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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

Introduction

30

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 where 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 ^{o}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 ^{o}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.jspacesystems.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 25th 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 180^0 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/) 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 1st principal

118 component (Table S1) was then used as a ground cover index.

119 **Mosquito Sampling:** To sample immature mosquito stages we made "ovitraps" (Zea

120 Iriarte et al. 1991) by using 350 ml Coca-Cola® cans painted black with an acrylic spray

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

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

154   2014 to December 1st 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 (^{0}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 4th 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   $r=\ln(N_t)-\ln(N_{t-1})$ (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    $N_t = \lambda_0 N_{t-1} exp(-bN_{t-1})$ (2)

213   Where λ_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    $N_t \sim NegBin(mean = \lambda_0 N_{t-1} exp(-bN_{t-1}), overdispersion = k)$ (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    $N_t \sim NegBin(mean = \lambda_0 N_{t-1} exp(-bN_{t-1}), overdispersion = kN_{t-1})$ (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    $N_t = \lambda_0 N_{t-1} exp(-bN_{t-1} + \gamma WV_{t-z})$ (5)

233   Where γ 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 $$mean = \lambda_0 N_{t-1} exp(-b N_{t-1} + \gamma WV_{t-z})$$ (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 4th 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 (± S.D.) number of adults

252 per sampling location was 4.22 ± 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 5th, 7th and 9th sampling biweek, i.e., July 12th, August 9th and September 6th

266   respectively, reaching a maximum of 34 individuals (Fig. 3A). From the 13th biweek of

267   sampling we did not catch any *Ar. subalbatus*. The average (± S.D.) number of adults

268   per sampling biweek was 8.14 ± 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 where 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

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

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

Figure Legends

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

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

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

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

Fig. 5 Temporal Abundance of *Armigeres subalbatus* (N_t) as function of its previous abundance (N_{t-1}) and Rainfall. In the plot dots are proportional to the biweekly abundance of *Ar. subalbatus* (N_t), which ranged from 1 to 34. The grey gradient indicates the expected number of *Ar. 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 (^{0}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
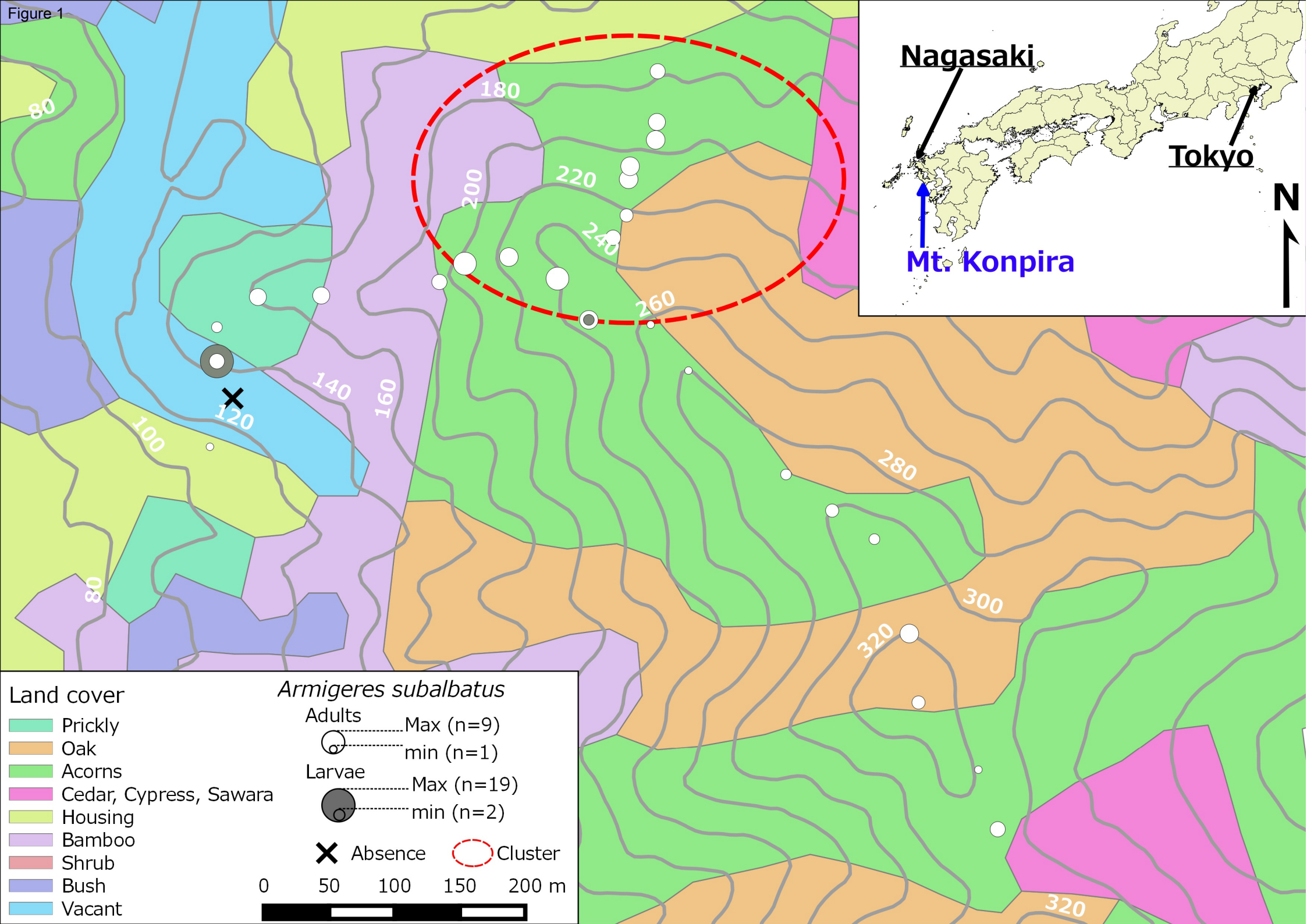
Land cover
- Prickly
- Oak
- Acorns
- Cedar, Cypress, Sawara
- Housing
- Bamboo
- Shrub
- Bush
- Vacant

