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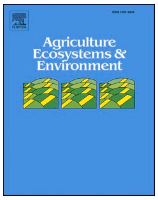

Associations between scale-dependent agroecosystem factors and cocoa swollen shoot virus incidence in Côte d'Ivoire

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ABSTRACT

Understanding the association between agroecosystem factors across multiple scales is essential for sustaining production in agroecosystems under disease pressure. Cocoa swollen shoot virus (CSSV) is a devastating and currently uncontrollable epidemic, posing the greatest threat to cocoa production in West Africa. The present study investigates the associations between CSSV incidence, meteorologic conditions, soil properties, agroforestry variables and landscape composition at different scales, using Self-Organizing Maps, an analysis method that handles nonlinearity and complex variable interactions. This study was based on data collected between 2021 and 2023 in 150 cocoa plots representing diverse cocoa-growing conditions in Côte d'Ivoire, which were clustered according to factor similarity. We found that low disease incidence was primarily associated with more frequent events of extreme precipitation and lower variation in temperature. On the contrary, a high incidence of CSSV was linked to a higher density of trees hosting the virus. We drew on existing knowledge of disease epidemiology, mealybug vector biology and cocoa tree physiology to interpret these results. Additionally, plots with low disease incidence were predominantly surrounded by non-host land, suggesting that large-scale management strategies could help mitigate CSSV incidence by promoting non-host land use at the landscape level.

1. Introduction

Extensive research on epidemic drivers in agroecosystems highlights global concerns regarding pathogen emergence and disease severity in agriculture (Jones, 2009). Sustainable strategies are needed to maintain and enhance agroecosystem services including crop production and pathogen control (Liu et al., 2022; Vega et al., 2023). Epidemic factors act through various ecological processes—biological, physical, and chemical—within agroecosystems, including environmental conditions (Szczepaniec and Finke, 2019) and agricultural practices (Gurr et al., 2017). These factors also operate at multiple spatial scales within the agricultural landscape (Angelella et al., 2016). At all scales, epidemic factors display a crucial role in shaping the complex interactions between pathogens and cultivated plants (Plantegenest et al., 2007; Prasad et al., 2022; Zahra et al., 2023). In vector-borne diseases, these factors also influence insect vectors, further complicating epidemiological processes (Islam et al., 2020).

Environmental factors such as meteorological conditions can directly influence epidemics in agroecosystems by influencing pathogen spread, abundance and pathogenicity. Temperature and humidity, for instance, can directly regulate pathogen replication and dissemination, up to an optimal threshold, through their direct effects on cellular mechanisms (Amari et al., 2021; Glasa et al., 2003). Meteorological conditions also indirectly impact vector-borne disease epidemics by affecting vector population dynamics, such as abundance and dispersion, notably through their effects on survival and flight activity (Morsello and Kennedy, 2009). Moreover, drought, heat, and extreme light conditions also modulate plant responses to pathogens, often weakening plant defenses

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(Mittler and Blumwald, 2010).

Soil properties, including physical, chemical and biological characteristics, can also play a crucial role in plant health and susceptibility to diseases (Ghorbani et al., 2008). Combined with meteorological conditions, they can indirectly influence pathogen-host interactions by inducing abiotic stress that weakens plant defences increasing plants susceptibility to infections (Atkinson and Urwin, 2012). Soil organic matter enhances water and nutrient retention (Banwart et al., 2014) while soil structure controls water flow, nutrients, oxygenation and root development (Bronick and Lal, 2005), and soil pH level regulates nutrient availability (Barrow and Hartemink, 2023), ultimately impacting plant resilience to disease.

Agricultural practices can directly affect pathogens or modify environmental conditions, either benefiting or hindering their development. In agroforestry systems, for example, shade trees mitigate air and soil extreme temperatures through light interception (Merle et al., 2022). This reduces plant physiological stress, generally making crops less susceptible to disease (Schroth et al., 2000). Furthermore, neighbouring plants in agroforestry systems can serve as alternative hosts for pathogens, provide habitats for vectors, or, conversely, support natural enemies of vectors, thereby contributing to disease natural regulation in crops (Avelino et al., 2023). Enclosing crops with non-host plants has been explored as a strategy to reduce vector-borne virus transmission (Hooks and Fereres, 2006), as non-host species serve as physical barriers that limit vector dispersion and act as pathogen sinks by capturing them when vectors land or probe, particularly in the case of non-persistent transmission (Fereres, 2000). In addition, depending on their composition and structure, landscapes surrounding crops can act as barriers over considerable distances, with similar biological processes involved. These landscapes typically form a mosaic of habitats that interact, providing a wide range of essential ecosystem services such as pest and disease regulation (Power, 2010; Vialatte et al., 2019; Zhang et al., 2007). Indeed, landscapes with diversified composition can help dilute pathogen inoculum, depending on land connectivity, with some areas serving as reservoirs while others act as pathogen sinks (Papaïx et al., 2014). The spatial arrangement of these habitats can either facilitate or hinder pathogen transmission by shaping vector movement through corridors or barriers (Tischendorf and Fahrig, 2000). As landscapes evolve, new conditions may emerge that promote vector establishment, potentially leading to new outbreaks (Meentemeyer et al., 2012).

The cocoa swollen shoot virus (CSSV) disease is the main viral threat to cocoa production in West Africa (Ploetz, 2016). Infected cocoa trees (*Theobroma cacao* L.*)* exhibit severe symptoms, including leaf chlorosis, shoot swelling, and substantial reductions in pod and bean production (Ofori et al., 2022). Typically, pod production declines sharply within three years of infection, ultimately leading to tree mortality (Crowdy and Posnette, 1947). CSSV is transmitted by at least fourteen mealybug species (Koffi et al., 2024 in press) which can acquire the virus within hours through feeding and retain it for a few days on their stylets (Obok et al., 2018; Roivainen, 1976). Mealybug dispersal mainly occurs locally through canopy migration, particularly via mobile first-instar nymphs engaged in active foraging, while older nymphs and adults are largely sedentary (Cornwell, 1958). Wind-borne dispersal is also possible but generally limited to localized spread under cocoa canopy (Cornwell, 1960) or further via tall host trees overhanging or surrounding cocoa plots, creating elevated pathways for extended dispersion. Moreover, human activities may facilitate broader dispersal by moving CSSV-infected planting materials, such as seeds (Quainoo et al., 2008) or seedlings (Assiri et al., 2009).

Current eradication strategies for CSSV rely on the roguing of symptomatic trees in disease outbreaks, including adjacent asymptomatic trees that may be infected (Thresh and Owusu, 1986). However, this approach is not widely adopted by cocoa farmers, as infected trees remain a source of income, despite decreasing production (Gyamera et al., 2023). Moreover, no curative treatment is available to date. Not only do farmers often fail to associate the disease with its mealybug vectors (Reyes et al., under review), but insecticides are also largely ineffective against these pests. The latter are protected by their waxy layer, by shelters built by tending ants or not accessible in crevices of wood (Hanna et al., 1955). Additionally, breeding programs for CSSV resistance have achieved only partial tolerance (Gyamera et al., 2023). However, planting CSSV non-host species around cocoa crops has shown promise in CSSV containment strategy in Togo (Oro et al., 2012), Ghana (Domfeh et al., 2016) and Côte d'Ivoire (Babin et al., 2023). In addition, agroforestry-based preventive strategies, particularly the integration of shade trees, have gained attention for their potential to mitigate CSSV severity compared to full-sun plots, especially when plot shade cover is around 50 % (Andres et al., 2018). Shade tree buffer temperature and humidity fluctuations (Abdulai et al., 2018), especially in the face of extreme climatic events (Niether et al., 2018). These conditions benefit cocoa physiology (Asitoakor et al., 2022; Mensah et al., 2022) and support mealybug predators and parasitoids, enhancing natural pest regulation (Bigger, 1981). However, certain tree species commonly found within cocoa plots, such as *Cola chlamydantha* K. Schum. (Malvaceae) or *Ceiba pentandra* (L.) Gaertn. (Bombacaceae), are alternative hosts for CSSV (Posnette et al., 1950; Tinsley, 1971), although their specific role in CSSV dynamics remains unquantified.

