMs for each
321 future time-period and SSP combination. We used the resulting density plots to assess potential
322 shifts in the distribution of annual mean temperature at low (<1500 m.a.s.l.) and high (>1500

m.a.s.l.) altitudes, using the ggplot2 package v3.5.0 (Wickham, 2016) in R.

# 3 | RESULTS

## 3.1 | Landscape structures influencing pathogen and pest risk

### 3.1.1 | Identifying locations with high cropland connectivity

The analysis of cropland connectivity in the Great Lakes region (i) indicates quantitatively how the geographic distribution of crop production could facilitate the potential spread of crop-specific pathogens and pests and (ii) identifies candidate priority locations for pathogen and pest surveillance for each food security crop (Figure 2). These maps of cropland connectivity highlight locations in the region that are likely important for understanding and managing the risk of crop-specific pathogens and pests.

In these maps of cropland connectivity, a higher CCRI-betweenness (Figure 2A) or CCRI-closeness indicates the potential to play an important role in the establishment and spread of crop-specific pathogens and pests affecting these crops, locations with high CCRI are candidate priorities for surveillance and mitigation programs. Although CCRI-betweenness and CCRI-closeness may not yield identical CCRI values, they highlight the same potential locations for prioritization (Figure 2A). The overall values of CCRI-closeness were higher than those of CCRI-betweenness, which may reflect the greater influence of proximity-based connectivity compared to pathway-based connectivity in the network. Combining these metrics could provide complementary insights into prioritizing key locations within the network. For banana, locations in Rwanda, Burundi, the DR Congo, Uganda, Tanzania, Ethiopia, Malawi, and Mozambique have a high CCRI (Figure 2).

343 Locations in the southern, eastern, and northern provinces of Rwanda have the highest CCRI-
344 betweenness (Figure 2A and 2B). For cassava, several locations across the region have a high
345 CCRI. In Burundi, locations in the Cibitoke, Bubanza, Kirundo, Ngozi, Bujumbura Rural and Gitega
346 provinces have the highest CCRI (Figure 2A and B). For potato, locations in Rwanda, Burundi, the
347 DR Congo, Uganda, Tanzania, Ethiopia, and Malawi have high CCRI-betweenness (Figure 2).
348 These maps also show that locations in the northern, western, and southern provinces of
349 Rwanda have the highest CCRI-betweenness (Figure 2A and B). For sweetpotato, locations in
350 Rwanda, Burundi, Uganda, Tanzania, Malawi, and Ethiopia have a high CCRI (Figure 2). These
351 maps indicate the important role that Rwanda and Burundi play for understanding and
352 mitigating the risks associated with the spread of pathogens and pests of these crops.

353 Maps of cropland connectivity (Figure 2B) also illustrate the potential roles of the locations we
354 selected for field sampling crop pathogens and pests in the Ruhengeri watershed in Rwanda and
355 in the Rusizi watershed in Burundi. The connectivity of these landscapes varies from crop to
356 crop. Some sampled locations had high cropland connectivity (e.g., cassava and sweetpotato in
357 Burundi transects and potato in Rwanda transects) compared to other locations. Overall, the
358 surveyed locations around Lake Kivu in Rwanda and Lake Tanganyika in Burundi, as well as other
359 locations in the two countries, are likely to be important candidate locations for surveillance for
360 the establishment and spread of banana, cassava, potato, and sweetpotato pathogens and pests
361 in both countries, based on cropland connectivity (Figure 2B).

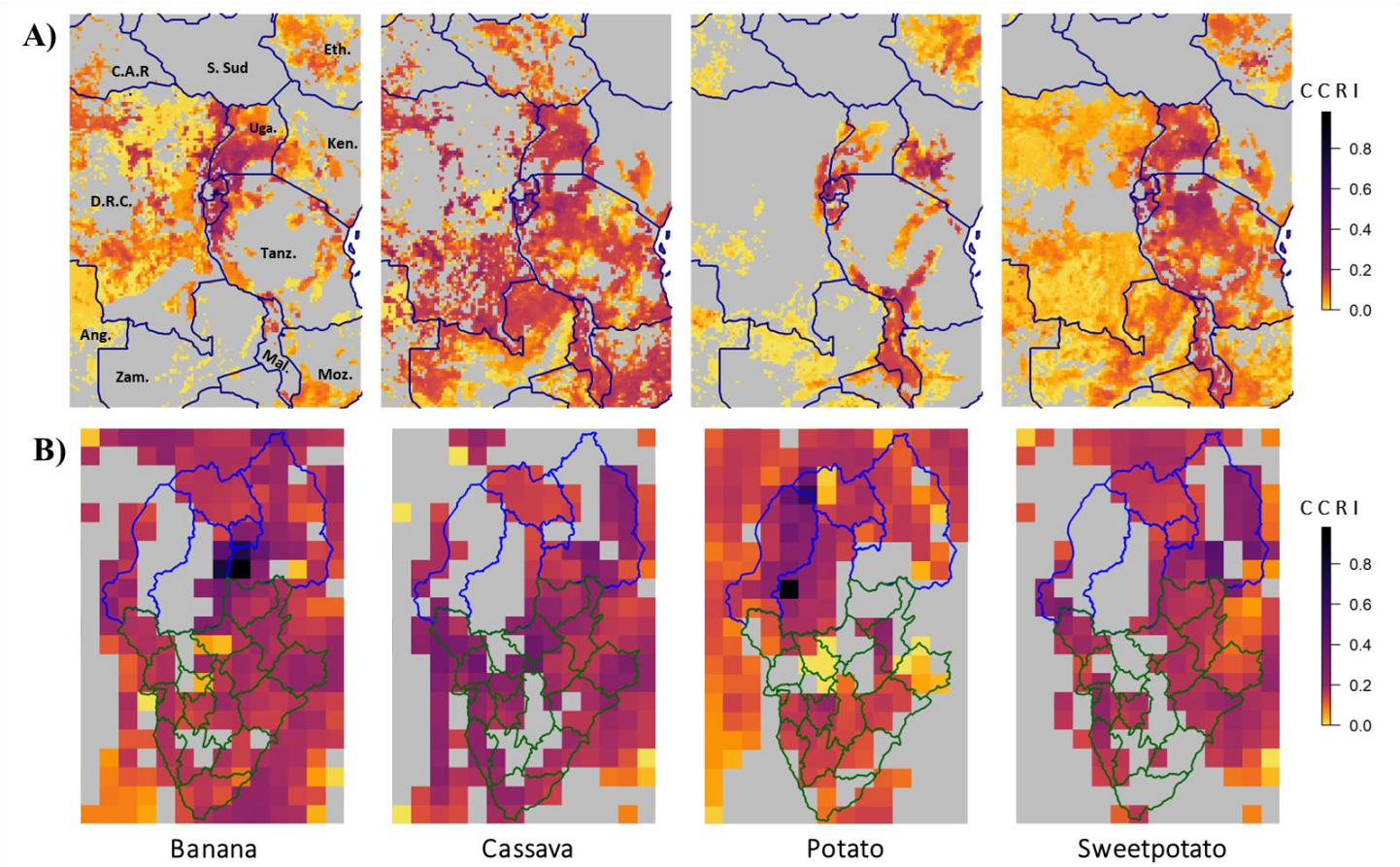


FIGURE 2 | Maps of a cropland connectivity risk index (CCRI-betweenness) for four food security crops in (A) the Great Lakes region of Africa and (B) in a focused geographical extent in Rwanda and Burundi. The CCRI indicates how important a location is likely to be for potential spread of a host-specific pathogen or pest, based on the network of host availability. The CCRI is a weighted mean of four network metrics, including betweenness centrality in the results shown here. In (A), dark blue lines indicate national boundaries. In (B), blue lines indicate the provinces of Rwanda and green lines indicate the provinces of Burundi.