Armigeres subalbatus

Adults
- Max (n=9)
- min (n=1)

Larvae
- Max (n=19)
- min (n=2)
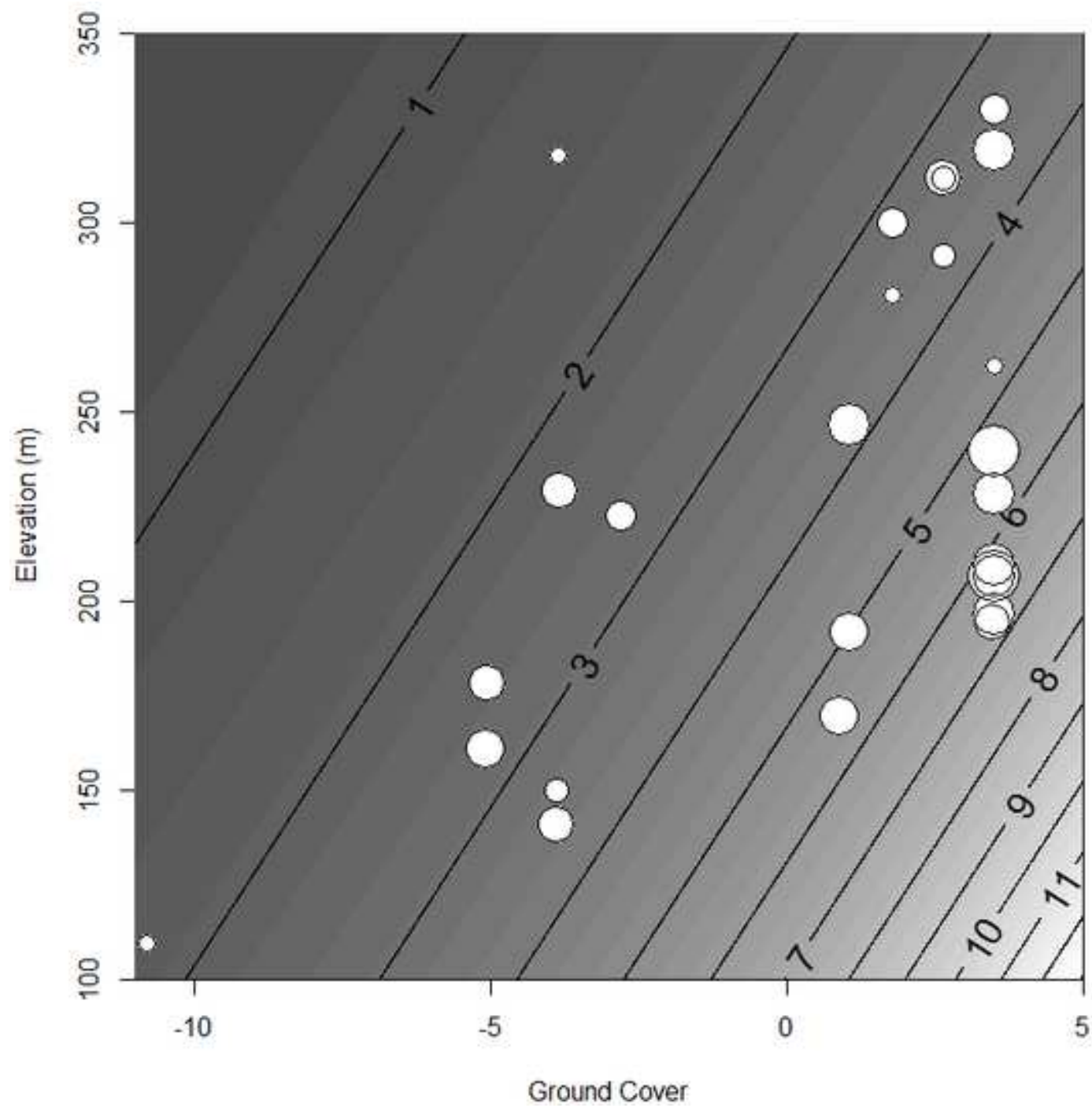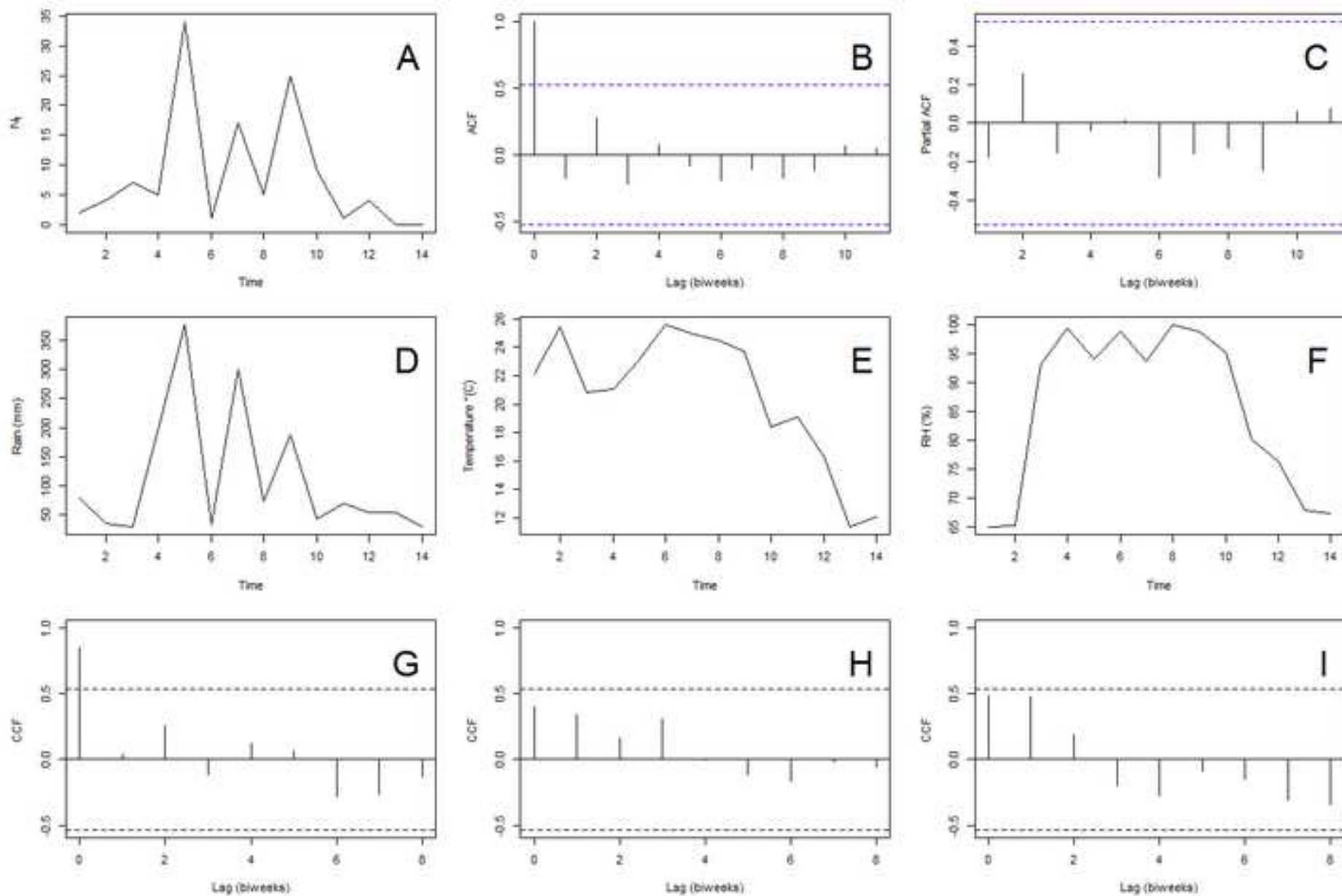
✕ Absence   Cluster

