

1 **Population dynamics of *Armigeres subalbatus* (Diptera: Culicidae) across a**  
2 **temperate altitudinal gradient**

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10 Short Title: **Population dynamics of *Armigeres subalbatus***

## 11 **Abstract**

12 Understanding the impacts of weather fluctuations, and environmental gradients, on the  
13 abundance of vectors is fundamental to grasp the dynamic nature of the entomological  
14 risk for disease transmission. The mosquito *Armigeres subalbatus* (Coquillet) is a  
15 common vector of filariasis. Nevertheless, its population dynamics have been relatively  
16 poorly studied. Here, we present results from a season long study where we studied  
17 spatio-temporal abundance patterns of *Ar. subalbatus* across the altitudinal gradient of  
18 Mt. Konpira in Nagasaki, Japan. Spatially, we found that abundance of adult *Ar.*  
19 *subalbatus* decreased with altitude and increased in areas where the ground was rich in  
20 leaf litter. Similarly, adult activity was observed only when relative humidity was over  
21 65%. Temporally, we found that peaks in abundance followed large rainfall events.  
22 Nevertheless, this mosquito was under significant density dependence regulation. Our  
23 results suggest that *Ar. subalbatus* population peaks following large rainfall events could  
24 reflect the recruitment of individuals that were dormant as dry eggs. We did not find a  
25 clear signal of temperature on abundance changes of this mosquito, but only on its  
26 phenology. Since ground cover seemed more critical than temperature to its spatial  
27 distribution, we propose that this mosquito might have some degree of autonomy to  
28 changes in temperature.

29 **Key-Words:** Schmalhausen's law, Ricker model, filariasis, density-dependence, forcing

## 30 Introduction

31 Mosquitoes have been widely studied because of their role as vectors of several  
32 pathogens affecting humans and animals (Silver 2008). Mosquito population dynamics  
33 are of particular interest because mosquito abundance shapes the entomological risk of  
34 vector-borne disease transmission (Dye 1990). Specifically, vectorial capacity, the  
35 ability of a pathogen to be propagated by the action of insect vectors, linearly increases  
36 with vector-abundance (Garrett-Jones 1964). Thus, the risk for disease transmission  
37 can be both spatially (Kitron 1998) and temporally (Chaves et al. 2011) linked to vector  
38 abundance. Nevertheless, a detailed knowledge of factors regulating the abundance of  
39 mosquitoes, such as density-dependence and the impact of weather changes over a  
40 heterogenous landscape, have been relatively poorly studied for species other than  
41 dominant vectors (Chaves and Koenraadt 2010), with few exceptions (Yang et al. 2008a,  
42 Hoshi et al. 2014a). Studies of mosquitoes over altitudinal gradients, in the context of  
43 climate change, allow to simultaneously evaluate mosquito abundance over the gradient  
44 of temperatures associated with elevation (Eisen et al. 2008), where, in general,  
45 temperature decreases with altitude. Similarly, information about mosquitoes with minor,  
46 or without any, medical importance is fundamental to understand possible evolutionary  
47 constraints on the response of mosquitoes, and the diseases they transmit, to climate  
48 change (Chaves and Koenraadt 2010).

49 The mosquito *Armigeres subalbatus* is a vector of filarial worms with medical  
50 importance, *Brugia pahangi* (Muslim et al. 2013) and with veterinary importance,  
51 *Dirofilaria repens* (Lee et al. 2007). *Ar. subalbatus* has also been found infected with  
52 Japanese Encephalitis Virus, JEV (Tanaka et al. 1979) and has been incriminated as a  
53 JEV vector in settings without rice fields (Chen et al. 2000). Regarding bloodfeeding, it  
54 has been reported that this mosquito was able to experimentally feed on humans, mice,  
55 chickens and reptiles, but not amphibians (Miyagi 1972), thus reinforcing the view that  
56 this mosquito can transmit zoonotic pathogens (Chaves et al. 2010).

57 The mosquito *Ar. subalbatus* is widely distributed in Asia (Tanaka et al. 1979,  
58 Amerasinghe and Munasingha 1988a, b) and has been observed across altitudinal  
59 gradients (Zea Iriarte et al. 1991), yet no detailed study has assessed its population

60 regulation. Studies on the natural history of *Ar. subalbatus* have shown that its larvae  
61 are common in nutrient enriched water (Senior-White 1925, Barr and Chellappah 1964),  
62 including septic tanks (Moriya et al. 1967), especially with high ammonia concentration  
63 (Rajavel 1992b), and the nutrient enriched water can be clear or turbid (Amerasinghe  
64 and Munasingha 1988b). This mosquito also colonizes bamboo stumps (Kurashige  
65 1963), artificial containers (Zea Iriarte et al. 1991) and treeholes (Tsuda et al. 1994).  
66 Overwintering occurs in the larval stage (Mogi 1996), and larvae seem to enter  
67 diapause because of a synergistic interaction between low temperature and short day  
68 length (Oda et al. 1978). It has also been suggested, based on laboratory observations,  
69 that dry conditions may lead to egg diapause (Barr and Chellappah 1964). The  
70 phenology of adults also seems to be strongly seasonal, with latitudinal variation. For  
71 example, in Taiwan adult *Ar. subalbatus* were absent from mosquito traps during  
72 January and February (Sun 1964), at the higher latitude of Shandong province, China  
73 from November to early May (Zhang et al. 1992). At the even higher latitude of Kyoto,  
74 Japan adult mosquitoes have been only observed from August to October (Nakata and  
75 Ito 1955). Rainfall has been suggested as an important factor for *Ar. subalbatus*  
76 population changes, with significant adult abundance increases during and after high  
77 rainfall (Amerasinghe and Munasingha 1988a). Here, we present results from a season  
78 long study of *Ar. subalbatus* abundance patterns in Mt. Konpira in Nagasaki, Japan. We  
79 asked what factors of the landscape were correlated with *Ar. subalbatus* abundance  
80 across the altitudinal gradient of Mt. Konpira, and whether its population dynamics were  
81 under density dependence regulation while accounting for potential impacts of weather  
82 changes on its abundance.

## 83 **Materials and Methods**

84 **Study site:** Larval and adult mosquitoes were biweekly sampled across 27 locations in  
85 Mt. Konpira (Fig. 1). Mt. Konpira is located in Nagasaki city, northwest Kyushu, western  
86 Japan (Fig. 1). Nagasaki has a temperate seasonal climate, with 4 well defined seasons.  
87 Temperature in the winter (from December to February) rarely drops below 0 °C and  
88 snowfall is minimal, often absent. By contrast, the summer (mid July to mid September)  
89 has both high relative humidity, above 65%, and temperature, above 27 °C (Isida 1969).