### 3.1.2 | Associations among altitude, landscape structure and climate

The associations among (a) altitude, (b) crop landscape structure, and (c) climate variables such as temperature and precipitation, were analyzed for the Great Lakes region. Higher temperatures were generally associated with lower altitudes. There was a strong negative correlation between altitude and most temperature-related bioclimatic variables (Tem, Tmin,

368 TColQ, TDriQ, TWetQ, TWarQ, Tmax, TColdQ). In contrast, altitude was weakly positively
369 correlated with some precipitation-related bioclimatic variables such as PrecS, PWetQ, and
370 PWetM, and negatively correlated with others, including Prec, PDriQ, PWarQ, and PColQ (Figure
371 3). In this region, higher cropland density and cropland connectivity of banana, cassava, potato,
372 and sweetpotato (Figure 3) were at higher altitudes (except cassava density). Cropland
373 connectivity of these crops showed a stronger positive correlation with altitude compared to
374 cropland density. Cropland density and cropland connectivity for each of these four crops were
375 negatively correlated with most temperature-related bioclimatic variables and positively
376 correlated with most precipitation-related bioclimatic variables (Figure 3).

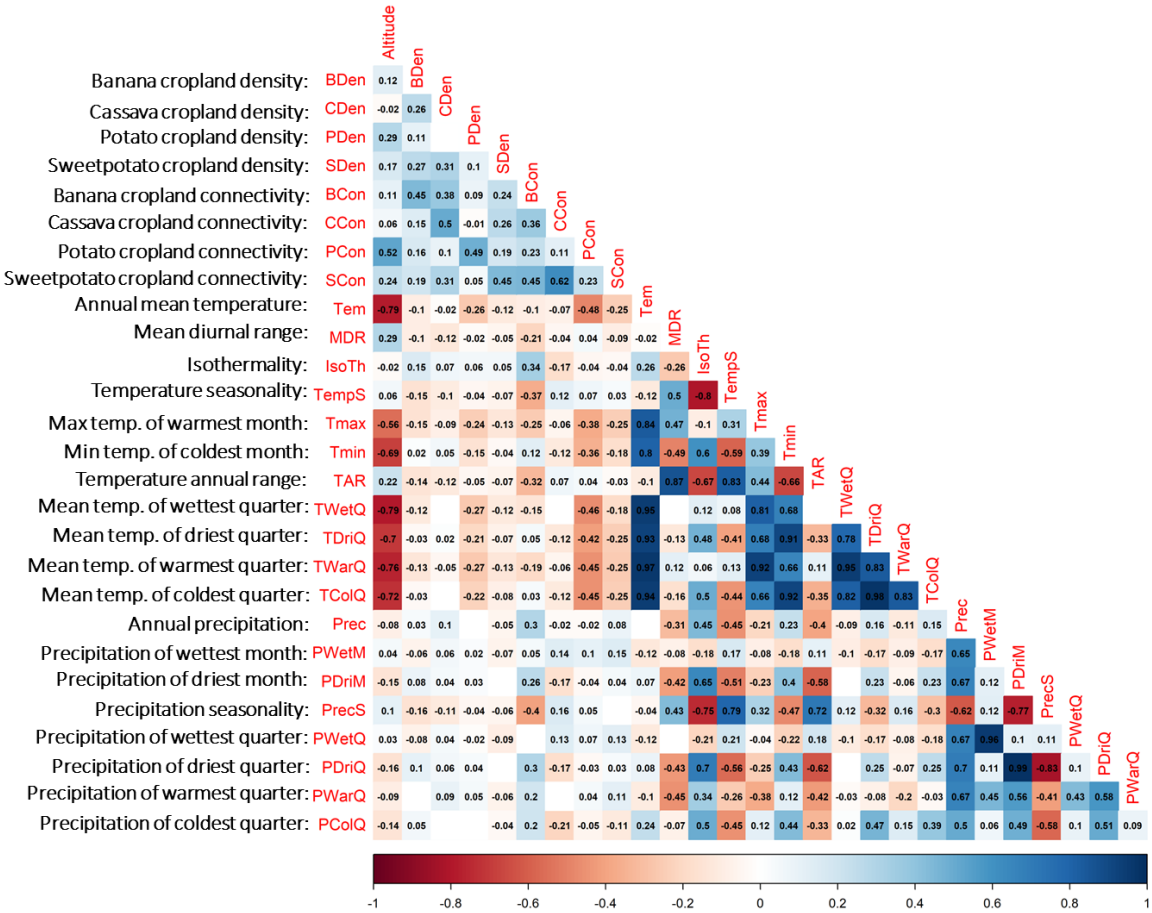


FIGURE 3 | Associations between altitude, bioclimatic variables, and crop landscape structure (crop density and cropland connectivity) in the Great Lakes region of Africa, based on Pearson's correlation. Strong positive correlations are in dark blue, while strong negative correlations are in dark red. White boxes without labels indicate no association.

## 3.2 | Pathogen and pest communities

### 3.2.1 | Spatiotemporal structure of pathogen and pest communities

Most of the targeted pathogens and pests were found in Burundi and Rwanda in both crop-growing seasons (Figure 4). Sweetpotato mealybugs, sweetpotato butterfly (*Acraea acerata*) and sweetpotato aphids were observed only in Burundi (Figure 4). The observed prevalence of each

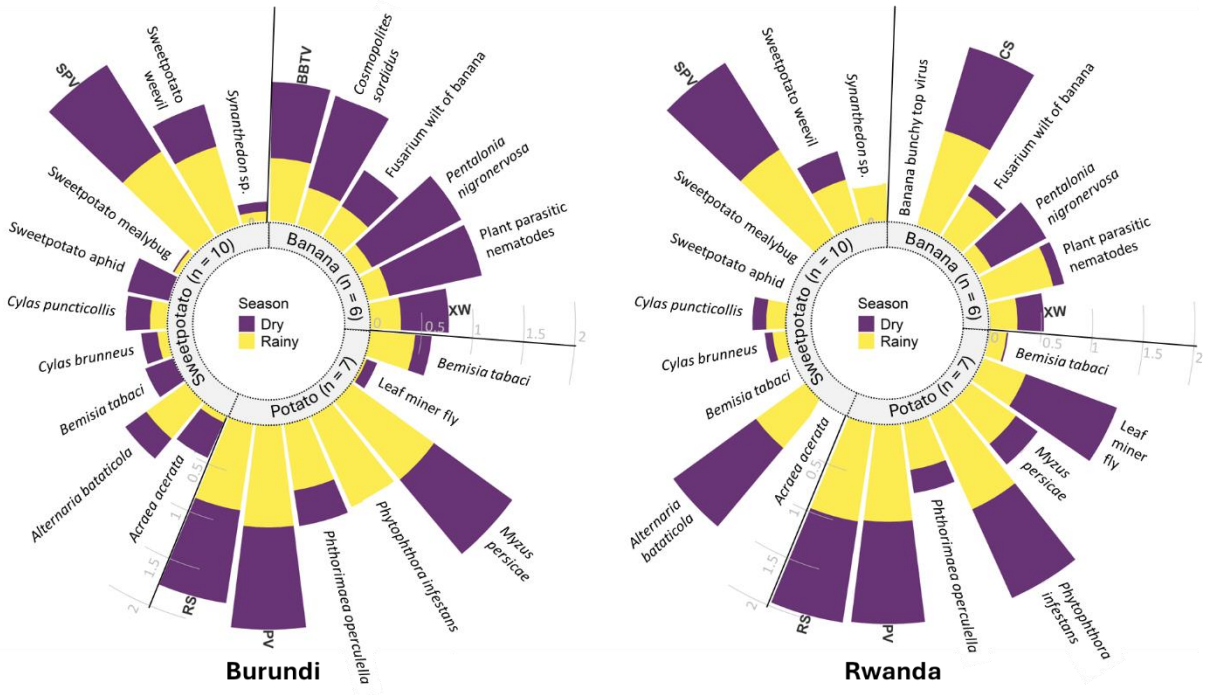


FIGURE 4 | Seasonal distribution of observed pathogens and pests in smallholder production of banana, potato and sweetpotato in Burundi and Rwanda. (Cassava data are not represented here). The length of the bars represents the prevalence for both seasons (where a total of 2 indicates presence in every field in both seasons). Abbreviations: Banana bunchy top virus (BBTV), *Cosmopolites sordidus* (CS), *Ralstonia solanacearum* (RS), sweetpotato virus (SPV), and Xanthomonas wilt of banana (XW).

pest or disease often varied by country, crop, and season. In both countries and seasons, the highest prevalence was observed for *Ralstonia solanacearum* and virus symptoms in potato, virus symptoms in sweetpotato, and *Cosmopolites sordidus* in banana.

