

## Mosquito Species (Diptera: Culicidae) Persistence and Synchrony Across an Urban Altitudinal Gradient

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### Abstract

Patterns of mosquito spatial persistence and temporal presence, as well as synchrony, i.e., the degree of concerted fluctuations in abundance, have been scarcely studied at finely grained spatial scales and over altitudinal gradients. Here, we present a spatial persistence, temporal presence, and synchrony analysis of four common mosquito species across the altitudinal gradient of Mt. Konpira in Nagasaki, Japan. We found that *Aedes albopictus* (Skuse) was more frequently found at the mountain base. In contrast, *Aedes japonicus* (Theobald) and *Aedes flavopictus* Yamada were common higher in the mountain, while *Armigeres subalbatus* (Coquillett) was uniformly present across the mountain, yet less frequently than the other species during the studied period. Our analysis showed that these spatial heterogeneities were associated with differences in landscape and microclimatic elements of Mt. Konpira. Temporally we found that presence across sampling locations was mainly synchronous across the four species and positively associated with rainfall and temperature. With the exception of *Ae. albopictus*, where no significant synchrony was observed, mosquito species mainly showed flat synchrony profiles in Mt. Konpira when looking at the geographic (2-D) distance between their sampling locations. By contrast, when synchrony was studied across altitude, it was observed that *Ae. flavopictus* tracked the temperature synchrony pattern, decreasing its synchrony with the separation in altitude between sampling locations. Finally, our results suggest that differences in mosquito species persistence, temporal presence, and synchrony might be useful to understand the entomological risk of vector-borne disease transmission in urban landscapes.

**Key words:** Asian tiger mosquito, Asian bush mosquito, *Aedes flavopictus*, entomological risk, urban land use

Mosquitoes (Diptera: Culicidae) are common insects in urban landscapes, whose bites are a common source of nuisance across the globe (Moriya 1974, Gleiser and Zalazar 2010, Medeiros-Sousa et al. 2015). Mosquitoes are also important vectors of pathogens affecting humans, wildlife, and domestic animals in urban areas (Bradley and Altizer 2007) where blood resources, especially from human hosts, get clustered, facilitating the transmission of pathogens that circulate between humans and mosquitoes, but also for zoonotic pathogens, i.e., with vertebrate hosts other than humans that also reside in cities (Edman 1988, Weaver and Reisen 2010, Hamer et al. 2012). Some aspects of mosquito ecology in urban environments have been studied in detail, for example, the recruitment of adult mosquitoes from water storage containers (Schneider et al. 2004, Harrington et al. 2008, Andreadis and Wolfe 2010), their habitat selection and development as related to waste water management (Chaves et al. 2009, 2011a), oviposition in relation to hourly (Reddy et al. 2007), daily (Chaves and Kitron 2011), and seasonal weather changes (Nguyen et al. 2012), mosquito species diversity

(Chaves et al. 2011b, Hoshi et al. 2014, Medeiros-Sousa et al. 2015), and bloodfeeding (Scott et al. 2000, Hamer et al. 2009, Chaves et al. 2010).

A topic that has been less studied is the synchrony of mosquitoes in urban environments, which is of special interest, as it might drive concerted epidemics of vector-borne diseases (Chaves et al. 2012). We have previously studied synchrony in the abundance of the house mosquito, *Culex pipiens* L., at a regional scale, i.e., with mosquitoes sampled in locations separated a few kilometers apart, and found the dynamics to show a flat synchrony that could reflect an uniform impact of rainfall on the activity and adult recruitment patterns of this mosquito species (Chaves et al. 2013). Nevertheless, in our previous study mosquito sampling was restricted to sites with similar altitude, restricting any potential inference about the role that temperature might play on the synchrony, beyond what we observed in the phenology, which started later in the year at northern colder latitudes for the house mosquito (Chaves et al. 2013). Unlike latitudinal gradients, altitudinal gradients offer the possibility of studying changes in

populations across environmental gradients whose physical separation does not need to be as large as the one where latitudinal changes in the environment are observed (Stevens 1992, Hodkinson 2005). In fact, for mosquitoes some studies have reported differences in species abundance across altitudinal gradients (Zea Iriarte et al. 1991, Eisen et al. 2008, Chaves et al. 2015, Chaves 2016), but have looked at mosquito cumulative abundance through seasons, not paying attention to the persistence of populations, i.e., how often are individuals from a given species present at fixed locations in a landscape (Dey and Joshi 2006), or temporally looking at how widespread, or present, are they across a landscape (Hanski 1999). These factors are important to understand the spatio-temporal dynamics of animal species, as they might provide insights into environmental factors that could affect the dispersal of a species and its metapopulation dynamics (Levins 1969, Hanski 1999).

The relative large scale of our previous approach to study synchrony in mosquitoes (Chaves et al. 2013) also had the limitation of not allowing to understand any impact of dispersal on mosquito population synchrony (Ranta et al. 2006). Mosquito dispersal commonly occurs within the scale of a few hundred meters, commonly below 500 m and is concentrated below 100 m (Harrington et al. 2005, Guerra et al. 2014, Hamer et al. 2014), a scale not considered in our previous study (Chaves et al. 2013) and which is critical to understand the synchrony of any animal species, especially regarding the test of hypothesis about the impact of dispersal on synchrony. Model simulations have repeatedly shown that synchrony initially decreases with distance when dispersal plays a role in synchrony (Ranta et al. 2006). Thus, to both investigate if mosquito population synchrony is partially shaped by mosquito dispersal and to test the hypothesis that mosquito spatial persistence and temporal presence might be associated with environmental differences detectable across a finely grained altitudinal gradient, here, we present the results from a season-long study on the persistence and synchrony patterns of mosquitoes across an urban altitudinal gradient.

## Materials and Methods

### Study Site and Mosquito Sampling

Our study took place in Nagasaki, a city in Kyushu island, western Japan (Fig. 1a). Nagasaki is in the southwestern tip of Nagasaki prefecture (Fig. 1b), and the landscape is highly urbanized, with >440,000 residents and a density of 1,100 people per km<sup>2</sup> according to the 2009 census (Statistics Bureau, Ministry of Internal Affairs and Communications of Japan, <http://www.stat.go.jp/index.htm>). Nevertheless, several mountains surrounding the human settlements host primary and secondary forests (Fig. 1b). Mt. Konpira is a mountain in the eastern side of Nagasaki city, mainly covered with natural vegetation (Fig. 1c). At the top of Mt. Konpira there is a Shrine which is frequently visited by the residents of Nagasaki city. Mt. Konpira comprises an altitudinal gradient (320 m at the highest point we sampled), where we chose 27 trees, distributed in three transects, to sample adult mosquitoes (Fig. 1d). Trees were chosen as fixed reference points to ease the systematic sampling of mosquitoes. Mosquitoes were biweekly sampled between May 18th and November 15th of 2014. For the sampling we used sweep nets around each one of the focal trees, where the order of the sampling locations was randomized each time mosquitoes were sampled, the time for sweeping time standardized to a total of 5 min (2 min sweeping, 1 min pause, 2 min sweeping), and the sweeping time was seasonally adjusted to start with sunrise. Further details about the sampling and mosquito

