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Research article

An increase in management actions has compensated for past climate change effects on desert locust gregarization in western Africa

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A R T I C L E I N F O

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A B S T R A C T

In response to high population density, the desert locust, *Schistocerca gregaria*, becomes gregarious and forms swarms that can cause significant damage to crops and pastures, threatening food security of human populations from western Africa to India. This switch from solitary to gregarious populations is highly dependent on favorable weather conditions. Climate change, which has been hypothesized to shift conditions towards increasing risks of gregarization, is therefore likely to have significant impacts on the spatial distribution and likelihood of outbreak events. However, the desert locust is intensely managed at large scales, which possibly counteracts any increased risk of outbreaks due to a more favorable climate. Consequently, understanding the changes in risks in the future involves teasing out the effects of climate change and management actions. Here we studied the dynamics of gregarization at the very early stages of potential outbreaks, in parallel with trends in climate and management, between 1985 and 2018 in western Africa. We used three different spatial scales, with the goal to have a better understanding of the potential effects of climate change per se while controlling for management. Our first approach was to look at a regional scale, where we observed an overall decrease in gregarization events. However, this scale includes very heterogeneous environments and management efforts. To consider this heterogeneity, we divided the area into a grid of 0.5° cells. For each cell, a climate analysis was performed for rainfall and temperature, with trends obtained by a harmonic decomposition model on monthly data. Analyses of gregarization showed only a few significant trends, both positive and negative, mainly found in western Mauritania where management effort has increased. To improve the statistical power, these cells were then grouped into larger homogeneous climatic clusters, i.e. groups of cells with similar climatic conditions and similar climatic trends over the study period. At this scale, gregarization events depend on the intersection between climate conditions and management efforts. The clusters where gregarization increased were also the ones with the highest increase of management. These results highlight the important effect of preventive management, which may counteract the positive effects of climate change on locust proliferation.

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1. Introduction

The intricate relationship between climate, management strategies and insect populations has been the subject of great interest in applied ecology [1]. Climatic parameters are known to have direct effects on insect population dynamics [2,3]. For example, warmer temperatures, changes in precipitation patterns, and altered seasons due to climate change may all contribute to changes in the distribution, abundance, and phenology of pest species [4,5], shifting the risk in different directions depending on the region. In turn, management strategies have greatly evolved in the last decades, due to new technological and methodological advances (e.g. large-scale monitoring systems, remote sensing, dynamic forecasting tools, new pesticides) that allow early detection and control of potentially dangerous outbreaks [6,7]. Understanding the interactions between climate change, management, and pest outbreaks, especially at large scales, has therefore become an important challenge to guarantee food security for a growing human population.

The impact of climate change on agricultural pests is complex. While climatic trends may produce population declines for some species, the same changes may trigger population outbreaks for others [8–10]. Changes in precipitation patterns and altered temperature regimes can also influence the geographic distribution of pests, potentially expanding their range into previously unaffected areas [5,11,12]. Indeed, some pests and pathogens of crops have already shifted their ranges poleward [13,14]. From a physiological point of view, insect species will struggle in the tropics as temperatures rise beyond currently existing ones, potentially exceeding their temperature tolerance limits [15], although some species will fare better than others. Morever, range expansions and contractions can be accompanied by changes in population dynamics within the range, which are also important to consider. For example, Youngblood et al. (2023) showed, with a physiology-based modelling approach, that climate change is expected to induce more intense outbreaks for the South American locust (*Schistocerca cancellata*) because warmer temperatures in parts of its range will improve its digestive rate, favoring population growth and leading to more swarms and range expansions during outbreaks. Such studies highlight the complex and context-dependent nature of the relationship between climate change and agricultural pest risk, as well as the importance of spatial heterogeneity.

Similar to the effect of climate on pest risks, the frequency and efficiency of management actions are highly variable and species-dependent. When it comes to pests that can affect very large areas, preventive management, which aims at early detection and targeted control actions to prevent large-scale outbreaks from occurring, has been broadly advocated as the best management strategy [16–19]. In this context, it is crucial to establish a monitoring network that covers most of the pest's distribution, especially when long-distance dispersal can play a role in accelerating pest outbreaks. In such situations, local management efforts need to be coordinated across borders to contain any emerging threats from spreading [12,20]. Collaboration and information sharing among neighboring regions is essential to ensure effective preventive pest control [21]. These large-scale monitoring efforts are fundamental to understand the interplay between climate change effects and management efforts, especially when considering long-term temporal horizons. Yet, large-scale and long-term monitoring databases are rare because they require a great human and economic investment [22,23].

In this context, the desert locust *Schistocerca gregaria* (Forskål, 1775) is an excellent case study. With a notorious reputation as one of the most destructive agricultural pests in large parts of northern Africa and south-west Asia [24], their populations have been monitored since the 1920s–1930s. Due to the desert locust's severe impacts on agriculture, the Food and Agriculture Organization (FAO) is coordinating an intergovernmental cooperation between affected countries from western Africa to India. The FAO advocated intensive field surveys with standardized guidelines for data collection since 1985. Our study focused on western Africa, which contains several frontline countries where the risk of gregarization leading to outbreaks is high. We focused on this area because it constitutes both an ecological and a management unit, with a relatively closed cycle in terms of population dynamics and outbreak potential, and with high quality monitoring data. Within the whole distribution of the desert locust, western Africa represents one out of three such ecological units (West, Centre and East) which are currently recognized and treated as functional management units [25]. In western Africa, preventive management is coordinated by the CLCPRO (Commission de Lutte contre le Criquet Pèlerin en Région Occidentale), a FAO commission including 10 western African member countries. Data from these countries provide long-term time series on occurrence of desert locusts in different stages of development, past outbreaks, and management operations carried out. This dataset therefore provides for a great opportunity to examine long-term, large-scale relationships between climate, management and population outbreaks.

The desert locust is native to arid and semi-arid regions of Africa, the Middle East, and Southwest Asia. When their populations reach high densities, desert locusts go through a transformation from a solitarious phase to a highly gregarious phase [26]. First, solitarious populations build up and concentrate in specific areas due to favorable weather conditions and aggregated vegetation structure, facilitating social interactions and further gregarious behavior [27,28]. This concentration leads to the multiplication of gregarious individuals [24]. Gregarization represents first a change in behavior but, through several generations, the morphology and physiology also change, which takes weeks or months depending on environmental conditions. Ultimately these series of processes lead to the formation of massive swarms that can cause significant damage to crops and pastures, eventually dispersing outside of the usual range of the solitarious individuals [29]. Such outbreaks are usually triggered by weather conditions [30–32], particularly temperature, humidity, and rainfall [30,31,33,34]. Therefore, elevated temperatures and altered precipitation patterns, which seem broadly characteristic of climate change, have been hypothesized to increase outbreak risks under future scenarios [35]. At the species range level, several studies have suggested that the potential distribution of the solitarious phase during recession periods is likely to shrink due to climate change [36,37]. However, some of these studies have highlighted the fact that this might not reduce outbreak risks in surrounding areas because, once gregarious populations form, they have a very large-scale dispersal potential [36]. Therefore, understanding what triggers gregarization and how this is likely to change under climate change and different management scenarios is fundamental to anticipate future trends in risks associated to the desert locust. Among those that have tried to tackle gregarization, Tratalos et al. (2010) focused on swarming frequencies instead of recession distributions, but did not manage to untangle climate change effects from inherent population dynamics during the gregarious phase, and they did not consider the effects of management efforts. To our knowledge, no previous study has attempted to relate changes of outbreak risks in the past to large-scale climate change while also considering management efforts.

