Modeling Dengue Vector Dynamics under Imperfect Detection: Three Years of Site-Occupancy by *Aedes aegypti* and *Aedes albopictus* in Urban Amazonia

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Introduction

Dengue is the most common arboviral disease of humans [1–3]. About 50 million people contract dengue annually, and an estimated 22,000 die from severe forms of the disease [3,4]. Dengue virus is transmitted by mosquitoes of the genus *Aedes*, particularly *Aedes aegypti* and *Aedes albopictus* [5]. In the absence of effective drugs or vaccines, prevention of dengue infections and severe dengue forms heavily relies upon vector control. However, despite massive spending and some encouraging results (e.g., [6–9]), neither vector populations nor, consequently, dengue transmission are currently under control; on the contrary, they are both clearly expanding [2,10]. In South America, dengue incidence increased from ~16,000,000 population in the 1980s to ~72,000,000 in 2000–2007 [11].

*Aedes aegypti*, a species native to Africa, has successfully adapted to urban environments around the world; it preferentially breeds in artificial containers (where desiccated eggs can remain viable for months), rests within houses, and feeds on human blood [12,13]. These traits have favored its man-mediated dispersal throughout the tropics [14,15], and, together with its capacity to transmit dengue virus, have transformed *Ae. aegypti* in a major public health concern [16]. *Ae. albopictus* is more ecletic; it exploits both urban and rural tropical-subtropical habitats, makes use of natural and artificial breeding sites, and feeds on either humans or non-human vertebrates [17,18]; this species, however, is less efficient than *Ae. aegypti* at transmitting dengue virus [18].

Dengue vector control is largely based on a combination of strategies aimed at eliminating *Aedes* breeding sites (either physically or by means of larvicides) and reducing adult mosquito populations through environmental insecticide application [6–9]. The design, implementation, and assessment of such strategies require detailed knowledge of vector population ecology, including the estimation of dwelling infestation rates [19,20]. In general, vector control interventions are expected to have a negative effect
on infestation by *Ae. aegypti* and *Ae. albopictus* at the local scale. Measuring such an effect requires reliable methods for ascertaining infestation; yet, detection of most animal species, including disease vectors, is rarely, if ever, perfect [21,22]. Here, we treat infestation as the probability that a dwelling is occupied by vectors (i.e. site-occupancy) and use a hierarchical modeling approach to analyze the dynamics of site-occupancy by *Ae. aegypti* and *Ae. albopictus*. Our analysis is based on three years of oviposition trap (ovitrap) data from a central-Amazon urban setting. Taking imperfect detection into account, we quantify the effects of routine control interventions and selected environmental variables on the main indicator used in vector control program management – dwelling infestation rates – and on its temporal change.

**Materials and Methods**

**Study Setting**

With a population of about 1.8 million, Manaus (3°6′S, 60°1′W) is the largest urban center of the Amazon basin (Figure 1). The city lies on the north bank of the Negro river and is surrounded by rainforest. The climate is tropical, warm and humid, with a relatively strong seasonality of rainfall and, to a lesser extent, temperature (Figure 2). After being declared eradicated from Brazil in the 1950s [15], *Ae. aegypti* reinfested Manaus in the late 1990s [23] and is currently widespread across all its neighborhoods [24]. *Ae. albopictus* was first recorded in 2002 [25], and is now also widespread [24]. Dengue transmission is endemic (i.e., occurs continuously) in the city, with recurrent epidemics and records of all known dengue virus serotypes [26]. As in other settings, dengue control in Manaus relies on dwelling visits by municipal or state agents, who physically eliminate breeding sites or treat them with larvicides; in “emergency” situations (in practice, when dengue cases begin to soar), environmental insecticide spraying aimed at reducing adult mosquito density is also used [27]. Vector control agencies also conduct regular infestation surveys on a random sample of dwellings in each neighborhood [see details in ref. [28]]. The results of these ‘rapid larval surveys’ are used to set priorities and make decisions about control interventions, with control teams usually deployed to a neighborhood when dwelling infestation rises above 2%; officially, the Brazilian control program aims to keep dwelling infestation below 1% [20].

