

Spatio-Temporal Modelling of *Culicoides* Latreille (Diptera: Ceratopogonidae) Populations on Reunion Island (Indian Ocean)

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Abstract

Background: Reunion Island regularly faces outbreaks of bluetongue and epizootic hemorrhagic diseases, two insect-borne orbiviral diseases of ruminants. Hematophagous midges of the genus *Culicoides* (Diptera: Ceratopogonidae) are the vectors of bluetongue (BTV) and epizootic hemorrhagic diseases of deer (EHDV) viruses. In a previous study, statistical models based on environmental and meteorological data were developed for the five *Culicoides* species present in the island to provide a better understanding of their ecology and predict their presence and abundance. The purpose of this study was to couple these statistical models with a Geographic Information System (GIS) in order to produce dynamic maps of the distribution of *Culicoides* throughout the island.

Methods: Based on meteorological data from ground weather stations and satellite-derived environmental data, the abundance of each *Culicoides* species was estimated for the 2,214 husbandry locations on the island for the period ranging from February 2016 to June 2018. A large-scale *Culicoides* sampling campaign including 100 farms was carried out in March 2018 to validate the model.

Results: According to the model predictions, no husbandry location was free of *Culicoides* throughout the study period. The five *Culicoides* species were present on average in 57.0% of the husbandry locations for *C. bolitinos*, 40.7% for *C. enderleini*, 26.5% for *C. grahamii*, 87.1% for *C. imicola* and 91.8% for *C. kibatiensis*. The models also showed high seasonal variations in their distribution. During the validation process, predictions were acceptable for *C. bolitinos*, *C. enderleini* and *C. kibatiensis*, with normalized root mean square errors (NRMSE) of 15.4%, 13.6% and 16.5% respectively. The NRMSE was 27.4% for *C. grahamii*. For *C. imicola*, the NRMSE was acceptable (11.9%) considering all husbandry locations except in two specific areas, the Cirque de Salazie – an inner mountainous part of the island- and the sea edge, where the model overestimated its abundance.

Conclusions: Our model provides, for the first time, an operational tool to better understand and predict the distribution of *Culicoides* in Reunion Island. As it predicts a wide spatial distribution of the five *Culicoides* species throughout the year and taking into consideration their vector competence, our results suggest that BTV and EHDV can circulate continuously on the island. It implies significant limitations for any preventive or control actions targeting vector populations. To assess other control strategies, our model could be coupled with an epidemiological model of BTV and EHDV transmission.

Background

Temporal and spatial variations of the climate and environment have an impact on vector populations and on the transmission of vector-borne diseases (VBDs) [1–3]. Statistical models help understand the interactions between climate – environment and vectors – VBDs [4]. When these models are incorporated into Geographic Information Systems (GIS), spatially explicit outputs such as distribution maps can be produced, making it possible to establish and rank the risk of exposure to vector bites and associated pathogens in a given geographical area [5, 6]. This approach is particularly relevant for areas where

surveillance data are lacking and the level of risk is unknown, as it provides a useful tool for health policy makers and vector-control agencies and the public [5].

Some biting midge species of the genus *Culicoides* are vector species of economically important viruses affecting livestock [7]. Because these viruses are exclusively transmitted to hosts by bites of *Culicoides* [8], their distribution and the intensity of infection are dependent on the distribution and abundance of their vectors [9, 10]. Epizootic events of bluetongue (BT), epizootic hemorrhagic disease (EHD) and African horse sickness (AHS), three *Culicoides*-borne viral diseases, respectively in Europe [11–13], in Mediterranean basin [14, 15 and in Africa {MacLachlan, 2010 #556, 16] have highlighted the need to map vector distribution and produce detailed predictive risk maps of *Culicoides*-borne diseases. Consequently, during the last decades, various studies conducted in Europe and Africa have mapped occurrence or abundance of *Culicoides* at a world-wide or country-wide scale [17–27] and less commonly at a local scale [4, 28, 29]. A spatio-temporal approach is particularly useful when the risk of exposure to vectors or VBDs is clustered in time and space [5]. This approach was favored by different authors [30–33].

Five *Culicoides* species have been recorded in Reunion Island [34, 35]: *C. bolitinos*, *C. enderleini*, *C. grahamii*, *C. imicola* and *C. kibatiensis*. Since the first detection of bluetongue virus (BTV) in 1979 [36] and epizootic hemorrhagic disease virus (EHDV) in 2003 [37] in Reunion Island, enzootic circulation of the former and epizootic circulation of the latter have been recorded [38]. Clinical cases were almost exclusively reported during or after the rainy season (November-April) and in the most recent cases (years 2016, 2018 and 2019) they were reported mainly on farms at high altitudes (GDS Réunion personal communication). This highlights the necessity to develop dynamic distribution maps of *Culicoides* in Reunion Island.

Statistical models were recently developed for each *Culicoides* species on Reunion Island [35] in order to provide a better understanding of their ecology and determine their periods of high abundance based on meteorological and environmental data. This first study focused on the temporal dimension of the *Culicoides* dynamics, but the spatial dimension was not addressed. The aim of this study is to couple previously developed statistical temporal models of *Culicoides* dynamics [35] with GIS techniques to provide spatio-temporal vector abundance maps for each *Culicoides* species in Reunion Island. It aims at addressing the needs expressed by different stakeholders, including breeders and veterinary services, to identify periods and areas when and where prevention and vector control strategies could be targeted.

Methods

Study sites

The study area is Reunion Island, a French department located in the southwestern Indian Ocean. The study sites include all the livestock (cattle, small ruminants, deer and horse) farms of the island. Livestock units are defined by the association of one breeder, one type of animal and one type of production (dairy farms, fatteners or pasture farms). In accordance to the 2016-2017 national census database and Groupement de Défense Sanitaire de La Réunion (GDS Réunion survey, the main

association of breeders of the island) survey, the island comprises 2,560 livestock units (figure 1) of cattle (1,337), goats (980), sheep (174), deers (12) and horses (57) distributed among 2,070 breeders. For the model, livestock units occupying the same production space, whatever the type of animal, were considered as a single geographic unit. Conversely, geographically separated livestock units of the same breeder were considered as separate units. Therefore, 2,214 husbandry locations with distinct geographical coordinates, composed of single or multiple livestock units, were defined and used as elementary geographic units in the *Culicoides* abundance model.

Meteorological and environmental data

The temporal dynamics models developed for each *Culicoides* species [35] include 11 categories of meteorological and environmental variables to estimate abundance: temperature, humidity, rainfall, wind speed at 2 m above ground, global radiation, vegetation index, eco-climatic area, land use, husbandry location density (i.e. the number of husbandry locations within defined buffered areas), animal density and building opening size. Corresponding data were acquired from different sources.

Time-dependent variables (i.e. temperature, humidity, rainfall, wind speed, global radiation, and vegetation index) were obtained for the January 2016 to June 2018 period.