Locust management can be either preventive, by anticipating a locust invasion before it occurs, or reactive, in response to a locust invasion. The preventive approach was proposed as early as the 1930s following Uvarov's discovery of phase polyphenism, and is nowadays generally preferred [16,17]. The aim is to find and break the dynamics of gregarization before it takes hold [38]. Based on the knowledge acquired on desert locusts, most invasions could be predicted by environmental factors at early gregarization stages. However, uncertainties due to local difficulties on the ground (e.g. armed conflicts, climatic emergencies), the capacity of the management teams to respond to urgent needs (e.g. lack of personnel and economic constraints), or lack of knowledge regarding future weather conditions, may lead to delayed or imprecise forecasts [39]. Therefore, even though management efforts have increased overall, they remain very heterogeneous both spatially and temporally. For example, the desert locust crisis that affected East Africa,

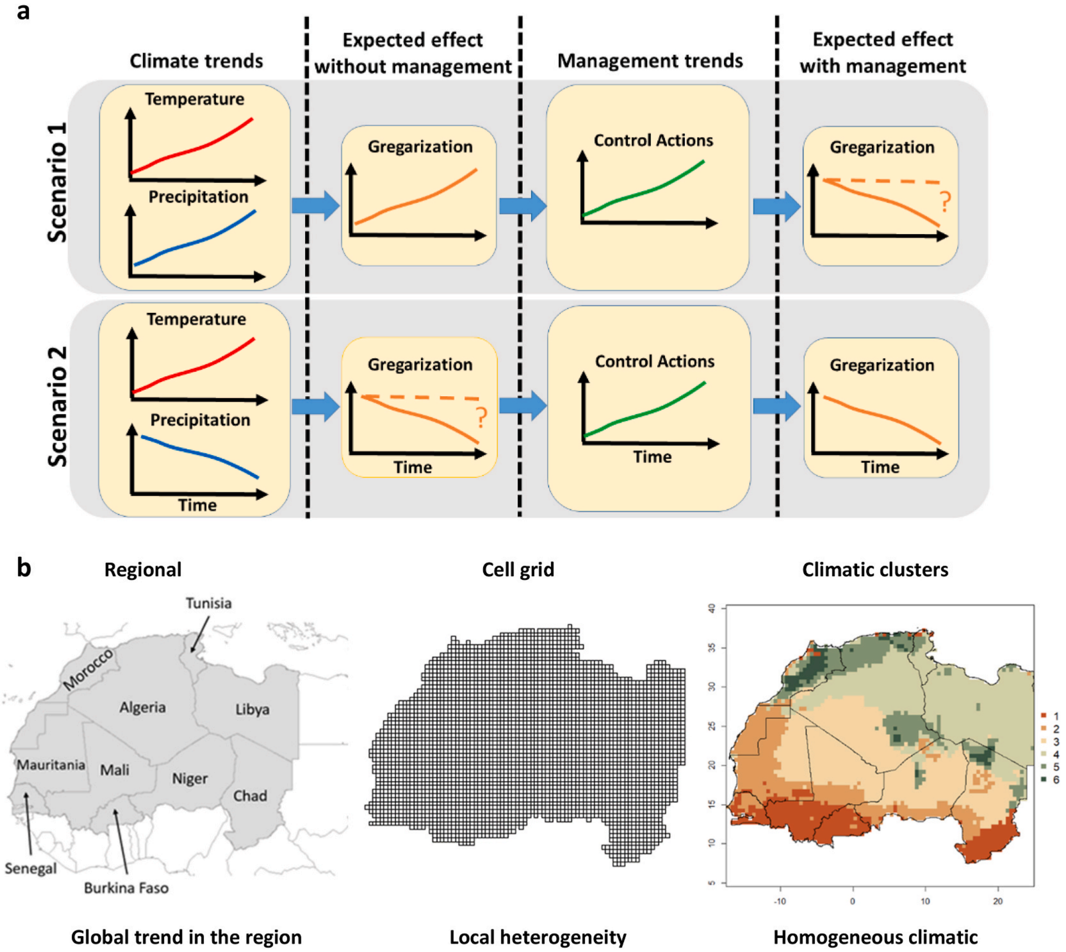

Fig. 1. Expectations and spatial scales of the study. Panel a represents gregarization trend expectations dependent on climatic and management trends. We present two scenarios. In scenario 1, both temperature and precipitation increase over time. Under these climate change conditions, we would expect an increased risk of gregarization. However, if control actions are also increasing during the same time period, we would expect that gregarization is either kept in check (i.e. constant gregarization over time) or even decrease, depending on the effectiveness of the management actions. Under scenario 2, temperature increases but precipitation decreases. The expectation regarding gregarization in this situation will depend on the overall balance between these opposing climatic trends, because the desert locust requires a minimum level of rainfall, even though temperature increases would generally favor gregarization. Overall, these conditions are expected to either keep gregarization constant, or even decrease. However, if management actions are also increasing over time, we would expect a decrease in gregarization risk. Panel b represent the three different scale of the analysis. Left map represent the countries which provided the occurences data for the analysis. The middle figure is the grid map of the finest scale (0.5° cells) used in this analysis. Right map is the cluster form based on similar climate conditions, used to highlight the effect of management. The colors on the map at the far right represent each climatic cluster, and they match those in Fig. 5 and Appendix D. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the middle-east and India in 2020–2021 was the result of a lack of preventive management in 2018 in the Arabian Peninsula and later in 2019 in the horn of Africa [40]. In contrast, the Mauritanian efforts to control locust outbreaks in 2009 and 2016 were probably key to avoid regional upsurges [40]. Therefore, any attempts to predict the potential effects of climate change on desert locust outbreak risks should also consider how management has helped contain past outbreaks.

In the large area covered by the CLCPRO, four climate classes can be found according to the Köppen-Geiger classification: BWh – Dry Arid Low Latitudes, BWk – Dry Arid Mid-Latitudes, BSh – Semiarid Low Latitudes, and Sk – Semiarid Mid-Latitudes [41]. Depending on these climatic conditions, gregarization risk is also expected to vary, along with management practices. Previous studies have demonstrated the connection between desert locust population dynamics and vegetation, with rare precipitation events in dry areas triggering vegetation growth that then fuels gregarization [42–44]. Here, however, we left vegetation out of our analyses because we aimed at understanding the specific interactions between climate change and management, including temporal and spatial variations between 1985 and 2018 in western Africa. We focus on the very early stages of gregarization (gregarious hoppers recorded outside of outbreak periods) of the desert locust, to consider environmental conditions that lead to gregarization, rather than gregarious populations that reproduce and disperse well outside of the usual solitarious range. It is generally expected that increases in temperatures and precipitation lead to an increase in gregarization within the potential range of the species [35,45], while effective management should decrease risk of gregarization (Fig. 1a). However, the outcome of the interaction between climate and management will depend on the intensity of pressures coming from these factors (Fig. 1a, scenario 1 versus scenario 2), which may be spatially heterogeneous: a combination of increased climatic risks and patchy or ineffective management would not compensate for the increased risk represented by weather conditions. To have a better understanding of the importance of these spatial variations, and the interactions between climate and management, we considered three scales of analysis (Fig. 1b). The regional scale allows analyzing overall temporal trends in climate, management and outbreak potential over time. We then analyzed the study area using 0.5° grid cells (roughly 55 km resolution), which allows considering spatial heterogeneity in all these variables. However, this also reduced sample size because not all grid cells have been visited consistently over time, and analyzing temporal trends requires at least three visits in the same sampling units. Finally, we chose a third, intermediate strategy, where we defined climatic clusters, i.e. sub-regions that have similar climatic conditions and trends. Within these clusters, we can highlight the effects of management while keeping climatic trends homogeneous and allowing a larger sampling size for analysis purposes.

2. Materials & methods

All data filtering, cleaning and analyses were conducted with R version 4.1.1 [46].

2.1. Study area and occurrence data

This study includes the ten West and North-West African countries that are members of the CLCPRO (Fig. 1): Algeria, Burkina Faso, Chad, Libya, Mali, Mauritania, Morocco, Niger, Senegal and Tunisia. These countries conduct regular surveys throughout the year to detect desert locusts at an early stage in potential breeding areas. During these surveys, geographically and chronologically referenced information is collected and stored. Field survey officers report locust population status (e.g. life stage, appearances, solitarious/gregarious behavior), a description of the management operations carried out (e.g. pesticide applications, treated surface) and ecological information describing the environment of the survey points, following FAO guidelines [47].

2.2. Locust data conditioning

Since we wanted to understand the climatic and management effects on the frequency of gregarization events, we focused on the observation of gregarious hoppers at the very beginning of a potential gregarization event. Indeed, the first signs of gregarization are the formation of crowds of nymphs resulting from the spatial proximity of the oviposition sites chosen by the gregarizing solitarious females [48,49]. Consequently, a gregarization variable was defined as the proportion of the number of observation points with presence of gregarious hoppers divided by the number of surveys carried out during a given year, outside of the known outbreak periods. This gregarization variable therefore represents the proportion of visited sites with recorded gregarization signs before any outbreak has been detected (see below).

