Globally invasive, withdrawing at home: *Aedes albopictus* and *Aedes japonicus* facing the rise of *Aedes flavopictus*

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Abstract

It has been suggested that climate change may have facilitated the global expansion of invasive disease vectors, since several species have expanded their range as temperatures have warmed. Here, we present results from observations on two major global invasive mosquito vectors (Diptera: Culicidae), *Aedes albopictus* (Skuse) and *Aedes japonicus* (Theobald), across the altitudinal range of Mt. Konpira, Nagasaki, Japan, a location within their native range, where *Aedes flavopictus* Yamada, formerly a rare species, has now become dominant. Spatial abundance patterns of the three species suggest that temperature is an important factor influencing their adult distribution across the altitudinal range of Mt. Konpira. Temporal abundance patterns, by contrast, were associated with rainfall and showed signals of density-dependent regulation in the three species. The spatial and temporal analysis of abundance patterns showed that *Ae flavopictus* and *Ae albopictus* were negatively associated, even when accounting for differential impacts of weather and other environmental factors in their co-occurrence patterns. Our results highlight a contingency in the expansion of invasive vectors, the potential emergence of changes in their interactions with species in their native communities, and raise the question of whether these changes might be useful to predict the emergence of future invasive vectors.

Key-words: Schmalhausen’s law, competition, mosquito, niche, Dengue, Japanese Encephalitis Virus.

Introduction

Temperature has been suggested as a factor potentially influencing the expansion of invasive vectors of disease (Lounibos 2002; Juliano & Lounibos 2005). For example, it has been suggested that the northward expansion of the Asian tiger mosquito *Aedes albopictus* has been modulated by temperature, locally in Japan (Kobayashi *et al.* 2002; Mogi & Tuno 2014), but also globally (Proestos *et al.* 2015). By contrast, it has also been suggested that high temperatures might have impaired the southward expansion of *Aedes japonicus* in North America (Kaufman & Fonseca 2014). Similarly, it has also been observed that changes in microclimate might lead to differential survival in invasive species, as well as, to variable outcomes in biological interactions between invasive species and native/longer time resident fauna (Lounibos *et al.* 2010). More generally, altitudinal and latitudinal changes have been observed in the distribution of many invertebrate species following the onset of climate change, where trends include both the expansion and contraction of habitat ranges (Parmesan 2006).

Nagasaki city, Japan is an ideal place to study climate change impacts on insect vectors of disease that have become global invasive species. Both *Ae albopictus,* a major vector of Dengue and other emerging arboviruses affecting humans (Paupy *et al.* 2009), and *Ae japonicus*, a competent vector for Japanese Encephalitis virus and West Nile virus (Kaufman & Fonseca 2014), are common species in Nagasaki city, which is within the native range of both species (Tanaka *et al.* 1979). Moreover, several studies have looked at diverse aspects of these mosquito species ecology (Omori *et al.* 1952; Mori & Wada 1978; Zea Iriarte *et al.* 1991; Tsuda *et al.* 1994). Of special interest are studies done along Mt. Konpira (Zea Iriarte *et al.* 1991; Tsuda *et al.* 1994), which recorded the presence of both *Ae albopictus* and *Ae japonicus* across an altitudinal gradient. These observations are valuable for comparison with current distribution patterns in these globally invasive species, because altitudinal gradients are ideal settings to study population dynamics in natural temperature gradients (Stevens 1992; Eisen *et al.* 2008), as well as, the impact of finely grained microclimatic differences on species co-existence (Hodkinson 2005; Chaves & Koenraadt 2010).

The comparison of *Ae albopictus* records in Mt. Konpira showed that adults have increased their altitudinal range by surpassing the 250 m limit observed in 1989 (Zea Iriarte *et al.* 1991), reaching the top of the mountain in 2014 (Chaves 2016). By contrast, *Ae japonicus* did not change its altitudinal distribution in Mt. Konpira (Chaves 2016). We also observed that a third mosquito species, *Ae flavopictus*, a competent vector of Dengue virus (Eshita *et al.* 1982), which used to be a rare species (Omori *et al.* 1952; Tsuda *et al.* 2003), was widely distributed across the altitudinal range of Mt. Konpira in 2014, and that land use and vegetation changes were unlikely drivers for this change (Chaves 2016). This pattern calls into consideration the possibility that climate change might have changed the nature of the biotic interactions (Post 2013) between these three mosquito species, in a way where *Ae flavopictus* population growth might have been facilitated. Specifically, the community formed by these tree-hole mosquitoes, where inter-specific interactions are likely mainly competitive, might have changed following the challenge by an emerging environmental templet that has increased the competitive ability of a previously rare species. Under the facilitation scenario, it is expected that *Ae flavopictus* might have a stronger negative impact on *Ae japonicus* and *Ae albopictus* population growth than viceversa, as expected from the analysis of their community matrix (Levins 1968). Here, we use spatial and time series statistical models, as well as a discrete time adaption of the Lotka-Volterra equation for competition (Hernandez 2009) to test whether the abundance and co-occurrence patterns of *Ae albopictus* and *Ae japonicus* with the, formerly rare, now common *Ae flavopictus* might support the existence of potential antagonistic interactions as inferred from the parameters estimated using finely grained spatio-temporal data on the abundance of adults from these three mosquito species. In our analysis we consider meteorological data to assess the role that changing weather patterns could have on the abundance and co-existence of these three mosquito species. Our results, based on both spatial and temporal analyses, robustly suggest that *Ae flavopictus* might be antagonistically interacting with *Ae albopictus*. However, before we can predict these species responses to climate change we need to better understand the ecology and evolutionary patterns of insect vectors of pathogens.

Methods

Data Collection

Study site

Nagasaki city is located in western Japan (Fig. 1A), in the west of Kyushu island (Fig. 1B). Mt Konpira, is in the eastern side of Nagasaki city (Fig. 1C) and comprises an altitudinal gradient of 320 m from the seaside level to its top (Fig. 1D). Along this altitudinal gradient we chose 27 trees to sample adult mosquitoes (Fig. 1D) with the same coordinates as a previous study (Zea Iriarte *et al.* 1991). Trees were chosen as reference for mosquito sampling given that fixed reference points ease the systematic sampling of mosquitoes (Zea Iriarte *et al.* 1991), and that the species of interest rest in vegetation near trees, since they naturally ovisposit in treeholes (Tsuda *et al.* 1994; Hoshi *et al.* 2014b). On May 25th 2014 we estimated the canopy cover and the dominant ground cover at each focal tree (Fig. 1D), following a method described in detail by Chaves *et al.* (2015). We also used an ASTER digital elevation model (http://gdem.ersdac.jspacesystems.or.jp/) to estimate elevation, slope and aspect, i.e., the direction of the slope (where 0° is north and 180° south), of each sampling location (Brunsdon & Comber 2015).