The location of meteorological stations recording temperatures (n=31), rainfall (n=31), wind speed (n=30), global radiation (n=28) and humidity (n=18) was obtained from meteorological service “Météo France” (<https://publitheque.meteo.fr>). The daily data recorded by these stations were downloaded from Smartis' web service (www.smartis.re). Missing data for wind (24.1%) and humidity (29.2%) were estimated by time linear interpolation. Meteorological stations recording wind speed provide measures either at 2 m or 10 m above the ground. To estimate wind speed at 2 m above the ground from 10 m above the ground measures, a correction method is applied based on the roughness categories of the land around the station, defined from the Atlas of Landscape and Roughness of Reunion Island (<https://sites.google.com/site/venturiec1/calendar>) [35]. Normalized Difference Vegetation Index (NDVI) was obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) measurements at 250 m spatial resolution (<https://lpdaac.usgs.gov/>) [39]. MODIS Terra 16-day composite images (product MOD13Q1) were acquired for the study period.

Eco-climatic area was obtained from the map of “Urban Planning and Native Plants Approach” (DAUPI) (Botanical Conservatory of the Mascarenes 2010; <http://daupi.cbnm.org/palette/#/taxons>).

A 2016-2017 land-use map [40, 41] was acquired from Cirad (<http://aware.cirad.fr>).

Husbandry location and characteristics (type of husbandry atelier and number of animals) data were obtained from 2016-2017 national and GDS Réunion census databases.

Altitude data were also required to take into account temperature variation between weather stations and husbandry locations. These data were acquired using the digital elevation model BD ALTI® from the National Geographic Institute (<http://professionnels.ign.fr/bdalti>).

Models of *Culicoides* presence and abundance

For each husbandry location, the abundance of each *Culicoides* species from February 2016 to June 2018 was estimated using the temporal dynamics models developed in [35]. This estimated abundance reflects the number of *Culicoides* that could have been captured near the animals by an OVI (Onderstepoort Veterinary Institute) light trap overnight. The temporal models are hurdle models, i.e. a presence/absence model combined with an abundance model, built from a two-year dataset of biweekly catches in 11 farms. For each species, the presence/absence model is a logit-link logistic regression model (Eq. 1):

$$p_i = \frac{e^{\beta_0 + \beta_j X_{ij}}}{1 + e^{\beta_0 + \beta_j X_{ij}}} \quad (Eq.1)$$

where p_i is the probability of presence at the husbandry location i , β_0 the intercept, β_j the coefficient of the explanatory variable X_j , X_{ij} the value of variable X_j at the husbandry location i .

The abundance model is a log-link mixed-effect zero-truncated negative binomial model (Eq. 2) with random effect on farms:

$$\lambda_i = \begin{cases} e^{\gamma_0 + \gamma_j X_{ij} + e_{farm(i)} + e_i} & \text{if } p_i \geq \alpha \\ 0 & \text{otherwise} \end{cases} \quad (Eq.2)$$

where λ_i is the estimated abundance (number of *Culicoides* per trap and per night) at the husbandry location i , γ_0 the intercept and γ_j the coefficient of the explanatory variable X_j , $e_{farm(i)}$ the random effect of farm for husbandry location i , e_i an error term for each prediction and α the threshold of positive realization.

All variables and coefficients used to estimate *Culicoides* abundances are presented in Additional file 1, tables S1 to S5.

To apply the models to the scale of Reunion Island, the random effect of farms in the count part of the hurdle model was neglected.

The environmental characteristics of the 11 farms used to build the temporal model define their validity domain: no predictions can be made on the husbandry locations with values of environmental characteristics outside the range of values of the predictive variables. The limiting variables are presented in Additional file 1, tables S1 to S5.

Preprocessing

The eco-climate area corresponding to each husbandry location, the husbandry location density, animal density and the percentage of land use coverage in different buffer sizes (0.5 km, 1 km or 2 km) around each husbandry location were all extracted using QGIS [42]. The altitude was extracted for each husbandry location and each weather station using QGIS. Building opening size was interpreted according to the general configuration of the type of farming observed in Reunion Island : from 0 to 25% for dairy farms, from 25 to 100% for fatteners, enclosure for pasture farms.

Spatio-temporal dynamics

The representation of the spatio-temporal dynamics of *Culicoides* was built with Ocelet language and open modelling platform (www.ocelet.org). Ocelet is an open-access domain specific language and simulation tool for modelling changes in geographical landscapes and facilitating the processing of geographical information [43].

Our model comprises four main elements called “entities”: *i*) the 2,214 husbandry locations (point geometry), characterized by their respective values of eco-climatic area, land use, husbandry location density, animal density and building opening size, *ii*) the weather stations (point geometry) whose daily minimum and maximum temperatures, rainfall, wind speed, global radiation and humidity are imported as text files (csv format), *iii*) the satellite-derived vegetation indices, imported as raster data, and *iv*) a 1 km wide hexagonal grid to map model output (Figure 2). The entities interact through spatial relations: for each husbandry location, the values of the meteorological variables were defined as those of the closest weather station, and the NDVI value was defined as the NDVI of the pixel in which the husbandry location was contained.

The scenario, which defines the sequence of operations and interactions between entities was defined as follows (Figure 2). Step 1: daily meteorological variable were read and attributed to each corresponding husbandry location. A correction of $-0.0075^{\circ}\text{C}\cdot\text{m}^{-1}$ [44] was applied to the temperature based on the altitude difference in meters between the station and the husbandry location. A correction of the 10 m above the ground wind speed measures was applied to convert them into 2 m above the ground wind speed estimates [35]. Step 2: daily NDVI values for each husbandry location were either read from a raster file if the date corresponded to the date of acquisition of MODIS NDVI, or estimated using a temporal linear interpolation. When the pixel corresponding to a husbandry location had a NDVI value lower than zero (suggesting that the pixel was masked by a cloud), the positive value of the nearest pixel was selected. Step 3: for each husbandry location, the probability of presence and the predicted abundance of each species was computed from Equations 1 and 2, provided they were within the validity limits of the model variables. Step 4: for each hexagonal grid, the abundance of *Culicoides* species was computed as the average values of *Culicoides* abundance of the husbandry locations it contained.

Validation

In order to validate the simulation of the spatial dynamics of each species, an entomological survey was carried out at the scale of the whole island. A total of 100 farms distributed throughout the island were

sampled representing 101 catches (one farm was sampled at two husbandry locations). The 11 farms used to build the temporal model in [35] were included in the survey. Single night catch collection was conducted from 07 to 22 March 2018 using OVI traps. The trapping and identification of *Culicoides* species was the same as described in [35].

Observed and predicted values at the date of capture were compared using the area under curve (AUC) of the ROC (Receiver Operating Characteristic) curve [45] for presence/absence and the Normalized Root Mean Square Error (NRMSE) standardized to the range of observations for abundance. These calculations were performed using R version 3.4.1 [46] with pROC [47] and hydroGOF [48] packages. Standardized differences, *i.e.* the difference between a prediction and an observation divided by the range of observed values, were also mapped to identify clusters of correct predictions, overestimations or underestimations.

Results

The total number of husbandry locations on which it was possible to estimate abundances (*i.e.* their environmental characteristics were within the validity domain of the model) was 1,807 (81.6%) for *C. bolitinos*, 1,534 (69.3%) for *C. enderleini*, 2,178 (98.4%) for *C. grahamii*, 1,866 (84.3%) for *C. imicola* and 1,922 (86.8%) for *C. kibatiensis*, out of the 2,214 husbandry locations in the sample size.