The locust database was downloaded from the FAO website that covers the period between 1985 and 2018 distributed between West Africa and India. We selected the survey points located in the CLCPRO region (169 627 points) and removed survey points recorded during periods of major outbreaks. To achieve this, we used a threshold of number of swarm observations per month following Piou et al. (2017) [50] (see more details in Appendix A) to filter out major outbreak periods. In short, a month was considered to be in an active major outbreak period if it met the following two conditions: (i) that there were ten or more swarm observations during the month in any part of the CLCPRO area; and (ii) that at least one of the three previous months, or the three following months, also included ten or more swarm observation points. We complemented this filter by subsequently eliminating some months that were well-known upsurge or plague periods according to the FAO bulletins [51]. Following this deletion of major outbreak periods, the database was composed of 105 221 survey points (Fig. 2).

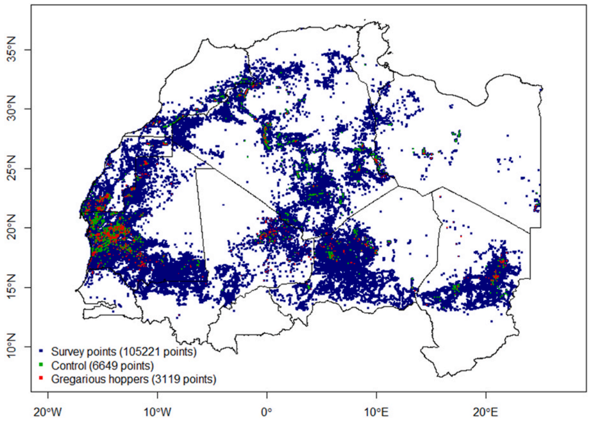

Fig. 2. The 105 221 survey points realized by the field officers of the CLCPRO countries (1985–2018), filtered to recession periods and used in the statistical analyses. Black dots: survey points. Green dots: management events (N1). Red dots: presence of gregarious hoppers (N2). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.3. Management variable

On the ground, monitoring and management effort has considerably increased throughout the period, with a very clear distinction before and after the 2000s. On top of that, there are important spatial variations, with some extremely remote areas such as the east of Mauritania-north-west of Mali, or high mountain areas such as Tibesti in Chad and the Hoggar in Algeria, that are surveyed rarely. In contrast, some areas in Mauritania have consistently increased their survey and management efforts. Notice that, although most control events consist of applying pesticides, there has also been limited use of other control measures, such as biological control agents. In the original database, management information regarding dosage and surface of pesticide use is heterogeneous throughout the study period (1985–2018). However, the mention of pesticide applications were always informed (even if lacking surface, dosage or type of pesticide used). Thus, we decided to consider only the number of management operations, i.e. pesticide applications, performed each year within a wider perimeter (see grid scale analysis section).

2.4. Climate data

Temperature and precipitation are among the environmental variables that condition locust development the most [25,26,52]. We extracted these climatic variables from CHELSA (Climatologies at high resolution for the earth's land surface areas), covering the period of 1980–2018 [53]. The dataset provides monthly climate output from a downscaling model, estimated at a horizontal resolution of 30 arc-seconds (approximately 1 km resolution at the equator). Among the different variables that could describe temperature and precipitation in the CHELSA database, we selected monthly average temperatures (°C) and monthly precipitation amount (mm). We chose monthly data to understand better climate change through the harmonic decomposition method (see section 2.5.2).

2.5. Trends analysis

2.5.1. Generalized linear model

To check on temporal trends of climate and management variables, we used Generalized Linear Models (GLM), with the year as the main predictor, and the target variable as the response. Additionally, for the locust gregarization variable, defined above as the proportion of observations with gregarious hoppers detected outside of major outbreak periods, we used the total number of surveys in each year as a weight in the GLM to account for sampling effort. We then applied an odds ratio logistic regression model. For the management variable, we used a negative binomial GLM with the log link function. For the climate variables, we averaged the 12 months of each year for each cell, and then calculated a regional average across grid cells (i.e. by grid cell, climatic cluster or overall in the CLCPRO region depending on the analysis, see below). Since we were interested in climate trends over time, these annual averages were then used as the response variables of linear models following a Gaussian distribution for both temperature and precipitation. This method was applied in the same way for the regional scale and in each climatic cluster.

For the management events in gridded data, a trend analysis requires at least three visits in the same grid cell, meaning at least three years with one observation of gregarious hoppers or more. This condition eliminates many grid cells from the analysis, setting aside large parts of the study area. For this scale we also determined climatic trends using a Harmonic seasonal decomposition, as described below.

2.5.2. Harmonic seasonal decomposition

Understanding climatic trends over a long period may be difficult because of large inter-annual variations, coupled with seasonal changes and occasional extreme events. For this reason, climatic time series are often divided in three main components: the trend, the seasonality and the “noise”.

A model for a time series $\{x_t : t = 1, \ldots, n\}$, where t is a time index and x is the variable of interest, can thus be written as follows:

$$x_t = m_t + s_t + z_t \quad (1)$$

With the trend m_t, the seasonal effect s_t and the residual term z_t which may be autocorrelated.

For time series that extend over many years, if the sampling interval is less than a year (e.g., monthly data), it is likely that seasonal variations are present. Therefore, a regression method adapted to variable time series called “Seasonal harmonic model” has been chosen (see more details in Appendix B). This method is based on trigonometric functions, which are appropriate to represent cyclical events. We followed the harmonic decomposition method described by Cowpertwait and Metcalfe [54].

To define a harmonic seasonal model, equation (1) can then be rewritten as follows:

$$x_t = m_t + \sum_{i=1}^{s/2} s_i \sin\left(\frac{2\pi t_i}{T}\right) + c_i \cos\left(\frac{2\pi t_i}{T}\right) + z_t \quad (2)$$

In equation (2), T represents the period associated with the repetitive pattern in the time series, t is a given time, s_i and c_i are parameters to be adjusted to the specific cyclic behavior of the variable of interest.

In practice, to apply a harmonic seasonal model to the climate data, we used monthly data to define t as a continuous variable from the first month in 1980 until the end of December 2018. Then, a first model containing all the coefficients for the sine and cosine functions were created. From this first full model, other model versions with some of the coefficients removed were tested. The model chosen to describe the series was the one that minimizes AICc for each 0.5° cell.

The climatic trends were directly retrieved as the coefficients of the trend m_t component.

2.6. Multi-scale analysis

We carried out our analysis at three different spatial scales: regional-scale, which considers the whole study area and allows us to have a general view of climatic, management and gregarization trends; a 0.5° resolution analysis (roughly 55 km resolution), that allows studying spatial heterogeneity in these trends, and a climatic clustering regionalization that allows focusing on management and gregarization trends within climatically-homogeneous regions, i.e. areas that have similar climatic means and similar climatic trends over time.

2.6.1. Regional-scale analysis

For this analysis, the whole study area was analyzed as a single unit. An average of the variable of interest (temperature, precipitation, number of management events, gregarization) was calculated per year and used in the temporal trend analysis.

We then looked at the annual trends of our 4 variables (temperature, precipitation, gregarization ratio, number of management operation) over the entire study area using the GLM approach described above.

2.6.2. Grid level analysis

We divided the area into a grid of cells of 0.5° (~55 km) (3532 cells in total). The CLCPRO zone is very large (around 10.5 million km^2), which implies a very low probability that the field teams would have conducted surveys at the same spatial coordinates over the years. Thus, increasing the size of the area for which we considered environmentally comparable points increased the chances of having several data points throughout the period in the same analysis unit. A grid of 0.5° resolution therefore represents a reasonable trade-off between increasing the area of each grid cell to maximize the number of sampling sites, while remaining within the scale of hopper potential movement to represent a biologically meaningful unit.