identification have been already presented elsewhere (Chaves et al. 2015, Chaves 2016). For this study we considered the four most common species that we caught during the studied season: *Aedes flavopictus* Yamada, with 1,118 individuals, the Asian bush mosquito *Aedes japonicus* (Theobald), 328 individuals, the Asian tiger mosquito *Aedes albopictus* (Skuse), 190 individuals, and *Armigeres subalbatus* (Coquillett), 114 individuals (Chaves et al. 2015, Chaves 2016). All these four species are medically important, as *Ae. albopictus* is a major dengue virus, Zika virus, and chikungunya virus vector (Weaver and Reisen 2010). *Aedes flavopictus* is a competent dengue virus vector (Eshita et al. 1982). *Aedes japonicus* is a competent Japanese Encephalitis Virus (JEV) and West Nile Virus vector, while *Ar. subalbatus* is an important vector of worms causing lymphatic filariasis and JEV in areas without rice fields (Chaves et al. 2015, Chaves 2016).

### Weather and Landscape Data

We recorded the air temperature and relative humidity with a portable thermohygrometer (model O-230, Dretec Co., Saitama, Japan) around focal trees when sampling adult mosquitoes, during each mosquito sampling session. Daily rainfall records for Nagasaki city (May 1st to December 1st, 2014) were obtained from the Japanese Meteorological Agency. Rainfall data were accumulated for the 14 d prior to the mosquito sampling, and only employed in the subsequent temporal analyses.

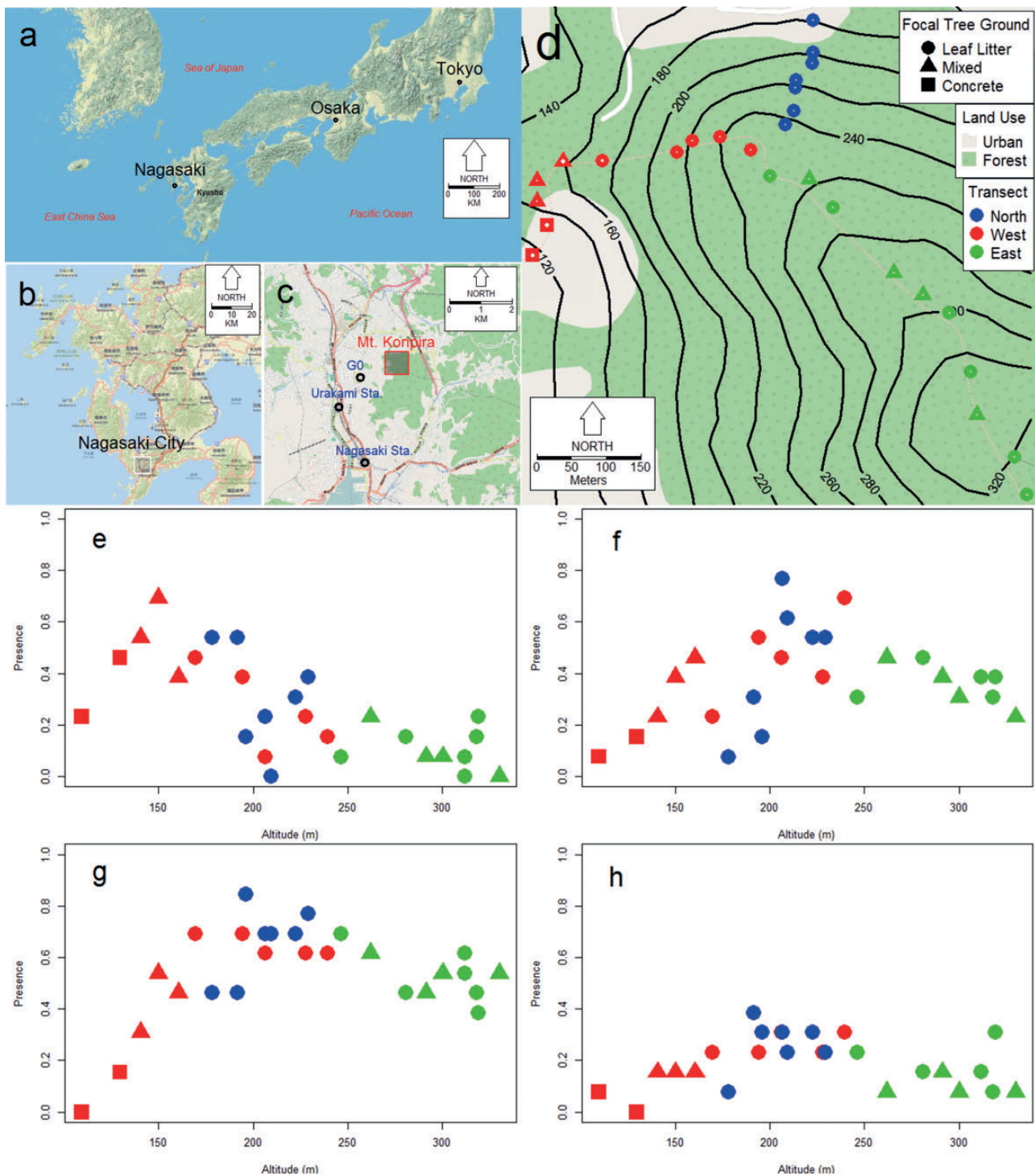
We estimated several components of the landscape around each of the reference trees, including a ground index that measured the dominant ground type (concrete or leaf litter) and the canopy openness around each one of the focal trees. We also used a digital elevation model to estimate the following landscape features: slope, aspect, and roughness. Further details about data collection and the estimation and processing of weather and landscape variables have been presented elsewhere (Chaves et al. 2015, Chaves 2016).

### Statistical Analysis

The spatial patterns of seasonal persistence for each mosquito species were studied using Poisson generalized linear models (Faraway 2006) that considered as independent variable the number of times a given mosquito species was sampled at a given location during our study season. An initial full model for each species included as covariates: an index for ground composition; the landscape slope, aspect, and roughness; the average and standard deviation of the canopy openness; as well as the season mean, SD, and kurtosis of relative humidity and air temperature at each sampling location.