During the 28 months of spatio-temporal dynamics simulation, *C. kibatiensis* followed by *C. imicola* were the most widespread species, present on average (minimum - maximum) in 91.8% (82.0% – 99.8%) and 87.1% (63.7% – 99.1%) of the husbandry locations respectively. In contrast, *C. grahamii* and *C. enderleini* were the least widespread species, present on average in 26.5% (6.8% – 74.0%) and 40.7% (17.3% – 64.3%) husbandry locations respectively. As for *C. bolitinos*, it was present on average in 57.0% (14.0% – 87.4%) of the husbandry locations.

A clear seasonal pattern was observed for all species (Fig. 3). *Culicoides bolitinos*, *C. enderleini* and *C. imicola* were present in fewer husbandry locations during the cold and dry season than during the hot and rainy season. These seasonal patterns could also be observed when considering husbandry locations with more than 10, 100 or more *Culicoides*. The opposite situation with an increased presence in study sites in the cold dry season was observed for *C. kibatiensis* and, to a lesser extent because seasonal patterns were harder to identify, for *C. grahamii*.

Interestingly, *C. bolitinos* was globally present in more sites during the period from early 2016 to the end of the 2016–2017 hot and rainy season than during the period from the end of the 2016–2017 hot and rainy season to mid-2018. In the former period, the average percentage (range in brackets) of positive husbandry locations was 69.5% (37.2% – 87.4%) and during the latter, it decreased to 45.8% (14.0% – 66.7%).

Estimated abundances remained generally low. Considering times points when the species were present, the median of estimated abundances (*Culicoides* per trap per night), 1st and 3rd quartiles in brackets,

were 12.1 (5.7–23.7) for *C. bolitinos*, 0.2 (0.03–1.1) for *C. enderleini*, 1.7 (0.5–3.7) for *C. grahamii*, 23 (1.2–148) for *C. imicola* and 3.7 (1.2–12.1) for *C. kibatiensis*. However, *C. imicola* was estimated to have a high abundance in an important number of husbandry locations compared to other species. On average for *C. imicola*, more than 1,000 individuals were estimated on 13.7% of the husbandry locations. This rate dropped below 0.1% for the other species. Considering a lower expectation of 100 individuals, the rate was 28.3% for *C. imicola* and less than 2.4% for the other species.

The abundance maps produced with a 7-day time step showed the spatial and temporal variation for each species (see examples of abundance maps in Fig. 4; Additional Files S2-6 for movies). According to the model, *C. imicola* occupied the island's coastal areas continuously and with high abundance. During the hot and rainy season, its distribution expanded and reached sites located further from the coast, towards the interior of the island.

Climatic and environmental conditions were favorable for the distribution of *C. kibatiensis* throughout the island, except on a thin southern and northeastern coastline during the hot and rainy season. However, areas of high abundance were only found in the highlands.

Culicoides bolitinos occupied a wide area from the coastal area to the interior of the island although the southern and western coastal areas become less favorable to its presence during the cold and dry season. The highest abundances were estimated for the mid- and high-altitude husbandry locations. Results highlighted also a high inter-annual variability, with a distribution of *C. bolitinos* much more restricted and less abundant in the western area in 2017 than in 2016.

Culicoides enderleini occupied the coastal areas of the island and during the cold and dry season, it persisted only in the southwest and in a small area to the northwest. Conversely, *C. grahamii* occupied very clearly the western and southwestern highlands and its distribution could extend to the northeast during the cold and dry season.

The survey conducted in March 2018 (Fig. 5) confirmed the presence of the 5 species identified by [34]. A total of 50,526 *Culicoides* were caught during the 101 nights campaign with a maximum of 8,091 individuals. No *Culicoides* were caught in 6 farms. For each species, the total number of individuals, mean and number of positive catches in brackets, was: 4,087 (40.5; 41) for *C. bolitinos*, 5,314 (52.6; 29) for *C. enderleini*, 154 (1.5; 20) for *C. grahamii*, 26,908 (266.4; 69) for *C. imicola* and 14,063 (139.2; 61) for *C. kibatiensis* (Additional file 7, table S6).

Predictive accuracy of presence and absence was acceptable for *C. imicola* and *C. kibatiensis* with ROC AUCs of 0.755 and 0.730 respectively. For *C. bolitinos*, *C. enderleini* and *C. grahamii*, predictions of presence were less good with AUCs of 0.557, 0.649 and 0.588 respectively. Regarding abundance estimates, the NRMSEs were 15.4% for *C. bolitinos*, 13.6% for *C. enderleini*, 27.4% for *C. grahamii* and 16.5% for *C. kibatiensis*. Considering all husbandry locations, the abundance predictions for *C. imicola* showed a high NRMSE of 252.5%. The maps of standardized difference (Fig. 6) showed a high variability between predictions and observations for *C. imicola* at the Salazie (inner mountainous area) husbandry

locations and at four other husbandry locations located in the south, southwest and northeast sea coasts, with a tendency to overestimate. Without considering the Salazie husbandry locations and the four other ones for which the model predicted more than 7,877 individuals per trap per night (maximum observation for *C. imicola*), the NRMSE was 11.9%.

The highest variabilities between observations and predictions were observed in the south and west for *C. bolitinos* and on the south coast for *C. enderleini*. For *C. grahamii*, a strong variability seemed to exist between the observations and the predictions. Finally, predictions for *C. kibatiensis* lead to underestimation of abundance, mainly in the western highlands.

Discussion

BTV and EHDV epidemics can cause severe economic losses to farmers [8, 14]. In Reunion Island, both a large-scale inventory and longitudinal monitoring allowed the identification of local *Culicoides* species, improving the understanding of their ecology and modelling high abundance periods [34, 35]. The present study provides, for the first time, a spatial model of the abundance of *Culicoides* in Reunion Island, designed to implement an operational tool to help stakeholders and farmers identify and communicate on disease risk periods and areas.

The abundance of each *Culicoides* species was estimated from mixed-effect zero-truncated negative binomial models developed in a previous study [35]. To apply these models to the entire island, the random effect of farms (Eq. 2) was neglected, as mixed models do not allow predictions on subjects that were not part of the original training data. However, the standard deviation of the random effects for farms provided in Grimaud *et al.* [35] was in the range of $2.8 \cdot 10^{-5}$ to $1.2 \cdot 10^{-4}$ for all species except *C. kibatiensis*. These orders of magnitude can be considered negligible and suggested that the estimated temporal dynamics for these four species were under the almost exclusive governance of climate and environment. Consequently, we can consider that the abundance estimates of *C. bolitinos*, *C. enderleini*, *C. grahamii* and *C. imicola* were not biased by the intrinsic effects of farms. However, for *C. kibatiensis*, the standard deviation of random effect was 0.596 and thus could not be considered as negligible. The modelled dynamics of *C. kibatiensis* allowed identifying the favourable areas according to climatic and environmental data only, but intrinsic characteristics of the farm could greatly impact these abundances.

