

Environmental Forcing Shapes Regional House Mosquito Synchrony in a Warming Temperate Island

LUIS FERNANDO CHAVES,^{1,2,3} YUKIKO HIGA,⁴ SU HYUN LEE,⁵ JI YEON JEONG,⁵
SANG TAEK HEO,⁵ MIOK KIM,⁵ NOBORU MINAKAWA,⁴ AND KEUN HWA LEE⁵

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ABSTRACT Seasonal changes in the abundance of exothermic organisms can be expected with climate change if warmer temperatures can induce changes in their phenology. Given the increased time for ectothermic organism development at lower temperatures, we asked whether population dynamics of the house mosquito, *Culex pipiens* s.l. (L.) (Diptera: Culicidae), in Jeju-do (South Korea), an island with a gradient of warming temperatures from north to south, showed differences in sensitivity to changes in temperature along the warming gradient. In addition, we asked whether synchrony, that is, the degree of concerted fluctuations in mosquito abundance across locations, was affected by the temperature gradient. We found the association of mosquito abundance with temperature to be delayed by 2 wk in the north when compared with the south. The abundance across all our sampling locations had a flat synchrony profile that could reflect impacts of rainfall and average temperature on the average of all our samples. Finally, our results showed that population synchrony across space can emerge even when abundance is differentially impacted by an exogenous factor across an environmental gradient.

KEY WORDS exogenous factors, phenology, *Culex pipiens*, Jeju-do, urban ecology

Changes in the phenology and distribution of organisms have become environmental concerns in light of climate change (Parmesan 2006). The expansion or contraction of species range in addition to changes in seasonal abundance/activity can result in new and unpredictable ecosystem dynamics. Insect vectors of disease are among the species raising major concerns, given their potential to extend the geographical range of vector-borne disease transmission to areas where disease transmission maybe limited by low temperature constraints on vector abundance and competence to transmit pathogens, or by altering the impact of exogenous environmental factors on vector population dynamics (Koenraadt et al. 2006, Chaves and Koenraadt 2010). For example, in temperate areas, West Nile Virus transmission season length is extremely sensitive to temperature changes, becoming longer at high temperatures (Ruiz et al. 2010; Chuang et al. 2011, 2012). Moreover, other weather factors,

such as rainfall, where recent changes have been associated with global warming (Zhou et al. 2001), can also influence changes in both vector abundance and infection (Chaves et al. 2011a). Hence, interconnectedness of weather variables requires a better understanding of environmental change impacts on the spatio-temporal patterns of insect vector abundance, even when their abundance is not strongly sensitive to temperature changes.

The house mosquito, *Culex pipiens* L. (Diptera: Culicidae) is a cosmopolitan species complex, vector of many arboviruses, for example, West Nile virus (Turell et al. 2001), St. Louis Encephalitis (Shaman et al. 2002), and parasites, for example, bird malaria (Hegner 1929) and lymphatic filariasis (Sasa 1965), whose seasonality (Hayes 1975, Hayes and Downs 1980) and overall population dynamics (Wada and Ofuji 1962, Scorza 1972, Mogi and Okazawa 1990) have been shown to be sensitive to environmental changes, especially in temperate environments (Madder et al. 1983, Barker et al. 2010). The development of the house mosquito, like other ectothermic organisms, is temperature dependent (Janisch 1932, Gu and Novak 2006), a fact that can influence population dynamics (Huey and Berrigan 2001). Furthermore, after warm winters, observations on earlier reproductive activity and earlier bloodfeeding have been recorded for the house mosquito, indicating an elongation of the active (i.e., nondiapausing) season in temperate environments (Reisen et al. 2010). All of these traits make the house mosquito an ideal model organism to test hy-

¹ Graduate School of Environmental Sciences and Global Center of Excellence Program on Integrated Field Environmental Science, Hokkaido University, Hokkai-dō, Sapporo-shi, Kita-ku, Kita 10, Nishi 5 A701, 060-0810, Sapporo, Japan.

² Programa de Investigación en Enfermedades Tropicales, Escuela de Medicina Veterinaria, Universidad Nacional, Apartado Postal 304-3000, Heredia, Costa Rica.

³ Corresponding author, e-mail: lchaves@ees.hokudai.ac.jp.