The temporal patterns of mosquito species presence were studied using time series models (Shumway and Stoffer 2011). For these models we built a time series for each species where observations corresponded to the proportion of locations where we sampled a given species during each sampling session, of the studied season. Covariates in the initial full time series model included: cumulative biweekly rainfall, average temperature, and relative humidity across the sampling locations. To select the lag for each covariate, we employed a cross correlation function, i.e., a graphical depiction of the correlation between two temporal variables (Shumway and Stoffer 2011).

Both spatial and time series “full” models were simplified by the minimization of the Akaike information criterion (AIC) through a process of backward elimination. In this method, through iterative steps, a covariate is removed if a model without it minimizes the AIC when compared with other models having the same number of parameters, until the AIC does not further decrease its value



**Fig. 1.** Study site and seasonal mosquito persistence, i.e., proportion of times a mosquito species was found at a given sampling location through the study season. (a) Nagasaki is located in Kyushu island, West of Osaka and Tokyo, in Western Japan. (b) Nagasaki city is located in the southwest of Nagasaki Prefecture, Western Kyushu. The highlighted area is Nagasaki City. (c) Mt. Konpira is east of the Ground Zero (GO) of the 1945 Atomic Bomb detonation. The study site on Mt. Konpira is highlighted in red in the map. (d) Sampling locations at Mt. Konpira. The contour lines are isoclines for altitude measured in m. Mosquito species persistence during the studied season—(e) *Ae. albopictus*, (f) *Ae. japonicus*, (g) *Ae. flavopictus*, and (h) *Ar. subalbatus*. Symbols indicate the dominant ground type and color the studied transects, ground colors the land use, see inset legends in (d) for details.

(Kuhn and Johnson 2013). Akaike information criterion is a metric that optimizes the trade-off between data fitting and the number of parameters in a statistical model (Faraway 2004). To ensure the validity of our inferences, we tested assumptions about spatial and

temporal independence in the residuals of the models selected as best. More specifically, for spatial models we estimated the Moran's I spatial autocorrelation index, a test whose null hypothesis is that spatial observations are independent (Brunsdon and Comber 2015).

For temporal models, we inspected the Autocorrelation Function of the residuals, which shows the temporal correlation of a time series with itself through different time lags, and which is expected to be nonstatistically significant for time lags  $> 0$  (Shumway and Stoffer 2011).

For the synchrony analysis, we proceeded in a two-way fashion. First, we examined the cross correlation functions between all possible pairs of mosquito species presence time series, to determine if the ubiquity of different mosquito species across the landscape were correlated. Then we also used the information from the cross correlation function between the presence time series of each mosquito species and rainfall, relative humidity, and temperature, to evaluate the role of these factors at explaining the synchronicity in the persistence of species across the landscape. Second, we estimated a correlogram (Ranta et al. 2006, Gouhier and Guichard 2014). The correlogram depicts the correlation between a set of time series as function of distance (Ranta et al. 2006). We estimated a Mantel correlogram for the abundance time series of each mosquito species (Gouhier and Guichard 2014). Inferences for the correlogram were based in a Monte Carlo randomization test, where the correlogram from the original data is tested against the distribution of correlograms that is generated by randomly shuffling the distance between the locations where the observations included in the time series were located (Bjørnstad and Falck 2001). For the inference, the null hypothesis is that synchrony at a given distance is equal to the average synchrony in the landscape, unless the estimate for a given distance is more extreme (Gouhier and Guichard 2014). Studies on time series data generated by models also suggest that synchrony should be higher in locations separated by a distance below the average dispersal distance of a species (Ranta et al. 2006). In general, mosquito dispersal mainly occurs below 100 m for mosquito taxa in the *Aedes* spp. genus (Guerra et al. 2014), a pattern illustrated by studies on *Ae. albopictus* dispersal in Nagasaki (Takagi et al. 1995c; Takagi et al. 1995a, b; Higa et al. 2000), the only species we studied where dispersal has been studied in detail. Thus, for correlogram

interpretation we will consider 100 m as a threshold for mosquito dispersal, and will assume dispersal estimates from the *Aedes* spp. genus extend to *Ar. subalbatus* given its phylogenetic relatedness to *Aedes* spp. mosquitoes (Wilkerson et al. 2015). We estimated correlograms that considered the geographic (2-D) distance between sampling locations and also their distance in altitude.

## Results

Panels e, f, g, and h in Fig. 1, respectively, show the persistence patterns of *Ae. albopictus*, *Ae. japonicus*, *Ae. flavopictus*, and *Ar. subalbatus* across the altitudinal gradient of Mt. Konpira. It can be observed that *Ae. albopictus* (Fig. 1e) was mainly common at the base of the mountain, while *Ae. japonicus* (Fig. 1f) and *Ae. flavopictus* (Fig. 1g) were more common at higher altitudes. By contrast, *Ar. subalbatus* (Fig. 1h) was present across the altitudinal gradient of Mt. Konpira, yet it was less persistent than the other species. The analysis of factors associated with the persistence of these mosquitoes is shown in Table 1. For *Ar. subalbatus* the ground index was the most important factor explaining its persistence in the landscape, the positive coefficient indicating that this species was more likely to persist in areas where leaf litter dominated the ground. For, both *Ae. japonicus* and *Ae. flavopictus* there was a negative association with mean temperature, indicating these species were more likely to persist in cooler (higher) locations. The Asian tiger mosquito, *Ae. albopictus*, on the other hand, had a negative association with temperature kurtosis, meaning that it was more likely to persist in places where temperature was more platykurtic, i.e., sampling locations more likely to be highly variable around the average conditions. *Aedes albopictus* persistence was also positively associated with the landscape slope. In all the models selected as best, there was no indication of significant remaining spatial autocorrelation, since for all species the Moran's I index of residual spatial autocorrelation was not significant ( $P > 0.05$ ), and all the models

**Table 1.** Parameter estimates for landscape variables associated with the seasonal persistence of medically important mosquitoes sampled by sweeping nets in 2014 at Mt. Konpira, Nagasaki, Japan

Parameter	Species	Estimate	S.E.	<i>t</i>	<i>P</i> -value
Intercept	<i>Ae. albopictus</i>	4.299	0.827	5.200	$<1e-5^*$
	<i>Ae. japonicus</i>	9.833	2.652	3.707	0.000209*
	<i>Ae. flavopictus</i>	9.492	2.143	4.429	$<1e-5^*$
	<i>Ar. subalbatus</i>	0.839	0.132	6.356	$<1e-5^*$
Kurtosis of Temperature	<i>Ae. albopictus</i>	-1.574	0.300	-5.243	$<1e-5^*$
Mean Temperature	<i>Ae. japonicus</i>	-0.403	0.130	-3.089	0.00201*
	<i>Ae. flavopictus</i>	-0.369	0.105	-3.500	0.000465*
Slope	<i>Ae. albopictus</i>	0.042	0.017	2.404	0.0162*
Ground Index	<i>Ar. subalbatus</i>	0.094	0.037	2.550	0.0108*
Moran's I	<i>Ae. albopictus</i>	-0.334	-	-	0.991
	<i>Ae. japonicus</i>	0.052	-	-	0.243
	<i>Ae. flavopictus</i>	-0.033	-	-	0.458
	<i>Ar. subalbatus</i>	0.062	-	-	0.216
$\Delta AIC_{FM}$	<i>Ae. albopictus</i>	14.91 <sup>a</sup>	-	-	-
	<i>Ae. japonicus</i>	21.80 <sup>a</sup>	-	-	-
	<i>Ae. flavopictus</i>	18.91 <sup>a</sup>	-	-	-
	<i>Ar. subalbatus</i>	19.53 <sup>a</sup>	-	-	-