90 Our sampling locations in Mt. Konpira followed those of a previous study in the same  
91 area, ranging from 109 to 330 m in altitude (Zea Iriarte et al. 1991). The sampling  
92 setting consisted of three radial transects, across an altitudinal gradient, joined at a  
93 middle point (Fig. 1). Our sampling locations were mainly located across a secondary  
94 forest, with diverse types of dominant vegetation according to the Japanese Ministry of  
95 the Environment (available at <http://www.vegetation.biodic.go.jp/>), but there were some  
96 urban sites in the periphery of all the sampling locations (Fig. 1). Exact coordinates for  
97 each sampling location were measured with a Garmin Oregon 650 GPS (Garmin Ltd,  
98 KS, USA), which was also used to measure the site altitude, in m. The altitude  
99 measures were compared with those from an ASTER digital elevation model, DEM, for  
100 Mt. Konpira (available at <http://gdem.ersdac.jpacesystems.or.jp/>), and given the low  
101 disagreement between the two measurements, we employed the DEM data in our  
102 analysis. At each sampling location we characterized the canopy cover in May 25<sup>th</sup> 2014  
103 by following a standard methodology (Frazer et al. 2001) where 4 photographs were  
104 taken with a fisheye ball lens located at ground level within a 1.5 m radius of a focal tree,  
105 i.e., a tree where an ovitrap was located. For the photos we used a EOS 40D camera  
106 (Canon Co., Tokyo, Japan) that had attached a normal lens (EF-S17-85mm F4-5.6 IS  
107 USM; Canon Co., Tokyo, Japan) and a 180° fisheye lens (Nordward optronics 0.25X  
108 Super fisheye lens 180° G2; Revel Royal Inc, Aichi, Japan), which allowed to take  
109 hemispherical photos. The images were subsequently analyzed with the gap light  
110 analysis mobile application for android tablets ([http://gap-light-analysis-mobile-  
111 app.android.informer.com/](http://gap-light-analysis-mobile-app.android.informer.com/)) to determine the average and S.D. of canopy cover for each  
112 sampling location. We also quantified the ground cover by sampling twelve 2.5 m long  
113 transects radiating from each focal tree. Each transect had an approximate angular  
114 separation of 30°. We categorized each transect as: grass, leaf litter, bush, trees,  
115 concrete and terrace, based on the dominant group type among those 6 categories. A  
116 matrix with the percent of transects in each category at each sampling point was then  
117 analyzed with principal components analysis (Chaves et al. 2011), and the 1<sup>st</sup> principal  
118 component (Table S1) was then used as a ground cover index.

119 **Mosquito Sampling:** To sample immature mosquito stages we made “ovitrap” (Zea  
120 Iriarte et al. 1991) by using 350 ml Coca-Cola® cans painted black with an acrylic spray

121 paint (Kanpe Hapio Co., Ltd., Osaka, Japan) inside and outside. We made one 5 mm  
122 opening to both hold the can to a tree, using a cord, and to drain excess water above  
123 280 ml. All traps were uniformly set at 1.2 m above the ground level. We selected this  
124 height given that previous reports indicated that *Ar. subalbatus* preferentially oviposits in  
125 containers around this height (Amerasinghe and Alagoda 1984). Ovitrap were filled  
126 with rain water collected during April 2014 and were set in May 18th, and then biweekly  
127 surveyed from June 1st until November 29<sup>th</sup> of 2014. During each survey we determined  
128 the presence of 1<sup>st</sup> to 3<sup>rd</sup> instar mosquito larvae of any species, and we counted the  
129 number 4<sup>th</sup> instar larvae of *Tripteroides bambusa* Yamada and *Ar. subalbatus*, due to  
130 their easy identification in the field (Tanaka et al. 1979), and removed all other 4<sup>th</sup> instar  
131 larvae and all pupae for laboratory rearing and identification of emerged adults (Hoshi et  
132 al. 2014a).

133         Adult mosquitoes were sampled using a sweep net (36-cm diam; Model 61-1B;  
134 Shiga Insect Co., Tokyo, Japan), a common tool to sample adult mosquitoes (Hoshi et  
135 al. 2014b). Sampling started at sunrise. We selected this sampling time given previous  
136 reports that indicated this mosquito is active at sunrise (Berlin et al. 1975). Also sweep  
137 nets are appropriate to sample this mosquito, which is predominant at ground level  
138 (Tsuda et al. 2003). The use of sweep nets was standardized by staying at a fixed point  
139 within a 2.5 m radius from the focal tree where the ovitraps were set up. After arriving to  
140 a sampling location the net was swept around the body of the person sampling for 2  
141 minutes, after this time period the person sampling stopped for 1 min and then swept  
142 the net for another 2 min. During each sampling session the order of the sampling  
143 locations was determined randomly in order to avoid any possible bias due to sampling  
144 the same locations always at the same time. Adult mosquitoes were biweekly sampled  
145 between May 4<sup>th</sup> and November 15<sup>th</sup> of 2014. We selected a biweekly sampling to have  
146 a sampling interval that coincided with the pre-adult developmental time of *Ar.*  
147 *subalbatus* (Weathersby 1962). Similarly, we started to collect mosquitoes in May, given  
148 that in Shandong Province, China, at the same latitude of Nagasaki, adult mosquitoes  
149 have only been caught after May 10<sup>th</sup> (Zhang et al. 1992).

150 **Weather Variables:** At each sampling session we recorded the air temperature and  
151 relative humidity using a portable O-230 termohygrometer (Dretec Co., Saitama, Japan).  
152 The water temperature in the ovitraps was measured using an AD-5617WP infrared  
153 thermometer (A&D Co., Tokyo, Japan). Data on daily records for rainfall from May 1<sup>st</sup>  
154 2014 to December 1<sup>st</sup> 2014 were obtained for Nagasaki city from the Japanese  
155 Meteorological Agency Website (<http://www.jma.go.jp/jma/index.html>). For the analyses  
156 we employed the cumulative amount of rainfall on the 14 days prior to the mosquito  
157 sampling. The weather station is located within a 5 km radius from our study site.

158 **Mosquito identification:** Fourth instar larvae and adult mosquitoes were identified  
159 using the taxonomic key of Tanaka et al (1979). Voucher specimens are available in the  
160 Entomological Collection in the Institute of Tropical Medicine of Nagasaki University,  
161 Japan and in the Mosquito Collection in the Walter Reed Biosystematics Unit –  
162 Smithsonian Institute, Washington DC, USA.

163 **Statistical analysis:** Larvae data of *Ar. subalbatus* were not analyzed given that we  
164 found them at two localities, once at one site, inside a vacant lot bordering a prickly  
165 forest, and two times at another other site, inside an area whose vegetation was  
166 dominated by acorns (Fig. 1).