0   50   100   150   200 m

Nagasaki   Tokyo   Mt. Konpira   N

Figure 2

Figure 3

Figure 4

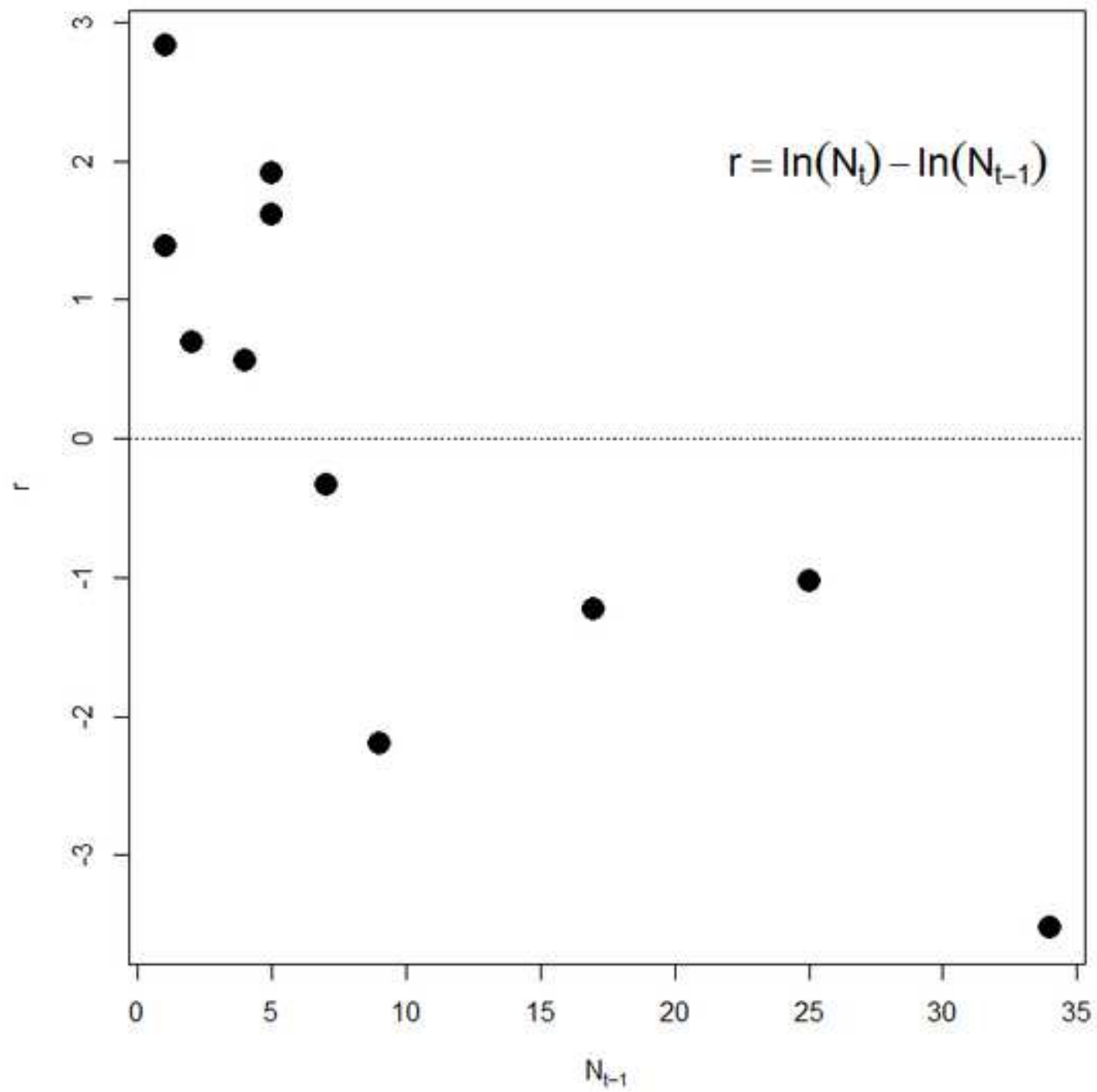