Mosquito Sampling

We sampled adult mosquitoes using a sweep net. Sampling started at sunrise (Zea Iriarte *et al.* 1991), each session randomizing the focal tree sampling order. The sampling with sweep nets was done at a fixed point within a 2.5 m radius from the focal trees. Upon arrival at a focal tree, the net was swept around the body of the person sampling for 2 minutes, stopping for 1 min, and then sweeping for another 2 min (Chaves *et al.* 2015). Mosquito sampling was biweekly between May 18th and November 15th of 2014. Further details about the sampling and taxonomic identification of mosquitoes are presented in the Supplement S1.

Weather Variables

We recorded the air temperature and relative humidity around focal trees, during each mosquito sampling session. Daily rainfall records for Nagasaki (May 1st to December 1st, 2014) were obtained for Nagasaki city from the Japanese Meteorological Agency. Rainfall data was accumulated for the 14 days prior to the mosquito sampling when used in subsequent analysis. Further details about weather data collection are presented by Chaves *et al.* (2015).

Statistical Analysis

*Patterns of adult **Aedes** spp. spatial abundance*

Patterns of spatial abundance of *Ae albopictus, Ae favopictus* and *Ae japonicus* were studied using generalized linear models (glm) for count data (Venables & Ripley 2002). As a default, we employed Poisson glm's, but in cases where counts were overdispersed we employed Negative Binomial models (Faraway 2006). For each mosquito species the "full" model had the following general form:

$$l(\mathrm{N_i}) = \mu + \textstyle\sum_j \beta_j \mathrm{Cov}_j \ + \varepsilon_i \qquad (1)$$

where N_i is the total cumulative mosquito abundance, i.e., for records spanning all the study period, for a focal species at location i, where i corresponds to each one of the 27 focal trees (Fig. 1D), $l()$ is a link function (for count glm's usually a natural logarithm), μ is the intercept of the model, the β_j's are coefficients for the impact of environmental covariates (Cov). Covariates included landscape features: elevation, slope, aspect, an index for ground cover (which increased when concrete predominated the ground, for details see Chaves *et al.* 2015) and canopy openness. Covariates also included weather variables: temperature and relative humidity. We considered both the mean and S.D. of the weather variables to measure the impact of both average conditions and their variability on mosquito abundance. We also considered the abundance of the other two *Aedes* mosquito species. Finally, the error, ε_i, was either Poisson or Negative Binomial (Venables & Ripley 2002).

*Impacts of weather fluctuations on adult **Aedes** spp. temporal abundance*

Time series for the adult abundance of each *Aedes* spp. were generated by adding the biweekly records from the 27 focal trees per sampling session. These time series were used to estimate autocorrelation functions (ACF), which, in this study, describe patterns of temporal autocorrelation in mosquito abundance (Chaves *et al.* 2012). More generally, an ACF presents the correlation of a time series with itself at different time lags (Shumway & Stoffer 2011). We also estimated cross correlation functions (CCFs), i.e., the temporal correlation function between two time series for different time lags (Shumway & Stoffer 2011), between all pair combinations of *Aedes* spp., and between each *Aedes* spp. and Rainfall, Temperature and Relative Humidity. This information was used to fit "full" time series models for each *Aedes* spp. The basic "full" model had the following general form:

$$\mathrm{N_{t+1}} = \mu + \varphi(\mathrm{N_t} - \mu) + \sum_i \beta_i \mathrm{Cov_{t-\tau}} + \epsilon_t \qquad (2)$$

Where N_t is mosquito abundance at time t, μ is the average mosquito abundance, φ is an autoregressive coefficient (which models temporal dependence in the data), the β_i's are coefficients for the impact of weather covariates (Cov), which were standardized by removing their mean value to ease interpretation (Shumway & Stoffer 2011). Weather covariates could also have a time lag $\tau \geq 0$. Finally, $\epsilon_t \sim N(0, \sigma^2)$, i.e., is an independent, identical and normally distributed error.

Density-dependence and inter-specific interactions in adult ***Aedes*** *spp. mosquitoes in* 2014

We started our analysis by plotting the per-capita growth rate ($r_t = \ln(N_{t+1}) - \ln(N_t)$) as function of abundance (N_t) for each *Aedes* spp*.* time series. A population is expected to reduce r_t as N_t increases when it is regulated by density-dependence (Turchin 2003). Given that data from each *Aedes* spp. fitted this qualitative expectation, we used a modified Ricker model of density-dependence to both quantify the impact of density-dependence and inter-specific interactions with other *Aedes* spp, on the regulation of each species. The "full" model is defined by the following equation:

$$\mathrm{N(i)_{t+1}} = \lambda_0 \mathrm{N(i)_t} exp\left(-b\mathrm{N(i)_t} - \alpha_j \mathrm{N(j)_t} - \alpha_k \mathrm{N(k)_t}\right) \qquad (3)$$

Where λ_0 is the intrinsic rate of population growth and *b* is a density-dependence coefficient (Turchin 2003) and α_j and α_k are the impact, or competition coefficient, of species j and k on species i. When *b*<0, it can be affirmed that a population undergoes density-dependent regulation (Turchin 2003), and similarly when $\alpha_j < 0$ and/or $\alpha_k < 0$ there is an antagonistic impact by species *j* and/or *k* on species *i* (Hernandez 2009). Further details about the Ricker model are presented elsewhere, including its deterministic (Turchin 2003; Mangel 2006) and several stochastic derivations (Melbourne & Hastings 2008).