Overall, the predicted spatio-temporal distributions of each *Culicoides* species coincide with the main observations made by [34] and [35]: *i)* low overall abundance, except for *C. imicola* in coastal areas; *ii)* higher abundances of *C. imicola* and *C. enderleini* at low altitude and during the hot and rainy season; *iii)* higher abundance of *C. bolitinos* at mid-altitude and during the hot and rainy season; *iv)* higher abundances of *C. kibatiensis* and *C. grahamii* at high altitude and during the cold and dry season. Our modelling results showed that *C. imicola* and *C. kibatiensis* have a wide spatial distribution and that there is virtually not a single husbandry location that would not be affected by *Culicoides*. This prediction was verified by data from the March 2018 campaign where *Culicoides* were found in 95 of the 101 catches.

This confirms that *Culicoides* species can occupy a wide variety of climates encountered on Reunion Island as already mentioned for the Palearctic region [7].

The spatial distribution of species observed during the March 2018 survey confirmed the global distribution described by Desvars *et al.* [34] and Grimaud *et al.* [35]. However, the greater sampling effort made and the use of the reference trap (OVI) enabled detecting a larger distribution of *C. bolitinos* in the south of the island and of *C. enderleini* on the northeast coast and on the highlands. A more extensive spatial distribution was also observed for *C. imicola* and *C. kibatiensis*, which is consistent with the predicted spatio-temporal distribution (Fig. 4).

When comparing modeled abundance predictions with field observations from the March 2018 survey, presence predictions were acceptable for the two most common species, *C. imicola* and *C. kibatiensis*. For the three other species (*C. bolitinos*, *C. enderleini* and *C. grahamii*), presence predictions were less good. With regard to abundance estimates, predictions were acceptable for *C. bolitinos*, *C. enderleini* and *C. kibatiensis*, but less good for *C. grahamii* and *C. imicola*.

It should be noted that the high variability of catches is a general problem in vector modelling [30]. As Baylis *et al.* pointed out [21], the number of *Culicoides* that can be caught per night using a light trap depends on the size of the local *Culicoides* population, the activity rate and the efficiency of the trap; the latter two are themselves affected by the local weather conditions. According to the same study, the absence of repeated captures over a short period of time reduces the accuracy of presence estimation, especially when *Culicoides* abundance is low. Also, the catches were made after a mild hurricane event that occurred on 05 March 2018, which still resulted in heavy rainfall (<http://www.meteofrance.fr/actualites/59989790-un-point-sur-le-cyclone-dumazile>). Thus, the model predictions were compared to one night catches data of March 2018, potentially impacted by the previous hurricane event, which could explain the lack of accuracy in the prediction of presence for the three species with the lowest observed abundances (*C. bolitinos*, *C. enderleini* and *C. grahamii*). Moreover, it should be stressed that NRMSE tends to be higher for low abundances even if the order of magnitude of observations and predictions is comparable, as it is the case for *C. grahamii* (maximum catch: 28 individuals per trap; maximum predicted abundance: 52 individuals per trap).

For *C. imicola*, model estimates of abundance were satisfactory only if outliers were not considered. *Culicoides imicola* abundance was overestimated in the municipality of Salazie and in some sites on coastal areas (Fig. 6). These sites are associated with a high percentage of bare rock, a variable originally associated with high *C. imicola* abundance. Because of the exponential function, the *C. imicola* abundance model is very sensitive to this variable, which can lead to high volatility in the predictions. This tends to have a strong impact on the NRMSE. In addition, the municipality of Salazie also has specific features. As a geological cirque, this municipality is a very isolated region of the island, surrounded by cliffs of several hundred meters, with very rugged relief and with stony and very gullied soils [49]. In this area, the climatic and environmental conditions taken into account in our models were very favorable for high *Culicoides* abundances, but its particular landscape and soil characteristics, which

were not exploited in the models, may explain the lower abundances observed in March 2018. Indeed, if landscape can play a role in local *Culicoides* abundance [29, 50, 51], the type of soil may limit *Culicoides* development, as in a *C. imicola*-free zone in South Africa, where the soil is sandy, poor in nutrients and too well-drained to sustain *Culicoides* larvae [52].

Another source of differences between predictions and the observations of March 2018 could come from the variables estimates. For example, the building opening size was estimated according to the general configuration of the type of production, and not from field observations as in [35]. Greater distances to weather stations could lead to approximates of climate data given the diversity of the island's microclimates.

Finally, the type of animal hosts in the vicinity of the traps could also be a source of variation. By construction, the predictions from temporal dynamics model built in Grimaud *et al.* [35] reflect the expected catches in the vicinity of cattle. The farms selected for the March 2018 campaign were mainly cattle farms (82 out of 100, Additional file 7) and therefore correspond to the conditions under which the temporal models were constructed in Grimaud *et al.* [35]. However, considering the predictions to all husbandry locations in this study, other animal types, such as sheep, goats, deer and horses, were included, assuming an equivalent importance of the host type on the composition of *Culicoides* species. However, some *Culicoides* species may be associated with one host type more than another by their host preference or the behavior [53–56]. Unfortunately, no comparative study was carried out in Reunion Island to take into account the differences induced by the type of host in the vicinity of the traps and therefore requires careful consideration of predictions.

From an epidemiological point of view, together the wide permanent distribution of *Culicoides* and their known vector competence [57, 58] suggests that BTV and EHDV can circulate throughout the year and throughout the island in vector *Culicoides* and in livestock. A serological survey conducted in 2011 [38] supports this hypothesis since: (1) two thirds of the cattle tested were EHDV positive and distributed throughout the island; (2) near 80% of cattle, 50% of goats and 21.5% of sheep were seropositive suggesting a high level of BTV circulation among these animals. However, each species showed spatial and temporal variations in abundance suggesting different implications in the transmission of the two viruses. As Donnelly *et al.* [59] pointed out, locally high abundance, although seasonal, and in addition to wide distribution, are conditions characterizing the primary role of a vector. Therefore, knowing these variations in abundance and distribution makes it possible to develop scenarios on how *Culicoides* species take turns to ensure a continuum of BTV and EHDV transmission across the island, but also to identify the species that would apparently be the most involved during an epizootic.

Given the close link between transmission and biting rates, it would be tempting to position *C. imicola* as the main vector of BTV and EHDV. Indeed, the four other species reach abundances of more than 100 individuals in an average of 2.4% of husbandry locations and more than 1,000 individuals in only 0.1% of husbandry locations on average, suggesting that their participation in transmission may remain low compared to that of *C. imicola*. However, other parameters such as virus replication pattern inside the

vector, host preference and association could provide effective mechanisms for the virus transmission [60]. A concrete example is *C. bolitinos*, whose biology closely associated with cattle and more adapted to cold environments than *C. imicola*, is a vector of prime importance during winter and in the coldest parts of South Africa [60, 61]. If, due to their abundance, *C. imicola* and *C. kibatiensis* are the ideal candidates in coastal areas and highlands respectively, it is not unreasonable to think that *C. bolitinos* could be the first-rate vector at higher altitudes in Reunion Island. The importance of the two other species (*C. enderleini* and *C. grahamii*) cannot be ruled out on the sole assessment of their abundance without assessing their vector competence. The presence of several vector or potential vector species, their wide distributions, their different trophic preferences and behaviors, reinforces the need to better understand the BTV and EHDV risk on Reunion Island. The calculation of the basic reproduction rate R_0 would be a very interesting approach to assess this risk [31, 62].