⁴ Institute of Tropical Medicine (NEKKEN) and Global Center of Excellence Program on Tropical and Emergent Infectious Diseases, Nagasaki University, 852-8523 Nagasaki, Japan.

⁵ Department of Microbiology and Immunology, School of Medicine, Jeju National University, Jeju-si 690-756, South Korea.

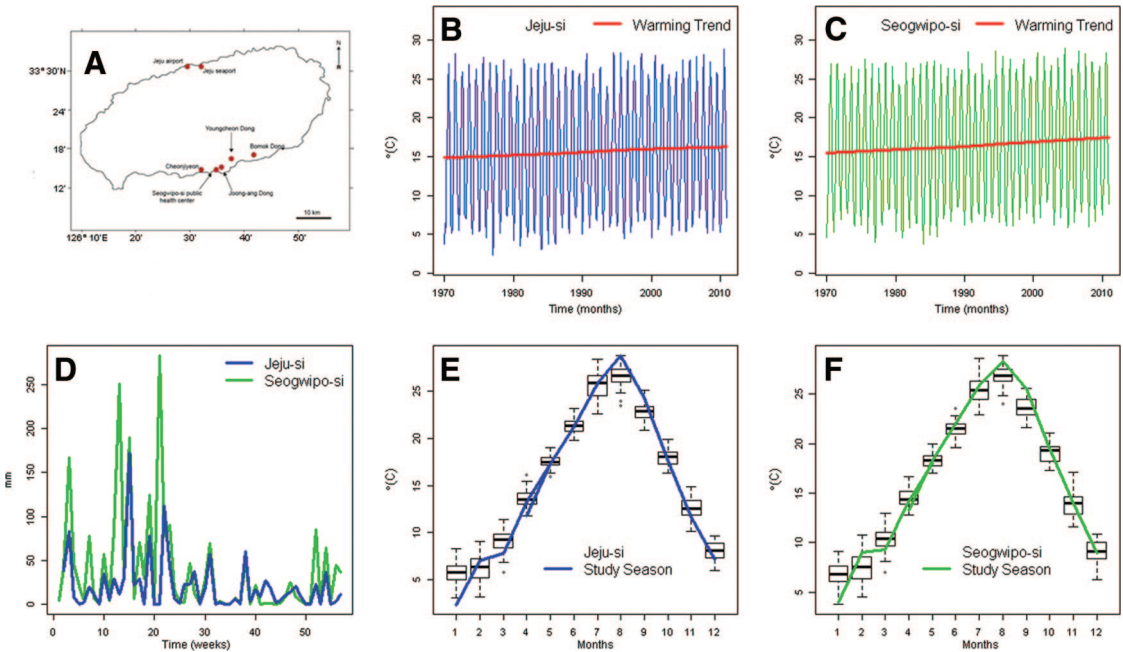


Fig. 1. Study locations and climatic variables: (A) map of the study locations in Jeju-do, (B) monthly Jeju-si temperature, (C) monthly Seogwipo-si temperature, (D) weekly rainfall during the study period, April 2010–April 2011, (E) seasonal temperature profile of Jeju-si, and (F) seasonal temperature profile of Seogwipo-si. Panels B, C, E, and F are based on monthly data from January 1970 to December 2010. In panels B and C temperature trends were obtained with a Lowess regression (Venables and Ripley 2002). Boxplots in panels E and F represent median and quartiles and numbers in the x-axis represent the different months of the year, solid lines represent the data for the studied seasons. (Online figure in color.)

pothesis about the impacts of changing environments on the spatio-temporal patterns of disease vector abundance.

To understand the impacts of the changing environment on a species abundance spatio-temporal patterns, records made across an environmental gradient can provide valuable information on the role of exogenous forcing factors in that species' population dynamics (Royama 1992, Turchin 2003). Jeju-do, an island off the coast of southern South Korea, provides an excellent scenario to do ecological studies of the house mosquito, a dominant vector species (Kim et al. 2005). Jeju-do has a natural temperature gradient between north and south, being the south $\approx 1.2^{\circ}\text{C}$ warmer than the north, a background on which a warming trend of 2°C has been recorded in the last 40 yr. This temperature gradient potentially implies a phenological delay in the emergence and seasonal activity of the house mosquito in the northern half of the island when compared with the warmer south, that is, a longer delay in the association of temperature with mosquito abundance, given the extended developmental time at lower temperatures (Ikemoto and Takai 2000, Gu and Novak 2006). In addition, synchrony patterns, that is, the degree of concerted fluctuations in abundance across locations (Ranta et al. 2006), can be expected to be independent of distance given that local mosquito populations have similar autoregressive structures and are forced in a similar manner by the same environmental factors. Here, we