To conclude, CSSV remains uncontrolled and continues to spread rapidly across West Africa, highlighting the urgent need to identify the key epidemic drivers in order to support more effective management strategies. Previous studies have primarily focused on microclimate and local soil properties as factors affecting the vector biology or individual cocoa tree response to infection. As emphasized by Ameyaw et al. (2024), little is known about how broader agroecological conditions, such as meteorological factors, soil characteristics, the presence of alternative host species, and landscape context, shape disease intensity at larger spatial scales. We hypothesize that environmental conditions unfavourable to cocoa health or conducive to vector development contribute to increased disease intensity. We also hypothesize that the presence of alternative host trees of the virus within agroforestry systems may increase disease spread particularly at long distance, and that the composition of the surrounding landscape plays a significant role in disease progression. Finally, we propose that these factors operate in combination, leading to the emergence of distinct cocoa plantation profiles with varying levels of vulnerability to the disease. To test these hypotheses, we applied unsupervised Self-Organizing Maps (Kohonen, 1982), a method widely used in ecological and epidemiological research for identifying complex, multidimensional patterns (Chon, 2011). By offering new insights into the epidemiology of CSSV, our study aims to support the development of more targeted and sustainable disease management strategies in Côte d'Ivoire.

2. Materials and methods

2.1. Studied cocoa production areas

The present study is based on data collected in smallholder cocoa plots selected across the cocoa-growing regions of Côte d'Ivoire. An initial survey identified 15 cocoa production areas (Fig. 1), chosen to capture a diverse range of climatic conditions (temperature and rainfall), vegetation types and soil properties, ensuring comprehensive representation of the country's cocoa-growing conditions (N'guessan et al., 2017). This also accounted for historical westward expansion of cocoa cultivation over the past seven decades (Ruf et al., 2015), which has led to considerable variation in technical practices, social and economic dynamics. In a second phase, 10 plots were selected in each cocoa production area to capture the diversity of cocoa growing conditions across the landscape. The structural complexity of the vegetation was considered within cocoa production area. Selected plots ranged from full-sun monocultures to complex agroforestry systems with varying levels of shade provided by associated tree species (details in Konan et al., 2023). Plots also varied in age, ranging from recently established

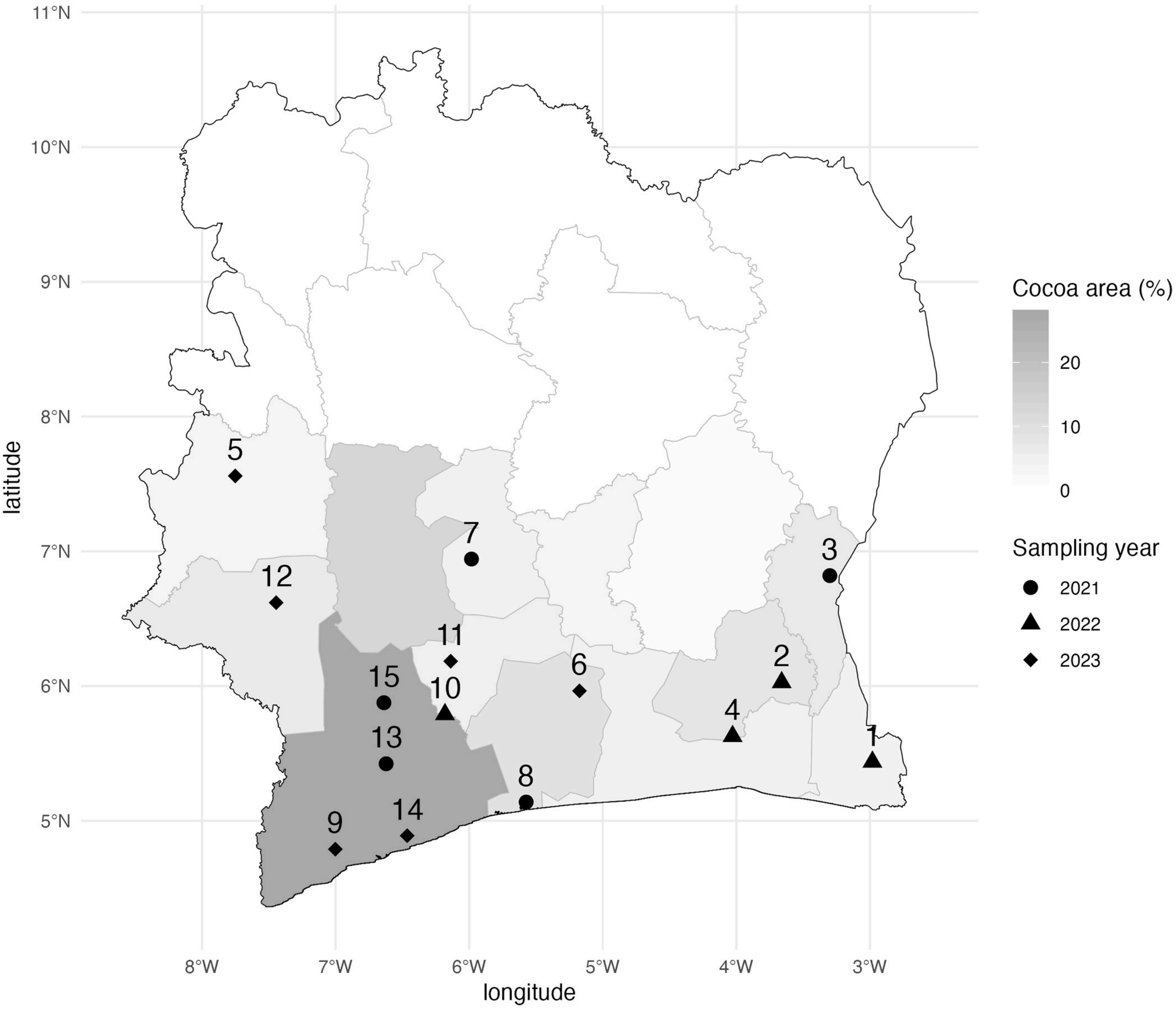

Fig. 1. Studied cocoa production areas distribution. The map illustrates the distribution of the 15 studied cocoa production areas (1: Aboisso, 2: Adzopé, 3: Agnibilékrou, 4: Azaguié, 5: Biankouma, 6: Blé, 7: Bonon, 8: Fresco, 9: Grand-Béréby, 10: Guéyo, 11: Guibéroua, 12: Guiglo, 13: Méagui, 14: San-Pédro, 15: Soubré), within which ten cocoa plots were selected. The CSSV disease incidence was assessed across different areas over multiple years, represented on the map by distinct symbols. The background represents the percentage of land dedicated to cocoa cultivation by region (Assiri et al., 2016), although the map does not necessarily delineate officially recognized national boundaries.

plantations of 4 years to old plantations up to 70 years, with an average plot age of 20 years across all selected plots. Within the same cocoa production area, the average age range of plots was 28 years. Differences in age between cocoa production area were not statistically significant, except for Biankouma, which had significantly younger plots of 9 years old in average compared to Gueyo, Meagui and San-Pédro (Dunn's test with Bonferroni correction, $p < 0.05$). Plot varied also in productivity, from low yielding, averaging in minimum 182 kg/ha, to highly productive plots, averaging in maximum 1862 kg/ha in cocoa production area. Moreover, plot sizes ranged from 0.3 to 5 ha, with a mean of 1.6 ha across all selected plots, and did not differ significantly between cocoa production area (Kruskal-Wallis rank sum test, $p = 0.2$). The high genetic diversity of cocoa (Guiraud et al., 2018) was not accounted for, as cocoa genotypes recombination remains largely uncontrolled due to the widespread use of planting material derived from informal, artisanal nurseries (Assiri et al., 2016). Geographic coordinates for each of the 150 plots were recorded using a GPS device (Garmin GPSMAP 64 s) to ensure precise georeferencing of cocoa plots.