388 3.2.2 | Associations among pathogens and pests

389 The NMDS analysis indicated few pathogens/pests whose levels are associated, although some
390 were common enough that they frequently co-occurred with others (Figure 5). A few pathogens
391 and pests were associated in terms of prevalence and severity/infestation in the crop fields.
392 Among banana diseases/pests, Fusarium wilt, Xanthomonas wilt and plant parasitic nematodes
393 were associated in terms of both prevalence and severity (Figure 5). In cassava, all pathogens
394 and pests except *B. tabaci* were associated in terms of prevalence. However, *B. tabaci* was
395 slightly associated with CMV in terms of infestation, which is expected as *B. tabaci* vectors CMV
396 (Figure 5). In potato, viruses and *R. solanacearum* were associated in terms of both prevalence
397 and severity/infestation (Figure 5). In sweetpotato fields, *B. tabaci* and sweetpotato aphids were
398 associated having similar infestation levels across fields.

399

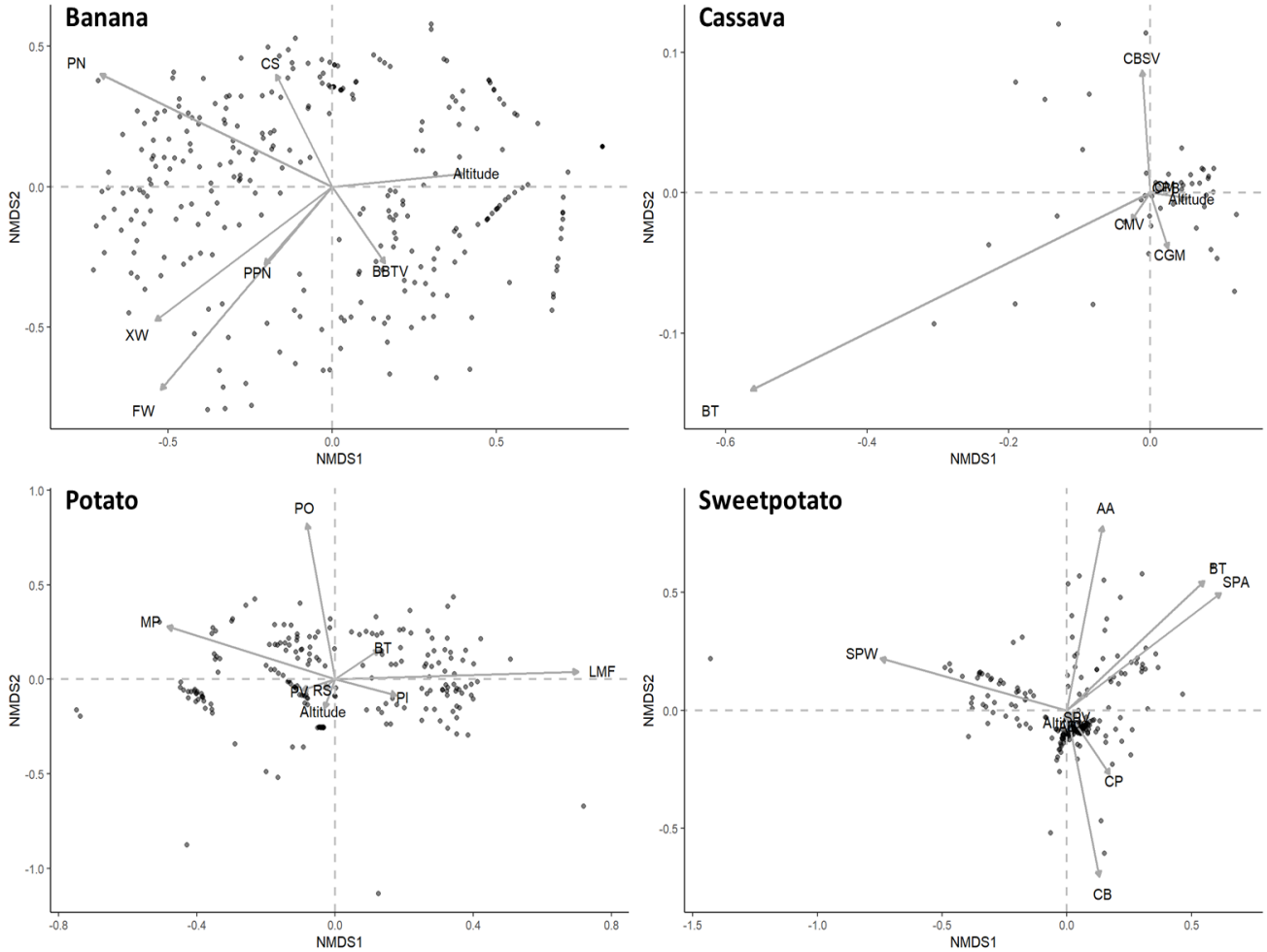


FIGURE 5 | Relationships among economically important pathogens and pests and altitude in four major crops in Burundi and Rwanda, using non-metric multidimensional scaling (NMDS) based on Bray's distance dissimilarities of disease severity or infestation intensity. Each dot represents a surveyed crop field. A line (or vector) indicates whether (line direction) and how strongly (line length) the pathogen or pest is associated with others. Nearly parallel lines in the same quadrant indicate pathogens and pests often co-occur in a crop. (Cassava data was collected only in Burundi for one season). Abbreviations: *Acraea acerate* (AA), *Alternaria bataticola* (AB), Banana bunchy top virus (BBTV), *Bemisia tabaci* (cassava, potato or sweetpotato whitefly; BT), cassava bacterial blight (CBB), Cassava brown streak virus (CBSV), cassava green mite (CGM), cassava mealybug (CM), Cassava mosaic virus (CMV), *Cylas brunneus* (CB), *Cylas puncticollis* (CP), *Cosmopolites sordidus* (CS), Fusarium wilt of banana (FW), leaf miner fly (LMF), *Myzus persicae* (MP), *Phytophthora infestans* (PI), plant parasitic nematodes (PPN), *Pentalonia nigronervosa* (PN), *Phthorimaea operculella* (PO), potato viruses (PV), *Ralstonia solanacearum* (RS), *Synanthedon* sp. (clearwing moth; Ssp), sweetpotato mealybug (SPM), sweetpotato virus (SPV), sweetpotato weevils ( SPW ), and Xanthomonas wilt of banana (XW).

400 Analyses of associations between pairs of pathogens/pests provide a more detailed perspective

401 on which syndromes are important. In banana, some pairs like *C. sordidus* and *P. nigronervosa*,
402 plant parasitic nematodes and Fusarium wilt, plant parasitic nematodes and *P. nigronervosa*, *P.*
403 *nigronervosa* and Xanthomonas wilt, and Fusarium wilt and Xanthomonas wilt were positively
404 correlated ($p < 0.05$) in terms of both prevalence and severity/infestation, while other pairs were
405 only positively correlated ($p < 0.05$) in terms of prevalence: *C. sordidus* and plant parasitic
406 nematodes, plant parasitic nematodes and Xanthomonas wilt, plant parasitic nematodes and
407 BBTV, *P. nigronervosa* and BBTV, and BBTV and Xanthomonas wilt (Figure 6).