We fitted the model presented in (3) using maximum likelihood methods described in our previous work (Chaves *et al.* 2012; Chaves *et al.* 2015). We assumed the time series had negative binomial distributions and that populations were subject to either: (i) environmental stochasticity, where all individuals are equally subject to stochastic variation and the overdispersion parameter (κ_E) of the negative binomial is constant or (ii), demographic stochasticity, where the impact of stochastic variation depends on population size, as well as, the overdispersion parameter ($\kappa_D \mathrm{N_t}$) of the negative binomial (Melbourne & Hastings 2008).

All models were simplified and selected based on the minimization of the Akaike Information Criterion (AIC), and model assumptions assessed with appropriate diagnostic tests. Further details are presented in Supplement S1.

Results

A total of 1636 adult *Aedes* spp mosquitoes where collected during the sampling period. *Ae flavopictus* was the most abundant with 1118 (68.34%) individuals, followed by *Ae japonicus* with 328 (20.05 %) and *Ae albopictus* 190 (11.61%). The statistical analysis of the spatial patterns of adult *Aedes* spp. abundance (Table 1), shows that both *Ae albopictus* and *Ae flavopictus* were positively associated with *Ae japonicus* presence, and negatively associated with each other. By contrast *Ae japonicus* spatial abundance was only associated with environmental factors. Both *Ae albopictus* and *Ae japonicus* adults were negatively associated with elevation (P<0.05), as depicted by Fig. 2A. *Ae albopictus* and *Ae flavopictus* increased their abundance with the landscape slope (Fig. 2B), while *Ae japonicus* with the aspect, suggesting the later prefers places with more natural shadow at our study site, since the direction of the mountain slope, in relation to light incidence, generates more shadow for southerly faced slopes along daylight hours during the season when adult mosquitoes are active in Mt. Konpira. *Ae albopictus* was the only species whose spatial patterns were associated with the ground cover, where the negative coefficient indicates an increased abundance in areas where the ground is dominated by concrete (Chaves *et al.* 2015). The canopy openness (Fig. 2C) was negatively associated with the abundance of *Ae japonicus*, but positively with *Ae albopictus*, re-inforcing the possibility that *Ae japonicus* prefers places with more shadow, while *Ae albopictus* can stay in places that are more exposed to sunlight. The relationship with the variability in relative humidity was positive for *Ae albopictus* and *Ae flavopictus*, but negative for *Ae japonicus* (Fig. 2D), meaning the latter species probably prefers places with more constant humidity when compared with the other two *Aedes* spp.

The relationship with temperature (Fig. 2E and 2F) was interesting, since the temperature mean value for each sampling location had a significant association ($P<0.05$) with *Ae albopictus* and *Ae flavopictus* abundance (Fig. 2E), where a convex polynomial, i.e., a function with a maximum, represented by:

$$ATemp - BTemp^2 = 0 \qquad (4)$$

describes the relationship of abundance with temperature (*Temp*). The maximum for the function presented in (4) can be obtained by taking the derivative (Larson & Edwards 2013) with respect to temperature:

$$Temp = \frac{A}{2B} \qquad (5)$$

which leads to an estimate of 2.21℃ for *Ae albopictus* and 0.66 ℃ for *Ae flavopictus* above the mean temperature across all sampling sites as the temperature leading to a maximum abundance, respectively, for each species. This result implies that, in principle, *Ae albopictus* is more abundant at hotter temperatures than *Ae flavopictus*. The variability, as measured by the temperature S.D. (Fig. 2F) was significantly

($P<0.05$) associated with abundance of *Ae flavopictus* and *Ae japonicus*, but it had a stronger impact in *Ae japonicus*, whose coefficient was over 5 times larger than that of *Ae flavopictus* (2.577 vs 0.482, Table 1). This result implies that these two species can cope with variable environments, *Ae japonicus* being more likely to be abundant under increasing temperature variability.

Temporal patterns of adult abundance are shown in Fig. 3. Fig. 3A shows the time series for each species, showing that *Ae flavopictus* was the most abundant species during the studied season, followed by *Ae japonicus* and *Ae albopictus*, respectively (see intercept parameter in Table 2). Only *Ae japonicus* had a significant partial autocorrelation at 1 biweek of lag (Fig. 3B, that was significant in time series models). *Ae albopi*ctus and *Ae flavopictus* had synchronuous fluctuations (Fig. 3C). By constrast, fluctuations in *Ae japonicus* led by one biweek the fluctuations of *Ae albopictus*, and were not significantly related to changes in *Ae flavopictus* abundance changes (Fig. 3C). Rainfall (Fig. 3D) was significantly ($P<0.05$) and positively associated with the abundance of the three *Aedes* spp without a lag (Fig. 3E). Relative humidity (Fig. 3F) was significantly associated ($P<0.05$) with *Ae albopictus* and *Ae japonicus* (Fig. 3G), but not important for the time series models (Table S1). Only *Ae albopictus* was significantly ($P<0.05$) and positively associated with temperature (Fig. 3H, 3I, and temperature parameter in Table 2). Thus, Rainfall (Fig. 3D) was the weather factor most likely associated (Fig. 3E) with peaks and troughs in abundance of the three mosquito species (Fig. 3A). The association between rainfall and abundance (rainfall parameter in Table 2) was weakest for *Ae albopictus* (Fig. 3J), strongest for *Ae flavopictus* (Fig. 3K) and intermediate for *Ae japonicus* (Fig. 3L, which also shows the autocorrelation with *Ae japonicus* abundance at 1 biweek of lag, i.e., N_{t-1}).

In the three *Aedes* spp. the per-capita growth rate (*r*) decreased with abundance (Fig. 3) and the density-dependent coefficient estimates (Table 3) were negative (i.e., $b<0$) as expected under density dependence, which can also partially explain the peaks and troughs in Fig. 3A. Model selection for the modified Ricker model presented in (3) suggests a negative impact of *Ae flavopictus* on *Ae albopictus* (Fig. 3M and Table 3) and of *Ae flavopictus* on *Ae japonicus* (Fig. 3O and Table 3). For *Ae flavopictus* (Fig.