167 To detect spatio-temporal clusters, i.e., hotspots, of *Ar. subalbatus* adults, we  
168 employed an elliptical cluster detection mode in a SCAN spatio temporal Poisson model  
169 (Kulldorff and Nagarwalla 1995, Kulldorff et al. 2005). We constrained the maximum  
170 cluster size up to 50% of the samples while scanning the whole study site. We chose  
171 the elliptical shape over a circular one given that our sampling followed transects  
172 (Kulldorff et al. 2006). For statistical inference we employed 999 Monte Carlo  
173 simulations. We then proceeded with a spatial analysis of *Ar. subalbatus* abundance in  
174 Mt. Konpira, Nagasaki. We fitted Poisson generalized linear models (Faraway 2006) to  
175 the total abundance per site. The total abundance per site was obtained by adding the  
176 abundance through the 14 biweeks of sampling at each sampling location (Fig. 1). We  
177 started by building a model that included elevation (m), mean and S.D. canopy  
178 openness (%), mean, S.D. and kurtosis of temperature (<sup>0</sup>C) and relative humidity (%),  
179 and the ground cover index. This model was simplified by a combined backward-

180 elimination and forward-addition algorithm (Kuhn and Johnson 2013) that minimized the  
181 Akaike Information Criterion (AIC). Briefly, AIC is a model selection criterion that weighs  
182 the trade-off between the goodness of fit in a model and the number of parameters, and  
183 the best model is chosen by minimizing the difference between a function of a model  
184 log-likelihood and the number of parameters (Kuhn and Johnson 2013). Moran's I test  
185 (Venables and Ripley 2002) was employed to test the spatial independence of residuals  
186 in the model selected as best, in order to ensure that inferences from the best Poisson  
187 generalized linear model were sound (Chaves 2010).

188 For the temporal analysis of *Ar. subalbatus* abundance we generated a 14  
189 observations adult abundance time series, given the absence of adult mosquitoes  
190 during May 4<sup>th</sup> 2014. The time series was generated by adding the biweekly records  
191 across the 27 sampled sites per sampling session. We used this time series for some  
192 preliminary time series statistical analysis. We estimated the autocorrelation (ACF) and  
193 partial autocorrelation (PACF) functions to describe the patterns of temporal  
194 autocorrelation in *Ar. subalbatus* abundance (Chaves et al. 2012, Chaves et al. 2013).  
195 The ACF presents the correlation of a time series with itself through different time lags,  
196 while PACF shows a similar profile that only considers the correlation between  
197 consecutive time lags (Shumway and Stoffer 2011). We also estimated the cross  
198 correlation functions (CCFs), i.e., the temporal correlation function between two time  
199 series for different time lags (Shumway and Stoffer 2011), between the *Ar. subalbatus*  
200 abundance time series and Rainfall, Temperature and Relative Humidity. We estimated  
201 the 95% confidence limits, CL, of the ACFs, PACFs and CCFs to test if the correlations  
202 departed from what would be expected by random, with only correlations outside the  
203 95% CL being considered statistically significant (Shumway and Stoffer 2011). Then,  
204 we proceeded to study of the density-dependence regulation of *Ar. subalbatus* adults.  
205 We started by plotting the per-capita growth rate ( $r$ ) of this mosquito as function of its  
206 total adult abundance ( $N_t$ ). The per-capita growth rate is defined by (Turchin 2003):

$$207 \quad r = \ln(N_t) - \ln(N_{t-1}) \quad (1)$$

208 Based on the results from this preliminary analysis, we fitted the Ricker model to the *Ar.*  
209 *subalbatus* time series data. The Ricker model has been widely used to study mosquito



210 populations (Yang et al. 2008a, Yang et al. 2008b, Hoshi et al. 2014a) and is defined by  
 211 the following equation:

$$212 \quad N_t = \lambda_0 N_{t-1} \exp(-bN_{t-1}) \quad (2)$$

213 Where  $\lambda_0$  is the intrinsic rate of population growth and  $b$  is a density-dependence  
 214 coefficient (Turchin 2003). When  $-b < 0$ , it can be affirmed that a population undergoes  
 215 density-dependent regulation (Turchin 2003). Further details about this model are  
 216 presented elsewhere, including its derivation (Turchin 2003, Mangel 2006) and several  
 217 stochastic versions (Melbourne and Hastings 2008).

218 To fit the models to our data we assumed biweekly adult counts had a negative binomial  
 219 (NegBin) distribution, given our observations had a variance larger than their mean, i.e.,  
 220 they were over-dispersed (Bolker 2008). This assumption for the model presented in (2),  
 221 when also assuming the model has an observation error, i.e., without feedback on  
 222 future states (Bolker 2008), coincides with the assumption that mosquito abundance  
 223 follows a negative binomial environmental stochastic Ricker model (Melbourne and  
 224 Hastings 2008):

$$225 \quad N_t \sim \text{NegBin}(\text{mean} = \lambda_0 N_{t-1} \exp(-bN_{t-1}), \text{overdispersion} = k) \quad (3)$$

226 Which implies stochasticity affects individuals, in this case *Ar. subalbatus* mosquitoes,  
 227 independently of their density. We also fitted the model assuming stochasticity was  
 228 demographic, i.e., a function of mosquito density (Melbourne and Hastings 2008):

$$229 \quad N_t \sim \text{NegBin}(\text{mean} = \lambda_0 N_{t-1} \exp(-bN_{t-1}), \text{overdispersion} = kN_{t-1}) \quad (4)$$

230 We expanded the model presented in (2) to account for the potential impacts of weather  
 231 variables (WV) on the dynamics, as follows:

$$232 \quad N_t = \lambda_0 N_{t-1} \exp(-bN_{t-1} + \gamma WV_{t-z}) \quad (5)$$

233 Where  $\gamma$  is a coefficient for the impact of a WV at any time lag  $z$ . The lag  $z$  for the WVs  
 234 was estimated with the CCFs previously described. To incorporate the forcing of

235 equation (5) into equations (3) and (4), we simply changed the mean of the negative  
 236 binomial to the following:

$$237 \text{ mean} = \lambda_0 N_{t-1} \exp(-bN_{t-1} + \gamma WV_{t-z}) \quad (6)$$

238 To fit the model presented in (3) and its forced version (6), we employed a  
 239 negative binomial generalized linear model (Faraway 2006), using the natural logarithm  
 240 of  $N_{t-1}$  as an offset, and  $N_{t-1}$  and  $WV_{t-z}$  as covariates. Nevertheless, to fit the model  
 241 presented in (4) and its forced version (6), we wrote an R function that is available as a  
 242 supplementary online material (Appendix S1). We computed the AIC of the models for  
 243 comparison.

244 All statistical analysis were implemented with the statistical software R version  
 245 3.2.0, with the exception of the SCAN cluster analysis that was performed with  
 246 SaTScan version 9.3.1.

## 247 **Results**

248 We collected a total of 114 adults and 21 4<sup>th</sup> instar larvae of *Ar. subalbatus*  
 249 during the duration of our study (Fig. 1). Adults of *Ar. subalbatus* were present through  
 250 all the land cover uses and vegetation types that we sampled, and were only absent  
 251 from one of the points that we sampled (Fig. 1). The average ( $\pm$  S.D.) number of adults  
 252 per sampling location was  $4.22 \pm 2.35$ , ranging from 0, i.e., a place where *Ar.*  
 253 *subalbatus* was never detected, to 9 individuals (Fig. 1). Fig. 1 also shows that adults of  
 254 *Ar. subalbatus* were clustered across the northernmost sampling locations, which were  
 255 all inside an area of the forest dominated by acorns.

256 The best spatial model showed that elevation and ground cover (Table 1) were  
 257 the best covariates explaining the spatial patterns of *Ar. subalbatus* abundance. The  
 258 lack of significance for the Moran's I index (Table 1) indicates spatial independence in  
 259 the residuals, thus fulfilling the assumptions for a sound statistical inference (Chaves  
 260 2010). Fig. 2 clearly shows how the number of adult *Ar. subalbatus* decreased with  
 261 elevation and increased with the ground cover index, where positive values indicate a

262 dominance of leaf litter over bushes and/or concrete (Table S1 online only), while  
263 negative values indicate an abundance of bushes and/or concrete over leaf litter.