408 In cassava, CBSV and mealybug were positively correlated ($r = 0.69$, $p < 0.001$ in terms of
409 prevalence but negatively correlated ($r = -0.44$, $p < 0.01$) in terms of severity/infestation (Figure
410 6). Only *B. tabaci* and CMV were positively correlated in terms of severity/infestation ($r = 0.64$, p
411 $< 0.001$) while other pathogens and pests were positively correlated in terms of prevalence ($p <$
412 $0.05$). In potato, viruses and *R. solanacearum* was positively correlated in terms of prevalence ($r$
413 $= 0.33$, $p < 0.001$) and severity ($r = 0.21$, $p < 0.01$), while *P. infestans* and *M. persicae*, and leaf
414 miner fly and *M. persicae* were negatively correlated ($p < 0.05$) in terms of prevalence and
415 severity/infestation, and leaf miner fly and *R. solanacearum* were positively correlated ($p < 0.05$)
416 in terms of prevalence but negatively correlated ($p < 0.05$) in terms of severity/infestation
417 (Figure 6). In sweetpotato, *C. brunneus* and *C. puncticollis* were positively correlated in terms of
418 prevalence ($r = 0.58$, $p < 0.001$) and infestation ($r = 0.18$, $p < 0.01$), while *A. bataticola* and
419 weevils (*Cylas* spp.) were negatively correlated in terms of prevalence ($r = -0.16$, $p < 0.05$) but
420 positively correlated in terms of severity/infestation ($r = 0.18$, $p < 0.05$) (Figure 6). *A. bataticola*
421 and mealybug, *A. bataticola* and aphids, *A. bataticola* and *B. tabaci*, *A. bataticola* and *Acraea*
422 *acerate*, and aphids and *Synanthedon* sp. were negatively correlated in terms of prevalence

(Figure 6).

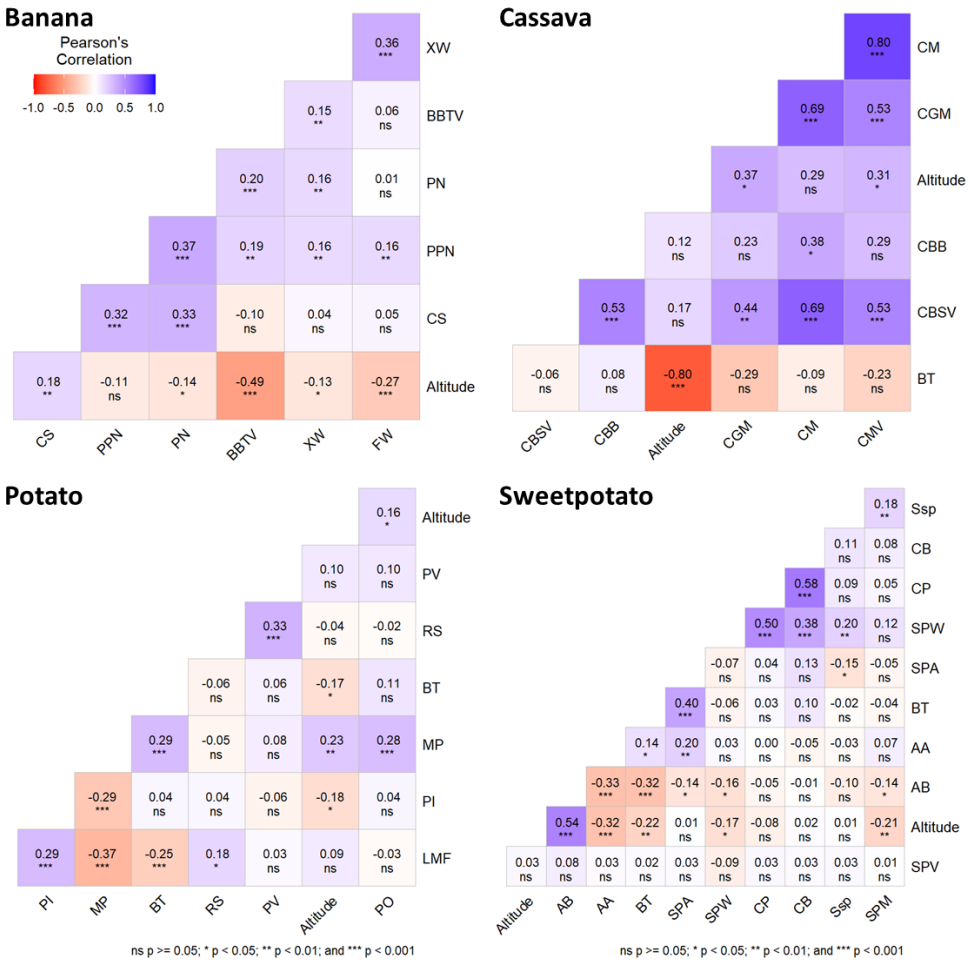


FIGURE 6 | Association of pathogens and pests in banana, cassava, potato, and sweetpotato in smallholder farms in Burundi and Rwanda, based on Pearson's correlation of prevalence. (Cassava data was collected only in Burundi for one season).
Abbreviations: *Acraea acerate* (AA), *Alternaria bataticola* (AB), Banana bunchy top virus (BBTV), *Bemisia tabaci* (cassava, potato or sweetpotato whitefly; BT), cassava bacterial blight (CBB), Cassava brown streak virus (CBSV), cassava green mite (CGM), cassava mealybug (CM), Cassava mosaic virus (CMV), *Cylas brunneus* (CB), *Cylas puncticollis* (CP), *Cosmopolites sordidus* (CS), Fusarium wilt of banana (FW), leaf miner fly (LMF), *Myzus persicae* (MP), *Phytophthora infestans* (PI), plant parasitic nematodes (PPN), *Pentalonia nigronervosa* (PN), *Phthorimaea operculella* (PO), potato viruses (PV), *Ralstonia solanacearum* (RS), *Synanthedon* sp. (clearwing moth; Ssp), sweetpotato mealybug (SPM), sweetpotato virus (SPV), sweetpotato weevil ( SPW ), and Xanthomonas wilt of banana (XW).

426 ### 3.3 | Prediction of pathogen and pest damage and geographic range shifts

427 #### 3.3.1 | Machine learning to predict pathogen and pest levels

428 We compared machine learning algorithms in terms of their ability to predict severity and
429 infestation in the field samples at monthly, quarterly, and annual intervals (Table 1). SVM and RF
430 had the highest model performance for some pathogens/pests. For the SVM model, the
431 performance characteristics across all pathogens and pests were 3-16% MAE for training, 7-20%
432 and 4-26% RMSE, and 0.20-0.72 and 0.09-0.72 R-squared for training and testing, respectively,
433 compared to the RF model with 3-17% MAE for training, 8-21% and 5-23% RMSE, and 0.23-0.72
434 and 0.12-0.73 R-squared for training and testing, respectively (Table 1). Among the 27 pathogens
435 and pests tested, the three with the highest predictive performance metrics per crop were
436 reported in Table 1.

437 The predictive performance was good for certain pathogens and pests, but poor for others
438 (Table 1). As an example, SVM and RF performed well in predicting the monthly, quarterly, and
439 annual infestation intensity of leaf miner fly in this region, explaining 69-71% of the variability in
440 the data (R-squared) with low errors. The RMSE was 17-18% during training and 16-17% during
441 prediction, demonstrating that both models generalized well to unseen data. In addition, the
442 MAE of 11-13% indicated a low average error in training. The tight alignment between training
443 and prediction metrics showed the robustness, stability and reliability of these models to predict
444 leaf miner fly infestation intensity.

445 Pathogens and pests differed in the importance of predictor variables. Contemporary weather

variables such as monthly temperature, precipitation, and relative humidity (extracted through NASAPOWER), generally had high contribution scores. Cropland structure variables also played significant roles, with contribution scores reaching 100 for cropland density, 81 for cropland connectivity, and 69 for altitude. For example, the key variables for predicting leaf miner fly infestation intensity (monthly) using SVM were monthly temperature, precipitation, and relative humidity, precipitation in the driest month, cropland connectivity, cropland density and annual temperature range (i.e. difference between the maximum temperature of warmest month and the minimum temperature of coldest month).