study the impact of weather fluctuations on population dynamics of the house mosquito in Jeju-do. We ask whether a delay on the impacts of temperature between south and north of the island can be observed given the extended developmental period at colder temperatures, such as those observed in the northern half of Jeju-do. We also ask whether the potential differences in temperature forcing delay can shape a synchrony profile that is independent from the distance between the sampling locations.

Materials and Methods

Mosquito Collection. Mosquitoes were collected weekly from various habitats and locations in Jeju island from April 2010 to April 2011. Figure 1A shows the specific locations where mosquitoes were collected, which included the Jeju Airport, Jeju Seaport, in Jeju-si, the northern half of Jeju-do, and Cheonjiyeon (near Seogwipo-si Seaport), Bomok Dong (a residential area), Seogwipo-si public health center (a residential area), Joong-ang Dong (a park), Young Cheon Dong (a location along the road crossing a forest) in Seogwipo-si, the southern half of Jeju-do. A more elegant selection of sampling sites, for example a transect from North to South, was not feasible because of Jeju-do topography, which has the volcano Halla-san (1,950 m), located in the geographic center of the island, creating an elevational gradient toward the center of the island. Because temperature de-

creases 0.6°C for each additional 100 m of elevation (Chaves and Koenraadt 2010), selection of the sampling sites was restricted to places whose altitude was between 50 and 150 m above sea level to avoid potential confusion in our inferences by the occurrence of an altitudinal temperature gradient. With the exception of Jeju Airport and Jeju Seaport, where sampling effort was duplicated with traps set apart by 300 m, at each place one black light trap was setup over one night each week. Mosquito traps were uniformly set at a height of 1.8 m, from 6 p.m. to 6 a.m., and the same weekday. Mosquitoes were identified using morphological characters described by Tanaka et al. (1979). In Jeju-do the *Culex pipiens* complex consists of the red house mosquito *Culex pipiens pallens* Couquillet and the autogeneus form of *Cx. pipiens*, which cannot be distinguished morphologically (Tanaka et al. 1979, Cheun et al. 2011).

Weather Data. Temperature and rainfall were obtained from the National Institute of Meteorological Research in Jeju-si (north) and Seogwipo-si (south) for the study period. Figure 1B–C show long-term temperature records for Jeju-si and Seogwipo-si, where a similar trend of temperature increase (2°C in the last 40 yr) can be observed on top of the south being slightly above 1°C warmer than the north. Figure 1D shows weekly rainfall records for the study period and Fig. 1E–F show boxplots for seasonal temperature records from the last four decades. Figure 1D–F show the south to be warmer than the north, and the north to be drier than the south.

Statistical Analysis. Time Series Analysis. To analyze the data we first computed an average time series for locations in the north (Fig. 2A), south (Fig. 2B), and for all locations (Fig. 2C). We estimated the averages given the lack of finely grained weather data for each of the locations where we collected the mosquitoes. We then performed an exploratory time series analysis, where we estimated the autocorrelation (ACF) and partial autocorrelation (PACF) functions for the north, south, and all locations average time series. ACF is the correlation profile of a time series with itself for different time lags. PACF is the ACF conditioned on the covariance of the previous lags, that is, PACF is a corrected ACF that provides information on the lag at which a time series is significantly autocorrelated (Shumway and Stoffer 2000). This analysis showed (Fig. 3) the time series to have a decreasing ACF with time and a significant PACF for 1 wk of lag time, which is common for time series that follow a first order autoregressive process, AR(1). We used this information to fit AR(1) models to each one of the time series and used the coefficients from these models to prewhiten the weather time series with the Kalman filter (Chaves and Pascual 2006). Briefly, prewhitening is a process that removes any possibility of considering the bogus correlation that emerges when two time series share a common autocorrelation structure (Chaves et al. 2012). We then used the residuals of the AR(1) model, that is, the residuals from a time series model where any current observation is a function of the observation from the previous time lag, and the pre-