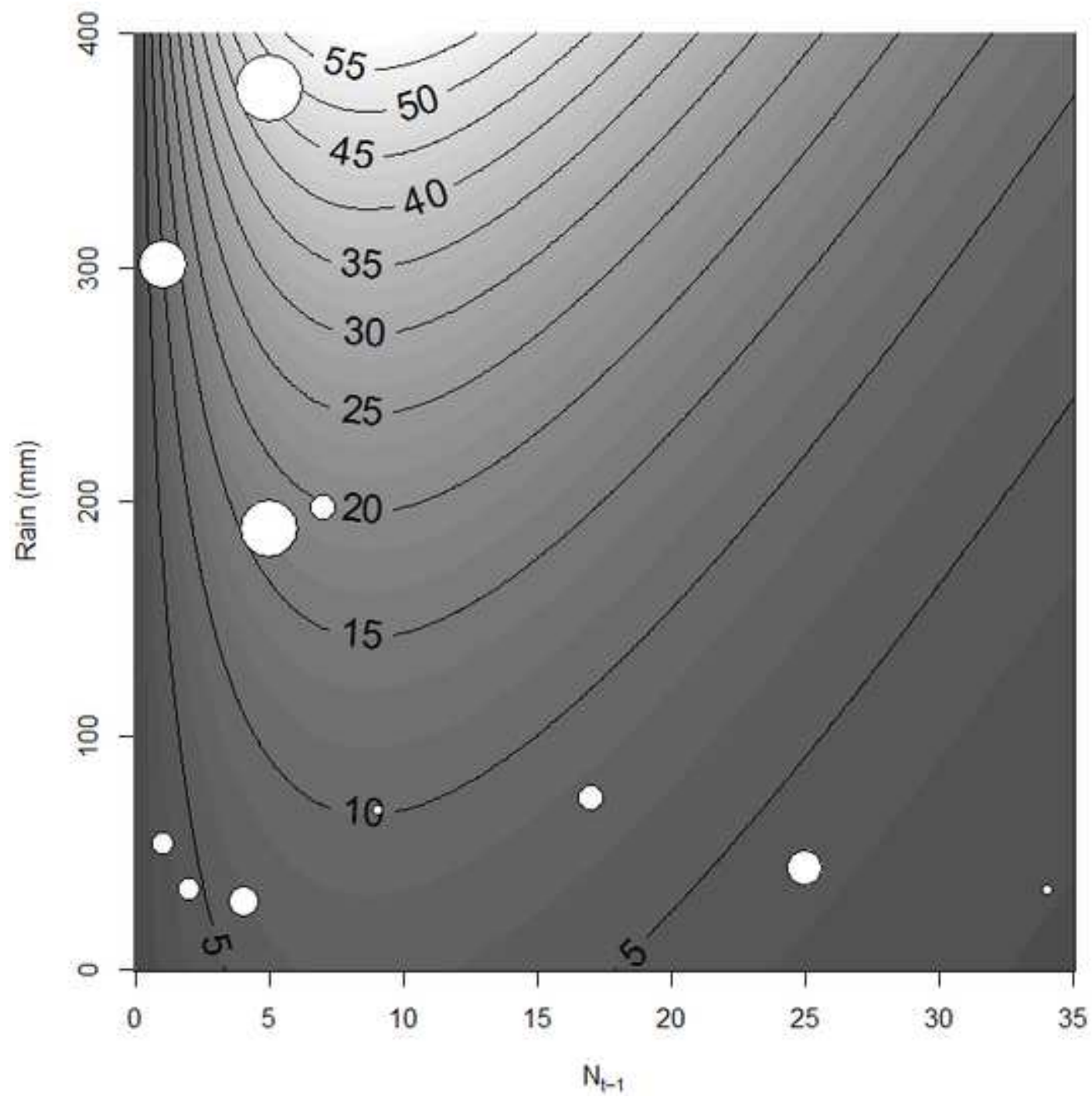$$r = \ln(N_t) - \ln(N_{t-1})$$

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)
```