**TABLE 1 |** Support vector machine (SVM) and random forest (RF) performance for predicting pathogen and pest levels in smallholder farms in Burundi and Rwanda, for selected species with higher model performance. The response variable was severity for the pathogens and infestation intensity for pests except for infestation rate for sweetpotato aphids.

| | | | SVM | | | | | Random Forest | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Training | | | Prediction | | Training | | | Prediction | |
| Crop | Pathogen/pest | Timeframe | %RMSE | R-squared | %MAE | %RMSE | R-squared | %RMSE | R-squared | %MAE | %RMSE | R-squared |
| Banana | *P. nigronervosa* | Monthly | 18 | 0.63 | 13 | 21 | 0.56 | 16 | 0.72 | 12 | 18 | 0.66 |
| | | Quarterly | 18 | 0.63 | 13 | 21 | 0.56 | 16 | 0.72 | 12 | 19 | 0.64 |
| | | Annual | 19 | 0.63 | 14 | 21 | 0.55 | 16 | 0.71 | 11 | 19 | 0.63 |
| | Banana bunchy top virus | Monthly | 7 | 0.22 | 3 | 4 | 0.10 | 8 | 0.25 | 4 | 5 | 0.12 |
| | | Quarterly | 7 | 0.22 | 3 | 4 | 0.11 | 8 | 0.23 | 4 | 5 | 0.13 |
| | | Annual | 7 | 0.20 | 3 | 4 | 0.09 | 8 | 0.24 | 4 | 5 | 0.13 |
| | Plant parasitic nematodes | Monthly | 11 | 0.42 | 6 | 15 | 0.29 | 10 | 0.42 | 6 | 14 | 0.31 |
| | | Quarterly | 11 | 0.40 | 6 | 15 | 0.25 | 11 | 0.37 | 7 | 14 | 0.32 |
| | | Annual | 11 | 0.39 | 6 | 15 | 0.23 | 11 | 0.37 | 7 | 14 | 0.29 |
| Potato | Leaf miner fly | Monthly | 18 | 0.69 | 13 | 16 | 0.71 | 18 | 0.70 | 12 | 16 | 0.71 |
| | | Quarterly | 18 | 0.69 | 13 | 16 | 0.71 | 18 | 0.71 | 11 | 16 | 0.69 |
| | | Annual | 18 | 0.70 | 13 | 16 | 0.72 | 17 | 0.72 | 11 | 17 | 0.69 |
| | *Ralstonia solanacearum* | Monthly | 14 | 0.30 | 10 | 14 | 0.13 | 13 | 0.40 | 10 | 15 | 0.12 |
| | | Quarterly | 15 | 0.28 | 10 | 14 | 0.13 | 13 | 0.41 | 10 | 15 | 0.12 |
| | | Annual | 15 | 0.28 | 11 | 14 | 0.16 | 12 | 0.39 | 10 | 15 | 0.13 |
| | Potato viruses | Monthly | 20 | 0.31 | 16 | 21 | 0.34 | 21 | 0.28 | 17 | 21 | 0.38 |
| | | Quarterly | 20 | 0.32 | 16 | 21 | 0.33 | 20 | 0.31 | 16 | 21 | 0.38 |
| | | Annual | 20 | 0.31 | 16 | 21 | 0.34 | 21 | 0.30 | 17 | 21 | 0.37 |
| Sweet | *Alternaria* | Monthly | 15 | 0.35 | 9 | 10 | 0.42 | 14 | 0.39 | 9 | 10 | 0.39 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| potato | *bataticola* | Quarterly | 14 | 0.41 | 9 | 9 | 0.43 | 13 | 0.45 | 8 | 9 | 0.42 |
| | | Annual | 15 | 0.35 | 8 | 9 | 0.47 | 14 | 0.38 | 9 | 9 | 0.43 |
| | Sweetpotato | Monthly | 19 | 0.44 | 10 | 25 | 0.26 | 18 | 0.38 | 10 | 22 | 0.44 |
| | weevils (*Cylas* | Quarterly | 19 | 0.42 | 10 | 26 | 0.21 | 19 | 0.38 | 11 | 22 | 0.41 |
| | spp.) | Annual | 20 | 0.41 | 10 | 25 | 0.27 | 19 | 0.36 | 11 | 23 | 0.40 |
| | Sweetpotato | Monthly | 14 | 0.60 | 6 | 9 | 0.60 | 10 | 0.53 | 5 | 7 | 0.73 |
| | aphids | Quarterly | 14 | 0.60 | 6 | 9 | 0.58 | 10 | 0.58 | 4 | 8 | 0.65 |
| | | Annual | 14 | 0.58 | 6 | 9 | 0.58 | 9 | 0.54 | 4 | 9 | 0.53 |

### 3.3.2 | Pathogen and pest communities across altitudinal gradients

For each crop, pathogen and pest communities differed at low versus high altitudes (Table 2). Although there was not strong evidence for differences across the altitudinal gradients for 5 out of 27 pathogens and pests (correlations with $p > 0.05$ in Table 1), likely due in some cases to high variability across samples, there was evidence for differences in some pathogens and pests that distinguished the pathogen/pest communities (correlations in Table 2 with lower p-values). For instance, crop production at higher altitudes (>1,500 m.a.s.l) had more *Myzus persicae*, *Phthorimaea operculella*, and cassava green mites. At lower altitudes, crop fields had more Fusarium wilt and Xanthomonas wilt of bananas, *P. infestans*, *A. acerate* and *Bemisia tabaci* (Table 2). The distribution of these pathogens and pests across altitudes was supported in the analysis combining observations from Burundi and Rwanda; overall, for banana, potato, and sweetpotato, there was evidence that 44% of the targeted pathogens and pests were more common at low altitudes, and that 17% were more common at higher altitudes.

When analyzing data for Rwanda and Burundi separately, differences across altitudes for pathogens and pests were specific to the measure being used (e.g., disease intensity; Table 2) or the country. For example, potato fields at high altitudes had a higher prevalence of potato leaf miner fly, while there was not evidence for a difference in the infestation intensity of this pest

476 across the altitudinal gradient. Similarly, there was stronger evidence that altitude was

477 negatively correlated with the prevalence and severity of banana Fusarium wilt in Burundi ($p < 0.001$) compared to Rwanda ($p = 0.069$ for severity and $p = 0.85$ for prevalence). At the

479 community level, potato fields in Rwanda and cassava fields in Burundi had higher pathogen and

480 pest richness at higher altitudes, while richer pathogen and pest communities were found in

481 banana fields at lower altitudes.

482 TABLE 2 | Correlation between altitude and pathogen and pest prevalence, severity, and
483 infestation in Burundi and Rwanda (PRV: prevalence, SEV: severity, Rate: infestation rate, INF:
484 infestation intensity, NUM: number of pests).
485