As a result, the variable to characterize the locust gregarization dynamics was a proportion of an annual sum of the number of observation events of gregarious hoppers over the total number of surveys carried out, for each of the 0.5° cells in the CLCPRO area. For the management variable, we considered the number of pesticide applications performed in a year for each 0.5° cell and a 3 × 3 grid-cell window around the focal grid cell. Finally, the resolution of the climate data was resampled to 0.5°, by applying an average over the area, to correspond to the locust data information. Therefore, each cell was associated to a monthly average precipitation and temperature time series over 1980–2018.

2.6.3. Climatic clusters

We used climate and elevation to identify environmentally homogeneous regions within the study area. The variables used for this spatial clustering were: the yearly average temperatures and precipitation, the trend coefficients (coming from the harmonic decomposition described above) of precipitation and temperatures, elevation and standard deviation of elevation as a measure of heterogeneity. Elevation variables were considered to avoid grouping together some North African mountain areas receiving the same amount of precipitation as the Sahel. The six variables were scaled and standardized. To identify the clusters, we applied a k-means cluster analysis [55,56], using the highest “Simple Structure Index” value [57] to identify the optimal value of k (the number of clusters).

3. Results

3.1. Regional-scale analysis

As expected, temperatures and precipitations increased during the study period at the regional scale (Fig. 3a and b). Management efforts also increased especially since the 2000s (Fig. 3c). Gregarization, however, decreased overall (Fig. 3d).

3.2. Gridded analysis

In the gridded analysis, temporal trends show important spatial variations (Fig. 4). Temperature has increased almost everywhere, except for some areas in southern Mali (Fig. 4a). There is a spatial gradient from the south-west, which has the smallest temperature increase (less than 0.2° in the last 38 years) to the north-east where temperatures have increased the most (up to 1.8°). Precipitation has been more variable, and a large portion of the study area has a non-significant trend (white cells in Fig. 4b). Where a significant temporal trend was detected, precipitation also increased over most of the countries, except for northern Algeria where precipitation has remained constant or even decreased. The precipitation increase is stronger in the Sahelian band and the Atlas Mountains area (Fig. 4b).

A large portion of the study area did not have enough data (i.e. > 3 observations) to study temporal trends in management and gregarization (striped area in Fig. 4c and d) at the scale of the gridded dataset. Of those with enough data, 249 grid cells (58%) showed a significant trend in management among the 426 in total. These grid cells showed an increase in management events with positive trends located in west Mauritania, south western Sahara, south and east of Morocco and the center of Algeria, and with some few positive trends in Niger and Chad. Regarding gregarization, only 42 grid cells had enough visits to analyze temporal trends; 23 of these grid cells (55%) showed a significant trend in gregarization. These grid cells were located mostly in Mauritania, with both negative (15 grid cells, representing 63%) and positive (8 grid cells) trends.

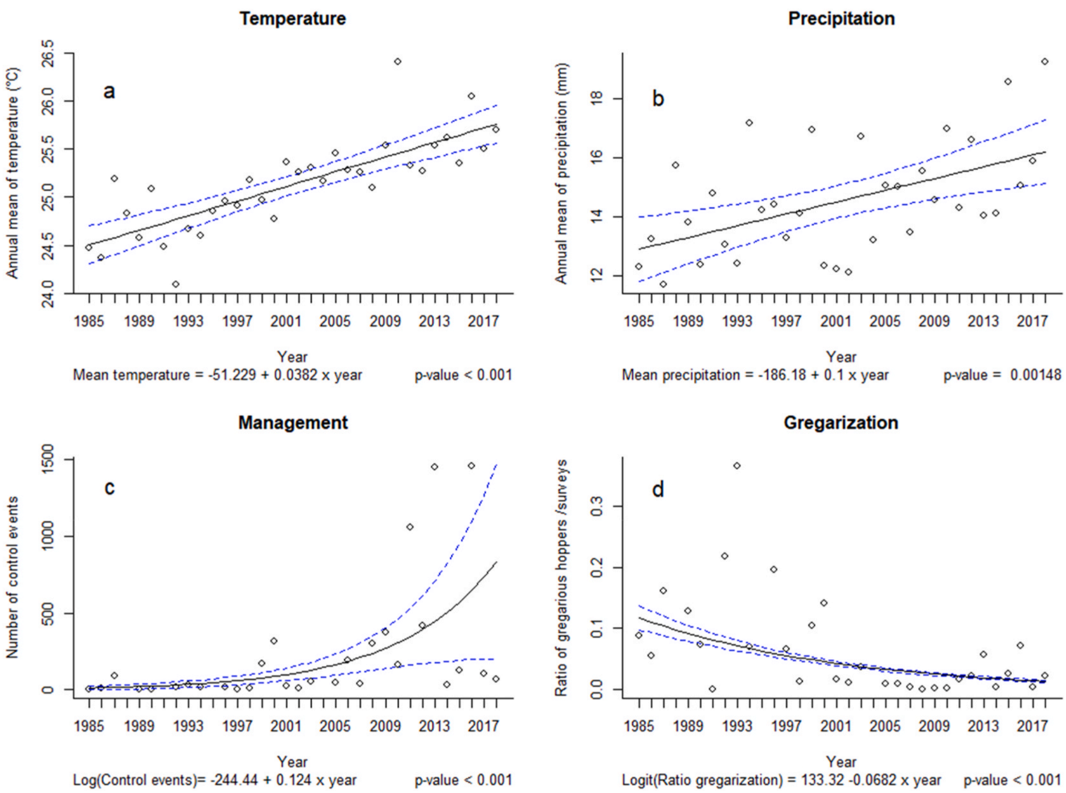

Fig. 3. Multiple trends in the CLCPRO area over 1985–2018. Figure a-Trend of annual mean precipitations (mm) and b- The trend of annual mean temperatures (°C). c- The trend of the control events each year. d- Annual trend of the gregarization risk (number of observation points with gregarious hoppers over total surveys). Blue lines show the confidence intervals for each model. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

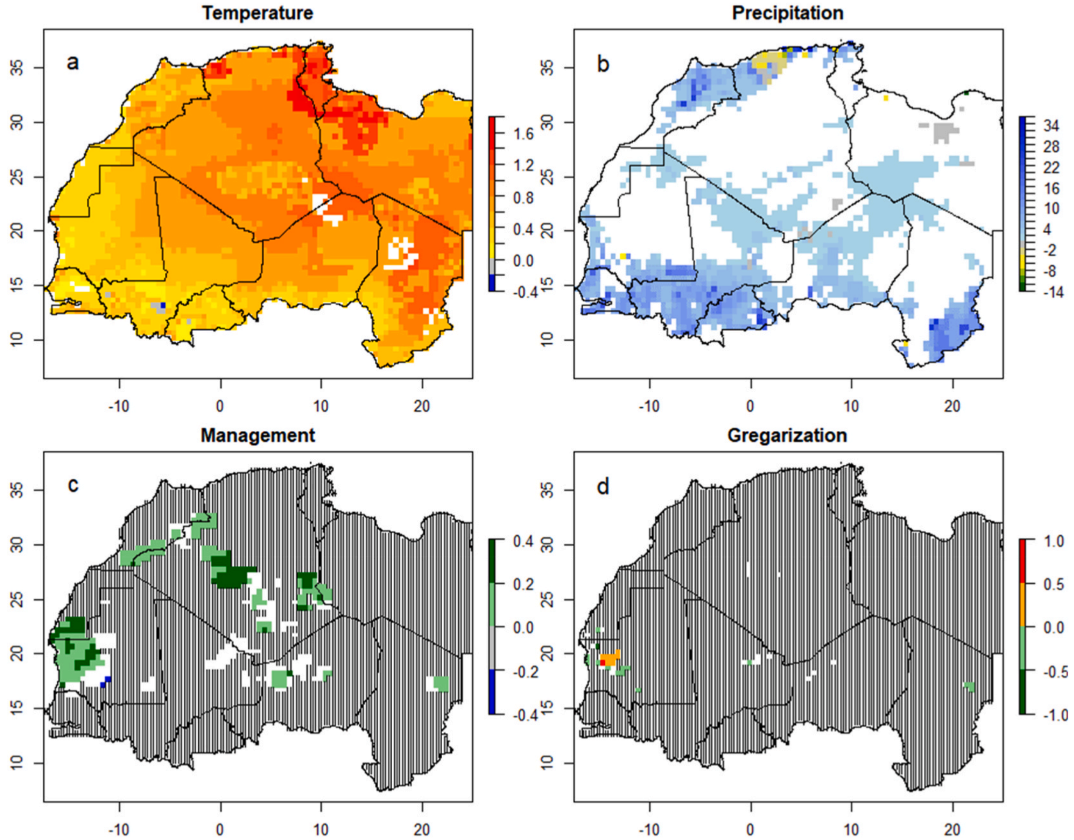

Fig. 4. Comparison of trend maps at 0.5° cells. The study area was divided in 0.5° grid cells. Only cells with significant temporal trends are colored: a-trend of annual mean temperatures (°C of increase/decrease) and b-trend of annual mean precipitations (mm of increase/decrease), which were both determined with the harmonic seasonal model; c- Trend of the number of pesticide applications each year (number per year). Vertical stripes indicate cells that were visited less than three times over the study period (had less than three years with management operations); d- Annual trend of the number of observation points with gregarious hoppers on total surveys (number per year). The vertical stripes on the area hide cells with less than three observations of gregarious occurrences.