Estimates come from the best Poisson Generalized Linear Models for each species, selected by a mixed forward and backward process of model selection. Moran's I indicates estimates for Moran's index of spatial autocorrelation estimated from model residuals through a 1000 replicates Monte Carlo.  $\Delta AIC_{FM}$  is the AIC difference between a full model that incorporated all landscape and weather covariates described in the methods section.

\*Statistically significant ( $P < 0.05$ ).

<sup>a</sup>The best model reduced the likelihood and number of parameters.

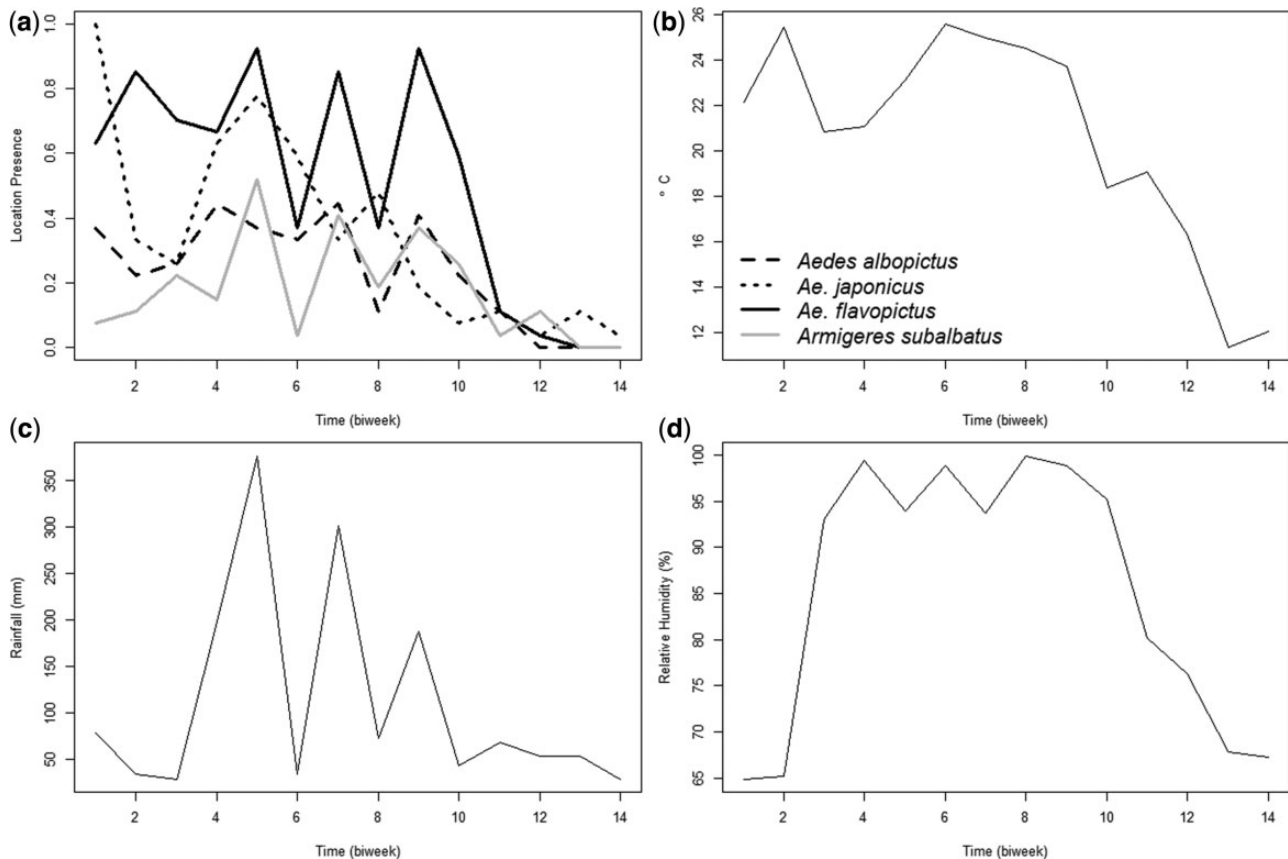
significantly decreased the AIC when compared with the full models for each species (Table 1).

Figure 2 shows the time series of mosquito species presence and weather variables. It can be seen that all four mosquito species were more likely to be widely present across the landscape (Fig. 2a) when temperature was high (Fig. 2b), with peaks coinciding with those of rainfall (Fig. 2c) and high relative humidity (Fig. 2d). A more formal cross correlation function analysis (Fig. 3) showed that *Ae. albopictus* temporal presence across the landscape was synchronous, i.e., significantly associated at lag 0, with *Ae. japonicus* (Fig. 3a), *Ae. flavopictus* (Fig. 3b), and *Ar. subalbatus* (Fig. 3c), that *Ae. japonicus* presence peaks preceded by one biweek the peaks in *Ae. flavopictus* (Fig. 3d) and two months (4 biweeks) the peaks of *Ar. subalbatus* (Fig. 3e), while *Ae. flavopictus* and *Ar. subalbatus* had a synchronous presence (Fig. 3f). Also, a positive association between presence and relative humidity was only statistically significant ( $P < 0.05$ ) for *Ae. albopictus* and *Ar. subalbatus* (Fig. 3g). Presence was positively and significantly associated with rainfall for all species but *Ae. japonicus* (Fig. 3h), and with temperature for all species but *Ar. subalbatus* (Fig. 3i). When time series models were fitted and simplified by AIC model selection (Table 2), rainfall was positively associated ( $P < 0.05$ ) with the presence of *Ae. albopictus*, *Ae. flavopictus*, and *Ar. subalbatus*, while temperature was positively associated ( $P < 0.05$ ) with *Ae. albopictus*, *Ae. japonicus*, and *Ae. flavopictus*. In all presence time series models relative humidity was left out of the final model by the AIC-based process of model selection. With the exception of *Ae. japonicus*, where only 32% of the variability in the presence time series was explained, temporal