3N) a model without interactions and where the stochasticity was environmental was selected as the best model (Table 3). For both *Ae albopictus* and *Ae japonicus* the stochasticty in the models was demographic (Table 3), meaning that stochastic variation depended on population size. The latter could also be expected given the smaller average population size of *Ae albopictus* and *Ae japonicus* when compared with *Ae flavopictus* (Fig. 3A and intercept parameter in Table 2). The intrinsic rate of population growth (λ_0) was largest for *Ae flavopictus*, followed by *Ae japonicus* and *Ae albopictus* (Table 3). By contrast, the density-dependence coefficient (*b*) was largest for *Ae albopictus*, followed by *Ae japonicus* and *Ae flavopictus* (Table 3). The negative impact (α) of *Ae flavopictus* was both proportionally, i.e, when compared to *b*, and numerically larger on *Ae japonicus* when compared to *Ae albopictus.* Nevertheless, in both cases the magnitude of the interaction was smaller than the impact of density-dependence, i.e., $|b| > |\alpha|$ (Table 2).

Finally, assumptions about spatial or temporal independence of the error for all models selected as best were not violated ensuring a sound statistical inference (Shumway & Stoffer 2011; Kuhn & Johnson 2013; Brunsdon & Comber 2015).

Discussion

Approaches to predicting changes in species distribution under climate change have tended to focus on associations between a focal species presence/abundance and weather records or climatic patterns (Proestos *et al.* 2015). As our results have shown, this approach might be improved by expanding the scope and looking at species co-occurring with focal species of interest. The latter is because patterns of co-occurrence could suggest potential biological interactions that might limit the distribution and abundance of species (Gotelli & McCabe 2002; Chaves *et al.* 2011). Our data illustrates a potential contingency under climate change, i.e., the emergence of “new” dominant vector species in communities currently associated with “known” disease vectors (Chaves & Añez 2016). Moreover, parameter estimates for the Lotka-Volterra modified Ricker model suggest that these changes might be occurring via changes in species interactions and/or a differential response to new environments (Levins 1968). That seems to be the case here with *Ae flavopictus,* the most abundant species of the trio we studied, which was also robustly, i.e., both temporally and spatially, negatively associated with *Ae albopictus* in an emerging pattern opposite to what has been historically reported for these two species in western Japan, where *Ae albopictus* was the dominant species (Kamimura 1968; Sota *et al.* 1992).

It is important to notice that *Ae flavopictus* is also a tiger mosquito with an external morphology very similar to that of *Ae albopictus,* i.e., with a brilliant longitudinal dorsal stripe (Tanaka *et al.* 1979). Nevertheless, *Ae flavopictus* has curved scales near the wing base, which are absent in *Ae albopictus* (Tanaka *et al.* 1979) and both species have remarkably different male genitalia (Yamada 1921). Both *Ae flavopictus* and *Ae albopictus* have also been confirmed as different species by biochemical (Gaunt *et al.* 2004) and molecular methods (Toma *et al.* 2002; Taira *et al.* 2012). Similarly, both species are unlikely to hybridize under natural conditions, yet low fitness hybrids have been obtained in the laboratory (Miyagi & Toma 1989). Phylogenetically both species are the most closely related in Japan (Taira *et al.* 2012). Moreover, *Ae flavopictus* is also a competent vector of dengue virus (Eshita *et al.* 1982) which should have raised an earlier interest on its potential to change its abundance and distribution patterns following climate change, especially considering its phylogenetic relatedness (Vamosi *et al.* 2009) with *Ae albopictus* and records about this later species expansion across different climatic conditions with global warming (Yamada 1921; Kamimura 1968; Mogi & Tuno 2014). Omori *et al.* (1952) were the first to report *Ae flavopictus* in Nagasaki, where it was a rare species, outnumbered by *Ae albopictus*, and only found deep inside a forest near Obama in 1948-1949, a town around 30 km east of Nagasaki city. The status of *Ae flavopictus* as a rare species seems to have been the rule in Nagasaki, as suggested by its absence in several studies in Nagasaki spanning from the 1950's to the early 2000's (Zea Iriarte *et al.* 1991; Tsuda *et al.* 2003) and observations from the 1990s in Saga, the province neighboring Nagasaki to the east, where *Ae flavopictus* was also rare in the 1990s (Mogi 1996; Sunahara & Mogi 2002).

Trends observed elsewhere in Japan also suggest changes in patterns of *Ae albopictus* and *Ae flavopictus* relative abundance. The former species used to be the most common where records of their co-occurrence have been reported (Kamimura

1968), the only exception being Hokkaido, where *Ae albopictus* has not been found (Mogi & Tuno 2014), and North East Honshu where *Ae flavopictus* was consistently the most abundant species (Yamada 1921; Kamimura 1968). However, *Ae flavopictus* is currently becoming an increasingly common mosquito in other locations over Japan (Yamauchi 2010; Shiraishi 2011; Yamauchi 2013). These emerging patterns call for further tests about the ecological mechanisms of co-existence for these two species. Traditionally, it was assumed that both species had different environmental requirements that segregated their habitats and co-existence (Kamimura 1968; Makiya 1974; Moriya 1974; Sota *et al.* 1992). Nevertheless, in an occasion it was observed that *Ae flavopictus* could easily outnumber *Ae albopictus* when they co-occurred as larvae in bamboo stumps (Kurashige 1961b, a). This last observation and our results raise questions about whether these two species compete, as suggested by the negative associations we found both temporally and spatially, and the observed change on adult dispersal between 1989 and 2014, where *Ae albopictus* adults were able, in 2014, to disperse all over Mt. Konpira, while in 1989 the species would not go beyond 250 m. To solve this question, we think it is necessary to look at abundance dynamics in the larvae, oviposition patterns and competition experiments (Juliano *et al.* 2004) which could further indicate if the observed pattern of lack of larval co-occurrence emerged mainly because of climate change altering habitat suitability or by emerging biological interactions. For example, the surge of *Ae flavopictus* could be related to its ability to cope with the variability of changing environments (Chaves *et al.* 2012; Chaves *et al.* 2014), as suggested by its association with measurements of environmental variability in the spatial model of Table 1. Alternatively, as suggested by parameters from the Ricker model, the two species might be antagonizing each other in a way where, although *Ae flavopictus* has a stronger negative impact on *Ae albopictus* population growth, both species still co-exist because for each species density-dependence is a stronger regulatory factor than competition (Hernandez 2009) as inferred by the parameter estimates of Table 3.