3.3. Climatic cluster analysis

The k-mean clustering analysis resulted in 6 regions with similar climatic means and trends (see Appendix D), which we named from south to north by numbers 1 to 6.

The mean temperature of the 6 clusters has increased significantly (Fig. 5a, Appendix E). This increase is higher in the northern clusters, where the mean temperature is lower than in the south. The Sahelian band, the Saharo-Sahelian area and the low mountains have a significant positive precipitation trend, but the Sahelian band stands out from the others by its precipitation amount, which is 3 times higher than other clusters (Fig. 5b).

In terms of management, apart from the Sahelian band and the high mountains which show non-significant trends (white areas in Fig. 5c), all other regions showed an increase in management events (Fig. 5c–Table 1), the strongest of which is in cluster 2 which covers the western and south western end of the species distribution during recession periods.

Regarding gregarization, four significant trends were found, covering the majority of the area except for the low and high mountainous areas (Fig. 5d). The Sahelian band and the south Sahara revealed a decrease of gregarization. In contrast, the Saharo-Sahelian area and the North Sahara have experienced an increase of gregarization. Note that the Saharo-Sahelian and the North Sahara clusters, which show an increase in gregarization, also show the strongest increase in management events (see more information on trends, including GLM results for each cluster and variable of interest in Appendix E).

4. Discussion

The multi-scale analysis of desert locust gregarization trends in western Africa provides valuable insights into the complex interactions between climate change, management actions, and outbreak potential. As expected, management, climate and outbreak potential are heterogeneous in space. Climate change has increased temperature and precipitation throughout the study area. This created more favorable conditions for desert locust development, especially in west Mauritania and southern Algeria, but the intensity

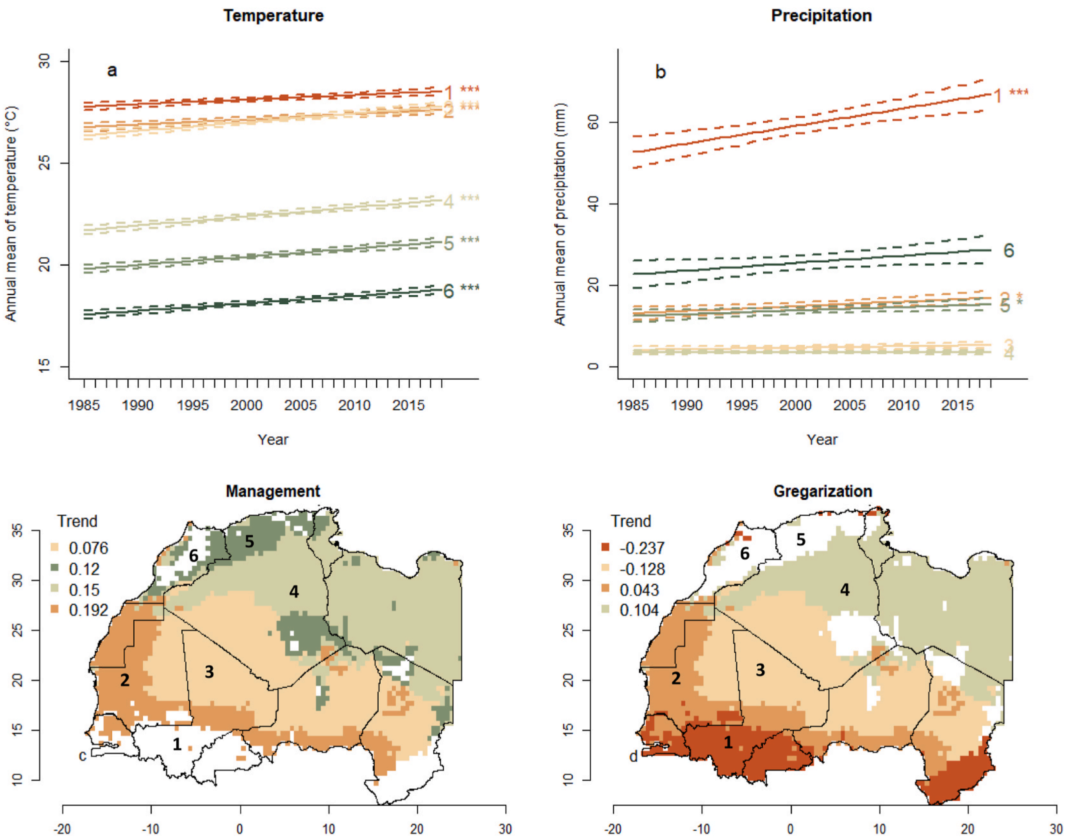

Fig. 5. Comparison of gregarization and management trends in climatic clusters. Each cluster is represented with a different color, which matches across panels: 1 = Sahelian band, 2 = Saharo-sahelian area, 3 = South Sahara, 4 = North Sahara, 5 = Low mountains, 6 = High mountains. Panels a- and c-are the averages of temperature and precipitation predicted by a GLM with Gaussian distribution for each year over the whole period. Each curve represents a cluster. The asterisks next to the cluster numbers represents the significance of the trend for each cluster. '***' for a p-value <0.001, '**' for a p-value <0.01, '*' for a p-value <0.05. c-is the map of the trend for each cluster of the number of pesticides application and d-is the map of the trend for each cluster of the annual ratio of gregarious hoppers observed by survey. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

of those changes has varied greatly over space. Therefore, based on the trends of climate only (temperature and precipitation), we were expecting an increase of gregarization (Fig. 1a). However, in most cases there was a decrease (or no change) in gregarization, on all three scales tested. This suggests that preventive management has been effective in compensating for an increased risk due to climatic trends in these regions. Management has also evolved at different rates in different regions, even though the efforts have increased consistently over time throughout the study area. These spatial heterogeneities reveal a fundamental interaction between management and climate change potential effects, which we will discuss in more detail below.

4.1. Gregarization and climate change

Until now, most of the studies about the effects of climate change on desert locust populations have focused on distributions under different scenarios of climate change. Some authors found a decrease of the potential range during recession periods, but also emphasized that this does not mean that the risk of gregarization and outbreaks will decrease within this area due to potential increases in population outbreaks within the range and their great dispersal capacity once the outbreaks emerge [36,37]. Other studies suggest that the warmer and more variable climate conditions are conducive to gregarization in locust populations [31]. In our study, we observed a clear increase of temperature and precipitation over the last 40 years in the study area overall. However, there is great spatial heterogeneity, with the most pronounced warming observed in the north-east, creating a gradient of increase from the least severe in the south-west to most severe in the north-east. On the other hand, while the coldest areas had the highest increases in temperature, precipitation patterns have become increasingly variable, with rising precipitation trends in some regions (north and south), and the highest increases concentrated in areas where there was already the most precipitation to start with (Appendix C). These observed climate change trends confirm previous studies, which had already shown an overall increase of temperatures and localized increase of precipitation in the Sahel, but also a strong spatial variability [58–60].