2.2. *CSSV disease assessment*

The CSSV disease intensity was assessed from May 2021 to April 2023 across the 150 (15 studied cocoa production areas x 10 plots) selected plots (Fig. 1, Fig. 3A). A plot was classified as infected if at least one cocoa tree exhibited CSSV symptoms, such as red banding, leaf chlorosis, and shoot swelling (Muller, 2016). Plots and outbreak zones were delineated using GPS to determine their total area. Outbreak zones included a 3-meter buffer around symptomatic trees to account for potential asymptomatic infections (Muller et al., 2001). CSSV incidence for each plot was calculated and defined as the total area of all outbreaks, including buffer zones, divided by the total plot area.

2.3. *Meteorological conditions*

We used meteorological data from AgERA5, provided by the Copernicus Climate Change Service and publicly accessible (Boogaard et al., 2020). This dataset, based on the fifth generation of ECMWF atmospheric reanalyses, provides meteorological variables at a spatial resolution of 0.1° × 0.1° (~10 km x 10 km) and a daily temporal resolution. The parameters considered include wind speed at 10 m above the ground level (m/s), temperature at 2 m above the ground surface (°C), precipitation flux (mm/day), and relative humidity at 15:00 h local time at 2 m above ground level (as a percentage of air water vapor saturation).

Given the complex interactions between meteorological conditions, plants physiology, vectors dynamics and CSSV incidence, meteorological data were analysed across multiple time windows using various statistical aggregations (Van de Pol et al., 2016). The statistical aggregations included mean, median, minimum, maximum and variance, capturing different biological processes, such as the effect of central tendencies in data distribution (Cao, 2021) or extreme weather events (Bailey and Van de Pol, 2016). Meteorological data were analysed over a five-year period (January 2018–December 2022) to assess both short- and medium-term climate influences on disease incidence (Fig. 3A). Seasonal variations were also considered by distinguishing four distinct periods: the major dry season (December–April), the minor dry season (August–September), the major rainy season (May–July) and the minor rainy season (October–November). A total of 596 meteorological variables were compiled for the 150 plots.

2.4. Soil quality indicators at the plot scale

To evaluate soil quality, we utilized a minimal set of soil quality indicators defined by Rousseau et al. (2012), based on scientific literature on to cocoa-based agroforestry systems and old-growth forests. Soil data were retrieved from SoilGrids (ISRIC, 2019) at a spatial resolution of 250 m (Hengl et al., 2017). The selected indicators included bulk density (kg/m3), soil pH and soil organic carbon content (g/kg) (Hengl et al., 2015). These global soil properties, derived from machine learning models and compiled between 2008 and 2014, are assumed to have remained largely stable and are thus considered representative of current conditions (Fig. 3 A).

2.5. Plot-scaled agroforestry characteristics

Between March 2021 and November 2022 (Fig. 3 A), a forest inventory was conducted to document trees associated with cocoa plots, with a diameter at breast height (DBH) ≥ 10 cm (Kouassi et al., 2023). Stand basal area (m^2/ ha) was used as standard proxy for evaluating plot shade levels (Bagny Beilhe et al., 2020; Mitchell and Popovich, 1997). Stand basal area ranges from 0.2 m^2/ha in full-sun cocoa plots to 26 m^2/ha in shaded cocoa systems. Within cocoa production areas, the standard deviation of stand basal area varies from 1 to 8 m^2/ha, reflecting both intra- and inter-area variability. Additionally, a literature-based list of 20 tree species known as alternative host of CSSV was compiled (Texte A1). Host tree density was assessed using the same proxy, defined as host tree basal area (m^2/ha) and goes from 0 to 7 m^2/ha.

2.6. Land cover of Côte d'Ivoire

The land cover of Côte d'Ivoire was mapped for 2017 and 2020, corresponding to four and one year prior the disease assessment, respectively (Fig. 3 A). Both maps were generated by the Centre d'Information Géographique et du Numérique (CIGN) of the Bureau National d'Etudes Techniques et de Développement (BNETD) using Sentinel 2 satellite images. The 2020 map is publicly available via the Africa GeoPortal (BNETD-CIGN, 2023), while the 2017 map is available upon request. As these maps used two different nomenclatures, a homogenized one was described in Tables A2 and A3. We grouped land cover types into four categories based on their potential to host CSSV: "non-cocoa" includes lands and crops that are not likely to host CSSV, but may be suitable for mealybug vectors, which are generally polyphagous (Strickland, 1951). The "natural vegetation" groups lands that could include alternative hosts of CSSV and serve as habitats for mealybug vectors. "Others" encompass lands that are unsuitable environments for both CSSV and mealybugs. Finally, "cocoa" includes cocoa lands that can become infected and serve as the primary host and reservoir of the virus. However, the classification in 2017 does not distinguish between cocoa and coffee and the cocoa category was named "cocoa/coffee" in 2017 but "cocoa" in 2020.

The landscape composition surrounding the 150 plots was assessed by calculating the relative proportions of the different land cover categories within varying buffer zones. Buffer sizes were selected based on current knowledge of CSSV transmission mechanisms. A buffer zone with a 50-meter radius was applied to represent local disease transmission, primarily through the short-distance movement of infectious mealybug vectors within the cocoa canopy or via wind transport within cocoa plots (Cornwell, 1960, 1958). Two larger buffer zones, with 300-meters and 1000-meters radius, were considered to account for the broader spread of CSSV, partly facilitated by human activities such as the movement of infected planting materials. Although wind-driven mealybug dispersal is unlikely beyond 50 meters within a cocoa plot, long-distance virus spread via mealybugs remains possible when tall host trees overhang or surround cocoa plots, creating elevated pathways for extended dispersion. Landscape composition within buffers zones were extracted using the *exactextractr* (Baston et al., 2023), *raster* (Hijmans et al., 2025), and *sf* (Pebesma, 2018) packages. In both 2017 and 2020, the landscape was predominantly composed of "cocoa" and "non-cocoa", with lower proportions of "natural vegetation" and "others", although some outliers were observed (Fig. 2). On average, "cocoa/coffee" was more present in 2017, while "non-cocoa" became the dominant land cover in 2020 across all spatial scales. In 2017, "cocoa/coffee" and "non-cocoa" exhibited greater differences in mean values and higher variability across spatial scales compared to 2020 (Fig. 2). However, in 2020, variation increased progressively from larger to smaller spatial scales.

2.7. Self-Organizing Map

The self-organizing map (SOM) is an automated data analysis method widely used for clustering and data exploration (Kohonen, 2013). It is particularly effective in handling nonlinearity, complex interactions, and strong correlations between variables (Koudenoukpo et al., 2021; Mendoza-Carranza et al., 2018; Stephan et al., 2022), while also handling high-dimensional data (Delgado et al., 2015; Wirth et al., 2011). These features make SOM particularly suitable for the analysis of complex ecological datasets. Network training was performed using the unsupervised *som* function from the *kohonen* package (Wehrens and Buydens, 2007). The algorithm performs a non-linear projection of multidimensional data, mapping input vectors onto a two-dimensional grid of nodes, each characterized by prototype vectors of the same dimension as the input vectors (Fig. 3B). The data were initially centred and scaled to ensure that variables with different units did not disproportionately influence the distribution of input vectors across the nodes (Stephan et al., 2022). During training, input vectors are fed into the network, and the 'best-matching unit', defined as the prototype vector closest to the input vector, is identified. Moreover, the network self-organizes by adjusting a node's prototype vector, and its neighbours within a defined radius to better match the input vector (Chon, 2011). At the end of the training, each node is thus characterized by a prototype vector that represents multiple input vectors. SOM can be combined with clustering methods to group prototype vectors, enabling quantitative analysis of both the map and the underlying data (Vesanto and Alhoniemi, 2000). In this study, we refer to this approach as the SOM-hclust algorithm. Hierarchical cluster analysis (hclust) was performed using Ward's aggregation criterion, which minimizes total within-cluster variance, with the *hclust* function from the *stats* package (R Core Team, 2024). The number of clusters was determined based on