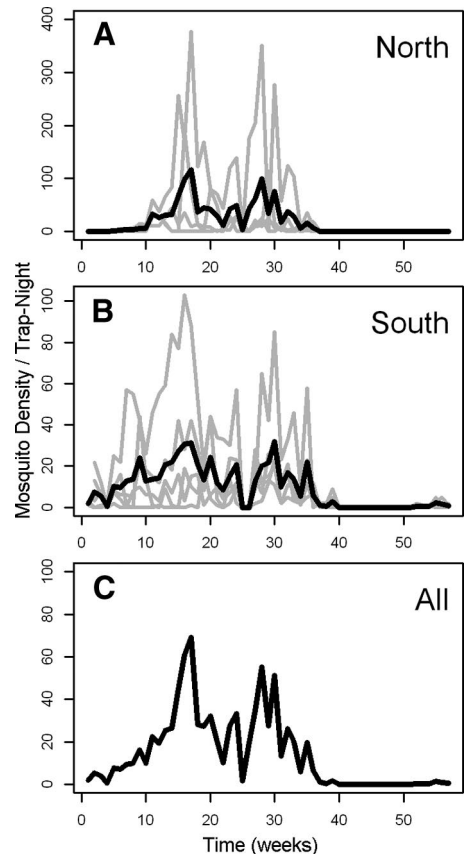


Fig. 2. Mosquito abundance time series (A) north, (B) south, and (C) all. Gray lines indicate original time series, black lines the average.

whitened weather variables time series to compute their cross correlation function (CCF; Fig. 4), which, in a sense, is equivalent to a PACF between time series of different variables. We then selected the lags with the highest significant cross-correlation to fit AR(1) models with co-variates, where we began by fitting a full model with all the significant covariates, and then proceeded with a simplification using backward elimination, that is, removing those variables uniquely associated with models having the worst fit, based on the Akaike Information Criterion (AIC), an index that allows the selection of model based on both the fit, that is, the likelihood (that is a probability based measure of model goodness-of-fit), and the number of parameters (Venables and Ripley 2002). In these models the covariates where de-meant to ease the interpretation of model intercept as the average mosquito abundance per trap/night (Chaves and Kitron 2011). Finally, time series models can be described by the following general equation:

$$Y_{t+1} = \mu + \phi(Y_t - \mu) + \beta_{\text{exo}}(\text{exo}) + \varepsilon_t \quad [1]$$

Where Y is mosquito abundance, μ is the average mosquito abundance in the time series, ϕ is the AR(1) coefficient, β_{exo} is the coefficient for any of the