| | | | Correlation in Burundi | | Correlation in Rwanda | | Correlation in both countries combined | |
|---|---|---|---|---|---|---|---|---|
| Crop | Disease/Pathogen/ Pest | Variables | r | P-value | r | P-value | r | P-value |
| Banana | Xanthomonas wilt | **PRV** | -0.08 | 0.28 | -0.07 | 0.49 | **-0.13** | **0.022** |
| | | **SEV** | -0.02 | 0.76 | -0.04 | 0.7 | **-0.13** | **0.028** |
| | Fusarium wilt | **PRV** | **-0.37** | **<0.001** | -0.02 | 0.85 | **-0.27** | **<0.001** |
| | | **SEV** | **-0.33** | **<0.001** | 0.18 | 0.069 | **-0.34** | **<0.001** |
| | Banana bunchy top virus | **PRV** | -0.13 | 0.065 | 0 | - | **-0.49** | **<0.001** |
| | | **SEV** | -0.01 | 0.9 | 0 | - | **-0.22** | **<0.001** |
| | Plant parasitic nematodes | PRV | -0.01 | 0.90 | 0.05 | 0.65 | -0.11 | 0.065 |
| | | INF | -0.13 | 0.07 | -0.03 | 0.78 | -0.02 | 0.72 |
| | Banana weevil *(Cosmopolites sordidus)* | **PRV** | 0.03 | 0.700 | -0.14 | 0.16 | **0.18** | **0.003** |
| | | **INF** | -0.07 | 0.37 | **-0.38** | **<0.001** | **-0.13** | **0.034** |
| | Banana aphid (*Pentalonia nigronervosa*) | **PRV** | 0.03 | 0.68 | -0.08 | 0.43 | **-0.14** | **0.018** |
| | | **INF** | 0.09 | 0.24 | 0.09 | 0.37 | **-0.25** | **<0.001** |
| | | **Richness** | **-0.16** | **0.028** | 0.80 | 0.41 | **-0.30** | **<0.001** |
| Potato | Leafminer fly | **PRV** | 0.16 | 0.16 | **0.26** | **0.006** | 0.09 | 0.22 |
| | | INF | 0.17 | 0.13 | 0.01 | 0.93 | 0.04 | 0.62 |
| | | Rate | 0.14 | 0.21 | 0.13 | 0.16 | 0.01 | 0.88 |
| | Potato aphid *(Myzus persicae)* | **PRV** | 0.02 | 0.86 | **0.24** | **0.011** | **0.23** | **0.001** |
| | | **Rate** | 0.07 | 0.54 | **0.25** | **0.008** | **0.21** | **0.004** |
| | Potato whitefly (*Bemisia tabaci*) | **PRV** | **-0.57** | **<0.001** | 0.04 | 0.7 | **-0.17** | **0.02** |
| | | **NUM** | **-0.38** | **<0.001** | 0.08 | 0.39 | 0.05 | 0.45 |
| | Potato tuber moth (*Phthorimaea operculella*) | **PRV** | **0.34** | **0.003** | 0.03 | 0.75 | **0.16** | **0.028** |
| | | **Rate** | **0.36** | **0.001** | -0.05 | 0.58 | 0.15 | 0.03 |
| | *Ralstonia solanacearum* | PRV | -0.09 | 0.41 | 0.10 | 0.31 | 0.04 | 0.61 |
| | | SEV | 0.04 | 0.73 | -0.08 | 0.41 | -0.03 | 0.66 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Potato viruses | PRV | 0 | - | 0.10 | 0.3 | 0.10 | 0.16 |
| | | **SEV** | 0.04 | 0.71 | **-0.21** | **0.025** | -0.61 | 0.4 |
| | *Phytophthora infestans* | **PRV** | -0.20 | 0.082 | 0.07 | 0.46 | **-0.18** | **0.014** |
| | | **SEV** | -0.21 | 0.068 | -0.06 | 0.53 | **-0.14** | **0.044** |
| | | **Richness** | -0.15 | 0.18 | **0.26** | **0.005** | 0.1 | 0.18 |
| Sweet Potato | *Alternaria bataticola* | **PRV** | **0.58** | **<0.001** | 0.05 | 0.61 | **0.54** | **<0.001** |
| | | **SEV** | **0.48** | **<0.001** | 0.04 | 0.65 | **0.32** | **<0.001** |
| | Sweetpotato viruses | PRV | 0.01 | 0.98 | 0 | - | 0.03 | 0.63 |
| | | SEV | 0.06 | 0.51 | -0.15 | 0.14 | -0.08 | 0.24 |
| | Sweetpotato whitefly (*Bemisia tabaci*) | **PRV** | -0.11 | 0.26 | 0 | - | **-0.22** | **0.001** |
| | | NUM | -0.05 | 0.61 | 0 | - | -0.11 | 0.13 |
| | Sweetpotato butterfly *(A. acerate)* | **PRV** | **-0.19** | **0.045** | 0 | - | **-0.32** | **<0.001** |
| | | **Rate** | -0.10 | 0.29 | 0 | - | **-0.19** | **0.005** |
| | | **NUM** | **-0.19** | **0.045** | 0 | - | **-0.22** | **0.001** |
| | Sweetpotato weevils (*Cylas* spp.) | **PRV** | -0.15 | 0.13 | 0.05 | 0.63 | **-0.17** | **0.016** |
| | | **INF** | 0.02 | 0.81 | 0.08 | 0.43 | **0.17** | **0.013** |
| | | **Rate** | -0.03 | 0.76 | -0.05 | 0.62 | **-0.17** | **0.013** |
| | *Cylas puncticollis* | PRV | -0.08 | 0.43 | 0.04 | 0.69 | -0.08 | 0.24 |
| | | **NUM** | **-0.23** | **0.016** | -0.06 | 0.54 | -0.04 | 0.61 |
| | *C. brunneus* | PRV | 0.08 | 0.39 | 0.06 | 0.58 | 0.02 | 0.8 |
| | | **NUM** | -0.01 | 0.99 | **-0.20** | **0.042** | -0.02 | 0.75 |
| | *Synanthedon* sp. | **PRV** | **-0.28** | **0.004** | **0.26** | **0.007** | 0.01 | 0.91 |
| | Sweetpotato mealybug | **PRV** | **-0.20** | **0.036** | 0 | - | **-0.21** | **0.002** |
| | Sweetpotato aphids | **PRV** | **0.24** | **0.013** | 0 | - | 0.01 | 0.94 |
| | | **Rate** | **0.45** | **<0.001** | 0 | - | **0.22** | **0.002** |
| | | **NUM** | **0.35** | **<0.001** | 0 | - | **0.17** | **0.01** |
| | | Richness | 0.05 | 0.6 | 0.10 | 0.34 | -0.02 | 0.8 |
| Cassava | Cassava whitefly (*Bemisia tabaci*) | **PRV** | **-0.80** | **<0.001** | - | - | **-** | **-** |
| | | **NUM** | **-0.32** | **0.032** | - | - | **-** | **-** |
| | Cassava green mite | **PRV** | **0.37** | **0.012** | - | - | **-** | **-** |
| | | INF | 0.06 | 0.68 | - | - | **-** | **-** |
| | Cassava mealybug | PRV | 0.29 | 0.057 | - | - | **-** | **-** |
| | | INF | 0.27 | 0.072 | - | - | **-** | **-** |
| | Cassava mosaic virus | **PRV** | **0.31** | **0.037** | - | - | **-** | **-** |
| | | **SEV** | **-0.52** | **<0.001** | - | - | **-** | **-** |
| | Cassava brown streak virus | PRV | 0.17 | 0.25 | - | - | **-** | **-** |
| | | **SEV** | **-0.47** | **0.002** | - | - | **-** | **-** |
| | Cassava bacterial blight | PRV | 0.12 | 0.43 | - | - | **-** | **-** |
| | | SEV | 0.25 | 0.093 | - | - | **-** | **-** |
| | | **Richness** | **0.78** | **<0.001** | - | - | **-** | **-** |

### 3.3.3 | Climate change and impact on regional temperature patterns

The frequency distribution of annual temperatures across altitudes in the Great Lakes region

489 illustrates the transformative impact of climate change (Figure 7). A progressive shift in
490 temperature distribution is expected, highlighting how currently cooler climates at higher
491 altitudes are likely to experience much higher temperatures (Figure 7). A general warming trend
492 is projected at both high and low altitudes. There is a greater temperature increase in the SSP5-
493 8.5 scenario than in the SSP1-2.6 scenario. Currently, the mean annual temperature in the region
494 ranges between 17-30°C at low altitudes, with the mode around 24°C, and between 10-22°C at
495 higher altitudes, with the mode around 17°C. As climate change progresses, and depending on
496 socio-economic pathways, this temperature landscape is likely to change substantially. Under
497 the SSP1-2.6 scenario, by 2090 (2081-2100), temperatures are expected to range between 20-
498 32°C at low altitudes, with the mode around 26°C, and between 10-25°C at high altitudes, with
499 mode 20°C. The high-emission scenario (SSP5-8.5) predicts that temperatures will range
500 between 22-36°C at low altitudes, with the mode around 28°C, and between 12-30°C at higher
501 altitudes, with the mode around 25°C.

502 These projections suggest future climate conditions at higher altitudes could become more
503 favorable for the 44% of pathogens and pests we evaluated that currently are more common at
504 lower altitudes (section 3.3.2). Likewise, pathogens and pests currently more common at higher
505 altitudes (17% of those evaluated in section 3.3.2) may become less common as the locations
506 warm in the future. These percentages are based on banana, potato, and sweetpotato, the three
507 crops for which we had the most complete data sets for analysis in predictive models based on
508 field data collected to allow direct comparisons across pathogens and pests.