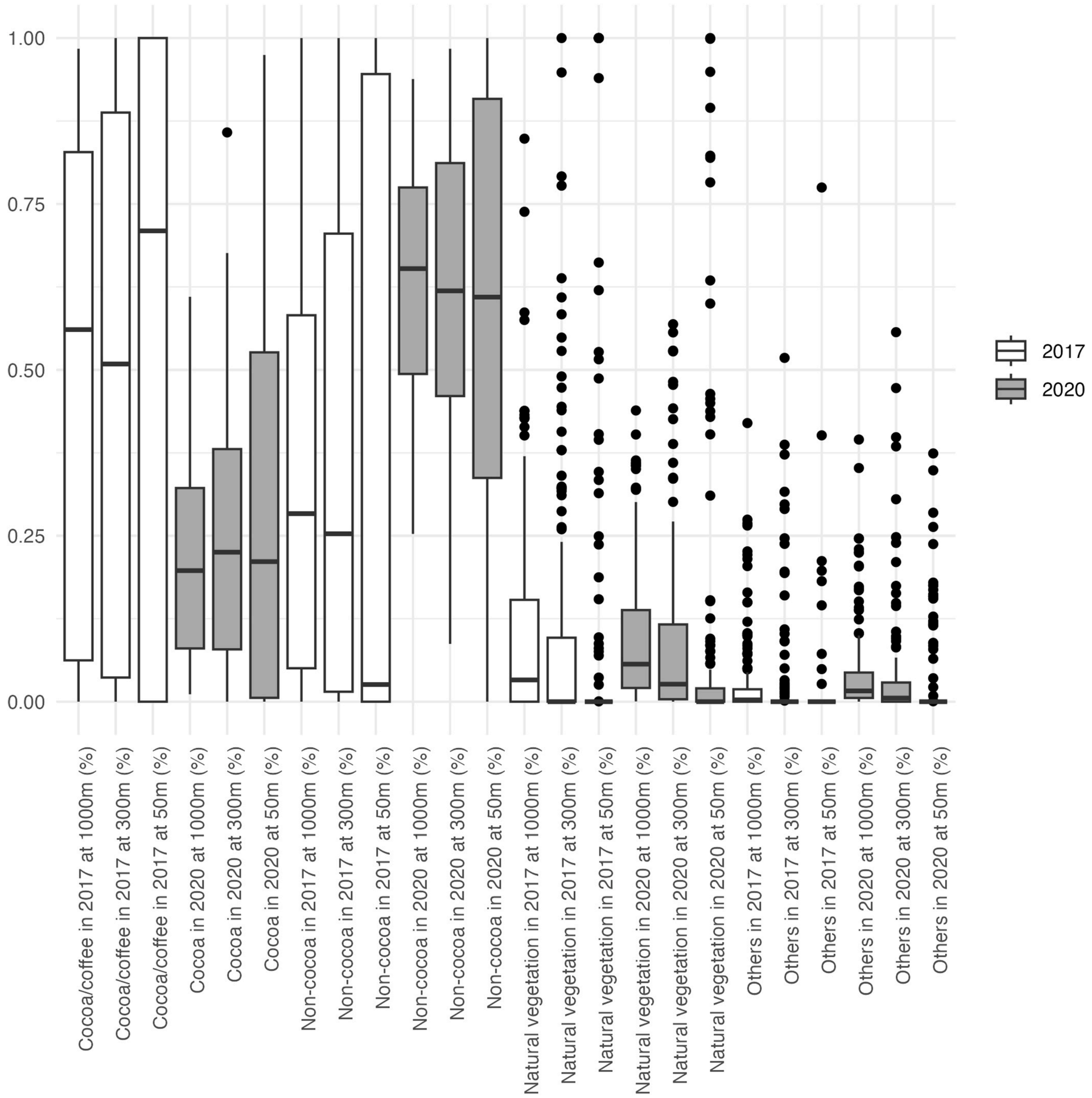

Fig. 2. Boxplots of land cover category proportion across spatial scales. Boxplots illustrate the proportions of four land cover categories (“cocoa”, “non-cocoa”, “natural vegetation”, “others”) across three buffer sizes (50 m, 300 m and 1000 m radius) for two years (2017 in grey and 2020 in white). Boxplots display the median, interquartile range, minimum and maximum values, with outliers represented as points beyond the whiskers.

the break in slope of the dendrogram and the subsequent jump in hierarchy, indicating distinct cluster separation (Fig. 3B), using the *aweSOMscreeplot* function from the *aweSOM* package (Boelaert et al., 2022). Dendrograms were segmented using the *cutree* function of the *dendextend* package (Galili, 2015).

2.8. Clustering based on agroecosystem factors and CSSV incidence

Cocoa plot clusters were identified by the SOM-hclust algorithm (Fig. 3B) based on 5 categories of standardized variables: CSSV incidence, meteorological conditions, soil properties, agroforestry and landscape composition and parameters described in Table A1. The selection of variables was guided by biological hypotheses: 596 meteorological variables, 4 soil property variables, 2 variables describing shade conditions and host tree presence, 24 variables representing landscape composition in 2017 and 2020 (at 50, 300, and 1000-meters of radius), and one variable characterizing CSSV incidence in each plot. Since all variables are equally weighted during SOM training, it was crucial to maintain a balanced number across categories to prevent biases in cocoa plot typology. Particular attention was given to selecting meteorological variables, which had a higher spatial resolution than the other variables. Due to this higher resolution, multiple cocoa plots shared similar values for wind speed, temperature, precipitation, and humidity, introducing a spatial structure among the plots that could bias