The climate has changed in a way that is generally favorable to locust outbreaks in most regions. However, it is important to note that the relationship between climate change and locust dynamics can be complex and context-specific. For similar species, rising temperatures can accelerate population development by improving their digestive rate for example, leading to more swarms and range expansions during outbreaks [61]. For desert locusts, temperature increases can have positive effects on gregarization in the areas that were at the lower temperature range to start with, but in extremely hot and arid deserts these further temperature increases could also impede population development [62]. Indeed, temperatures exceeding their temperature tolerance limits can trigger heat stress for which their chances of survival depend strongly on shade availability, hydration state, and also oxygen supply during the first instar [63,64]. However, increased precipitation can reduce these risks, as shown for some species of grasshoppers, by counterbalancing the impact of warming on egg development for example [65]. Increases of precipitation are often associated with increased locust gregarization [34,66]. We observed here an increase of gregarization in two regions. In the Saharo-Sahelian area, this increased gregarization could be explained by an increase in precipitation and the high mean temperatures already characteristic of this region, which remain within the thermal limits of the species. In the northern Sahara, precipitation have remained very low and with no significant change over the last 40 years. However, mean temperature there, which is lower than the mean temperature in the Saharo-Sahelian cluster, has been rising, probably reaching more favorable conditions for desert locust development. These two areas therefore illustrate increases in gregarization risks under two different past climate change trends.

However, the two areas cited above were the only ones with an increase of gregarization. For example, the South Sahara, which already has high temperatures that continue to rise, and very low precipitation, displayed a decrease in gregarization. This could mean that temperatures have become too high, falling out of the thermal range of the species, or that other factors, including management, have played a role (see below). Similarly, the Sahelian band, has experienced a decrease in gregarization, concomitant with a slight increase in temperature and a strong increase in precipitation. This area is at the southern limit of the recession potential distribution, which is predicted to shift upward with further climate change [36]. Hence, the decrease of gregarization is potentially due to the climate becoming much more humid than the usual optimum for development of desert locusts [67].

Two climatic clusters did not show any trends in gregarization risk. The high mountains are not a usual desert locust habitat, and have not been prospected enough to determine any temporal trends. The case of the low mountains is more interesting though. Here, the changes in precipitation are similar to the ones in the Saharo-Sahelian area, and despite not being as high, temperature has also increased. If the evolution of its climate continues in the same direction, it could become an area of more frequent gregarization of desert locusts. Indeed, with rising temperatures, the altitude at which desert locusts can thrive is expected to increase, potentially leading to changes in their distribution and migration patterns [68]. However, the lack of a positive trend in gregarization over the last 40 years in these low mountain areas suggests that it might be linked to the observed increase in management treatments.

4.2. Preventive management and gregarization

Management effort has increased in the whole area of the CLCPRO (Fig. 3c). We observed these increases at all our scales of analysis, from regional to grid cells. These observations of increase are in agreement with the heightened focus on proactive locust management in recent years to prevent large-scale outbreaks and mitigate economic losses [10,17,40,69]. However, the evolution of management actions varied across regions, indicating differing responses to the locust threat. Despite a consistent overall increase in management efforts throughout the study area, the effectiveness of these actions varied geographically. This is particularly visible at the cluster scale, as climate is homogeneous within each cluster, making it easier to dissociate the effects of climate from the effects of management.

The absence of change in gregarization for the low mountain cluster, despite favorable climatic conditions, might be due to the increase of management efforts, acting as a compensatory effect. A similar phenomenon is observed for the South Sahara, with a decrease of gregarization as the climate was already less propitious. However, management also increased in the Saharo-Sahelian area and the northern Sahara. It is actually the highest in those areas where gregarization increased. The increase in management efforts in the Saharo-Sahelian area over the past 40 years, despite not having a negative effect on the global gregarization trend, has probably prevented very strong outbreaks favored by climate. In the north of the Sahara, management efforts have been continuous in Algeria, but Libya has experienced a decrease since 2011 because of political insecurity. Thus, the lack of surveillance in Libya could lead to a build-up of gregarious populations, despite the control efforts of neighboring countries. This is probably what happened in 2012 during the last outbreak in this cluster in Libya [70].

The heterogeneous response to climate change and management highlights the need for area-specific intervention strategies to effectively control locust populations. Nevertheless, the arrival of uncontrolled locust populations following their seasonal migration cycle [24,52] may still occur and need an international cooperation.

4.3. Population dynamics of gregarization for desert locust

Studies of swarm migrations have revealed a cyclical population dynamics in desert locusts, including seasonal reproduction patterns throughout the year [71]. For the CLCPRO region, these migrations follow predictable patterns, from south to north during July to December, and from north to south during January to June [35,50]. At the end of summer, locusts migrate from the southern breeding areas in the Sahel to northern regions, and often gregarize on heterogeneous habitats [72]. Moreover, the ability of desert locusts to cover vast distances (hundreds of kilometers in a day) during these migrations is a noteworthy aspect of their population dynamics [24,73]. Therefore, taking into consideration their population dynamics over large spatial scales is crucial. These cycles allow to better understand some of our results. The Sahelian band, with a decrease of local gregarization events, still remains a potential breeding ground for solitarious individuals. The migration of these solitarious locusts between this cluster and the Saharo-Sahelian area probably favored the development of populations and the gregarization in the latter cluster. Likewise, the strongest increase of management efforts in the Saharo-Sahelian may be at the origin of the lowered gregarization in the South Saharan area because of lowered migrations in September–December. Similarly, the spring migrations towards the South Sahara, Saharo-Sahelian and Sahelian clusters may have been decreased thanks to the increase in management efforts in the northern Sahara cluster. Collaborative efforts such as the "Emergency Prevention System for Transboundary Animal and Plant Pests and Diseases" (EMPRESS) program in the regional commission (CLCPRO and others) have played a crucial role in coordinating international responses and effective management in front of these cyclic migrations [62].

Since this known cyclic spatial dynamic of desert locusts is linked to the seasonality of the weather, it is still uncertain how climate change will influence these movements. Insect migrations are essentially linked to abiotic changes as triggering factors [74], which are likely to be affected by climate change [75], especially temperatures. Warmer temperatures have been positively correlated with the increasing number of butterflies and moths migrating into Britain [76,77]. The aphid spring migration has been found across Europe to advance by 14 days for every degree Celsius rise in temperature [78]. Migratory birds, which have also been extensively studied, are expected to undergo major changes in their migrations, in terms of synchrony [79–81]. Additionally, migrating species are more vulnerable to climate changes as they rely on multiple habitats and therefore have to adapt to several changing environments [74]. It is hence still to be investigated how the increases in temperature and changes in precipitation patterns may affect desert locust migration cycles and the population build-up that lead to gregarization.

5. Conclusion

Our study has provided a spatial view of the temporal trends in gregarization in the CLCPRO countries since 1985. These results show that gregarization patterns are highly heterogeneous and cannot be explained solely through climate change, as management plays a large role as well in the outcome. While this study cannot definitively establish causation, it strongly suggests that effective management actions have contributed to the observed decrease in gregarization in certain regions and that all the efforts made by CLCPRO to survey and manage populations have helped to limit outbreaks. Nonetheless, the efficacy of management measures will stay constrained if significant effects to locate and manage bands and swarms in a region are counteracted by untreated infestations in other areas, either within the same country or in neighboring nations. This underlines the importance of continuing efforts and allocating resources to desert locust preventive management [16,82].

A main limitation is that occurrence analysis such as this study do not include population dynamics and migration processes that are important in locust gregarization [83]. Previous studies showing potential range contractions under climate change conditions [36,37] ignore the internal dynamics of local populations. These limitations might be counteracted by mechanistic models which allow to describe the population dynamics that are needed to go further on the comprehension of environmental condition at the emergence of gregarization and represent the cyclic migrations [84].

As seen in this study, it is also challenging to understand the impact of climate change on pest species when human actions, such as management or land use, have concurrent effects on these populations. In anthropized systems, the effect of climate change may be hidden by the direct impact of management practices or indirect effects related to land use changes [85]. This complex interplay of factors makes it essential to disentangle the specific contributions of climate change [86,87]. Indeed, without a clear understanding of the impact of a changing climate due to the effects of human actions, it is hard to forecast future trajectories of risk.

Data statement

All the raw datasets used in this study were downloaded from open databases. Locust occurrence and control operations data are available on https://locust-hub-hqfao.hub.arcgis.com/. Climatic data are available on https://chelsa-climate.org/timeseries/. All data and scripts needed to replicate this analysis are available in the following directory: https://doi.org/10.18167/DVN1/1FO9M6.