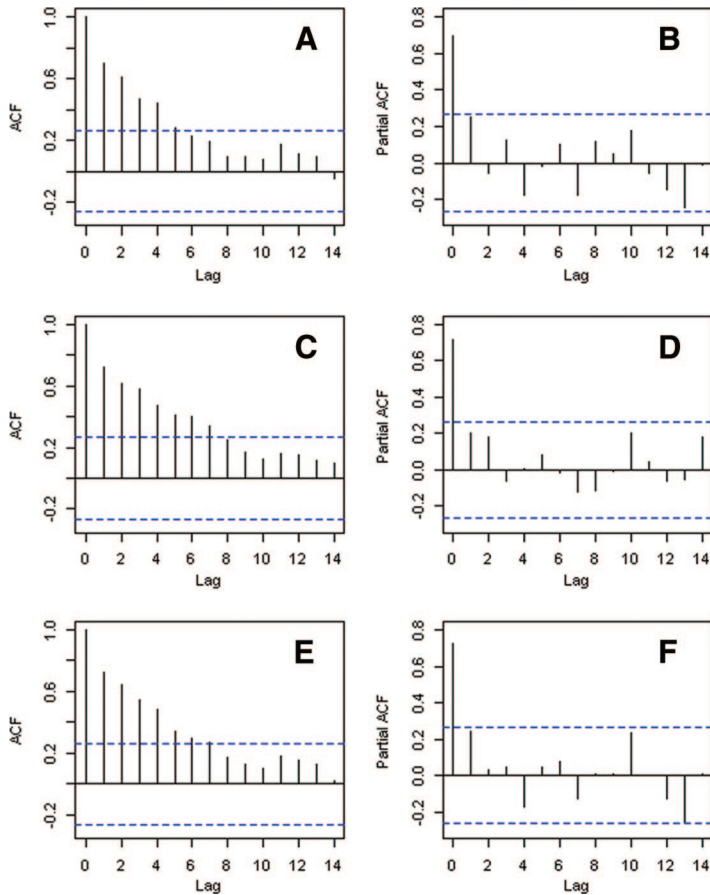


Fig. 3. Autocorrelation, ACF, and partial autocorrelation functions, PACF. North locations average time series (A) ACF (B) PACF. South locations average time series (C) ACF (D) PACF. All populations average time series (E) ACF (F) PACF. Dashed lines are the 95% point-wise CIs of the autocorrelation in a time series that can be expected by random. (Online figure in color.)

weather covariates(exo): Rainfall (R), Maximum (Tmax), Minimum (Tmin), and Average (T) temperature and $\varepsilon_t \sim N(0, \sigma^2)$, is a normally distributed error with variance σ^2 .

Synchrony Analysis. To study synchrony, that is, the degree of concerted fluctuation in abundance across all our sampled locations, we used the spline correlogram (Bjørnstad and Falck 2001). This technique uses smoothing splines to generate a functional correlogram, that is, an assumption free and smooth function depicting spatial autocorrelation, among several time series, as function of the distance between locations. This technique, like other methods for synchrony analysis, assumes that time series reflect fluctuation patterns in a population measured at different locations using a standardized sampling method, but the analysis is independent of the studied variables magnitude, like any simpler correlation estimate between two variables (Ranta et al. 2006). For inference we generated a null distribution from the estimator by computing spline correlograms from random time series. The random time series were constructed by sampling without replacement the original time series.

This procedure was repeated 1,000 times to extract the 2.5 and 97.5% quantiles of the null distribution, which correspond to the 95% confidence envelope of the spline correlogram (Bjørnstad and Falck 2001). For smoothing the mosquito abundance time series we used three degrees of freedom (edf).

Results

Patterns of Mosquito Abundance. Figure 2 shows the time series for each sampling location, the average for the locations in the north, that is, those in Jeju-si (Fig. 2A), the locations in the south, that is, locations in Seogwipo-si (Fig. 2B), and all the locations (Fig. 2C). The north populations presented relatively larger fluctuations in size than those in the south. In total, 7,198 individuals of *Cx. pipiens* s.l. were collected over 495 trap/nights, near half of the individuals were collected at Jeju-si Airport (3,491 over 105 trap/nights) and Bomok Dong had the lowest number of collected mosquitoes (164 over 57/trap nights). We believe most of the mosquitoes we caught were *Cx. pipiens pallens* provided the null abundance of *Cx. pipiens* s.l.