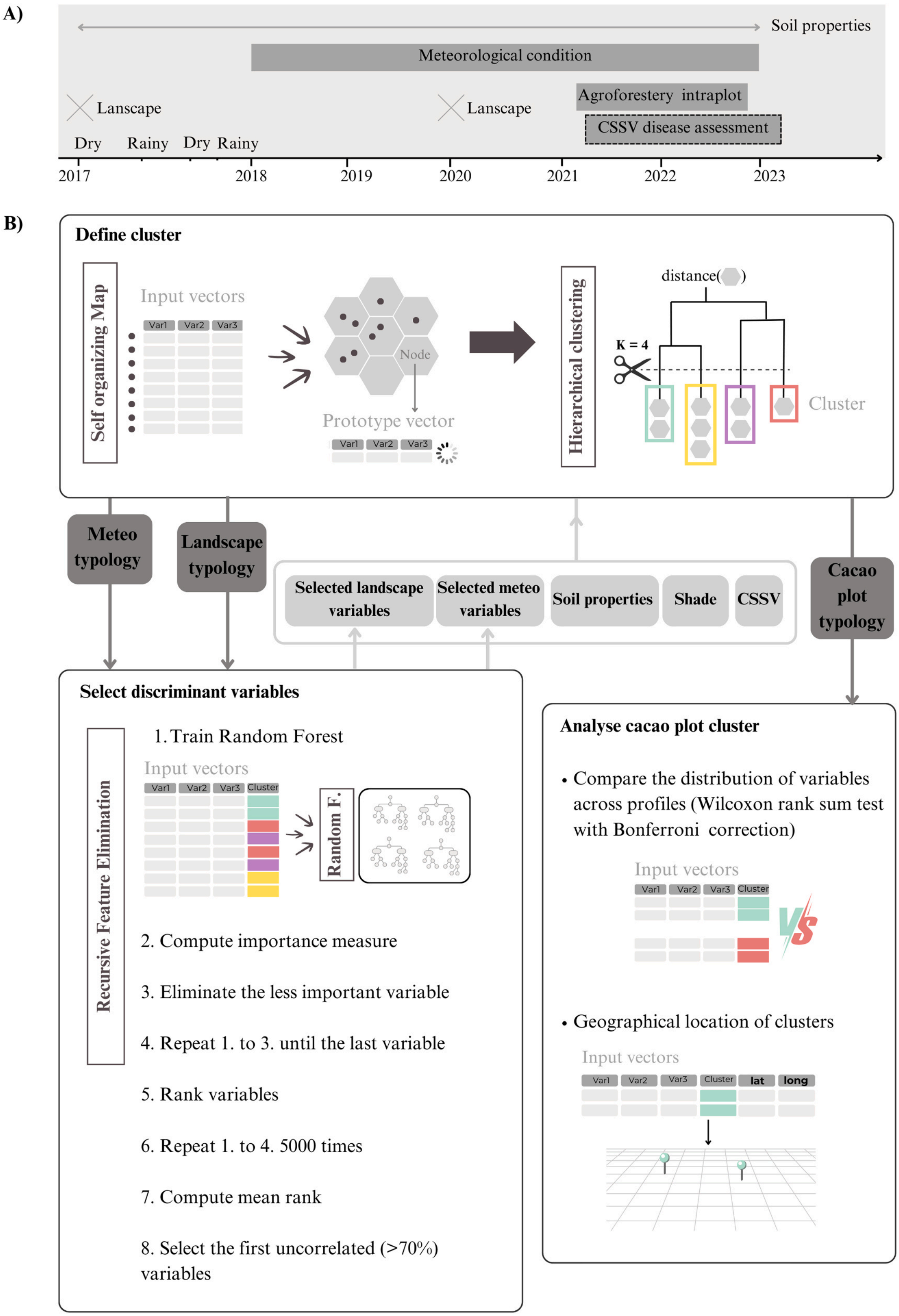

Fig. 3. Overview of data collection timing and analysis A) Timeline of study data: boxes represent variables within specific time windows; double arrows indicate variables that remained constant throughout the disease assessment period; crosses denote variables with a one-year timeframe. B) Methodological summary: A self-organizing map and hierarchical clustering defined typologies of cocoa plots. A meteorological typology identified the most discriminative variables among 596 related to wind speed, humidity, temperature, and precipitation. Similarly, a landscape typology was based on 24 variables describing landscape composition in 2017 and 2020 across various buffer sizes. Finally, a cocoa plot typology was created and analysed using the selected variables.

the cocoa plots profiling process. For this reason, the number of meteorological and landscape variables was reduced by selecting only those most representative of the meteorological and landscape typology of the studied area.

2.9. *Variable selection*

Meteorological and landscape typologies were identified by the SOM-hclust algorithm, with parameters detailed in Table A1. Since variable importance was not directly given in the unsupervised SOM-hclust process, a post-hoc analysis was necessary to estimate the relative contribution of variables. This estimation was achieved by training a supervised model on the typology, using Random Forest as the selection method (Gregorutti et al., 2017) with the *randomForest* and *importance* functions from the *randomForest* package (Liaw and Wiener, 2002). However, Random Forest is sensitive to correlations since random variables permutations can influence importance criteria (Toloşi and Lengauer, 2011). To address this issue, variables were screened using Recursive Feature Elimination (RFE) (Fig. 3B). As described by Gregorutti et al. (2017), RFE is a backward selection algorithm that iteratively removes the least important variable in the Random Forest classification. Its robustness to correlation stems from its approach to updating variable importance measures. The Mean Decrease Accuracy (MDA) was recommended to assess variable importance, as outlined by Gregorutti et al. (2017). This metric evaluates the impact of excluding a variable on the model's overall accuracy. A total of 5000 RFEs were conducted, and the mean rank was computed over these iterations to ensure a robust selection process. The top-ranked variables were considered the most important to be selected. If two variables shared the same biological significance and had a Person correlation exceeding 70 % (Bhatt et al., 2013), then only one was selected. Correlations were computed and visualized using the chart.*Correlation* function from the *PerformanceAnalytics* package (Peterson et al., 2024). To ensure balance across variable categories, selection was restricted to three meteorological variables and three landscape variables.

2.10. *Analysis of cocoa plot clusters*

First, we analysed the distribution of all selected variables across cocoa plot clusters generated by the SOM-hclust algorithm using boxplots. Variables in different clusters were found to be non-normally distributed and did not exhibit equal variances. Consequently, non-parametric tests were used to compare variables distributions across clusters (Blair and Higgins, 1980). Pairwise comparisons between clusters were conducted using the Wilcoxon rank sum test (Wilcoxon, 1945) with the pairwise.wilcox.test function from the stats package. The Bonferroni correction was applied to the Wilcoxon tests due to the multiple tests being conducted ($N = 180$, $\alpha = 3e\text{-}04$) (Armstrong, 2014). Given that cocoa plots are geospatially referenced, we mapped the plots according to their cluster assignments.

3. Results

3.1. *Variable selection*

The analysis of landscape composition variables led to their classification into six distinct groups, derived from 24 initial variables. Through the Recursive Feature Elimination (RFE) process, the most representative variables were the areas occupied by “cocoa (cocoa/coffee)” and “non-cocoa” in 2017 and 2020 across multiple spatial scales. These variables exhibited higher mean ranks (greater than 10) compared to “natural vegetation” or “others” (Fig. 4A). Among the top three selected variables, the most frequently chosen were “cocoa/coffee” in 2017 at the 50-meters radius, as well as “cocoa” in 2020 at both the 50-meters and the 1000-meters radius. Since the correlation coefficients among variables remained below 0.7, the top three selected variables were retained. The selected variables were strongly correlated with their respective land category ($r > 0.7$, $p < 0.001$) and negatively correlated with “non-cocoa” at different scales ($r < -0.7$, $p < 0.001$), supporting similar biological meaning.

Similarly, meteorological variables were classified into six groups, derived from an initial set of 596 variables. Using the RFE selection process, temperature and precipitation variables were identified as the most representative of these groups (Fig. 4B). Among the representative variables (mean rank greater than 10), the most frequently chosen were the temperature range and variance during the short rainy season of 2020. Due to their strong correlation ($r = 0.96$, $p < 0.001$), these two variables convey similar information on thermal variability, reflecting low temperature fluctuations during this period. Since the “range” variable demonstrated better classification performance, it was retained. Following a similar approach, the mean precipitation during the short rainy season of 2019 was preferred over the median precipitation during the main rainy season of 2020 ($r = 0.84$, $p < 0.001$). Likewise, the maximum precipitation during the short dry season of 2019 were selected over the precipitation range ($r = 1$, $p < 0.001$), as the minimum precipitation value in this case was always zero.

3.2. *3Description of cocoa plot clusters*

The SOM-hclust algorithm classified cocoa plots into six distinct

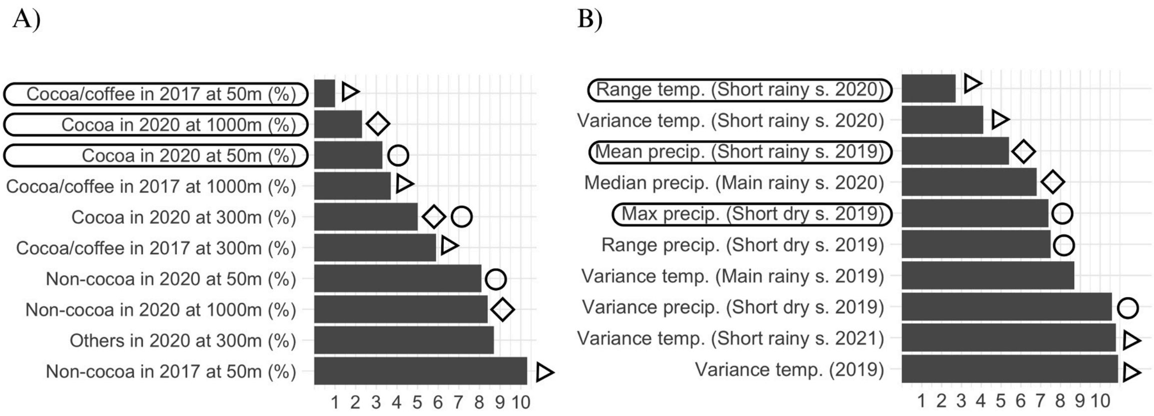

Fig. 4. Variable selection based on average ranks over 5000 iterations of Recursive Feature Elimination (RFE). RFE was applied to typologies generated by the SOM-hclust algorithm on 150 plots representing cocoa-growing conditions in Côte d'Ivoire. The top ten variables are displayed, with the first rank representing the most important variable. Selection was performed separately for A) landscape composition variables and B) meteorological variables. The top three selected variables are highlighted with enclosing lines. High correlations (above 70 %) between selected variables and other variables are indicated by symbols.

clusters (1–6), based on agroecosystem factors (Fig. 5). Cluster 1 consists of 9 plots, Cluster 2 of 10, Cluster 3 of 52, Cluster 4 of 59, Cluster 5 of 14, and Cluster 6 of 6 plots. A significant trend was observed from Cluster 3 to Cluster 6, characterized by an increase in the mean incidence of CSSV disease from 6 % to 44 %, an increase in temperature ranges from 2°C to 3°C, and an increase in the proportion of land composed of "cocoa/coffee" in 2017 from 50 % to 100 %. Conversely, maximum precipitation decreased along this gradient, from 50 mm/day to 24 mm/day. No significant trends were detected from Cluster 3 to Cluster 6 for soil pH, mean precipitation, the proportion of land composed of "cocoa" in 2020, stand basal area, which averaged 6 m^2/ha across all clusters, and the basal area of CSSV host trees, which averaged 1 m^2/ha.