CRediT authorship contribution statement

Fanny Herbillon: Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Cyril Piou:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Christine N. Meynard:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

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

During the preparation of this manuscript, the main author used ChatGPT to improve readability and language of the first draft of the introduction. After using this tool, all authors reviewed and edited the content as needed, and they take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Cyril Piou reports financial support was provided by Food and Agriculture Organization of the United Nations. If there are other authors, they 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. Large outbreak periods filtering

Before explaining the process of filtering the upsurge and plague periods, we first provide an explanation of each term used, which is a situation-specific vocabulary for the desert locust, with definitions from the FAO.

Groups of wingless hoppers are called **bands** and groups of winged adults are defined as **swarms**.

Outbreak refers to a sudden and marked increase in the population of desert locusts in a given area. It occurs when environmental conditions, such as increased rainfall and vegetation growth, provide ideal breeding conditions for the insects. Within a month or two, they start to concentrate and gregarize which, can lead to the formation of bands or swarms, if not controlled. It usually occurs in one part of a country.

An **upsurge** in desert locusts refers to a sudden and large increase in their population, which can lead to a plague. It generally affects an entire region. Unlike a plague, an upsurge may not necessarily result in significant damage to crops or vegetation, as it depends on the timing and location of the upsurge and the availability of control measures to manage the insects. However, upsurges can be a warning sign of a potential plague and require monitoring and early detection measures to prevent further spread.

A **plague** of desert locusts is a more severe form of upsurge. It occurs when desert locust populations become so large that they spread over a wide area. Plagues are periods of one or more years during which there are widespread and heavy locust infestations, the majority of which occur as bands or swarms. A plague can occur when favorable breeding conditions are present and management operations fail to stop a series of local outbreaks from developing into an upsurge that cannot be contained. It takes at least one year or more for a plague to develop through a sequence that commences with one or more outbreaks and followed by an upsurge.

Filtering: To be able to select what corresponds to recession periods in the database, we set a swarm observation point threshold per month. A month was considered to be in a large outbreak period if it met the two following conditions. The first one is that this month counted ten or more swarm observation points, considering the whole CLCPRO area. The second one is that at least one of the 3 previous months or 3 following months also includes ten or more swarm observation points. This threshold of ten swarm observation points was chosen to correspond to a potential large outbreak situation where there would be at least one swarm in each of the ten countries belonging to the CLCPRO. After verification, this threshold appeared to be globally effective (Figure A1). Certain months, not identified by this threshold, but which belonged to well-known upsurge or plague periods, were manually identified based on FAO bulletins reporting locust situations. The choice of a three-month window before or after, was based on the knowledge of the generation time of desert locust [30].

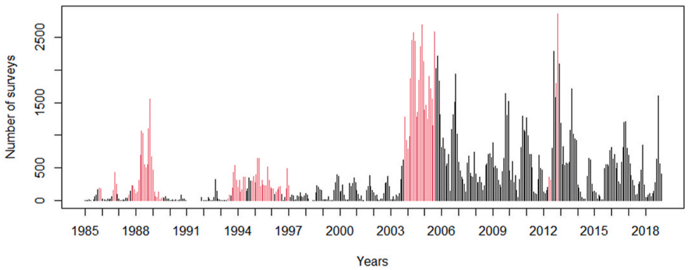

Fig. A1. Visualization of months considered in large outbreak situation (red) over the period 1985–2018.

Appendix B. Harmonic seasonal decomposition

A model for a time series $\{x_t : t = 1, \ldots, n\}$, where t is a time index and x is the variable of interest, can thus be written as follows:

$$x_t = m_t + s_t + z_t \tag{1}$$

With the trend $\boldsymbol{m_t}$, the seasonal effect $\boldsymbol{s_t}$ and the residual term $\boldsymbol{z_t}$ which may be autocorrelated (e.g. a high precipitation during a given month increases the chances that the month right before or right after was also very rainy).

For time series that extend over many years, if the sampling interval is less than a year, for example if the measured data are monthly, it is likely that seasonal variations are present in the series. Therefore, a regression method adapted to variable time series that is based on the use of sine and cosine functions to account for seasonal changes has been chosen. This method is called "Seasonal harmonic model".

This method is based on trigonometric functions, which are appropriate to represent cyclical events. These trigonometric functions are called "harmonic" in the sense that they are chosen to have frequencies that are integer multiples of the fundamental frequency, determined by the size of the data series. To best represent the data, the harmonic function shifts laterally to match the peaks and troughs of the data series.

We followed the harmonic decomposition method described by Cowpertwait and Metcalfe [54].

Considering a harmonic sine wave y_t of amplitude A, of period T and phase shift or phase angle φ, it can be expressed as equation (2):

$$\mathrm{y_t} = \mathrm{A}\ \sin\left(\frac{2\pi\ \mathrm{t}}{\mathrm{T}} + \varphi\right) \tag{2}$$

Then, a time series represented by $\{x_t : t = 1,\ldots,n\}$, can thus be written as a combination of different sine and cosine signals as follows:

$$x_t = A_1\ \sin\left(\frac{2\pi\ t}{T} + \varphi_1\right) + A_2\ \sin\left(\frac{4\pi\ t}{T} + \varphi_2\right) + \ldots + A_n\ \sin\left(\frac{2n\pi\ t}{T} + \varphi_n\right) \tag{3}$$

To obtain a more useable expression, we apply to equation (3) the trigonometric identity approach:

$$A\ \sin\left(\frac{2\pi\ t}{T} + \varphi_1\right) = \alpha_s \sin(2\pi ft) + \alpha_c \cos(2\pi ft) \tag{4}$$

with $\alpha_s = Acos(\varphi)$ et $\alpha_c = Asin(\varphi)$ which are regression coefficients.

Seasonality can therefore be defined as the sum represented in equation (4), more commonly known as the Fourier series, where $\boldsymbol{A}$ represents the amplitude of the seasonal component, $\boldsymbol{T}$ represents the period associated with the repetitive pattern in the time series, $\boldsymbol{t}$ is a given time, and $\boldsymbol{f}$ is the frequency and $\boldsymbol{\varphi}$ is the phase shift.

To define a harmonic seasonal model, equation (1) can then be rewritten as follows:

$$x_t = m_t + \sum_{i=1}^{n} \{s_i\ \sin\ (\ 2\ \pi i\ t\ /\ \ s) + c_i\ \ \cos\ (2\ \pi i\ t\ /\ \ s)\} + z_t \tag{5}$$

The expression used to define the seasonality $\boldsymbol{st}$ is thus linear in equation (5), which subsequently makes it possible to use the least squares method to estimate the parameters s_i and c_i.

The higher value $\boldsymbol{i}$ is, the more the seasonal pattern is allowed to be "wavy". For example, with $\boldsymbol{i} = 1$, it is a simple sine curve. Subsequently, the value of $\boldsymbol{K}$ will be selected by minimizing the AICc value. However, for a time series $\{\boldsymbol{xt}\}$ with s seasons, there is [$\boldsymbol{s}$/2] possible cycles.

In the end, we get the expression of the harmonic seasonal model as equation (6) below:

$$x_t = m_t + \sum_{i=1}^{s/2} s_i\ \sin\left(\frac{2\pi t_i}{T}\right) + c_i\ \cos\left(\frac{2\pi t_i}{T}\right) + z_t \tag{6}$$

with s_i and c_i which are parameters to be determined.

In practice, to realize a harmonic seasonal model, we create the variable $\boldsymbol{t}$ which represents the increase of time along my time series. This variable is constructed by standardizing the time variable by the mean and the standard deviation.

Then, we will create a first model containing all the coefficients for the sine and cosine functions. From this first model, other models will be tested for which more or less coefficients have been removed. The harmonic coefficients are known to be independent, which means that all harmonic coefficients that are not statistically "significant" can be dropped. The model chosen to describe the series is the one that minimizes the AICc value.