In contrast, *Ae japonicus* had patterns of co-occurrence with *Ae albopictus* that, as summarized elsewhere (Kaufman & Fonseca 2014), suggest that biological interactions are unlikely or weak between these two species, mainly given their differences in habitat selection and resource use (Kaufman & Fonseca 2014). None of these two species, for example, were negatively associated with each other spatially (Table 1) and temporally (Tables 2 and 3). The relationship of *Ae japonicus* with *Ae flavopictus* is less clear. Spatially, there is no sign of antagonism, and indeed *Ae japonicus* was positively associated with *Ae flavopictus* adult abundance (Table1). Temporally, it seems that *Ae flavopictus* had a negative impact on *Ae japonicus* (Table 3), but this might have emerged from both species having different associations with environmental variables, e.g., spatially with relative humidity variability where the association was positive for *Ae flavopictus* but negative for *Ae japonicus* (Table 1).

For the three *Aedes* spp rainfall seemed to be a major force driving their population dynamics. This result could be related with the fact that rainfall is the more platykurtic weather variable in Nagasaki city (Chaves 2016). According to Schmalhausen's law (Chaves & Koenraadt 2010), the biological principle stating that organisms are more likely to be sensitive to environmental factors more variable around the mean than towards the extremes, i.e., the environmental factors with a more platykurtic distribution. This particular pattern was also shared by *Ar. subalbatus* adults, another common mosquito in Mt. Konpira (Chaves *et al.* 2015). Parameters of the Ricker model also suggested that the three species had stable populations. For the three species $\ln(\lambda_0) < 2$, the necessary condition for stability in that model (Mangel 2006). This pattern of stability was also shared by *Armigeres subalbatus* at Mt. Konpira (Chaves *et al.* 2015) and has been commonly observed in other mosquito species where density-dependence has been formally studied with the Ricker model (Yang *et al.* 2008; Hoshi *et al.* 2014a).

Finally, our results suggest that, beyond the need to include *Ae flavopictus* as a species requiring an enhanced surveillance in Japan and East Asia, a better understanding of the forces driving relative abundance changes in *Ae albopictus* and *Ae flavopictus* might be reached by looking at their evolutionary changes over ecological time scales (Khibnik & Kondrashov 1997). One possibility is that evolutionary changes that might have followed climate change (Egizi *et al.* 2015) could have altered the interaction between *Ae albopictus* and *Ae flavopictus* by changing traits fundamental to their co-existence. Alternatively, the environmental context (Juliano 2009), which becomes more variable with climate change (Chaves & Koenraadt 2010), might be driving the new patterns of co-existence between *Ae flavopictus* and *Ae albopictus*. Similarly, it should not be surprising if the new patterns of environmental variability and genetic change are synergistically driving the change, since the latter is unlikely independent of the former (Levins 1968). It would also be interesting to see if the emerging pattern of *Ae flavopictus* observed in Japan also extends to Korea, where the mosquito used to be rare (Yamada 1921), and where it is frequently reported in mosquito surveys (Kim *et al.* 2007) or if the species is now present in Taiwan, where it was absent (Yamada 1921) when it was described.

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Table 1 Factors associated with the spatial patterns of adult *Aedes albopictus*, *Aedes flavopictus* and *Aedes japonicus* abundance*,* sampled by sweeping nets in 2014 at Mt. Konpira, Nagasaki, Japan. Parameter estimates are for the best Poisson generalized linear model (glm) selected through a process of backward elimination. Moran's I indicates the Moran's I index of spatial autocorrelation estimated from model residuals through a 1000 Monte Carlo replicates. ΔAIC is the difference between the AIC from the "full" model, including all potential covariates, and the "best" model.

Species	Parameter	Estimate	S.E.	z	P
Aedes albopictus	Intercept	-3.322	2.582	-1.29	0.19818
	Ae flavopictus	-0.030	0.011	-2.75	0.0059*
	Ae japonicus	0.034	0.013	2.57	0.01016*
	Elevation (m)	-0.011	0.004	-2.91	0.00363*
	Landscape Slope (^{o})	0.039	0.017	2.24	0.02544*
	Ground	-0.117	0.041	-2.87	0.00412*
	Canopy openness (%)	0.036	0.013	2.82	0.0048*
	S.D. Relative Humidity (%)	0.470	0.173	2.71	0.00676*
	Temperature (^{o}C)	-1.035	0.555	-1.86	0.06236
	Temperature^{2}	-0.234	0.080	-2.91	0.00363*
	Moran's I	-0.152	-	-	0.802
	ΔAIC	4.33	-	-	**
Aedes flavopictus	Intercept	-0.692	1.306	-0.53	0.596292
	Ae albopictus	-0.029	0.007	-4.12	3.81E-05*
	Ae japonicus	0.016	0.003	5.94	2.92E-09*
	Landscape Slope (^{o})	0.012	0.004	2.75	0.005942*
	S.D. Relative Humidity (%)	0.123	0.041	3.00	0.002735*
	Temperature	-0.417	0.115	-3.64	0.000277*
	Temperature^{2}	-0.317	0.082	-3.88	0.000105*
	S.D. Temperature	0.482	0.212	2.27	0.023033*
	Moran's I	-0.196	-	-	0.894
	ΔAIC	7.26	-	-	**
Aedes japonicus	Intercept	-2.888	4.751	-0.61	0.5433
	Elevation (m)	-0.007	0.003	-2.43	0.01515*
	Landscape Aspect (^{o})	0.003	0.001	2.75	0.00601*
	Canopy openness (%)	-0.053	0.022	-2.42	0.01575*
	S.D. Relative Humidity (%)	-0.392	0.120	-3.27	0.00109*
	S.D. Temperature	2.577	0.951	2.71	0.00672*
	Overdispersion***	3.84	1.39	-	-
	Moran's I	-0.121	-	-	0.726
	ΔAIC	4.13	-	-	**

*Statistically significant ($P<0.05$), **The "best" model significantly reduces the number of parameters and/or loglikelihood, *** data were overdispersed, thus a Negative Binomial glm was fitted.

Table 2 Parameter Estimates for the time series models of the number of adult *Aedes albopictus*, *Aedes flavopictus* and *Aedes japonicus* abundance*,* sampled by sweeping nets*,* as function of weather variables. Columns indicate the estimates (**± S.E.)** for each species. ∆AIC is the difference between the AIC from the "full" model, including all potential covariates, and the "best" model.