Cluster 2 stood out as particularly distinct from the other clusters, exhibiting higher soil organic carbon and lower bulk density ($p < 3e\text{-}04$ for all comparisons). Additionally, compared to Cluster 1, Cluster 2 was characterized by a greater temperature range, a higher proportion of land under cocoa cultivation in 2020 within a 1000-meter radius, lower maximum precipitation, and a lower stand basal area, which averaged 18 % in Cluster 1 ($p < 3e\text{-}04$ for all comparisons). Similarly to Cluster 1, Cluster 2 did not record any CSSV infection and showed no significant differences in mean precipitation, pH and the proportion of land under

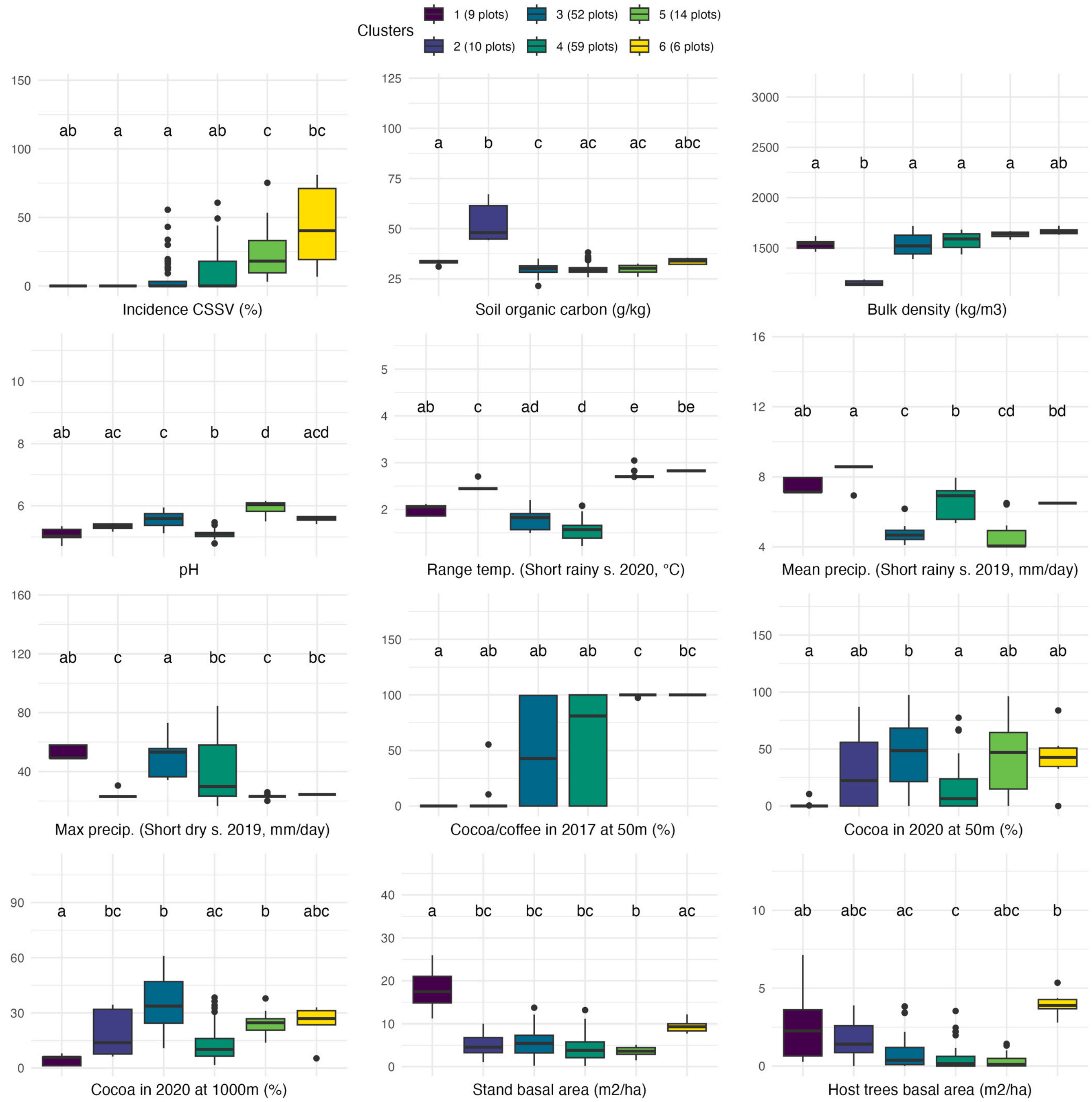

Fig. 5. Boxplots of CSSV incidence and agroecosystem factors across five cocoa plot clusters. Cocoa plot clusters were generated by SOM-hclust algorithm applied to 150 plots representing cocoa-growing conditions in Côte d'Ivoire. Boxplots display the median, interquartile range, minimum, maximum, and outliers, which are represented as points beyond the whiskers. Wilcoxon rank sum tests were performed between clusters with a Bonferroni correction (N = 180) for multiple tests comparison. Clusters sharing the same letter are not significantly different.

cocoa cultivation in 2017 ($p > 3e\text{-}04$ for all comparisons).

Cluster 4 appeared to be an intermediate cluster between Clusters 3 and 6. It shared similarities with Clusters 3 and 6 in terms of CSSV incidence, soil organic carbon, bulk density, and the proportion of land composed of "cocoa" in 2017 ($p > 3e\text{-}04$, for all comparisons). It also resembled Cluster 3 in terms of temperature range ($p = 2.0e\text{-}03$) and host tree basal area ($p = 1.8e\text{-}02$), while sharing similarities with Cluster 6 in terms of mean precipitation ($p = 8.5e\text{-}01$), maximum precipitation ($p = 2.0e\text{-}01$) and the proportion of land composed of "cocoa" in 2020 at 50-meter and 1000-meters radii ($p > 3e\text{-}04$).