264 Temporal patterns of *Ar. subalbatus* (Fig. 3) showed that its abundance peaked  
265 during the 5<sup>th</sup>, 7<sup>th</sup> and 9<sup>th</sup> sampling biweek, i.e., July 12<sup>th</sup>, August 9<sup>th</sup> and September 6<sup>th</sup>  
266 respectively, reaching a maximum of 34 individuals (Fig. 3A). From the 13<sup>th</sup> biweek of  
267 sampling we did not catch any *Ar. subalbatus*. The average ( $\pm$  S.D.) number of adults  
268 per sampling biweek was  $8.14 \pm 10.23$ . In general, *Ar. subalbatus* abundance time  
269 series had temporally independent observations, as indicated by the lack of significant  
270 lags in its ACF (Fig. 3B) and PACF (Fig. 3C). Regarding fluctuations in the weather  
271 variables, it can be seen that peaks in mosquito abundance (Fig. 3A) overlapped with  
272 those of rainfall (Fig. 3D), but not those of temperature (Fig. 3E) nor relative humidity  
273 (Fig. 3F), nevertheless, these two last factors seem to be related with the presence of  
274 adult mosquitoes, which were only captured when their values were high. CCF  
275 analysis showed that *Ar. subalbatus* abundance was significantly associated with  
276 rainfall without a temporal lag (Fig. 3G), but not with temperature (Fig. 3H), nor with  
277 Relative Humidity (Fig. 3I).

278 As expected in a population undergoing density-dependent regulation (Fig. 4) we  
279 found that the per capita growth rate of *Ar. subalbatus* decreased with its population  
280 size.

281 Estimates of the environmental negative binomial Ricker model (Table 2)  
282 outperformed those of the demographic one (Table S2, online only). Table 2 shows the  
283 fit considering the forcing by rainfall was better, i.e., with a lower AIC, than an  
284 autonomous model. The effect of rainfall on the density dependent regulation of *Ar.*  
285 *subalbatus* (Fig. 5) was to increase the number of mosquitoes, nevertheless, in all  
286 cases the abundance of *Ar. subalbatus* was under a strong density dependence, with  
287 the per capita growth rate diminishing with adult abundance in all instances.

## 288 Discussion

289 We found that temporal changes in adults of *Ar. subalbatus* were autonomous  
290 from changes in temperature and relative humidity. Nevertheless, these two factors may

291 be important for the phenology of *Ar. subalbatus* adult activity, since we only found the  
292 species when temperatures were above 14 °C and relative humidity above 65%. In fact,  
293 we found that phenology of adults of *Ar. subalbatus* at our study site was similar to  
294 observations at a similar latitude in China, where adult mosquitoes were only observed  
295 from May to October (Zhang et al. 1992). Moreover, our spatial model indicated that  
296 abundance of *Ar. subalbatus* adults decreased with altitude, further supporting that  
297 temperature might be important to the phenology and distribution of this mosquito, as  
298 suggested by observations across different latitudes (Nakata and Ito 1955, Sun 1964,  
299 Zhang et al. 1992) and studies on its overwintering (Oda et al. 1978). However, spatially  
300 we also found that adults of *Ar. subalbatus* were more common on grounds with  
301 abundant leaf litter, suggesting that organic matter necessary for enriching potential  
302 larval habitats (Senior-White 1925, Rajavel 1992b) is a factor that might modulate  
303 habitat use by adults. This ground cover also resembles the habitats where this  
304 mosquito has been found transmitting filarial worms (Muslim et al. 2013). Therefore,  
305 ground cover might be important to understand landscape heterogeneities in pathogen  
306 transmission risk by *Ar. subalbatus*.

307         The positive impact of rainfall on adult *Ar. subalbatus* abundance can be related  
308 to two aspects of its biology: (i) under dry conditions, eggs can enter diapause (Barr and  
309 Chellappah 1964) and (ii) the low variability in oviposition above the water surface,  
310 where more than 75% of the eggs were within a “threshold” of 16 mm above the  
311 waterline (Amerasinghe and Alagoda 1984), suggest that any rainfall above the  
312 oviposition “threshold” has the potential to synchronously trigger egg hatching in *Ar.*  
313 *subalbatus* larval habitats, which can lead to an eventual “outbreak” or sudden large  
314 change in mosquito abundance (Chaves et al. 2014), as we observed in our study site,  
315 a pattern also observed in Sri Lanka (Amerasinghe and Munasingha 1988a).  
316 Unfortunately, the scarcity of larval samples did not allow us to connect any potential  
317 changes in larval density with adult abundance. However, a previous study (Rajavel  
318 1992a) suggests that at high larval density *Ar. subalbatus* keeps its numbers in check  
319 by cannibalizing larvae, especially if *Ar. subalbatus* does not co-occur with other  
320 mosquito species, and in that regard we can mention that we found 4<sup>th</sup> instar larvae of  
321 *Ar. subalbatus* only co-existing with larvae of *Tp. bambusa*, the most common and

322 abundant mosquito in our ovitraps, following a similar pattern also observed by Zea  
323 Iriarte et al (1991) in our study area. However, we were unable to assess any potential  
324 interaction between these two species given the scarce *Ar. subalbatus* larval data that  
325 we collected.

326 Our results clearly indicate that there is density dependence regulation in *Ar.*  
327 *subalbatus*. The density dependence parameter  $b$  in the Ricker model was negative as  
328 expected under density dependence regulation (Turchin 2003), and in congruence with  
329 patterns observed in several mosquitoes (Makiya 1973, 1974, Yang et al. 2008a, Yang  
330 et al. 2008b, Chaves et al. 2012, Hoshi et al. 2014a). However, although rainfall can  
331 transiently increase the number of adults, population growth still decreases with  
332 population abundance, highlighting the importance of density dependence regulation. It  
333 is also interesting to note that for the autonomous environmental stochastic Ricker  
334 model, the natural logarithm of the intrinsic rate of population growth parameter, i.e.,  
335  $\ln(\lambda_0) = 1.98$ , was close to the threshold value for weather independent oscillations,  
336 a.k.a., bifurcations, which is  $\ln(\lambda_0) \geq 2$  (Mangel 2006). Nonetheless, when considering  
337 rainfall it became clear that any potential periodicities likely reflected rainfall patterns.  
338 Finally, we can conclude that population dynamics of adult *Ar. subalbatus* follows  
339 Schmalhausen's law, the prediction that systems are more sensitive to environmental  
340 variables more unpredictable around their mean (Chaves and Koenraadt 2010, Chaves  
341 et al. 2012). Rainfall, the only weather variable associated with abundance changes in  
342 *Ar. subalbatus* adults, undergoes less extreme changes in its mean behaviour than  
343 temperature or relative humidity at our study site, which although more extreme, have a  
344 more predictable pattern of change and seem to impact *Ar. subalbatus* phenology, but  
345 not its abundance dynamics.