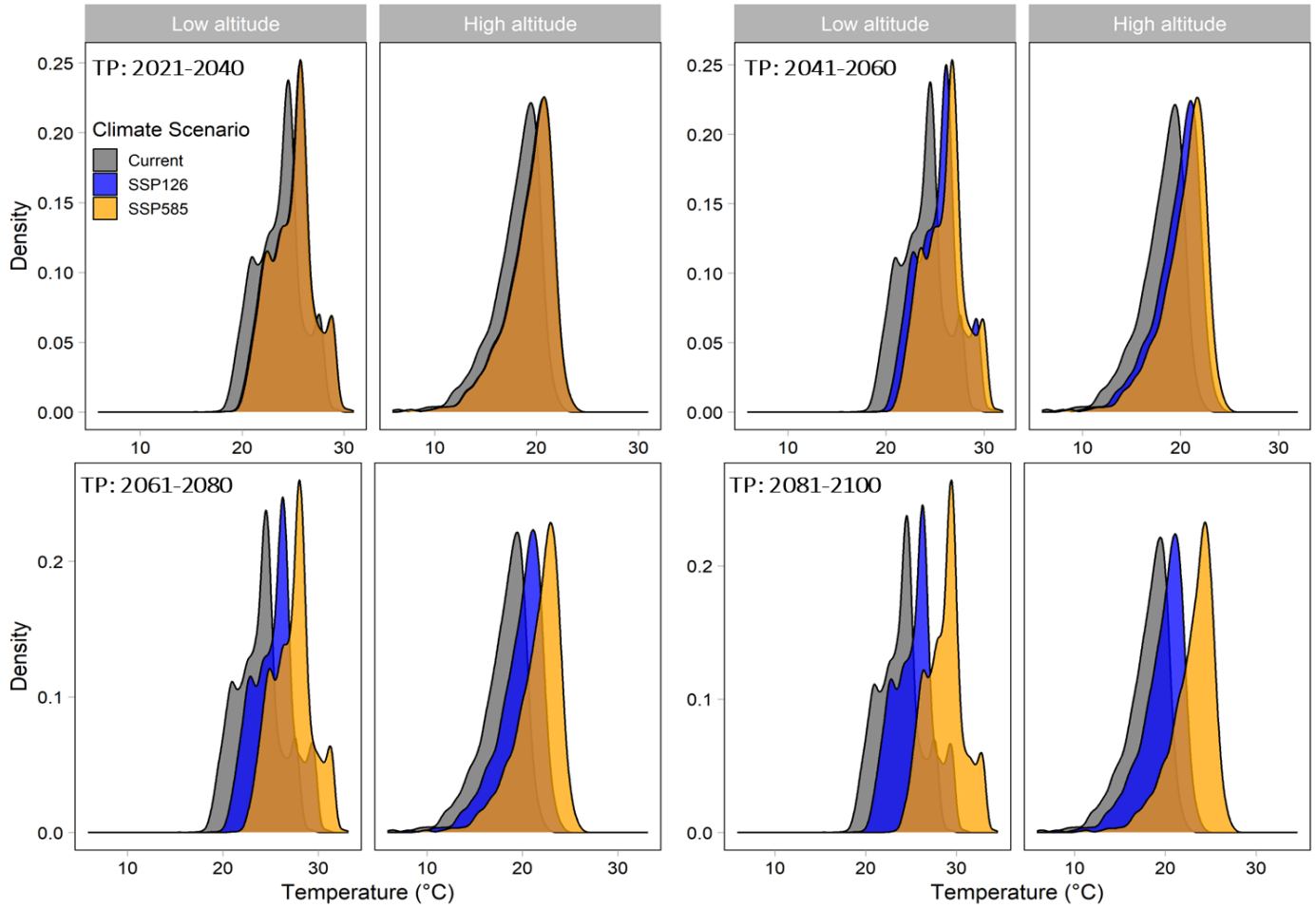


FIGURE 7 Shift in annual temperature range at lower and higher elevations in the Great Lake region of Africa. Density is the probability density or likelihood of temperature rates occurring at locations in the Great Lakes region of Africa. TP: time period of the projections (while the 'Current' reference remains the same). SSP: Shared Socioeconomic Pathway, sustainability (SSP1-2.6) and fossil-fueled development (SSP5-8.5) emission scenarios. Here, high altitude refers to locations above 1500 m.a.s.l. and low altitude those below 1500 m.a.s.l.

## 4 | DISCUSSION

This study identified candidate surveillance locations based on cropland connectivity, a starting point in understanding geographic spread and establishment of crop-specific pathogens and

514 pests in four key food security crops in the Great Lakes region. We also quantified the current
515 geographic and seasonal distribution of 27 economically important pathogens and pests across
516 climate gradients. We evaluated future climate scenarios, with evidence that 44% of the
517 pathogens and pests would become more common at higher altitudes while 17% would become
518 less common.

519 **4.1 | Pathogen and pest risk across landscape structures**

520 The cropland connectivity analysis provides a first approximation to the potential geographic
521 distribution of pathogen and pest risk. This analysis helped us identify candidate priority
522 locations for general surveillance and mitigation of the potential spread of crop-specific
523 pathogens and pests based on networks of host availability (Figure 2). Analysis of cropland
524 connectivity provides a baseline for quantifying invasion risks for pathogens and pests at a
525 national or global scale (Andersen Onofre et al., 2021, Etherton et al., 2025, Mouafo-Tchinda et
526 al., 2024). In the Great Lakes region, locations in Rwanda and Burundi had a high CCRI for all four
527 food-security crops, highlighting their vulnerability to pathogen and pest spread in the absence
528 of phytosanitary measures. Maps of cropland connectivity are particularly relevant for
529 monitoring outbreaks of introduced or emerging diseases and pests, as tools for national plant
530 protection organizations (NPPOs).

531 Ongoing improvements to understanding other components of pathogen and pest risk regionally
532 – such as the effects of climate change, local trade, and genetic resistance deployment – could
533 be integrated in more complete habitat connectivity analyses as additional resources become
534 available (Keshav et al., 2024). The disaster plant pathology framework emphasizes the

535 importance of developing and implementing disease management strategies before, during, and
536 after disasters (Etherton et al., 2024). Human-driven crises like the ongoing Boko-Haram and
537 separatist conflicts in Cameroon played a key role in human migration and informal movement
538 of cassava and sweetpotato planting material between neighboring villages (Mouafo-Tchinda et
539 al. (2024). The recurrence of crises in the Great Lakes region can increase pathogen and pest risk
540 nationally or internationally, especially in production regions with high cropland connectivity.
541 These threats motivate strengthening monitoring of informal seed movement in highly
542 connected cropland.

543 4.2 | Pathogen and pest communities

544 Our analysis of the on-farm distribution of 27 pathogens and pests highlights how these
545 communities change along climate gradients, in terms of seasonal abundance (Figure 4),
546 community structure (Figure 5), and interspecific pathogen/pest associations (Figure 6). Previous
547 studies have typically addressed how individual pathogens or pests are distributed along climate
548 gradients (Ebregt et al., 2005, Okonya & Kroschel, 2013, Nyang'au *et al.*, 2021), yet a community
549 perspective provides a more realistic scenario for understanding regional pest management
550 (Makiola *et al.*, 2021, Savary *et al.*, 2000, Were *et al.*, 2013). Our study addresses this knowledge
551 gap by identifying which pathogens/pests are most prevalent across seasons, which pathogen
552 and pest occurrences are associated, and how climate gradients are likely to influence disease
553 severity and pest infestation. Evaluating these interactions and cumulative effects of multiple
554 pathogens/pests in specific production environments can increase our understanding of injury
555 profiles (Savary et al., 2000), the cumulative damage to crops caused by the set of biotic

556 stressors including insects, pathogens and weeds.

557 Our findings highlight injury profiles for food security crops across climate gradients. Some
558 associations are already well-known; as expected, BBTV and its vector *P. nigronervosa* were
559 positively correlated (Blomme et al., 2020, Hu *et al.*, 1996). BBTV has been present in Africa for
560 decades, its spread continues to have an impact on new regions, and its management remains a
561 major challenge (Ngatat *et al.*, 2024, Rybicki, 2015, Ocimati *et al.*, 2024). We also found strong
562 associations between certain pathogens and pests; Fusarium wilt, Xanthomonas wilt and plant
563 parasitic nematodes were associated in banana, viruses and *R. solanacearum* in potato, and *B.*
564 *tabaci* and aphids in sweetpotato. These pathogen/pest associations underscore the need for
565 integrated management strategies that address the spread and combined impacts of multiple
566 pathogens and pests on crops (Alcalá Briseño *et al.*, 2023, Mouafo-Tchinda *et al.*, 2022).