Most of the time, for *Culicoides*, the spatial and temporal components of their abundance distribution are modelled separately. Only Brugger & Ruble [30] and Rigot *et al.* [32] built spatio-temporal models on *C. obsoletus* spp. and *C. imicola* respectively. However, these models did not incorporate environmental variables such as land use, eco-climate, host type and density although Conte *et al.* [63] and Purse *et al.* [50] suggested the increased model accuracy when estimating *Culicoides* abundance. In this study, environmental and host variables as well as the entrance size of buildings, which may influence *Culicoides* abundance depending on their exophilic or endophilic behaviors, were included for the first time to model the spatio-temporal distribution of *Culicoides*. It should be noted that the use of Ocelet modelling platform, a free software dedicated to the modelling of spatial dynamics, greatly facilitated the integration and processing of the geographic information corresponding to the climate, environment and host variables [43]. In particular, its capacity to facilitate the formalization of the link between these data and entities, the interactions between entities and the definition of a scenario were proved to be extremely useful.

Recently, spatio-temporal models of arthropod vectors have sparked the interest of public health authorities in Reunion Island and its close sister island, Mauritius. Indeed, a similar model was developed for *Aedes albopictus*, a vector of dengue and chikungunya viruses in the Indian Ocean, and transferred to local authorities [64] to help prioritize action areas where public awareness and vector control measures should be implemented. For *Culicoides*, control methods are not as developed as for mosquitoes [65], limiting, for the moment, the development of an applied tool used by pest management units. The development of control actions is further challenged by the fact that our results suggest that vectors are present nearly in every farm in Reunion Island, and during sufficiently long periods of time to support BTV and EHDV transmission. Yet, a tool equivalent to that developed for mosquitoes in Reunion Island would help raise awareness, train and support decision-making relative to prevention strategies and enable testing control methods. In addition, for horses that may develop summer dermatitis because of *Culicoides*, such a tool could be useful to anticipate when and where protective measures for these animals should be implemented.

Conclusions

The modelling approach developed enabled to develop dynamic maps of abundance for the five *Culicoides* species present in Reunion Island for the first time. The use of GIS and Ocelet spatial modelling platform enabled easy integration of different climatic and environmental variables and facilitated the development of dynamic risk maps. From an operational point of view, the results suggest that any preventive and control actions targeting the vectors would be limited by their large distributions and long activity periods. It now appears crucial to evaluate the vector competence of each species to better assess the risk of BTV and EHDV transmission.

Abbreviations

AHS

African horse sickness; AUC:area under curve; BT(V):bluetongue (virus); DAUPI:urban planning and native plants approach; EHD(V):epizootic hemorrhagic disease (virus); GIS:geographic information system; GDS:groupelement de défense sanitaire; MODIS:moderate resolution imaging spectroradiometer; NDVI:normalised difference vegetation index; (N)RMSE:(normalised) root mean square error; OVI:Onderstepoort Veterinary Institute; ROC:receiver operating characteristic; VBDs:vector-borne diseases.

Declarations

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Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

All sample and Ocelet codes are available upon request to the corresponding authors.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

Y.G., A.T., S.B., H.G. and C.G. designed the study; Y.G., F.B. and HG collected the samples, Y.G. and C.G. identified the *Culicoides* samples, Y.G. and S.B. analyzed the data with the help of A.T.; S.B., O.E., C.C.S. and E.C. contributed to the manuscript after its first draft by Y.G, A.T., H.G. and C.G.; all authors read and commented on the final manuscript version. All authors read and approved the final version of the manuscript.

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Additional Files

Additional file 1 (.docx): Table S1. Model parameters for *C. bolitinos*. **Table S2.** Model parameters for *C. enderleini*. **Table S3.** Model parameters for *C. grahamii*. **Table S4.** Model parameters for *C. imicola*. **Table S5.** Model parameters for *C. kibatiensis*.

Additional file 2 (.mp4): Movie of the spatio-temporal distribution of *C. bolitinos*.

Additional file 3 (.mp4): Movie of the spatio-temporal distribution of *C. enderleini*.

Additional file 4 (.mp4): Movie of the spatio-temporal distribution of *C. grahamii*.

Additional file 5 (.mp4): Movie of the spatio-temporal distribution of *C. imicola*.

Additional file 6 (.mp4): Movie of the spatio-temporal distribution of *C. kibatiensis*.

Additional file 7 (.docx): Table S6. Observed *Culicoides* abundance during the sampling campaign from 07 to 22 March 2018.