Parameter	*Aedes albopictus*	*Aedes flavopictus*	*Aedes japonicus*
Intercept (μ)	13.57 ± 0.94*	79. 86 ± 16.51*	21.81 ± 12.74
AR1 (φ)	-	-	0.59 ± 0.20*
Rainfall (β_1)	0.068 ± 0.010*	0.693 ± 0.154*	0.113 ± 0.046*
Temperature (β_2)	1.095 ± 0.225*	-	-
Error variance (σ^2)	12.42	3814	452.7
∆AIC(with "full" model)	-1.74**	8.53**	0***

*Statistically significant (P<0.05), **The "best" model significantly reduced the number of parameters and/or increased the loglikelihood, *** The "full" and best model are the same

Table 3 Parameter estimates for the best Ricker-like model explaining changes in the temporal abundance of *Aedes albopictus*, *Aedes flavopictus* and *Aedes japonicus* adults sampled with sweep nets during 2014 in Mt. Konpira, Nagasaki, Japan. The column "Species" indicates the focal species followed by the competitor species (i.e., focal vs competitor), when only one species is presented it means the focal species was autonomous from changes in the abundance of any of the other two species. Parameter $\widehat{\lambda_0}$ indicates the estimated population growth rate, $-\hat{b}$ the density dependence coefficient, $-\hat{\alpha}$ the competition coefficient of the competitor species on the focal species, while $\widehat{\kappa_D}$ and $\widehat{\kappa_E}$ are, respectively, the overdispersion terms for the negative binomial Lotka-Volterra modified Ricker model in presence of demographic or environmental stochasticity. ΔAIC_{SM} is the difference between the AIC from the "best" model and a simpler model. ΔAIC_{FM} is the difference between the AIC from the "full" model, including all tested covariates, and the "best" model.

Species	Parameter	Estimate	95% CL	
Aedes albopictus vs *Aedes flavopictus*	$\widehat{\lambda_0}$	2.807	2.267	4.580
	$-\hat{b}$	0.0247	0.0160	0.0698
	$-\hat{\alpha}$	0.00514	-0.0032	0.00616
	$\widehat{\kappa_D}$	0.846	0.324	1.262
	ΔAIC_{SM}	-2.74*		
	ΔAIC_{FM}	1.96**		
Aedes flavopictus	$\widehat{\lambda_0}$	6.589	2.837	20.134
	$-\hat{b}$	0.0143	0.0069	0.0201
	$\widehat{\kappa_E}$	0.772	0.343	1.536
	ΔAIC_{SM}	-6.82*		
	ΔAIC_{FM}	4.87**		
Aedes japonicus vs *Aedes flavopictus*	$\widehat{\lambda_0}$	5.769	3.007	27.247
	$-\hat{b}$	0.0151	-0.0031	0.0183
	$-\hat{\alpha}$	0.0103	0.0092	0.1179
	$\widehat{\kappa_D}$	0.126	0.054	0.272
	ΔAIC_{SM}	-10.27*		
	ΔAIC_{FM}	1.03**		

*Significant information is lost in the simpler model, **Best model significantly reduced the number of parameters and/or increased the loglikelihood