567 4.3 | Climate-based predictions of pathogen and pest levels

568 In the Great Lakes region, temperatures decreased with increasing altitude (Figure 3), where
569 higher temperatures were associated with an increase in the prevalence and severity of some
570 pathogens and pests and a decrease in others (Table 2). Whiteflies were more common at low
571 altitudes for cassava, potato and sweetpotato. Aphids were more common at low altitudes for
572 banana, but more common at high altitudes for potato. The observed differences in the
573 altitudinal distribution of these pests could be attributed to their species composition, host
574 specificity, and the influence of species-specific ecological adaptations (McCulloch & Waters,
575 2023, Aleuy & Kutz, 2020). Aphid communities included different species, with *P. nigronervosa*
576 more frequent in low-altitude crops, and *M. persicae* more frequent in high-altitude crops (Aleuy

577 & Kutz, 2020, Wells & Clark, 2019, Malumphy *et al.*, 2017, Wieczorek *et al.*, 2019).

578 The distribution of host availability across a landscape can influence pathogen/pest prevalence,
579 severity/infestation, and richness (Etherton et al., 2025, Buddenhagen et al., 2022, Poveda et al.,
580 2012). In this study, the availability of banana, potato, and sweetpotato increased with altitude
581 while cassava decreased slightly (Figure 3), which may contribute to differences observed in the
582 pathogen and pest communities of these crop species. As a crop species becomes more
583 common, insect and microbial communities may become dominated by specialist species
584 infesting that crop (Poveda et al., 2012).

585 Weather variables are well known to be useful for predicting disease severity (Fenu & Malloci,
586 2021, Kaundal et al., 2006, Carisse & Fall, 2021). Cropland geography variables (cropland density,
587 connectivity), altitude, and climate variables (annual mean temperature, temperature annual
588 range, and annual precipitation) were key for most of the pathogens and pests we evaluated.
589 The performance of machine learning algorithms depends on data availability, the predictor
590 variables, and the biological features of pathogens and pests (Xiao *et al.*, 2018, Fenu & Malloci,
591 2021). The data for Rwanda and Burundi supported prediction of some pathogens, while others,
592 like BBTV, would require more study. The models effectively predicted leaf miner fly infestation
593 intensity, accounting for 69-71% of the variability with low training and predicting errors. These
594 models could serve as a baseline for predictive models of leaf miner fly infestation intensity in
595 this region (Table 1).

596 Temperature influences the life cycle, reproduction, and migration patterns of pathogens and
597 pests (Mouafo-Tchinda *et al.*, 2021, Yamamura & Kiritani, 1998, Awmack *et al.*, 1997). In

598 response to regional warming, certain pathogens and pests may become more common at
599 specific altitudes (Datta *et al.*, 2017, Poveda et al., 2012, Blomme et al., 2020), which will require
600 adaptation of pathogen and pest management to future conditions. Several studies suggest that
601 climate change shifts species ranges to higher altitudes (Colwell et al., 2008, Bebber *et al.*, 2013,
602 Bale *et al.*, 2002), and the new results from this study clarify the specific effects on individual
603 pathogens and pests in Rwanda and Burundi for key food security crops.

604 Pathogen/pest richness in banana decreased with altitude, while it increased in cassava. In
605 addition, the severity of certain pathogens/diseases such as BBTV, CMV, *P. infestans* and
606 Fusarium wilt decreased with altitude, while the severity or infestation of *A. bataticola* and
607 aphids in sweetpotato increased. In general, we found evidence that 44% of the pathogens and
608 pests currently more common at low altitude in banana, potato, and sweetpotato could shift to
609 higher altitudes under climate change, based on climate matching. Specifically, those expected
610 to become more common at higher altitudes are Xanthomonas wilt, Fusarium wilt, BBTV, and *P.*
611 *nigronervosa*, in banana; sweetpotato mealybug, *A. acerate*, sweetpotato weevils in
612 sweetpotato; and *B. tabaci* in potato and sweetpotato. The 17% currently more common at high
613 altitudes could become less common. Cropland connectivity was positively correlated with
614 altitude and was a key predictor of severity/infestation of some pathogens and pests. This
615 suggests that food-security crops at higher altitudes may experience substantial flows of
616 pathogens and pests, amplifying the risk of damage. Customizing risk assessments for these
617 specific pest/pathogen communities across altitudes could make management strategies better
618 adapted to the challenges posed by climate change for each crop in the region.

619 ### 4.4 | Translating pathogen and pest risk to support current and future agriculture

620 Historically, global and national research and extension efforts have been employed to manage
621 diseases and pests in the Great Lakes region (RTB, 2013, Kroschel et al., 2014). Integrated
622 management systems combining cultural control, surveillance, awareness creation and involving
623 policy makers and farmers have been adopted (Gotor *et al.*, 2022, Legg *et al.*, 2006). There has
624 been support for active management programs where clean planting material is provided to
625 farmers to encourage them to destroy diseased plants. Efforts have been made to create
626 awareness and empower farmers to recognize and destroy diseased plants. A challenge for these
627 efforts is availability of resources to support ongoing, sustainable plans by governments and
628 national programs, especially after project lifespans are over. The results of this new study can
629 help to inform prioritization and efficient use of available resources. Currently, for many food
630 security crops, efforts are underway to improve seed health, obtain resistance to key pathogens
631 and pests, and adapt these improved technologies and techniques for use in humanitarian
632 settings (Andrade-Piedra *et al.*, 2020, Andrade-Piedra *et al.*, 2023, RTB, 2013).

633 Pathogen and pest risk analysis can help to ensure the economic, social, and environmental
634 sustainability of crop production (Carisse & Fall, 2021, Fall *et al.*, 2016, Kaundal et al., 2006).
635 Image analysis apps such as the PlantVillage Nuru app and the Tumaini app can help smallholder
636 farmers in the region diagnose crop damage caused by pests and diseases, and offer national
637 plant protection organizations and extension staff a tool for surveillance and disease mapping
638 (Ramcharan *et al.*, 2019, Kreuze *et al.*, 2022, Selvaraj *et al.*, 2019). Predicting the timing of
639 pathogen and pest threats would enable farmers to adjust management strategies in the short

640 run and would support prioritization in research and breeding programs in the long run.

641 Ongoing improvements in predicting pathogen and pest impacts depend on weather data
642 availability, which is often limited in low-income and disaster-prone countries. Satellite platforms
643 like NASA POWER offer a useful alternative (Sparks, 2018), providing near-real-time weather
644 data and allowing researchers in resource-limited settings to develop useful models without the
645 need for extensive ground observations. Another challenge is detection of transient pests such
646 as aphids, which move frequently and rapidly across fields (Loxdale, 2018). Addressing this
647 requires the use of innovative sampling techniques, such as suction traps and environmental
648 DNA (eDNA) analysis, to monitor pest populations more accurately (Poppinga *et al.*, 2016,
649 Taberlet *et al.*, 2012). However, implementing these advanced approaches in low-income and
650 disaster-prone areas such as the Great Lakes region remains a challenge due to limited resources
651 and technical capacity, requiring scalable and cost-effective solutions.

652 In disaster-prone regions, humanitarian organizations and government agencies must prioritize
653 key areas where abandonment or poor management of staple crops is particularly important to
654 regional spread of pathogens and pests (Etherton et al., 2024, Mouafo-Tchinda et al., 2024). This
655 study identifies candidate priority locations for mitigation of the establishment and spread of
656 pathogens and pests, characterizes pathogen and pest associations (injury profiles), and
657 evaluates potential altitudinal shifts under the influence of climate change. Future research can
658 build on these results by validating and refining the models for each pathogen/pest, and
659 developing tools that growers and policymakers can easily implement. Iterative improvement
660 can increase the adaptability and effectiveness of crop health management strategies, a no-

661 regrets adaptation strategy as agricultural systems face increasing challenges due to climate
662 change.

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