Figures

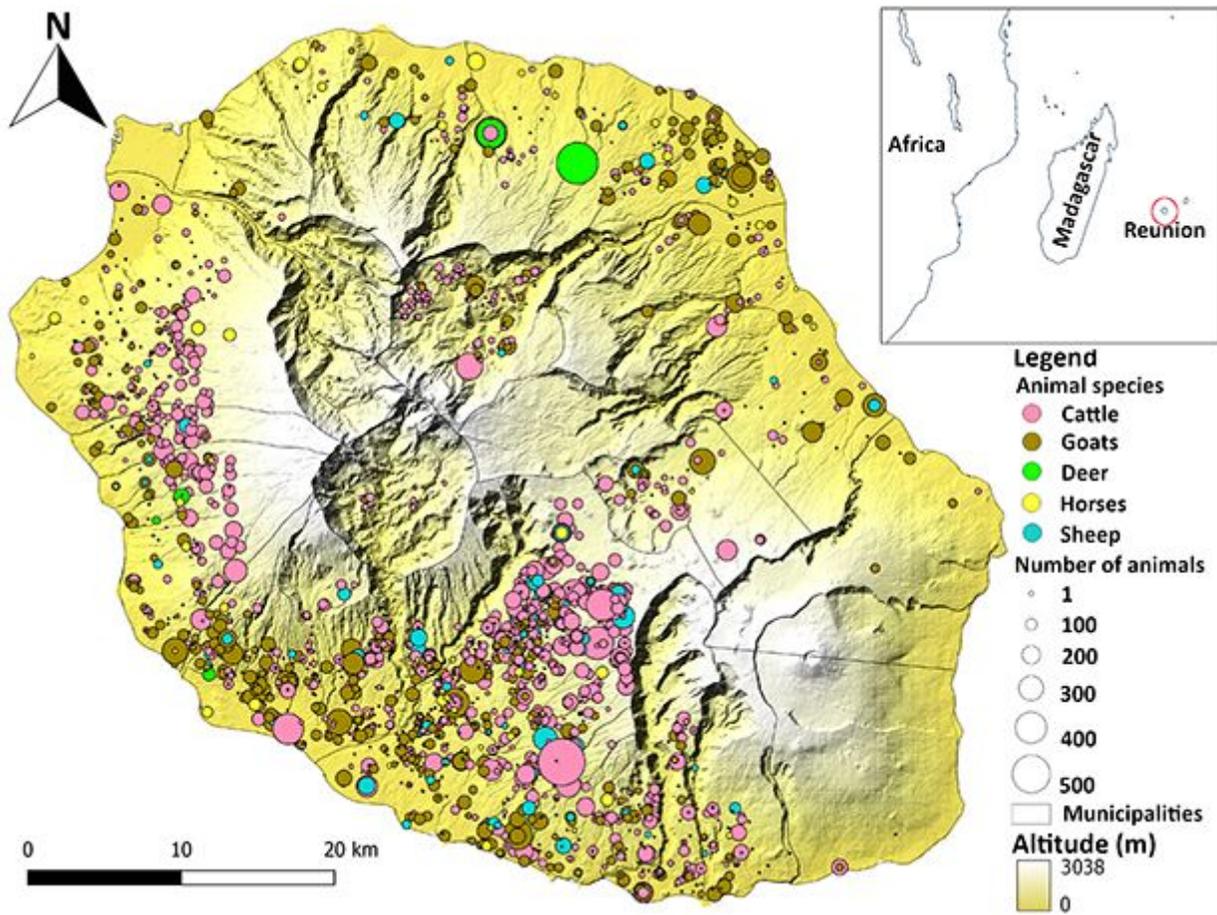


Figure 1

Spatial distribution of cattle, goats, sheep, deer and horses on Reunion Island. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

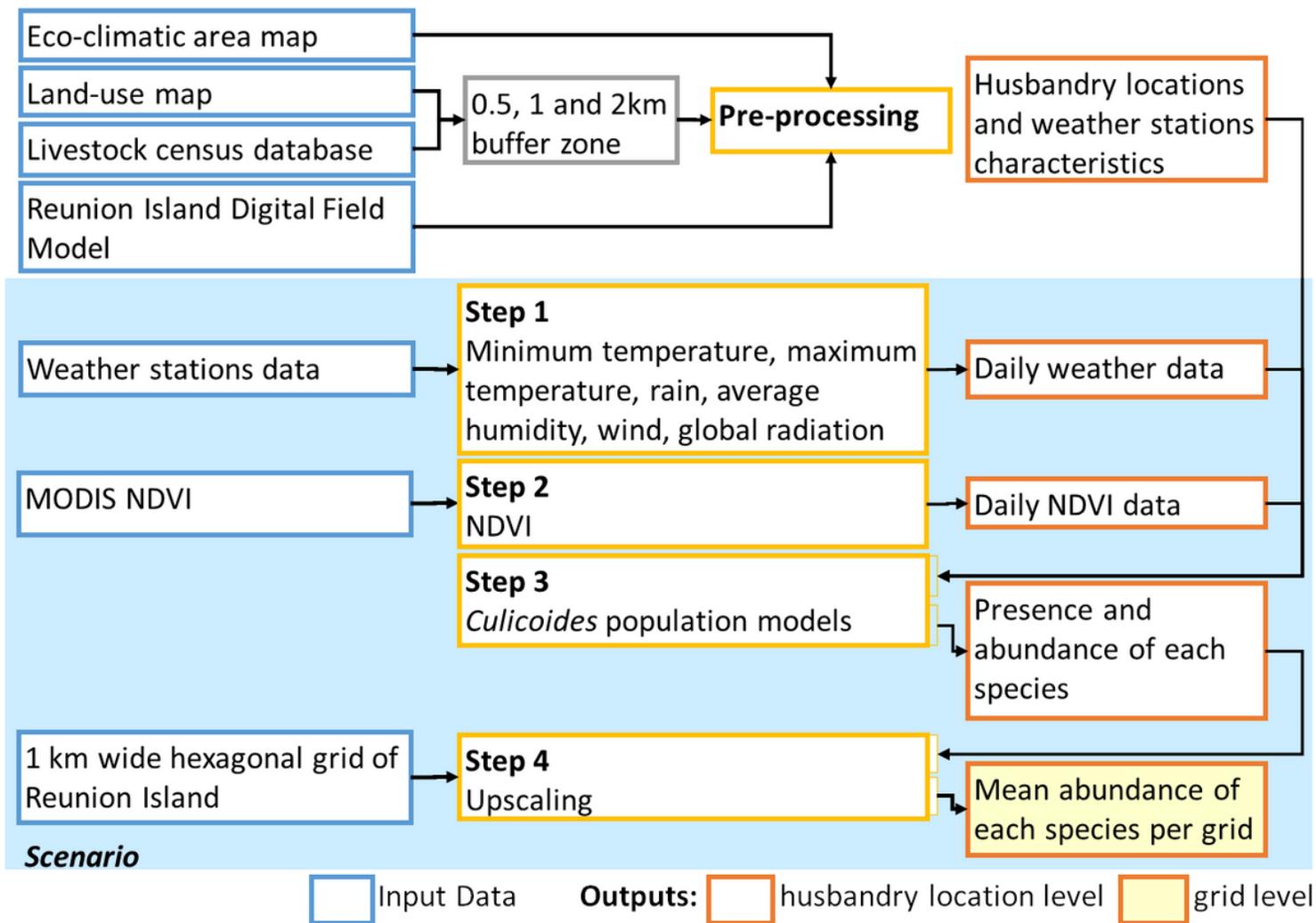


Figure 2

Workflow diagram for the application at Reunion Island scale of the *Culicoides* spatio-temporal models.