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## 352 **Figure Legends**

353 **Fig. 1** Map of sampling locations. The inset figure shows the location of Mt. Konpira in Nagasaki,  
 354 Japan. Contour lines indicate the elevation. The inset legend indicates the land use types and  
 355 vegetation cover, and there is also a guide to the total abundance of *Armigeres subalbatus*  
 356 adults and 4<sup>th</sup> instar larvae sampled during May to November 2014. A dashed red line indicates  
 357 a significant spatio-temporal cluster.

358 **Fig. 2** Spatial patterns of *Armigeres subalbatus* abundance. Dot size is proportional to  
 359 abundance of *Ar. subalbatus*, ranging from 1 to 9, as function of ground cover and altitude. The  
 360 grey gradient indicates the abundance estimated with the model presented in Table 1.

361 **Fig. 3** Temporal patterns of *Armigeres subalbatus* abundance. (A) Time series of *Ar. subalbatus*,  
 362 TSAS, biweekly abundance from May 18<sup>th</sup> to November 15<sup>th</sup> 2014. (B) Auto-Correlation function,  
 363 ACF, of TSAS, (C) Partial ACF, PACF, of TSAS. Time series of weather variables: (D) Rainfall,  
 364 (E) Temperature and (F) Relative Humidity, RH. Cross-Correlation functions between TSAS  
 365 and: (G) Rainfall, (H) Temperature and (I) RH.

366 **Fig. 4** Per capita population growth rate ( $r$ ) of *Armigeres subalbatus* as function of its density,  
 367 ( $N_{t-1}$ ), in Mt. Konpira, Nagasaki, Japan.

368  
 369 **Fig. 5** Temporal Abundance of *Armigeres subalbatus* ( $N_t$ ) as function of its previous abundance  
 370 ( $N_{t-1}$ ) and Rainfall. In the plot dots are proportional to the biweekly abundance of *Ar. subalbatus*  
 371 ( $N_t$ ), which ranged from 1 to 34. The grey gradient indicates the expected number of *Ar.*  
 372 *subalbatus* according to the Ricker model forced by Rainfall (for parameters see Table 2).

373 **Table 1** Parameter estimates for the best spatial Poisson Generalized Linear model explaining  
 374 *Armigeres subalbatus* abundance across an altitudinal gradient. This model was selected by a  
 375 combined backward-elimination and forward-addition algorithm, from a model that included  
 376 elevation (m), mean and S.D. canopy openness, mean, S.D. and kurtosis of temperature ( $^{\circ}\text{C}$ )  
 377 and relative humidity (%), and a ground cover index. The AIC of the starting model was 124.05,  
 378 and the AIC for the model presented here is 111.25.  
 379

Parameter	Estimate	S.E.	z	P
Intercept	2.46	0.45	5.496	<0.0001*
Elevation (m)	-0.0051	0.0020	-2.521	<0.01*
Ground Cover	0.124	0.032	3.881	<0.0001*
Moran's I	-0.0652	-	-	0.574

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

381

382

383 **Table 2** Parameter estimates for the negative binomial environmental stochastic Ricker model  
 384 fitted to the time series of *Armigeres subalbatus* biweekly abundance. Models were fitted with  
 385 (Forced) and without (Autonomous) rainfall as covariate. AIC stands for the Akaike Information  
 386 Criterion.

387

Parameter	Forced				Autonomous			
	Estimate	S.E.	z	P	Estimate	S.E.	z	P
Intrinsic rate of population growth ( $\hat{\lambda}$ )	2.17	1.08	2.01	*	7.37	2.75	2.68	*
Density dependence coefficient ( $\hat{b}$ )	-0.12	0.03	-4.50	**	-0.15	0.03	-5.38	**
Rainfall coefficient ( $\hat{\gamma}$ )	0.0054	0.0020	2.70	**	-	-	-	-
Negative binomial overdispersion ( $\hat{k}$ )	2.68	1.53	-		1.43	0.66		
AIC	74.44				78.00			

388 NS= not significant ( $P>0.05$ ), \*\*Statistically significant ( $P<0.001$ ), \*Statistically significant  
 389 ( $P<0.05$ )