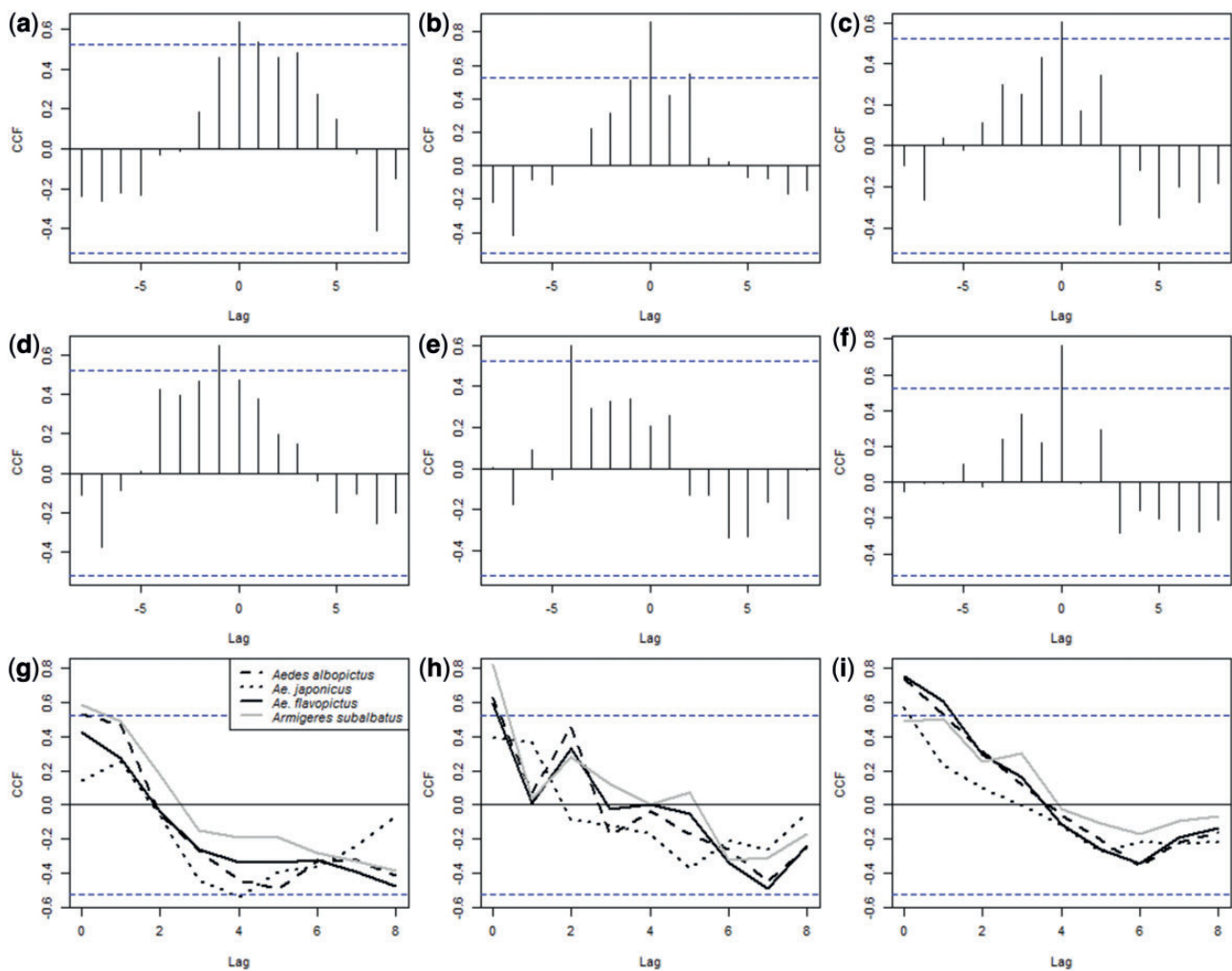
models for all species explained about 67% of the variability in the presence time series. Residuals from all models presented in Table 2 showed no significant temporal autocorrelation for time lags  $> 0$ , ensuring a valid statistical inference.

Figure 4 shows the abundance time series for each mosquito species and sampling location. Data for *Ae. albopictus* suggest this species was synchronous in the locations where it was persistent, mainly in the West transect (Fig. 4a). In contrast, *Ae. japonicus* had different peaks across the different transects, but similar peaks in each transect (Fig. 4b). Meanwhile, *Ae. flavopictus* was highly synchronous across most of the sampling locations, and had the most synchronous fluctuations across the four species (Fig. 4c). Contrasting with the three *Aedes* spp., *Ar. subalbatus* had concerted peaks in abundance in the East and West transects, but not in the North transect (Fig. 4d).

Figure 5 shows the results of a formal synchrony analysis for the abundance of mosquito species, temperature, and relative humidity as function of the geographic (2-D) distance between sampling locations. The first result is that *Ae. albopictus* was asynchronous, being its synchrony not different from random (Fig. 5a). By contrast, *Ae. japonicus* was more synchronous at short distances, around 70 m, the synchrony becoming flat over the range of distances studied (Fig. 5b). Meanwhile, *Ae. flavopictus* had a flat synchrony profile, with an overall higher synchrony than other species (Fig. 5c). The synchrony profile of *Ar. subalbatus* (Fig. 5d) was similar to that of *Ae. japonicus*, with a significantly higher synchrony at short distances, around 70 m, but also around 550 m, the synchrony decreasing at intermediate distances of around 400 m. This synchrony pattern might reveal the scarce abundance of *Ar. subalbatus* across



**Fig. 2.** Time Series. (a) Mosquito species presence, i.e., proportion of the sampling locations where a mosquito species was found during each sampling session. Each line corresponds to a mosquito species, see panel b for details. (b) Temperature, (c) Rainfall, and (d) Relative Humidity.



**Fig. 3.** Cross correlation functions (CCF) of mosquito species persistence and weather variables across the sampling locations—(a) *Ae. albopictus* and *Ae. japonicus*, (b) *Ae. albopictus* and *Ae. flavopictus*, (c) *Ae. albopictus* and *Ar. subalbatus*, (d) *Ae. japonicus* and *Ae. flavopictus*, (e) *Ae. japonicus* and *Ar. subalbatus*, (f) *Ae. flavopictus* and *Ar. subalbatus*, (g) mosquito species and relative humidity, (h) mosquito species and rainfall, and (i) mosquito species and temperature. The legend of panel g indicates the line associated with each mosquito species in panels g, h, and i. In all panels, the dashed blue lines indicate the 95% confidence intervals of the correlation functions, which is significantly different from random when it is outside the area between the dashed blue lines.

Mt. Konpira. Over the same spatial scale temperature synchrony tended to decrease with distance (Fig. 5e) while only for short distances relative humidity (Fig. 5f) was more synchronous than the average over the range of distances studied.