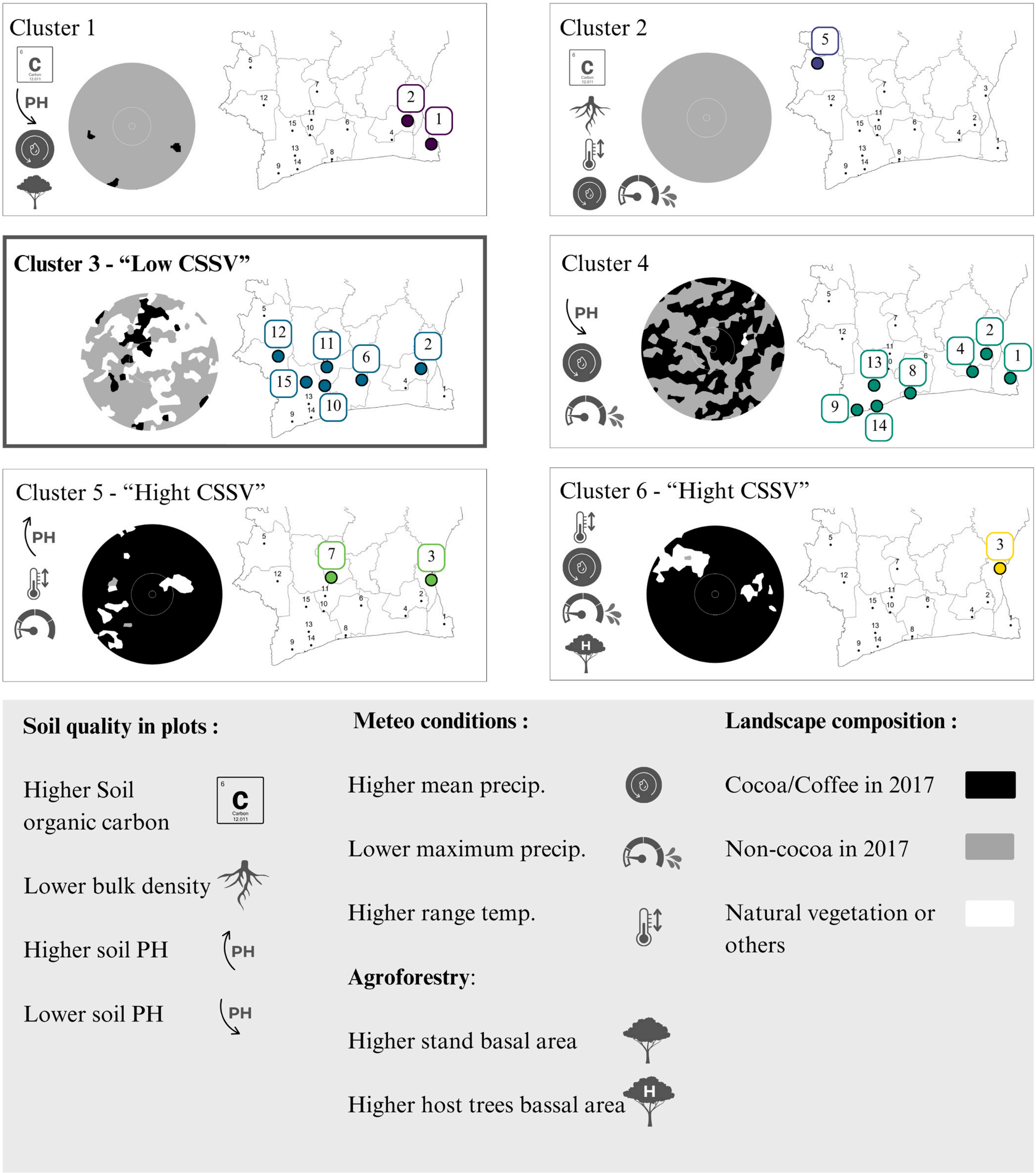

Fig. 6. Spatial distribution of cocoa plot clusters and associated agroecosystem characteristics. The spatial distribution of the studied cocoa areas in each cluster is highlighted using the same colours as in Fig. 5. Significative differences of agroecosystem factors between Cluster 3 and the other clusters were represented using distinct symbols. To provide insight into the surrounding landscape composition, a 1 km buffer zone was mapped around a representative plot from each cluster, based on 2017 land cover data. The background map outlined the location of the studied cocoa production areas, described in Fig. 1.

3.3. CSSV profiles comparison

Clusters 1, 2, and 4 did not exhibit significant differences in mean CSSV incidence (Fig. 5, $p > 3e\text{-}04$). Clusters 1 and 2 contained no infected plots. Cluster 1 was located in Adzopé and Aboisso, near the Ghanaian border in southeastern Côte d'Ivoire, while Cluster 2 was found exclusively in the Biankouma region, at the northwestern edge of the cocoa-growing area (Fig. 6). In contrast, Clusters 3, 4, 5, and 6 included both infected and non-infected plots, with mean CSSV incidence of 6 %, 10 %, 26 %, and 43 %, respectively (Fig. 5). Cluster 3 was distributed across Blé, Guéyo, Guibéroua, Guiglo, and Soubré, in western Côte d'Ivoire, with two additional plots in Adzopé. Further south, Cluster 4 was concentrated in Azaguié, Fresco, Grand-Béréby, Méagui, and San-Pédro, while also including three plots in Adzopé and six in Aboisso. Cluster 5 was located between Bonon and Agnibilékrou, whereas Cluster 6 was exclusively found in Agnibilékrou (Fig. 6). CSSV assessments were conducted in 2022 for Cluster 1, in 2023 for Cluster 2, from 2021 to 2023 for Clusters 3 and 4, and in 2021 for Clusters 5 and 6 (Fig. 1. and Fig. 6).

Among clusters with multiple CSSV-infected plots (Clusters 3, 4, 5, and 6), three significantly different profiles emerged (Fig. 6): a "Low CSSV" incidence profile (Cluster 3) and two "High CSSV" incidence profiles (Clusters 5 and 6). The analysis of factors associated with disease incidence indicated that CSSV incidence was primarily associated with maximum precipitation and landscape composition in 2017, followed by temperature range (Figure A1). The "Low CSSV" profile was characterized by nearly twice the maximum precipitation and half the temperature range compared to the "High CSSV" profiles ($p < 3e\text{-}04$ for all comparisons). Additionally, the "Low CSSV" profile exhibited a lower proportion of land under cocoa cultivation in 2017 ($p = 1.7e\text{-}05$) compared to Cluster 5. Regarding Cluster 6, it had 2 mm/day higher mean precipitation ($p = 6e\text{-}05$) and a significantly higher host tree basal area, with an average of 4 m^2/ha, compared to 1 m^2/ha in the "Low CSSV" profile ($p = 1.7e\text{-}04$). Furthermore, between 2017 and 2020, the proportion of land under cocoa cultivation decreased by 55 % in Cluster 5 and 58 % in Cluster 6, both classified as "High CSSV" profiles, whereas it declined by only 3 % in the "Low CSSV" profile (Fig. 5 and Fig. 6).

4. Discussion

This study investigated the associations between environmental factors (meteorological conditions and soil properties), agroforestry factors (shade levels and alternative host trees), the surrounding landscape composition, and CSSV incidence in cocoa orchards of Côte d'Ivoire. Notably, low CSSV incidence was associated with extreme precipitation events, low temperature variations and high mean precipitation. In contrast, in one 'High CSSV' profile, a greater presence of host trees was observed. Moreover, this was the first study to examine CSSV epidemics at landscape level. Our analysis reveals an association between CSSV incidence and the composition of host and non-host lands surrounding cocoa plots, providing insights for large-scale management strategies.

Our results demonstrated a strong association between CSSV disease and extreme precipitation events, particularly in the 'Low CSSV' profile, which experiences higher maximum precipitation compared to the 'High CSSV' profiles. In contrast, higher mean precipitation levels were found in a "High CSSV" profile. Based on these findings, we suggest that high mean precipitation may be less limiting than initially thought, as we had expected it to impact the vulnerability of cocoa trees to CSSV. However, extreme precipitation appeared to be more limiting, potentially facilitating the leaching of cocoa trees from vector mealybug populations (Oyedokun et al., 2022) and limit their aerial dispersal (Cornwell, 1960). Such events may therefore reduce both the transmission of the virus and the spread of mealybugs, effectively limiting the expansion of existing outbreaks and preventing the emergence of new outbreaks from the initial sites of infection. Our analysis also reveals that higher temperature range was strongly associated with high CSSV incidence in both "High CSSV" profiles, located at the northern margins of cocoa-growing regions that experience high temperature fluctuations. This association can be explained by the fact that temperatures exceeding an optimal range create suboptimal conditions for cocoa physiology, potentially weakening the plants and increasing their susceptibility to disease (Hebbar, 2007). Elevated temperatures can also accelerate the population dynamics of mealybugs by increasing their reproduction rate and food intake, which in turn enhances CSSV transmission (Roivainen, 1976). Moreover, this profile, which exhibited higher CSSV incidence, seemed to be associated, although not significantly, with higher bulk density, indicating lower soil quality for cocoa cultivation (Araujo et al., 2018). By reducing soil porosity and aeration, high bulk density may limit biological activity and restrict root development, which are both critical for maintaining plant health (Passioura, 2002; Shah et al., 2017). This suggests that environmental stressors, such as high temperature fluctuations and compacted soils, may act synergistically to weaken cocoa trees and increase their vulnerability to CSSV. To the best of our knowledge, this hypothesis has not been explored in the context of CSSV, highlighting the need for further research in this area.