390



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Figure 1

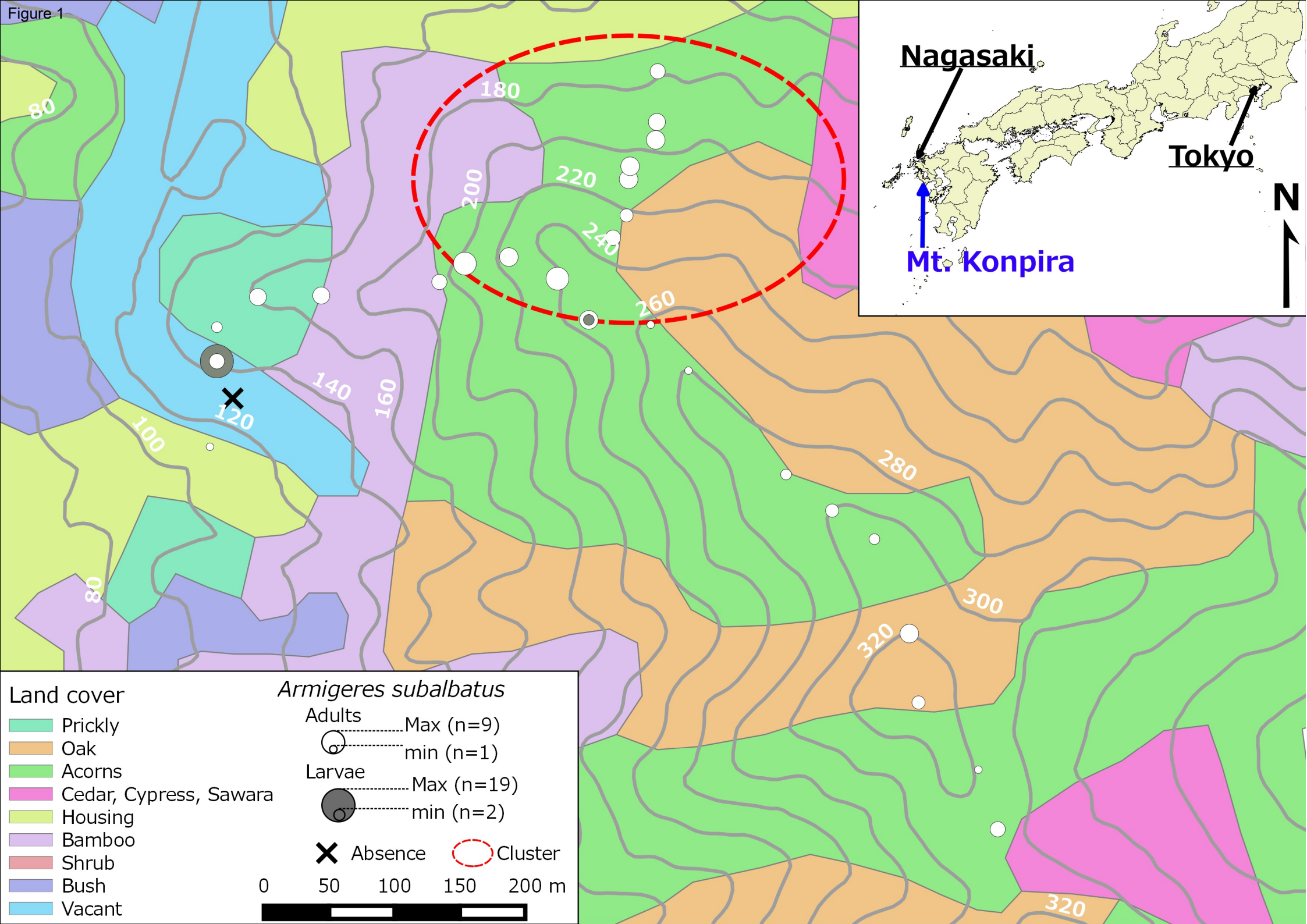


Figure 2

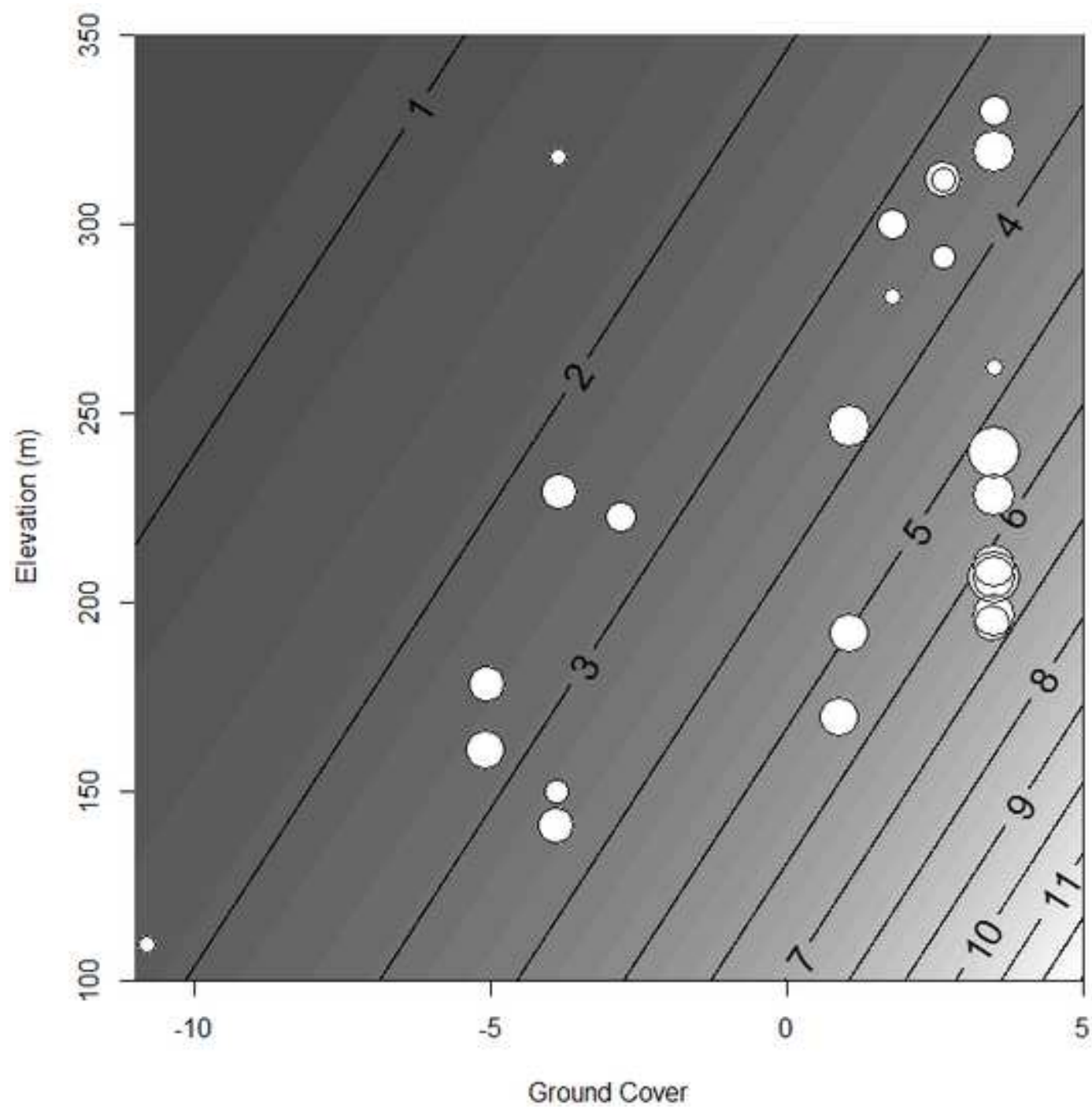


Figure 3

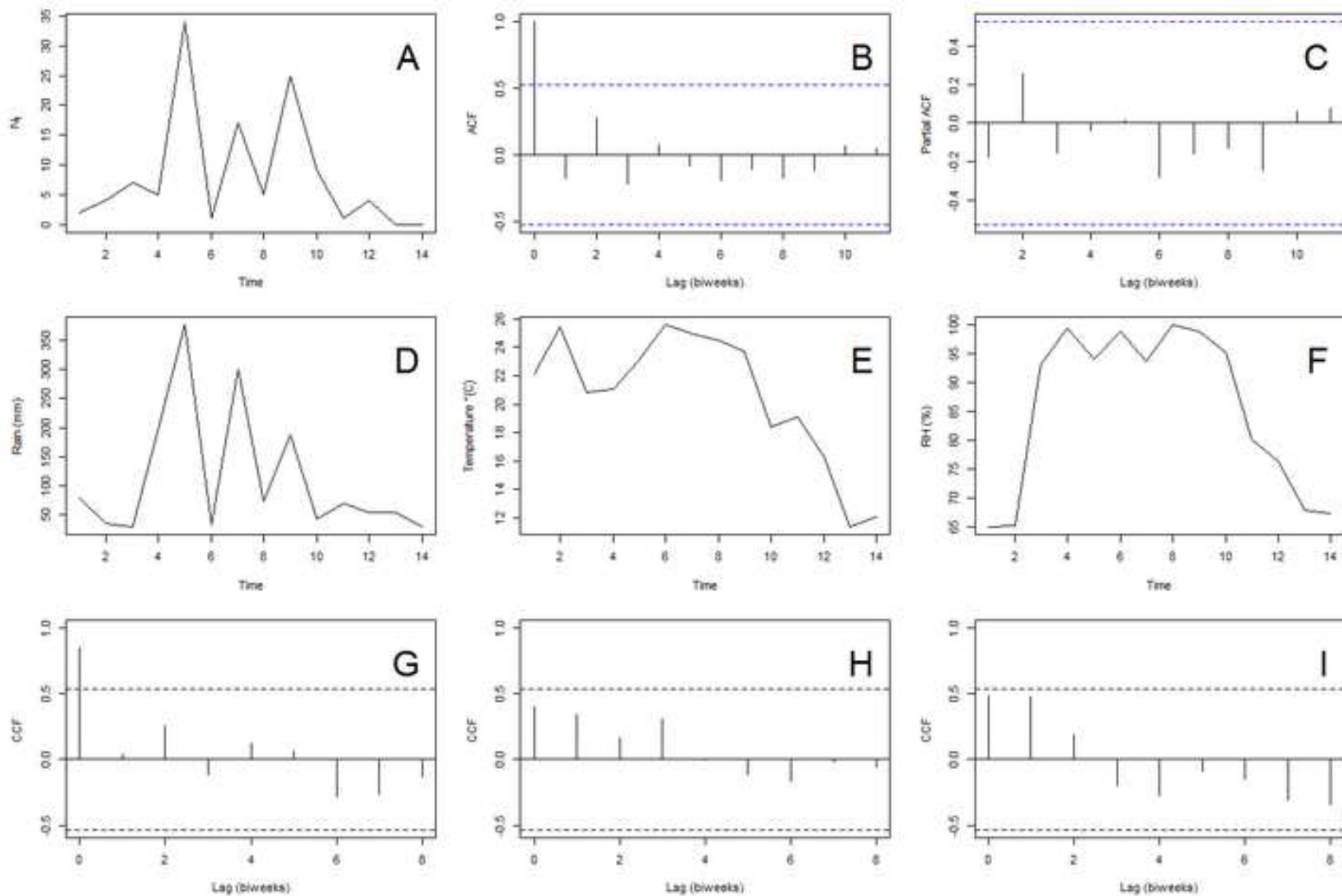


Figure 4

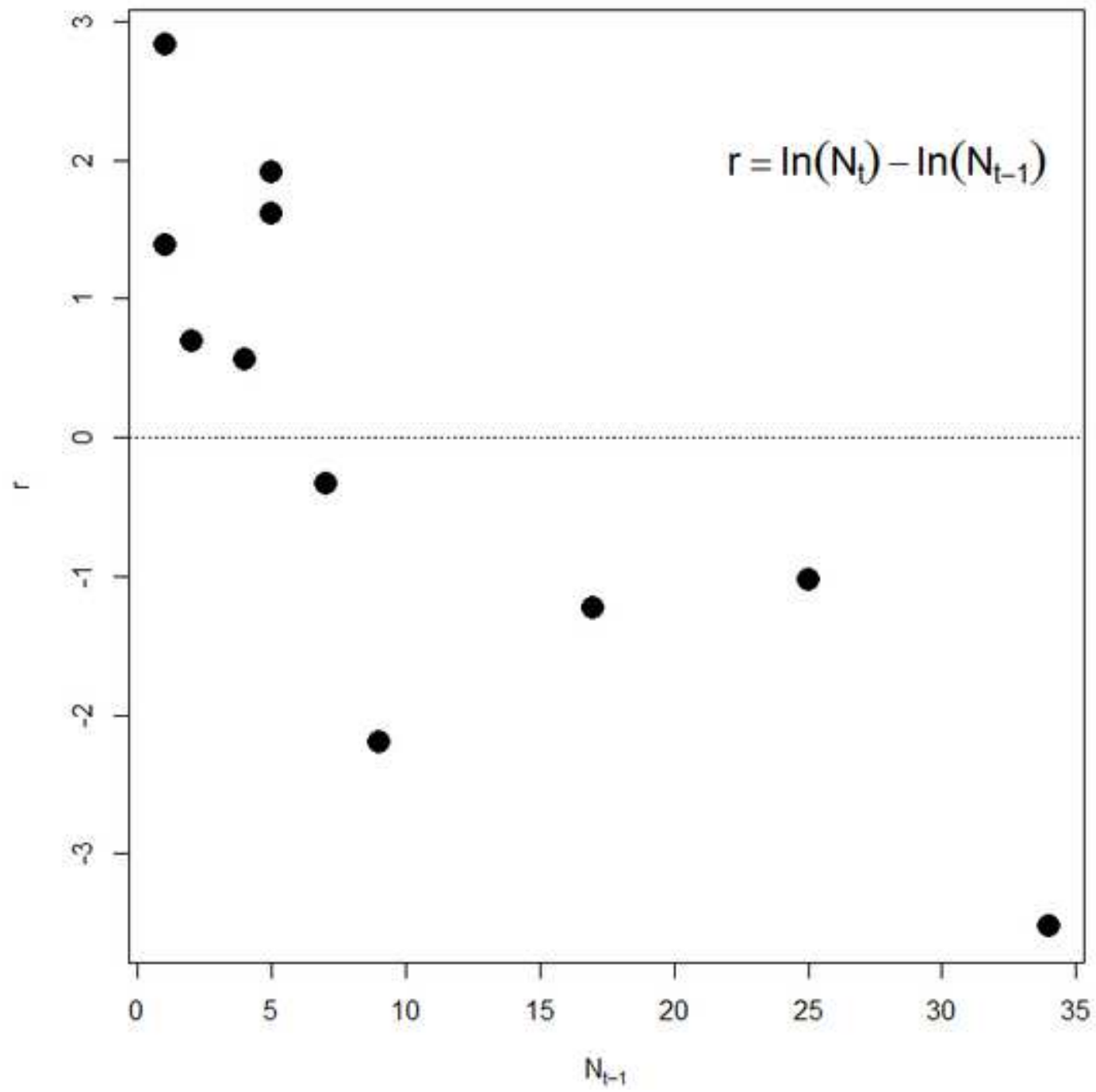


Figure 5

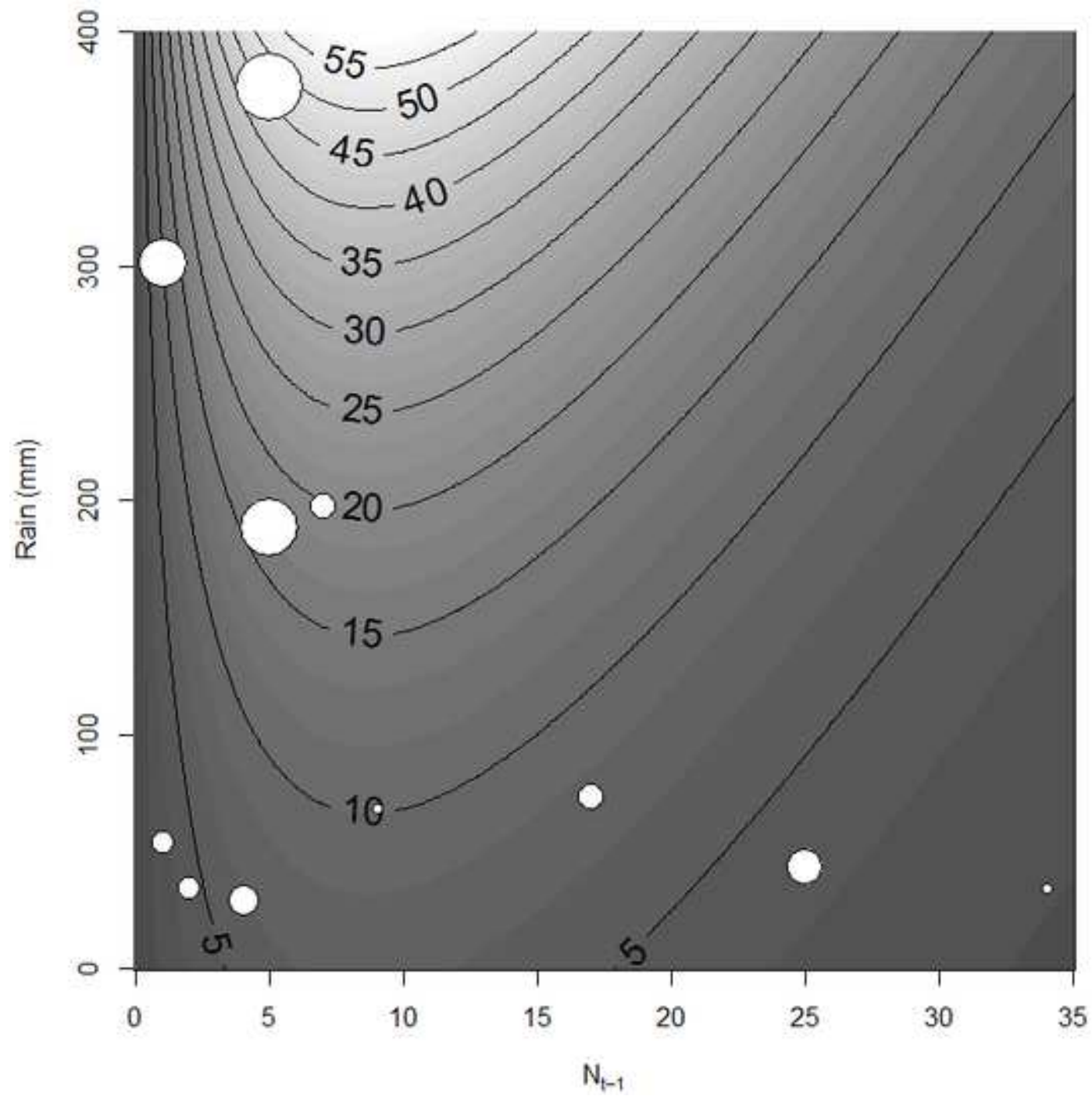




Table S1

**Table S1** Principal Component Analysis for the estimation of a ground cover index

Ground Cover	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5
Terrace	0	0	0	-0.2	0.979
Grass	0	0	-0.764	0.458	0
Tree	0	0.122	-0.255	-0.829	-0.178
Bush	-0.390	-0.730	0.334	0	0
Leaf Litter	0.836	0	0.294	0.113	0
Concrete	-0.381	0.671	0.39	0.221	0
% Variance	0.738	0.196	0.033	0.027	0.005
Cumulative Variance	0.738	0.935	0.968	0.995	1.000

Table S2

**Table S2** Parameter estimates for the negative binomial demographic stochastic Ricker model fitted to the time series of *Armigeres subalbatus* biweekly abundance. Models were fitted with (Forced) and without (Autonomous) rainfall as covariate. AIC stands for the Akaike Information Criterion.

Parameter	Forced				Autonomous			
	Estimate	S.E.	z	P	Estimate	S.E.	z	P
Intrinsic rate of population growth ( $\hat{\lambda}$ )	1.57	0.83	1.88	NS	5.40	2.25	2.39	*
Density dependence coefficient ( $\hat{b}$ )	-0.10	0.02	-4.18	**	-0.13	0.02	-5.69	**
Rainfall coefficient ( $\hat{\gamma}$ )	0.0054	0.0021	2.51	*	-	-	-	-