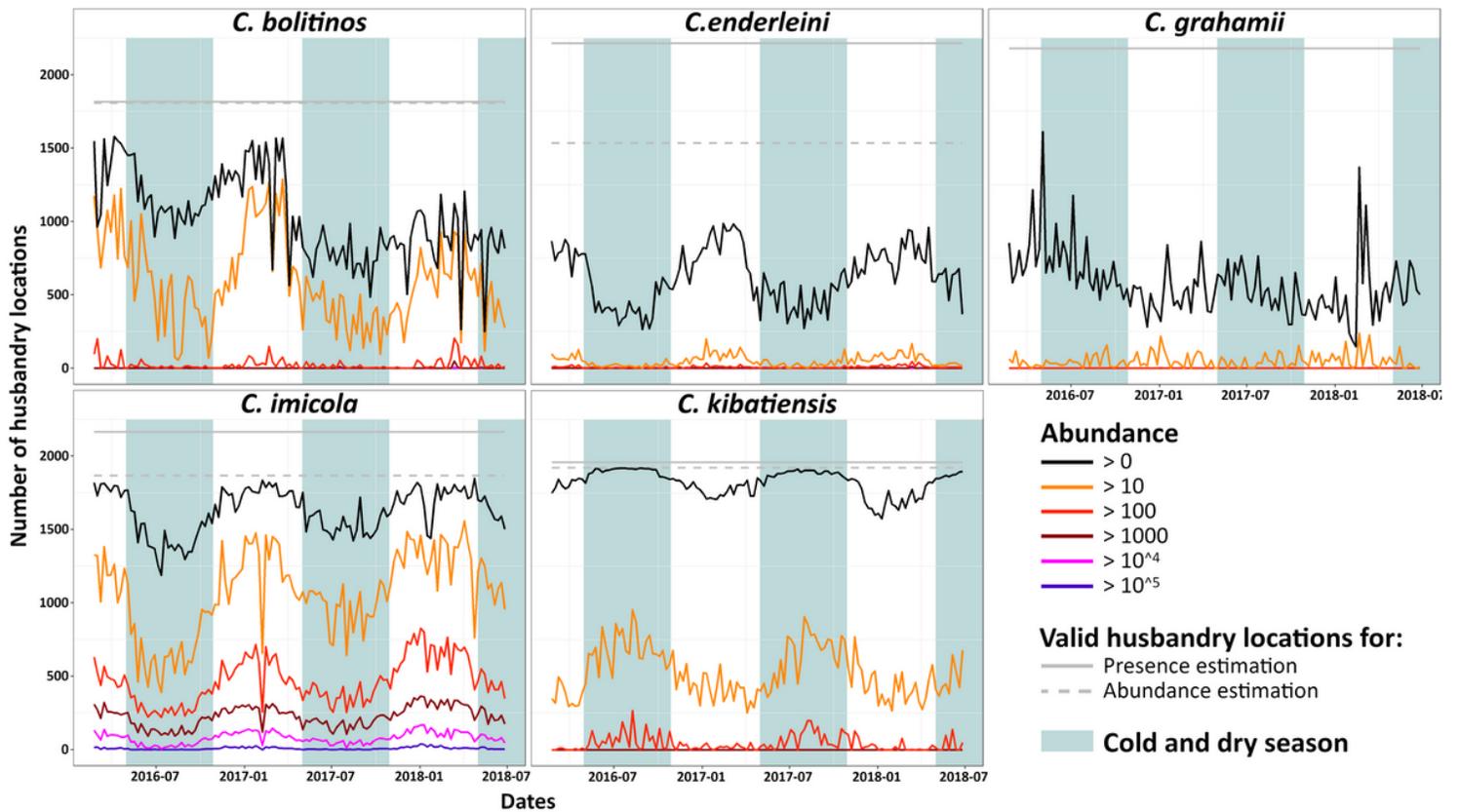


Figure 3

Temporal variations in the number of husbandry locations with an estimated positive abundance for each of the *Culicoides* species. Husbandry locations with more than 10¹ to 10⁵ individuals are also shown.

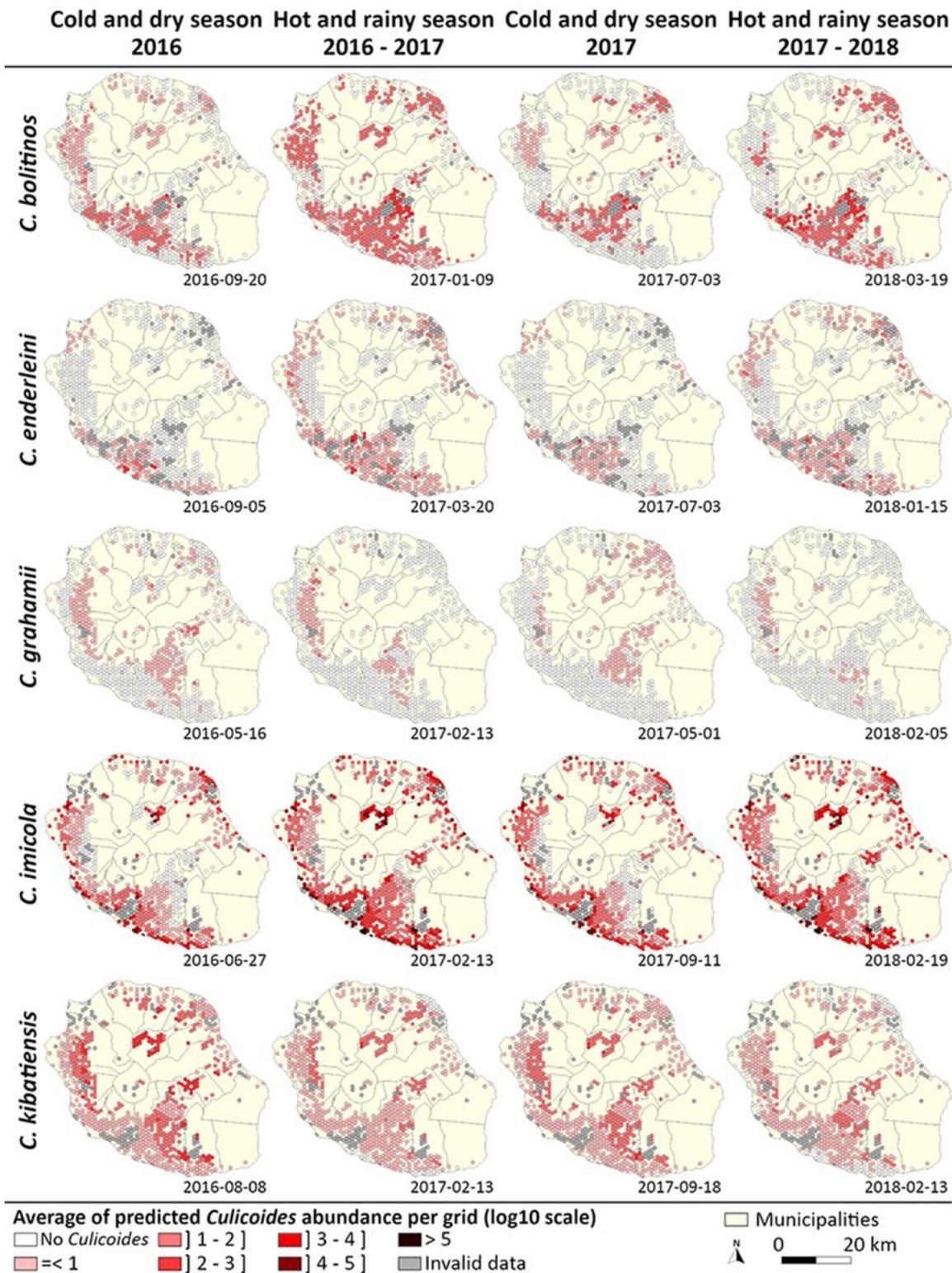


Figure 4

Example of modelled density maps of each *Culicoides* species, Reunion Island, 2016-2018. The examples chosen are those closest to the 3rd quartile of the number of positive husbandry locations during the hot and rainy season for *C. bolitinos*, *C. enderleini*, and *C. imicola* and during the cold season for *C. grahamii* and *C. kibatiensis*. For the opposite seasons, the examples are the closest to the 1st quartile. Note: The designations employed and the presentation of the material on this map do not imply the expression of