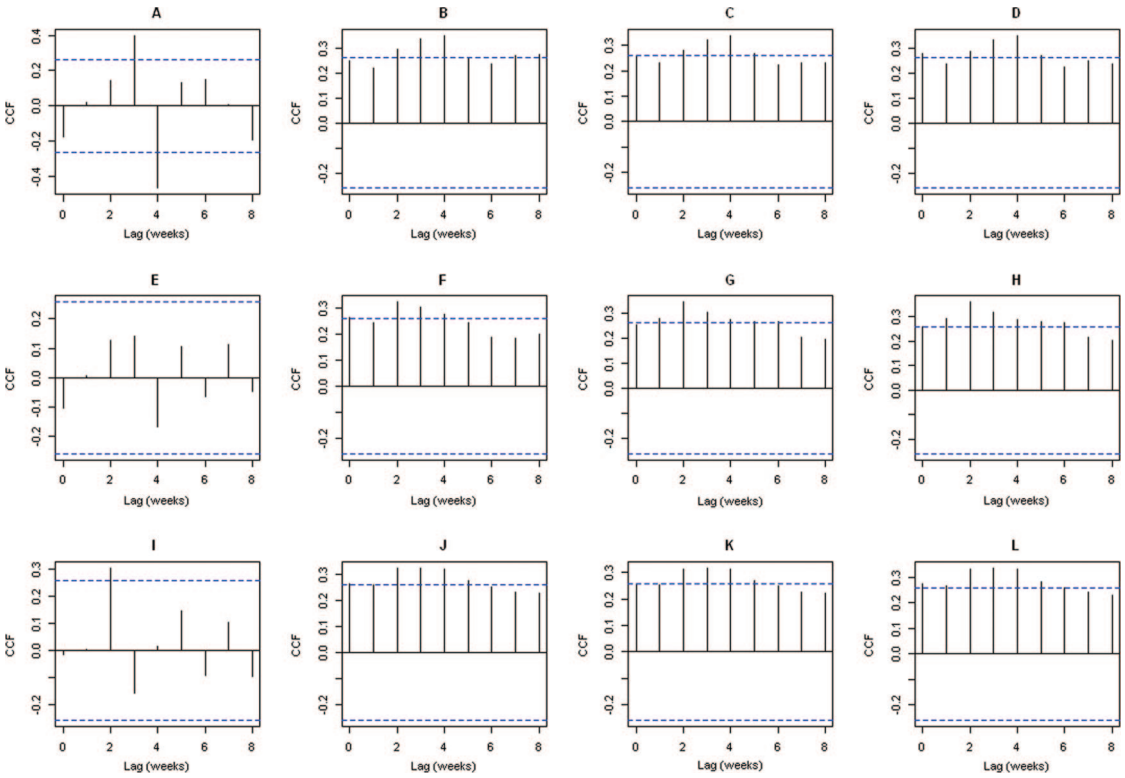


Fig. 4. Cross correlation functions, CCF. North locations average time series with (A) rainfall, (B) average temperature, (C) maximum temperature, and (D) minimum temperature. South locations average time series with (E) rainfall, (F) average temperature, (G) maximum temperature, and (H) minimum temperature. All locations average time series with (I) rainfall, (J) average temperature, (K) maximum temperature, and (L) minimum temperature. Dashed lines are the 95% point-wise CIs of the cross-correlation between two time series that can be expected by random. (Online figure in color.)

in the traps from December to February, months when the autogenous *Cx. pipiens* form (sometimes referred as *Cx. pipiens molestus*) is active at similar latitudes in Japan (Spielman 1971). However, to acknowledge the limitations in species identification we will refer to *Culex pipiens* s.l. through the manuscript.

Time Series Analysis. The process of model selection revealed that population dynamics in the northern locations were sensitive to changes in rainfall, maximum temperature, and average temperature with

a delay of 4 wk (Supp. Table 1 [online only]). Dynamics in the south were sensitive to changes in minimum temperature, with a lag of only 2 wk (Supp. Table 2 [online only]). The average population was sensitive to changes in rainfall and temperature with a 2 wk lag (Supp. Table 3 [online only]). Interestingly for temperature, in all the three cases, correlations were significant between 2–4 wk of lag (Fig. 4). Parameter estimates for the best models are shown in Table 1. In general, models had a good fit with >60%

Table 1. Parameter estimates for the best autoregressive time series models fitted to the avg populations from northern, southern, and all (i.e., northern and southern) locations

Parameter	Lag	Estimate (\pm SE)		
		Northern	Southern	All
Intercept ($\hat{\mu}$)	—	20.37 \pm 3.67	9.69 \pm 1.48	14.41 \pm 2.36
Autoregressive ($\hat{\phi}$)	1	0.42 \pm 0.13	0.44 \pm 0.12	0.41 \pm 0.13
Minimum temperature ($\hat{\beta}_{Tmin}$)	2	NBM ^a	0.89 \pm 0.18	NBM
Maximum temperature ($\hat{\beta}_{Tmax}$)	4	-17.55 \pm 7.62	NBM	NBM
Average temperature ($\hat{\beta}_T$)	4	20.64 \pm 7.74	NBM	NBM
Rainfall ($\hat{\beta}_R$)	2	NBM	NBM	1.54 \pm 0.31
	4	-0.26 \pm 0.06	NBM	NBM
Error variance ($\hat{\sigma}^2$)	—	NBM	NBM	0.070 \pm 0.030
		244	37	105
R^2	—	0.70	0.61	0.65

^a NBM indicates parameters not present in the best model for the avg pop of a given set of locations.