Figure 6 shows the synchrony analysis for the mosquito species, temperature, and relative humidity as function of the altitudinal distance between sampling locations. For *Ae. albopictus* (Fig. 6a), the pattern of asynchrony was similar to what was observed when considering the geographical distance. By contrast, for *Ae. japonicus* (Fig. 6b) the synchrony was flat across the altitudinal gradient. For *Ae. flavopictus* (Fig. 6c) the synchrony decreased as the altitudinal distance increased. For *Ar. subalbatus* (Fig. 6d) synchrony was flat, but became not different from what is expected by random when the altitudinal distance between sampled locations exceeded 150 m and became negative for altitudinal distances around 200 m. Just like it was the case when geographic distance was considered temperature synchrony decreased with distance, yet more abruptly as the altitudinal distance increased (Fig. 6e), and synchrony for relative humidity (Fig. 6f) decreased with the altitudinal distance, yet not as abruptly like temperature. It is remarkable how the synchrony patterns of *Ae. flavopictus* (Fig. 6c) tracked the synchrony patterns of temperature

(Fig. 6e), yet the synchrony was smaller in the mosquito than in the environment.

## Discussion

Synchrony, population persistence, and presence across landscapes have been, in general, relatively poorly explored for mosquitoes, and especially across altitudinal urban gradients. Our previous results suggested that for the four studied mosquito species population dynamics were under density dependence regulation (Chaves et al. 2015, Chaves 2016), and the results presented here help to gain additional insights about the population dynamics of these species in their adult life stage.

As our analysis suggest, factors associated with the persistence of the four species across the altitudinal gradient of Mt. Konpira were different. For the persistence of *Ar. subalbatus* the ground type was the most important factor, which was also important to explain its abundance patterns in Mt. Konpira (Chaves et al. 2015). By contrast, for *Ae. flavopictus* and *Ae. japonicus* it was a cool environment what was most important, while for *Ae. albopictus* it was

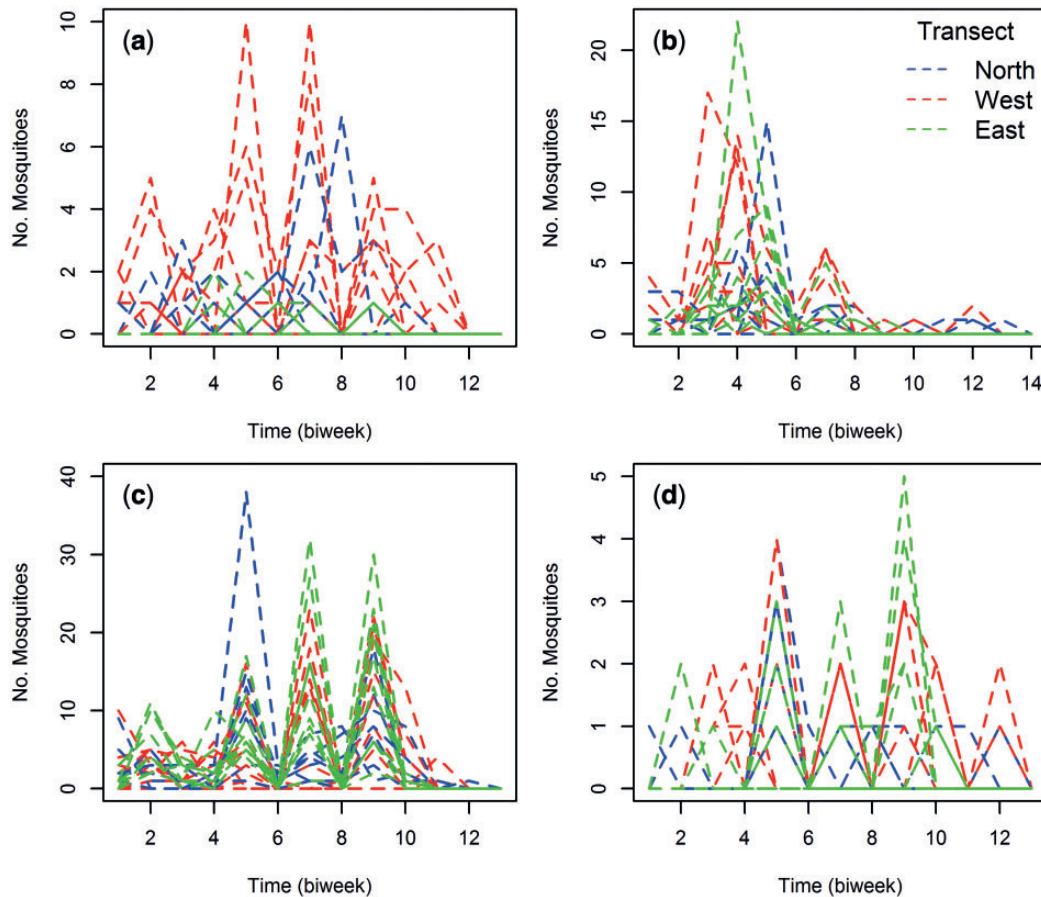
**Table 2.** Parameter estimates for weather variables associated with the temporal presence of medically important mosquitoes, sampled by sweeping nets, across 27 sampling locations in 2014 at Mt. Konpira, Nagasaki, Japan

Parameter	Species	Estimate	S.E.	<i>t</i>	<i>P</i> -value
Intercept	<i>Ae. albopictus</i>	−0.261	0.128	−2.040	0.066
	<i>Ae. japonicus</i>	−0.400	0.323	−1.239	0.239
	<i>Ae. flavopictus</i>	−0.581	0.273	−2.130	0.056
	<i>Ar. subalbatus</i>	0.0448	0.0372	1.208	0.250
Rainfall	<i>Ae. albopictus</i>	0.00062	0.00027	2.282	0.0434*
	<i>Ae. flavopictus</i>	0.00115	0.0058	1.993	0.0717
	<i>Ar. subalbatus</i>	0.00119	0.00024	4.940	0.000342*
Temperature	<i>Ae. albopictus</i>	0.0207	0.0064	3.212	0.00828*
	<i>Ae. japonicus</i>	0.0366	0.0153	2.392	0.034*
	<i>Ae. flavopictus</i>	0.0463	0.0138	3.367	0.00628*
$R^2$	<i>Ae. albopictus</i>	0.687	—	—	—
	<i>Ae. japonicus</i>	0.323	—	—	—
	<i>Ae. flavopictus</i>	0.680	—	—	—
	<i>Ar. subalbatus</i>	0.670	—	—	—
$\Delta AIC_{FM}$	<i>Ae. albopictus</i>	1.77 <sup>a</sup>	—	—	—
	<i>Ae. japonicus</i>	1.82 <sup>a</sup>	—	—	—
	<i>Ae. flavopictus</i>	1.87 <sup>a</sup>	—	—	—
	<i>Ar. subalbatus</i>	0.108 <sup>a</sup>	—	—	—