Negative binomial overdispersion ( $\hat{k}$ )	0.56	0.39	-		0.27	0.14		
AIC	79.32				81.89			

NS= not significant (P>0.05), \*\*Statistically significant (P<0.001), \*Statistically significant (P<0.05)

### Appendix S1 R functions to fit the Stochastic Ricker Model

### Time Series

```
### Armigeres subalbatus abundance at t+1 (biweeks 2-12)
nt1<-c(4, 7, 5, 34, 1, 17, 5, 25, 9, 1, 4)
### Armigeres subalbatus abundance at t (biweeks 1-11)
nt<- c(2, 4, 7, 5, 34, 1, 17, 5, 25, 9, 1)
### Cumulative bi-weekly rainfall before t+1
RR<- c(34.5, 29.0, 197.5, 376.5, 34.0, 301.0, 73.0, 188.0, 43.5, 68.5, 53.5)
```

### Calling a library with the Negative Binomial Generalized linear model fitting function library(MASS)

```
### Fitting the environmental stochastic Ricker model as a Neg-Bin GLM (Autonomous)
rglmnba<-glm.nb(nt1~offset(log(nt))+nt)
### Calling the model summary (to see parameter estimates)
```

summary(rglmnba)
### Fitting the environmental stochastic Ricker model as a Neg-Bin GLM (Forced by Rainfall)

```
rglmnbF<-glm.nb(nt1~offset(log(nt))+nt+RR)
```

### Calling the model summary

```
summary(rglmnbF)
```

### Likelihood functions

### Calling a library with convenient functions to fit Maximum likelihood models library(bbmle)

```
###Function to fit the environmental stochastic Ricker model (Autonomous)
renva <- function (lambda0, b, kappa){