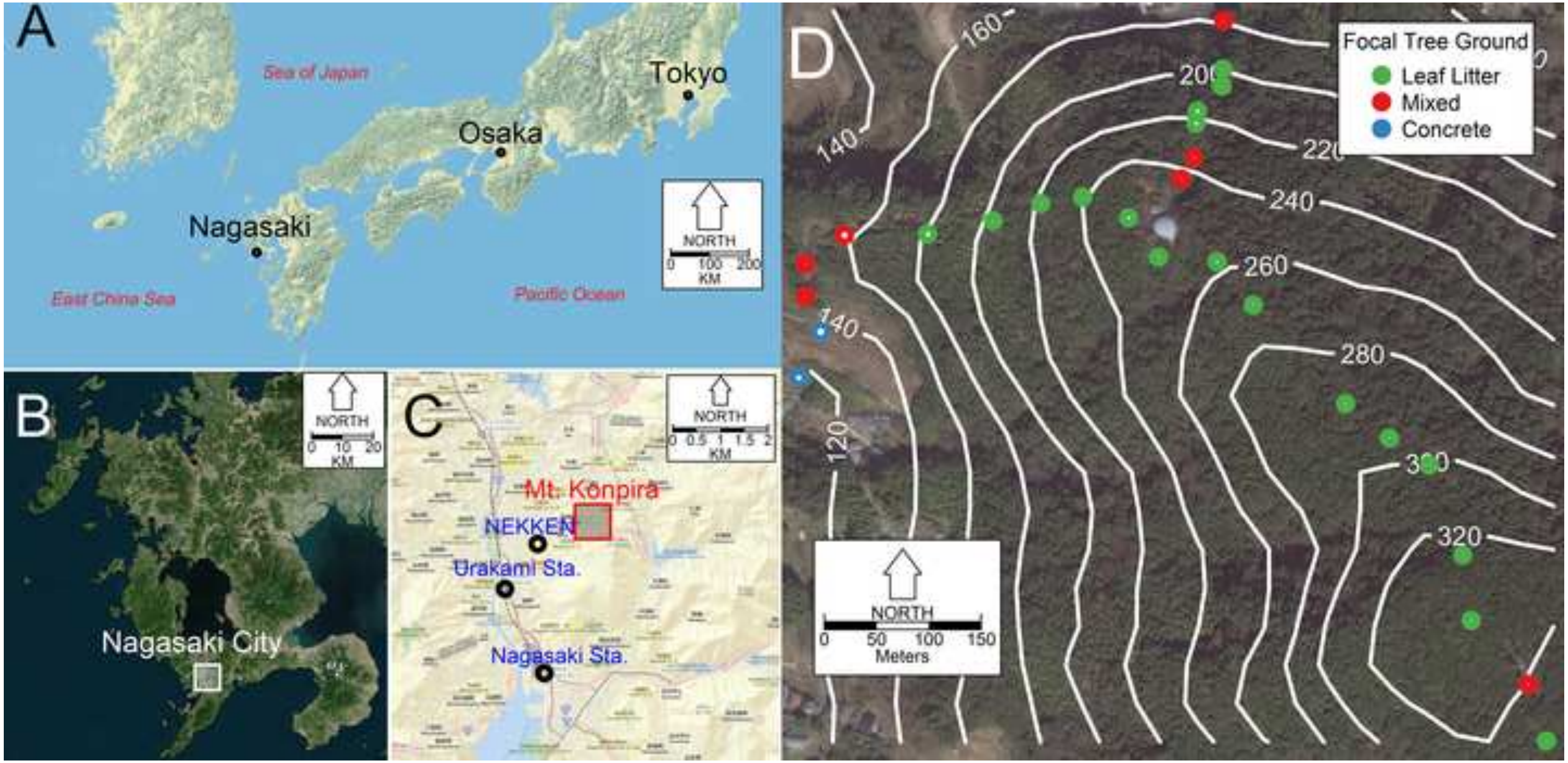
Figure Legends

Figure 1 Study Site (A) Relative location of Nagasaki in temperate East Asia. For reference, the cities of Osaka and Tokyo are also shown (B) Location of Nagasaki City in west Kyushu, the area of the city is highlighted (C) Location of Mt. Konpira in Nagasaki. Reference points include the two main train stations in the city, as well as, the Nagasaki University Institute of Tropical Medicine, NEKKEN (D) Location of the focal trees where ovitraps were set in Mt. Konpira. Isoclines are shown, and colors indicate the dominant ground type around the focal trees, see legend for details. The size of the white spot is proportional to the canopy openness around each focal tree.

Figure 2 Patterns of spatial (N_i) abundance of adult *Aedes albopictus*, *Aedes flavopictus* and *Aedes japonicus* as function of landscape features and climatic variables at Mt. Konpira in 2014. (A) Elevation (B) Landscape slope (C) Canopy openness (D) S.D. of relative humidity (E) Mean temperature (F) S.D. of temperature. The inset legend in panel (C) indicates the symbol for each mosquito species.

Figure 3 Temporal patterns of adult *Aedes albopictus*, *Aedes flavopictus* and *Aedes japonicus* abundance (N_t), weather factors and per capita population growth rate ($r_t = \ln(N_{t+1})-\ln(N_t)$) from May to November 2014 in Mt. Konpira. (A) Adult abundance. The inset legend indicates the color for each species in this and subsequent panels, unless otherwise noted (B) Partial auto-correlation functions, PACF, for each mosquito species (C) Cross-correlation functions, CCF, between pairs of mosquito species, the inset legend indicates combinations of species, where albo=*Ae albopictus*, flavo=*Ae flavopictus* and japo=*Ae japonicus* (D) Rainfall time series (E) CCF between Rainfall and the abundance of each mosquito species (F) Relative humidity, RH, time series. The time series is the average from measurements taken around each focal tree (G) CCF between RH and the abundance of each mosquito species (H) Temperature time series (I) CCF between Temperature and the abundance of each mosquito species (J) *Ae albopictus* N_t and (K) *Ae flavopictus* N_t and (L) *Ae japonicus* N_t as function of $Rain_t$. Population growth rate (r_t) of: (M) *Ae albopictus* and (N) *Ae flavopictus* and (O) *Ae japonicus* as function of N_t. Time series presented in: (A) are the totals from the 27 sampling locations, (D) is from the Nagasaki City weather station, (F) and (H) are the averages from measurements taken at the sampling locations. In (B), (C), (E), (G) and (I) the dashed lines indicate the 95% confidence limits for correlations expected by random. The size of the circle is proportional to: *Ae japonicus* N_{t-1} in (L) and *Ae flavopictus* N_t in (M) and (O). For a guide to mosquito abundance in panels, (L), (M) and (O), please refer to the inset legend with black dots in panel (L).

Figure 1


A
Sea of Japan
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Osaka
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NORTH
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East China Sea
Pacific Ocean
B
NORTH
0 10 20
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Nagasaki City
C
NORTH
0 0.5 1 1.5 2
KM
Mt. Konpira
NEKKEN
Urakami Sta.
Nagasaki Sta.
D
160
140
200
220
240
260
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300
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Focal Tree Ground
Leaf Litter
Mixed
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0 50 100 150
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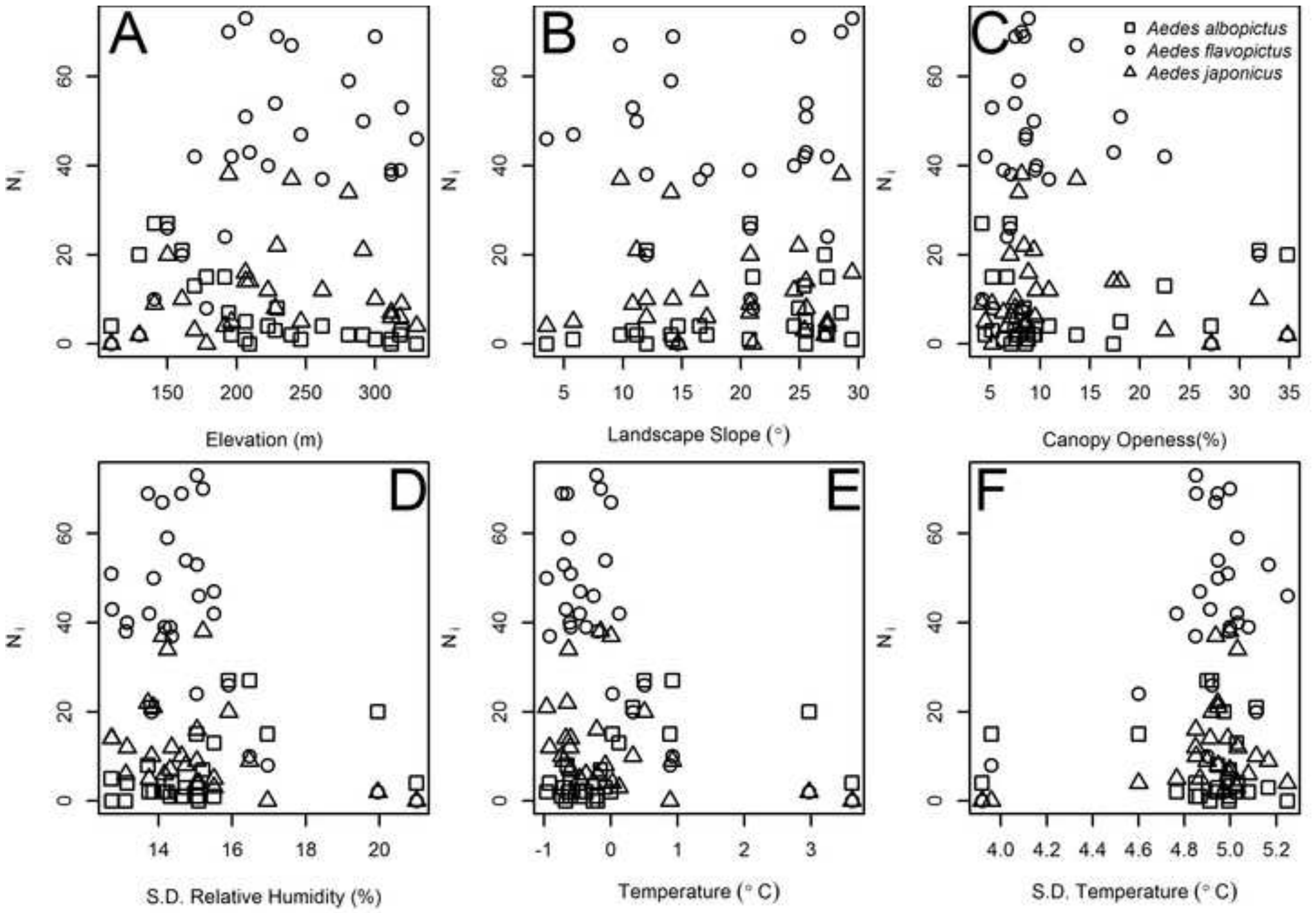
Figure 2