Appendix C. Maps of monthly mean precipitation and temperature

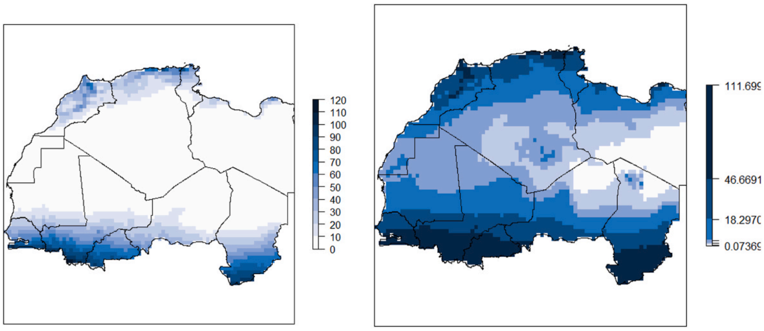

Fig. C.1. Maps of the average monthly precipitation amount between 1985 and 2018. To the right, a representation by quantiles (10% = 0.6, 25% = 1.7, 50% = 3.7, 75% = 18.3, 90% = 46.7).

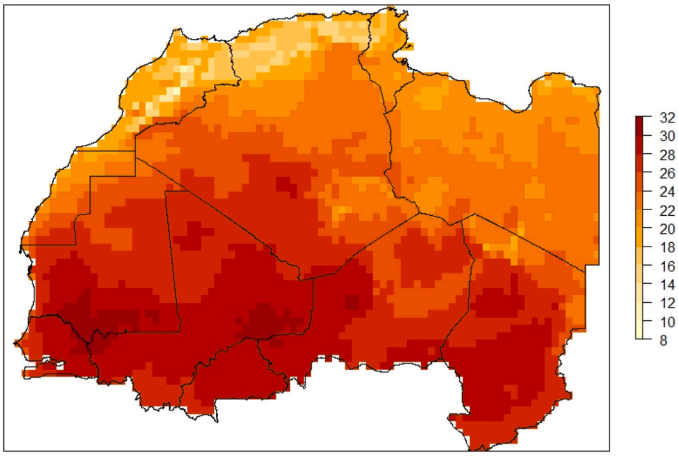

Fig. C.2. Maps of the average monthly mean temperature between 1985 and 2018.

Appendix D. Climatic and geomorphologic clusters

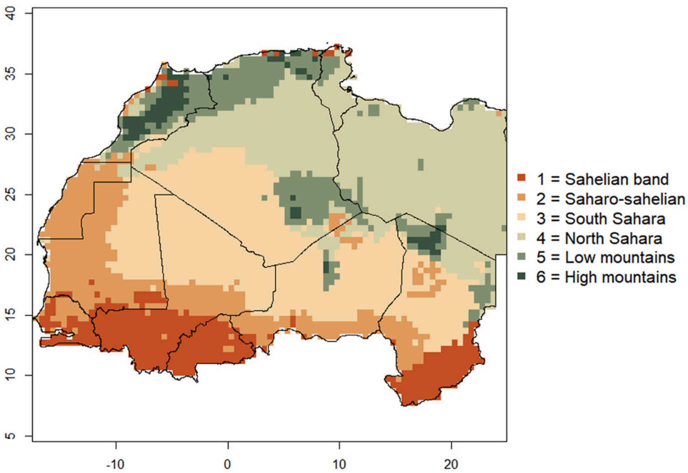

Fig. D.1. Clusterization results of the CLCPRO region based on climatic and geomorphic characteristics. The colors on the map represent each cluster.

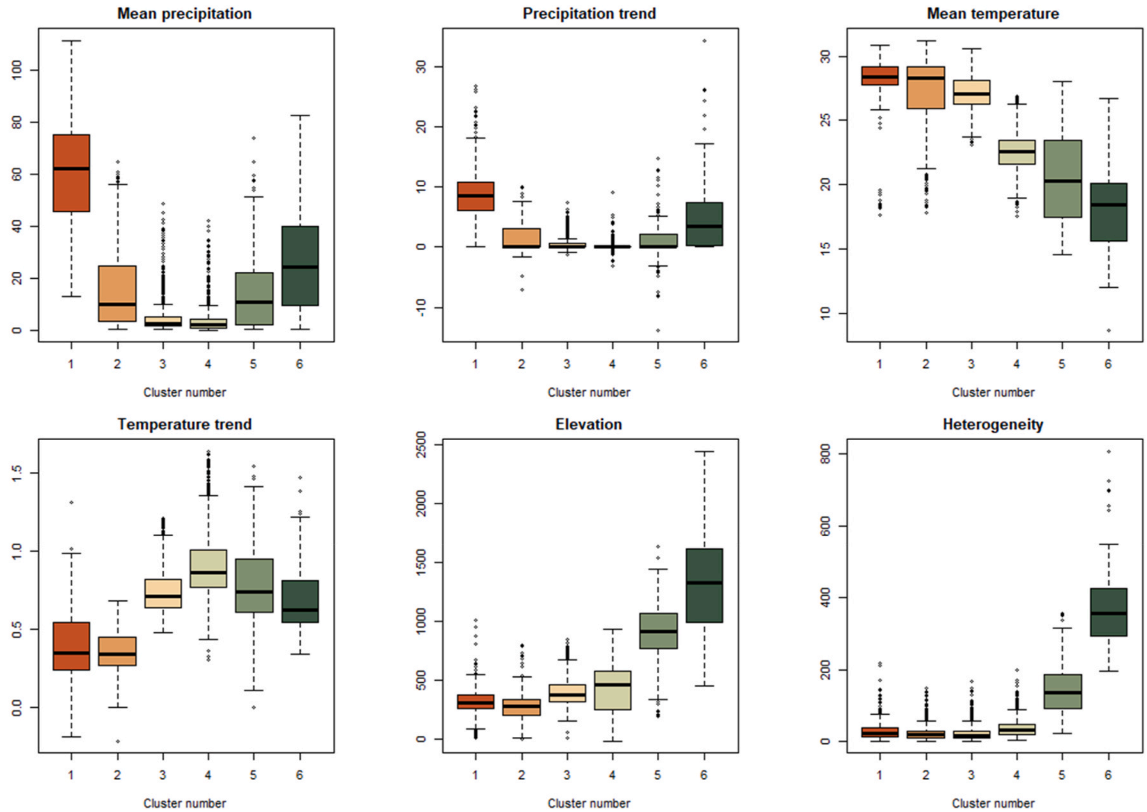

Fig. D.2. Climatic and geomorphic characteristics of each cluster obtained inside the CLCPRO region by k-mean clustering.

The box represents the interquartile range (IQR) between the first and third quartiles, with the median depicted by a line inside the box. The whiskers extend to the minimum and maximum values within a range of 1.5 times the IQR, and any data points beyond this range are considered outliers, displayed as individual point. The boxplot does not convey information about standard deviations. "Heterogeneity" refers as the standard deviation of the elevation.

Appendix E. Summary of climatic clusters results

Appendix E provides a summary of the different trends recorded for each climatic cluster.

Table 1
Summary of climatic clusters results. White cells represent non-significant trends, while significant trends are represented with backgrounds in shades of color: orange for positive trends, blue for negative ones, darker tones for stronger trends. NA = not available; trends for High mountains cluster management events could not be calculated because there were less than 3 years with at least 1 observation of control events. This makes sense because high mountains are not a usual desert locust habitat.

Cluster		Sahelian band	Saharo-Sahelian	South Sahara	North Sahara	Low mountains	High mountains
Temperature	Mean	28.162	27.198	27.093	22.458	20.462	18.158
	Trend	**0.023**	**0.026**	**0.043**	**0.045**	**0.040**	**0.037**
	p value	**1.25e-04**	**8.38e-05**	**5.97e-08**	**1.21e-08**	**4.81e-08**	**2.33e-07**
Precipitation	Mean	59.869	14.972	4.641	3.500	13.845	25.724
	Trend	**0.432**	**0.118**	0.036	-0.001	**0.087**	0.187
	p value	**2.17e-04**	**0.011**	0.136	0.939	**0.039**	0.050
Management	Trend	0.038	**0.192**	**0.076**	**0.150**	**0.120**	NA
	p value	3.44e-01	**9.05e-10**	**2.68e-03**	**4.84e-06**	**1.62e-03**	NA
Gregarization	Trend	**-0.237**	**0.043**	**-0.128**	**0.104**	0.017	NA
	p value	**4.06e-17**	**3.16e-26**	**6.99e-133**	**7.48e-08**	2.57e-01	NA

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