  nt1<-nt1
  nt<-nt
  -sum(dnbinom(nt1, mu=(lambda0*nt*exp(-1*b*nt)),size=kappa,log=TRUE))
}
```

```
### Fitting the model
fitrenva=mle2(renva,start=list(lambda0=7.37, b=0.15, kappa=1.43))
### Calling the model summary
summary(fitrenva)
```

###Function to fit the environmental stochastic Ricker model (Forced by Rainfall)

```
renvF <- function (lambda0, b, kappa,g){
  nt1<-nt1
  nt<-nt
  RR<-RR
  -sum(dnbinom(nt1, mu=(lambda0*nt*exp(-1*b*nt+g*RR)),size=kappa,log=TRUE))
}
```

```

### Fitting the model
fitrenvF=mle2(renvF,start=list(lambda0=2.1714, b=0.115, kappa=2.678,g=0.0054))
### Calling the model summary
summary(fitrenvF)

###Function to fit the demographic stochastic Ricker model (Autonomous)
rdema <- function (lambda0, b, kappa){
  nt1<-nt1
  nt<-nt
  -sum(dnbinom(nt1, mu=(lambda0*nt*exp(-1*b*nt)),size=kappa*nt,log=TRUE))
}
### Fitting the model
fitrdema=mle2(rdema,start=list(lambda0=5.4005, b=0.1314215, kappa=0.2724))
### Calling the model summary
summary(fitrdema)

###Function to fit the demographic stochastic Ricker model (Forced by Rainfall)
rdemF <- function (lambda0, b, kappa,g){
  nt1<-nt1
  nt<-nt
  RR<-RR
  -sum(dnbinom(nt1, mu=(lambda0*nt*exp(-1*b*nt+g*RR)),size=kappa*nt,log=TRUE))
}
### Fitting the model
fitrdemF=mle2(rdemF,start=list(lambda0=1.5716, b=0.0979, kappa=0.5574,g=0.00536))
### Calling the model summary
summary(fitrdemF)

```