A
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□ Aedes albopictus
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△ Aedes japonicus
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40
60
150
200
250
300
Elevation (m)
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10
15
20
25
30
Landscape Slope (°)
5
10
15
20
25
30
35
Canopy Openess(%)
14
16
18
20
S.D. Relative Humidity (%)
-1
0
1
2
3
Temperature (° C)
4.0
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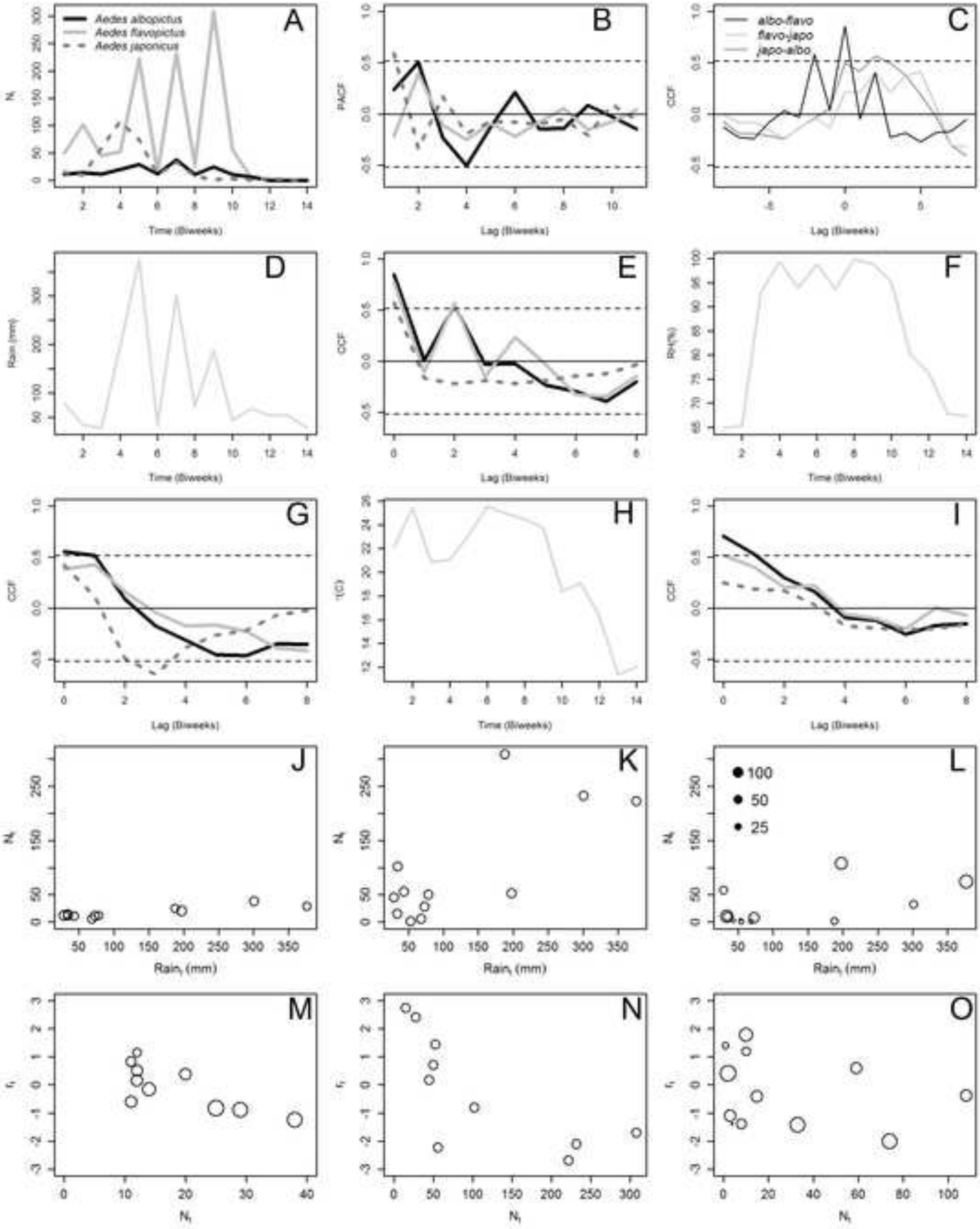
4.4
4.6
4.8
5.0
5.2
S.D. Temperature (° C)

Figure 3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Aedes albopictus
Aedes flavopictus
Aedes japonicus
albo-flavo
flavo-japo
japo-albo
N
PACF
CCF
Rain (mm)
RH(%)
T(C)
N_t
r_t
Time (Biweeks)
Lag (Biweeks)
$Rain_t$ (mm)
N_t
● 100
● 50
● 25