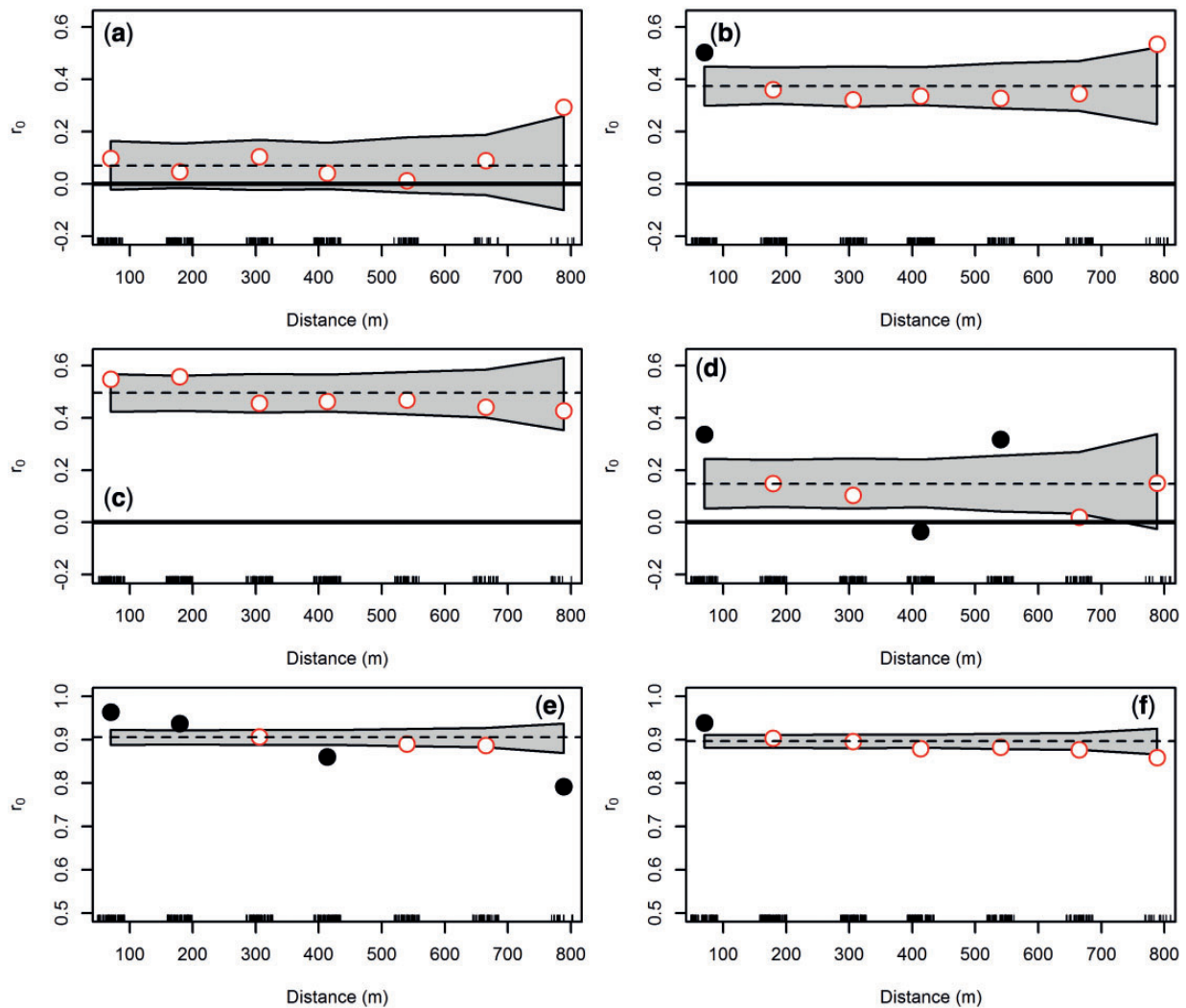
Estimates come from the best linear regression model for each species, selected by a mixed forward and backward process of model selection.  $R^2$  is the coefficient of determination which explains the proportion of variance in the data explained by each model.  $\Delta AIC_{FM}$  is the AIC difference between a full model that incorporated all landscape and weather covariates described in the methods section.

\*Statistically significant ( $P < 0.05$ ).

<sup>a</sup>The best model reduced the likelihood and number of parameters.



**Fig. 4.** Mosquito abundance time series at each sampling location—(a) *Ae. albopictus*; (b) *Ae. japonicus*; (c) *Ae. flavopictus*; (d) *Ar. subalbatus*. The inset legend in panel (b) shows the color coding for the transect where each “sampling location” time series was collected.