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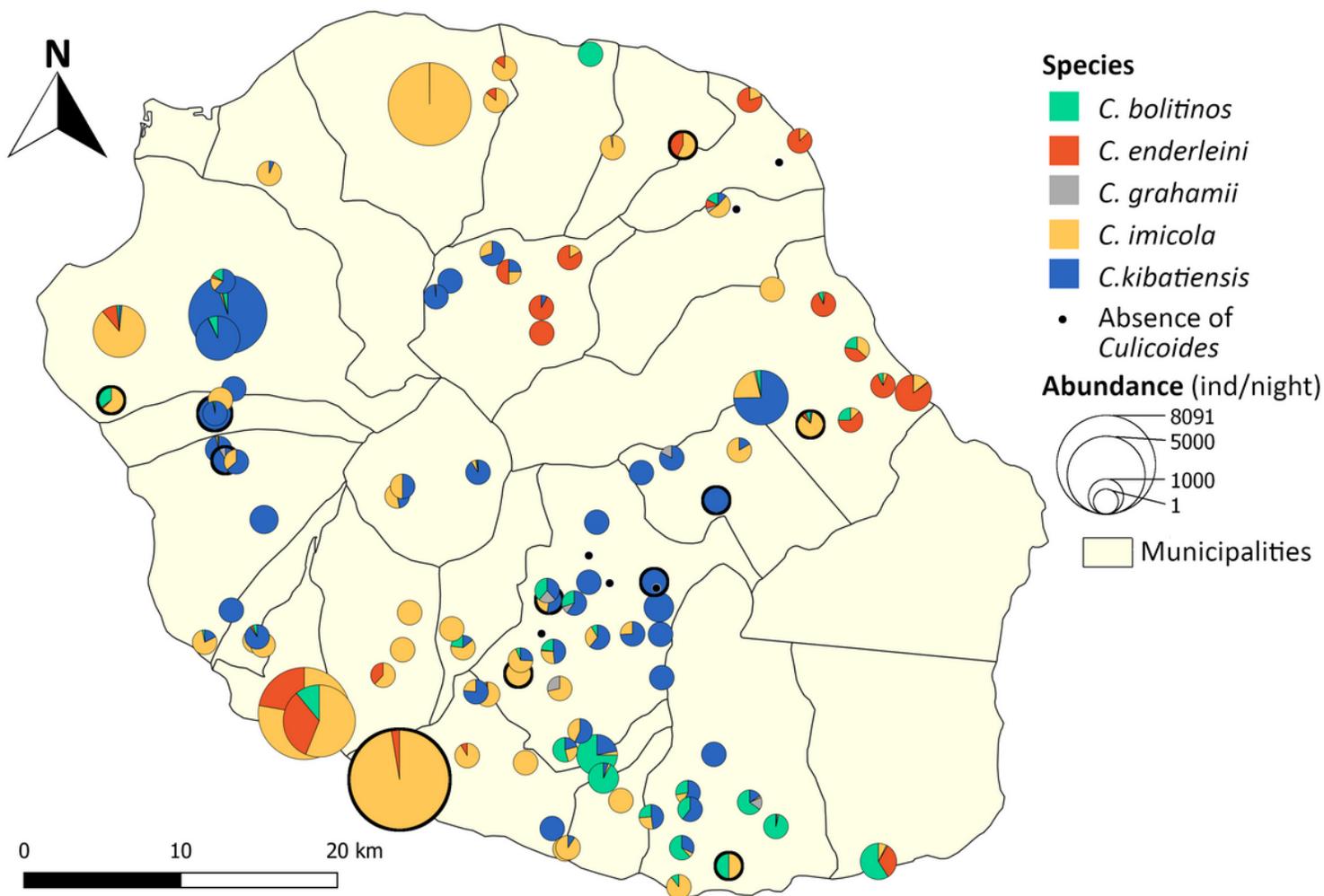


Figure 5

Spatial distribution of *Culicoides* species observed during the March 2018 sampling campaign. The bold circles correspond to the 11 farms used to build the temporal model in [35]. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

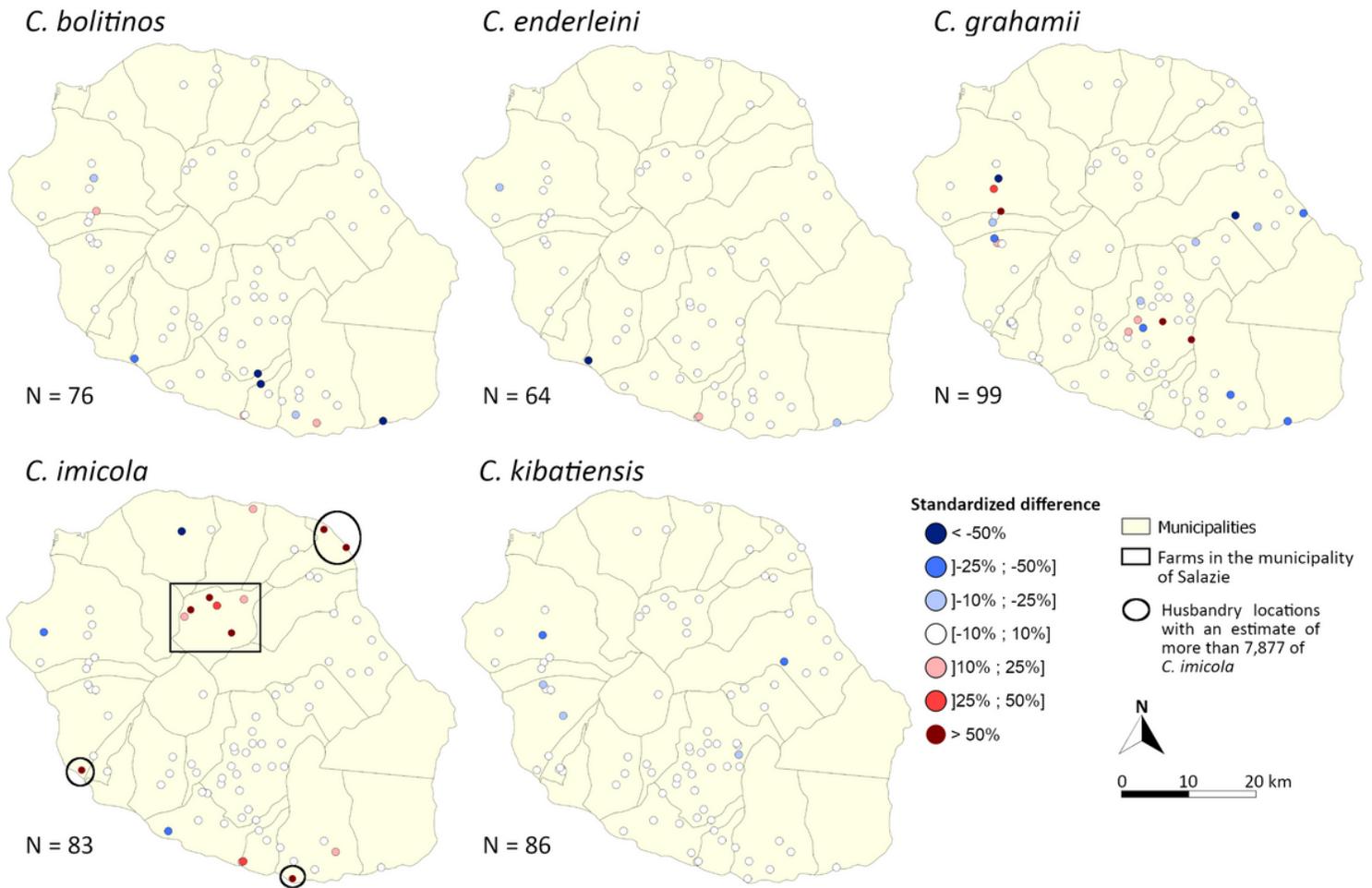


Figure 6

Maps of standardized differences between predictions and observations from the March 2018 sampling campaign Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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