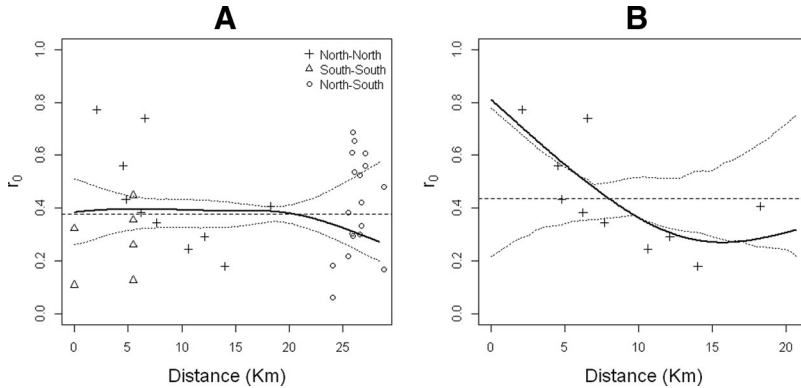


Fig. 5. Synchrony analysis. Mosquito abundance time series correlogram at lag 0, r_0 , as function of the two-dimensional distance (2D) between: (A) all localities, symbols indicate r_0 estimates for northern (north–north), southern (south–south), and all (north–south) populations, see legend for further details (B) southern locations. Dashed line is for the regional synchrony, dotted lines indicate the 95% confidence envelope for the smoothed correlation function, solid line, obtained with 1,000 data permutations.

of the variance explained by the models. Average mosquito density per trap night was two-times larger in the north when compared with the south (≈ 20 vs. ≈ 10 individuals per trap night) and the variability, measured by the error variance, was six-fold larger in the north when compared with the south (≈ 240 vs. ≈ 40), meaning that although populations where, on average, larger in the north they also had a larger variability, something that can be appreciated in Fig. 2. In the north, south, and the average population from all locations the autoregressive coefficient was ≈ 0.4 , meaning that in both north and south populations follow similar autoregressive dynamics to those of the average population, a necessary condition for the emergence of synchrony. Regarding the forcing, that is, the impact of exogenous weather factors on the dynamics, it is interesting to see (Table 1) that rainfall was primarily important in the north. In the north maximum temperature was negatively associated with the dynamics while average temperature was positively associated with mosquito abundance, probably indicating that extremely hot temperatures can be detrimental for mosquito abundance, yet abundance increases with overall temperature, highlighting a possible nonlinear response to temperature. In the southern locations minimum temperature was positively associated with mosquito abundance. In addition, the maximum association lag between temperature and mosquito abundance was delayed by 2 wk in the north (4 wk of lag) when compared with the south (2 wk of lag). The average population from all locations was positively associated with both rainfall and average temperature with 2 wk of lag.

Synchrony. Results from the spline correlogram can be observed in Fig. 5A. The smoothed cross-correlation between all the sampled locations showed that association between the sampled locations did not decrease with distance being constant and not significantly different from the estimated regional synchrony. However, in the southern locations the degree of association between the time series decreased with

distance (Fig. 5A), in a fashion that was significantly different from the estimated regional synchrony (Fig. 5B), with the association between abundance at different locations being significantly larger than the regional synchrony at short distances, and smaller than the regional synchrony at long distances.

Discussion

Our time series analysis showed the association between temperature and mosquito abundance to be delayed by 2 wk in the north of the island when compared with the south. This can be related with the longer developmental time of *Cx. pipiens* s.l. at lower temperatures, a fact documented for aquatic stages in the laboratory (Kramer 1915, De Boissesson 1930, Tekle 1960, Shelton 1973) and controlled field conditions (Gu and Novak 2006, Chaves et al. 2011b). Similar delayed correlation patterns have been observed in the field, both for larvae (Hayes and Hsi 1975, Madder et al. 1983) and adults (Hayes 1975, Hayes and Downs 1980, O'Meara and Evans 1983). Mathematical models have shown that this dependence can be mechanistically explained by the dependence of enzymatic activity on temperature (Ahumada et al. 2004, Gong et al. 2011), a plausible mechanism in accordance with long-term records that have shown the seasonality of this mosquito species complex to be associated with relatively dry and hot environmental conditions (Spielman 2001, Barker et al. 2010). Moreover, further experimental studies have shown that development of the house mosquito is not sensitive to photoperiod, that is, daylength (Mogi 1992), or population geographical origin along a latitudinal gradient (Mori et al. 1988). In that sense, our results are in accordance with previous observations, yet to the best of our knowledge, we are the first to use time series analysis to show a difference in the delay of association between mosquito abundance and temperature. We consider that observed differences between the north and south in the sensitivity to temperature can reflect