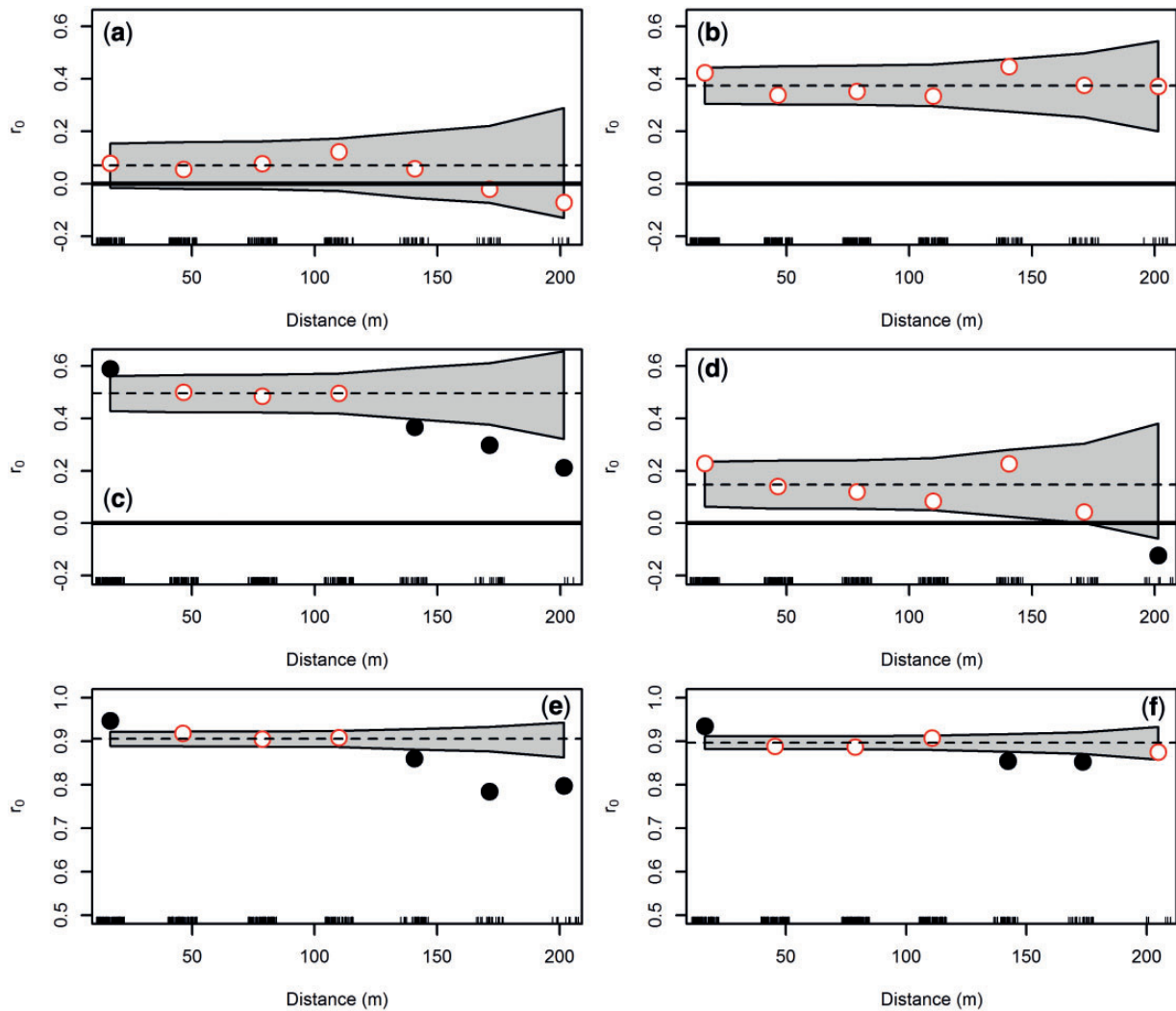
**Fig. 5.** Synchrony of mosquito species abundance, temperature, and relative humidity as function of the geographic distance between sampling locations—(a) *Ae. albopictus*; (b) *Ae. japonicus*; (c) *Ae. flavopictus*; (d) *Ar. subalbatus*; (e) air temperature (°C); (f) relative humidity (%).

locations with a slope and platykurtic temperature variability, which are relatively simple factors if we consider that many more factors, for example, canopy openness, were necessary to explain differences in their abundance across Mt. Konpira (Chaves 2016). Similarly, unlike what we observed when studying temporal patterns of mosquito abundance, where *Ae. flavopictus* seems to have an antagonistic relationship with *Ae. albopictus* and *Ae. japonicus* (Chaves 2016), the pattern of association in temporal presence across the landscape was positive and mainly synchronous across most species pairs, being both rainfall and temperature weather factors that seemed important for this synchronicity in presence. The positive effect of temperature on temporal presence might be related to the impact of temperature on mosquito activity, especially considering sweep nets catch mosquitoes flying into the net, either by the disturbance made by the sweeping or by being attracted to humans (Hoshi et al. 2014). However, the positive association might also be related to a temperature-dependent accelerated adult mosquito recruitment from aquatic stages (Alto and Juliano 2001, Chaves et al. 2014). Meanwhile, the positive impact of rainfall might be related with the recruitment of new individuals for the mosquito species we studied, independently of any potential impacts of heterogeneous rainfall, and/or water collection by larval habitats, at the more finely grained

spatial scale of our sampling. For both *Ae. albopictus* and *Ar. subalbatus* it is known that larval recruitment from eggs follows rainfall, as eggs previously oviposited above the water line get submerged in water and hatch into larvae (Amerasinghe and Alagoda 1984).

Patterns of abundance synchrony were robust for *Ae. albopictus*, which was asynchronous both across the range of geographic and altitudinal distances that we considered, and this can be related to its relative low spatial and temporal persistence when compared with the other mosquito species at Mt. Konpira. The lack of synchrony could also arise from adult mosquito emergence from artificial water containers, which could recruit mosquitoes depending on their use (Eshita and Kurihara 1979, Sota et al. 1994, Paupy et al. 2009). For *Ae. japonicus*, on the other hand, when the geographic distance was considered a spike in synchrony at short distances, i.e., below 100 m, within the usual range of mosquito dispersal (Guerra et al. 2014), is followed by a flat synchrony. This pattern is suggestive of dispersal playing a role in the synchrony of this mosquito (Ranta et al. 2006), and the effect is likely due only to distance, given that the synchrony becomes totally flat when studied across altitude. By contrast, *Ae. flavopictus* showed a different pattern, where synchrony, which was the highest across all the four species studied, was flat when geographic distance was considered, yet it tracked the pattern of





**Fig. 6.** Synchrony of mosquito species abundance, temperature, and relative humidity as function of the altitudinal distance between sampling locations—(a) *Ae. albopictus*; (b) *Ae. japonicus*; (c) *Ae. flavopictus*; (d) *Ar. subalbatus*; (e) air temperature ( $^{\circ}\text{C}$ ); (f) relative humidity (%).

temperature synchrony when studied across the altitudinal gradient of Mt. Konpira, suggesting that if dispersal plays a role on *Ae. flavopictus* synchrony, it might be tied to impacts of temperature on it. It is recognized that relative humidity and temperature play major roles in mosquito activity, especially movement (Dow and Gerrish 1970). This result, however, highlights the need to better understand the impacts of changing weather conditions on mosquito dispersal, especially in light of the diverse patterns we observe with the four mosquito species we studied. Here, it is also important to discard the possibility of a Moran effect, since the environmental synchrony was larger than the population synchrony observed in the four mosquito species (Liebhold et al. 2004, Ranta et al. 2006). *Armigeres subalbatus* had the most intriguing synchrony pattern, which suggests mosquitoes moved across the altitudinal gradient of the mountain, given the negative synchrony for altitudinal distances of 200 m, and when considered in conjunction with the fluctuating synchrony patterns observed across the range of geographical distances, as well as the raw abundance data for each sampling location, suggest travelling waves in the distribution of this mosquito during the studied season, i.e., that locations where *Ar. subalbatus* was most abundant changed through time (Ranta et al. 2006).

Finally, our results suggest that synchrony in populations of vectors is a suitable hypothesis to test when looking for drivers in the synchrony of vector-borne disease epidemics (Chaves et al. 2012), given that vectors can synchronize their population dynamics over short and relatively long spatial scales (Chaves et al. 2013). Our results also highlight open questions about the dependence of mosquito dispersal on changing environmental conditions and how changing weather patterns could influence transmission by facilitating vector movement across population of hosts at finely grained spatial scales. Also, understanding the persistence, presence, and synchrony of mosquito vectors of disease can help to better understand the entomological risk factors underpinning the transmission of vector-borne diseases.

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