Additionally, shading did not show significant differences between profiles with varying levels of CSSV incidence. However, this does not imply that agroforestry has no impact on CSSV disease dynamics, as shown by previous studies on CSSV (Andres et al., 2018), as well as other cocoa diseases (Ramos et al., 2024). It appears that weather and landscape factor exert a stronger influence on the cluster characteristics than management practices within the plots, which did not differ significantly across clusters. To further investigate shading effects in regions under disease pressure, a finer-scale analysis with increased spatial and temporal observations per cluster could be conducted. Given that the 'High CSSV' profiles experience higher temperature fluctuations and shading mitigates temperature under the canopy (Niether et al., 2018), it would be of interest to specifically assess shading effects in these regions. However, given that we found an association between a high number of host trees in Cluster 6 and CSSV incidence, we recommend that farmers limit the presence of host trees within and around cocoa plots and introduce non-host shade trees. It is important to note that our study does not allow us to determine whether shading or the presence of host tree has a greater impact on CSSV incidence, so these recommendations should be considered with caution. Another limitation of our study is that the presence of herbaceous and subsistence crops that can host the virus under cocoa canopies was not taken into account in the plots. Additionally, other management practices, such as pesticide use, soil fertilization or cocoa tree spacing, were not included in the study due to the lack of available data, even though these factors may influence CSSV incidence.

Beyond meteorological conditions, soil properties and intra-plot management practices our results reveal that CSSV incidence was also associated with the surrounding landscape composition, with a significant difference between the "Low CSSV" and one of the "Hight CSSV" profile, four years before the first disease assessment in 2017. Notably, plots with lower CSSV incidence were surrounded by a higher proportion of "non-cocoa", from the plot scale to the broader landscape scale. This suggests that "non-cocoa" influences disease dynamics and may act as a sink for the pathogen or as a barrier to the spread of mealybug vectors. Indeed, non-host plants could reduce CSSV transmission by either limiting opportunities for mealybugs to acquire the virus or causing mealybugs to lose their infectivity when feeding on them (Obok et al., 2018). Moreover, this landscape discontinuity may amplify this effect by increasing the spacing between cocoa plots. Experimental studies in Ghana further support this finding at the plot scale, showing that cocoa plots bordered by non-host species exhibited significantly lower CSSV incidence than those surrounded exclusively by "cocoa" (Domfeh et al., 2016). While these findings highlight the potential role of landscape composition in shaping disease dynamics, further research is needed to disentangle the relative contributions of sink and barrier effects to understand the underlying mechanisms. Given the “correlative” nature of our approach and the available data, our study only allows us to make assumptions rather than establish causal relationships at this level of detail.

Moreover, our study found that in 2020, one year before the first disease assessment, the proportion of “cocoa” drastically decreased compared to 2017 in the “High CSSV” profiles, becoming not significantly different from the “Low CSSV” profile. In 2017, the "Low CSSV" profile was characterized by a more diversified landscape, whereas the "High CSSV" profile is almost exclusively surrounded by “cocoa”. This suggests that areas with higher CSSV incidence experienced a greater reduction in the proportion of “cocoa” between 2017 and 2020. However, caution is needed when interpreting these results, as the maps used did not have the same level of precision. In particular, the 2017 map does not distinguish between cocoa and coffee, which may impact direct comparisons. We can still suppose that this is a consequence of high CSSV pressure, which decimated cocoa plantation, leading most farmers to switch to other crops (Ruf et al., 2019).

The absence of CSSV disease in Cluster 1 and the Cluster 2, located on opposite sides of the country, suggests that shared environmental and landscape characteristics may create conditions unfavourable for the virus’s spread or establishment. Both clusters are characterized by higher mean precipitation and lower proportion of the landscape composed of “cocoa” in 2017, which make cocoa plots more isolated from each other. This could indicate that reduced cocoa farm density in high-rainfall regions may limit CSSV spread. However, the history of cocoa westward expansion in Côte d’Ivoire should be seriously considered as a potential factor in the current distribution of the disease, as shown by the localisation of Clusters 1 and 2, respectively in the last and the first zones of cocoa crop expansion (Barima and Konan, 2020). The virus may not have reached newly established cocoa production zones or may have already passed through the oldest ones. Additional cocoa plots should be sampled to confirm whether the virus is truly absent in these regions. As some evidence suggests the presence of CSSV in the Cluster 1 region (Ameyaw et al., 2024), it would also be valuable to use molecular tools to detect latent or asymptomatic CSSV infections. This would help verify whether the apparent absence of the disease is due to underreporting of asymptomatic infections, as our current disease data are based on visible symptoms. A study has also investigated the diversity of CSSV strains, their geographic distribution, and their associated disease severity (Kouakou et al., 2012), which may explain the absence of symptoms in cluster 2. These studies have shown that isolates from groups E and F, which are predominantly found in clusters 1 and 2 in our analysis, tend to be relatively mild and are associated with a slower progression of symptoms. In contrast, the highly aggressive group B isolates identified in clusters 5 and 6, where disease incidence was highest, have been linked to more severe outbreaks. While this viral diversity was not integrated into the current model due to the lack of isolate-specific molecular data at the plantation scale, we nevertheless observed a certain consistency between the clusters formed based on agroecological factors and the distribution of CSSV strains across the Ivorian landscape. This suggests potential interactions between agroecosystem structure and the spatial patterns of viral diversity. This underscores the need for future research to integrate molecular diagnostics and viral genotyping in order to better characterize the relationship between isolate aggressiveness, and agroecosystem factors.

Our findings underscore the importance of the landscape composition surrounding cocoa plantations as a key factor in CSSV management. However, current control strategies typically focus on individual plot-level interventions rather than broader spatial scales. In light of these results, we advocate for further research exploring landscape-scale strategies for CSSV mitigation, with an emphasis on integrating “non-cocoa” lands into the agricultural landscape to reduce disease pressure. Such management strategies should be driven by the goal of identifying an optimal landscape composition that balances short-term and long-term economic benefits (Forster and Gilligan, 2007). To implement this approach, additional studies are required to determine the optimal proportion of “non-cocoa” land and its spatial configuration within the agroecosystem (Papaïx et al., 2018). The feasibility of this strategy will largely depend on farmers’ willingness to collaborate and adopt these management measures, which may be constrained by uncertainties regarding the potential benefits and the complexities involved in coordinating multiple producers (Matthews et al., 2024). However, since cocoa production is often organized around cooperatives that connect farmers within the same region, this structure may provide an opportunity for implementing large-scale collective action. Cooperatives could serve as institutions that would facilitate resource sharing, knowledge exchange, and the adoption of best practices tailored to local conditions and constraints, ultimately supporting the successful implementation of such a strategy (Garcia-Figuera et al., 2024).

CRediT authorship contribution statement

Konan Kouamé Isaac: Data curation, Resources. **KOIGNY Kouadio Juslin Hervé:** Resources. **Deron Kouakou Koffi Alain:** Data curation, Resources. **Loreleï Guéry:** Validation, Project administration, Investigation, Conceptualization, Writing – review & editing, Supervision, Methodology, Funding acquisition. **Dago Marie Ruth:** Data curation, Resources. **Kouassi Kouadio Aimé:** Data curation, Resources. **Régis Babin:** Validation, Investigation, Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Hérault Bruno:** Writing – review & editing. **Dumont Agathe Blanche:** Writing – original draft, Validation, Investigation, Data curation, Visualization, Methodology, Formal analysis, Conceptualization. **Fabienne Ribeyre:** Visualization, Methodology, Funding acquisition, Writing – review & editing, Supervision, Investigation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Chat GPT/ Mistral in order to improve the readability of some sentences. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109851.

Data availability

C4F project data are not yet publicly available. The analysis scripts for the current study are available in the GitHub repository https://github.com/Agathedumont/SOM_agroeco_CSSV.git.

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