a nonlinear response to temperature in the north, where extremely hot temperatures can be detrimental for mosquito abundance, yet the abundance increases with overall temperature (Chaves et al. 2012), and the sensitivity to low temperatures in the south maybe related to the growth of a population in an environment where temperature is never hot enough to become detrimental, thus being primarily sensible to be above the threshold for development (Gu and Novak 2006, Wang et al. 2011).

Although there was a difference in the delay of high temperature impacts on mosquito population dynamics between north and south, populations presented a flat synchrony profile, suggesting that differential delays on the impacts of temperature on mosquito development are not strong enough to produce a phase difference between locations, a.k.a., asynchrony at the regional level, which is measured by a spline correlogram that is not independent of the distance between the sampled locations (Ranta et al. 2006). This can be related to the hypothesis that populations of mosquito can be synchronized by environmental exogenous forcing (Ranta et al. 2006). Interestingly, the dynamics of the average population for the whole island was sensitive to both rainfall and temperature making plausible an island wide synchronization of mosquito abundance via a rainfall associated reproductive phase locking (Shaman and Day 2007). In addition, synchrony does not necessarily catch phenological differences, but focus on the correlation of the whole time series, thus, as long as abundance across locations have similar fluctuations during most of the season, synchrony can be expected to be high even when there are phenological differences across sampled locations, as suggested by Fig. 2B, where southern populations have increased abundances earlier in the studied season. However, data limitations, especially the lack of finely grained weather time series precluded a more detailed mechanistic analysis on the role that weather can have on synchronized house mosquito abundance across Jeju-do. Multiple mechanisms seem to be ruling synchrony patterns at the more local scale. In the north synchrony was flat, suggesting an environmentally mediated mechanism for synchrony. By contrast, in the south synchrony decreased with distance, suggesting a role for mosquito dispersal, not at the level of a moving individual but in the sense of a population diffusing across the landscape shaping the local patterns of synchrony in the south (Ranta et al. 2006). We believe this might be the case given the association of *Cx. pipiens* s.l. with degraded aquatic environments associated with human activity, such as polluted water bodies (Britton 1914, Wada and Ofuji 1962, Kumada et al. 1972, Makiya 1973) or septic tanks (Mackay et al. 2009, Burke et al. 2010) including *Cx. pipiens* ability to oviposit (Chaves et al. 2009, Chaves and Kitron 2011, Nguyen et al. 2012) and colonize environmentally degraded urban creeks (Mogi and Okazawa 1990, Mogi et al. 1995, Mogi and Sota 1996, Calhoun et al. 2007). In fact, the closest locations in the south are located inside the urban areas of Seogwipo-si, the biggest city in the

south of Jeju-do, a place with many suitable larval habitats for the house mosquito (Kim et al. 2005, Cheun et al. 2011). The farther away locations in the south of Jeju-do where Joong-ang Dong and Young cheon Dong, which are outside Seogwipo-si and relatively far away from large human settlements and potential larval habitats to maintain viable populations year round, either by the superior environmental quality of water bodies (Mogi et al. 1995, Mogi and Sota 1996), the lack of suitable places for overwintering (Hayes 1973) or potential interactions with other mosquito species (Chaves et al. 2011a).

Finally, our results showed the house mosquito to have a delayed sensitivity to the impacts of temperature at lower environmental temperatures (north of Jeju-do) and that population synchrony across space can emerge even when local populations are differentially impacted by the same exogenous factors. In light of global warming our results suggest that season length for insect pests could not only become longer in temperate areas, but pest abundance might more closely track environmental fluctuations as the environment becomes hotter, thus making necessary the development of new control strategies that consider these dynamical aspects of insect pest population dynamics for an effective control.

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