**Sampling Strategy**

We selected an area of ~250,000 m² within the Manaus neighborhood of Tancredo Neves (Figure 1) for vector monitoring. This neighborhood is frequently infested by both target mosquito species, and about 1500 dengue cases were notified during the study period [refs. [24,29,30] and unpublished Municipal Health Department data]. The typical Tancredo Neves dwelling – our sampling unit are positively correlated, values close in time are more similar than those separated by longer periods [40]. Apart from rainfall and temperature, we also registered dwelling-level traits throughout the last 13 months of monitoring. Following criteria from Tun-Lin et al. [36] adapted to our setting, we separately assessed houses and courtyards; for each of these, we defined a covariate with values of 1 (poor overall maintenance, garbage accumulation, and, for courtyards, overgrown vegetation) or 0 (well-maintained houses or courtyards). Finally, we noted whether routine control interventions were or were not performed in our study area in each of the last 13 months of monitoring. These interventions were carried out by municipal/state agents and military staff, and involved elimination of breeding sites, physically or with larvicides [20,27]; while campaigns are designed to target all dwellings, interventions are effectively limited to houses whose owners are present at the time of the visits and allow control agents to inspect their property.

**Data Analyses**

Our analytical approach involved two main steps. First, we used descriptive statistics, tables, and graphs to explore the data [37], and calculated naïve infestation rates (i.e., rates that assume perfect detection of vectors) of both target species for later comparison with model-based estimates (see below). Second, we implemented a set of hierarchical models of occupancy dynamics. These models explicitly account for imperfect detection, providing estimates of detection probability (denoted *p*) conditioned on occupancy (denoted *ψ*), and treat temporal changes in occupancy as a first-order Markov process [38–40]. Thus, the probability of a site being occupied in month *t* depends on the occupancy state of that site in the previous month, *t*−1. This also accounts for a form of temporal autocorrelation: when observations on the same sampling unit are positively correlated, values close in time are more similar than those separated by longer periods [40]. Apart from *p* and *ψ*, our occupancy dynamics models also provide information...
Figure 1. Study area. Manaus, state of Amazonas, Brazil (A) and Tancredo Neves neighborhood (B). doi:10.1371/journal.pone.0058420.g001

Figure 2. Observed dwelling infestation and meteorological variables during the study period. Dwelling infestation (%) by *Aedes aegypti* and *Ae. albopictus*; total monthly rainfall (mm; right y axis); and monthly averages of daily mean, minimum, and maximum temperatures (\(^\circ\)C; left y axis). doi:10.1371/journal.pone.0058420.g002
about the probability that a dwelling that is infested at time \( t \) becomes uninfested at time \( t - 1 \) will become uninfested at time \( t \) (named local extinction probability, or \( \psi \)) or that an uninfested dwelling at time \( t - 1 \) becomes infested at time \( t \) (colonization probability, \( \gamma \)). Models can use a variety of parameterizations to represent the same occupancy-dynamic process: we chose to focus on the estimation of \( \psi \) and \( \gamma \), which, combined, can yield information on \( \varepsilon \). Parameters \( p, \psi, \varepsilon, \) and \( \gamma \) can be modeled as functions of sampling or environmental covariates. For simplicity, we model covariates on \( p \) and \( \psi \).

The main assumption of the models is population closure – i.e., site-specific occupancy remains unchanged within each sampling month. In our case, closure was guaranteed by the simultaneous assessment of all traps set within each dwelling. This design could however result in nonindependence of traps set within a single dwelling: if detection in one trap increases detection probabilities in the others, this would result in some overestimation of \( p \) and, therefore, a negatively biased \( \psi \) estimate. Finally, the usual assumption of independence of dwellings with regard to infestation also applies; if violated, this would inflate the precision of occupancy estimates.

As summarized above, estimation of \( p \) requires detection histories from repeated samples or multiple traps. A ‘011’ detection history for a dwelling and month, for example, indicates that one trap was false-negative; on the other hand, all-zero histories may result from two scenarios: either the dwelling was truly uninfested or it was infested yet all traps failed to detect the vectors [38–40]. Since detection probability (\( p \)) is conditional on site-occupancy, it can be interpreted as the sensitivity of the vector-detection method – its ability to detect the presence of the vectors in dwellings that are actually infested.

Models were fit by likelihood maximization and ranked according to the Akaiake information criterion corrected for small sample size (AICc) [41]. Model fitting and ranking were carried out with the freely-available software PRESENCE 4.0 [42]. To avoid repetition, further details on model specification, comparison, and selection are presented in the Results section and in Tables 1, 2, and S1.

We fit occupancy dynamic models separately to (i) the 13-month subset of data for which we recorded vector control interventions and house/courtyard covariates and (ii) the full 38-month dataset. This resulted in a two-stage analysis. On the first stage, we focused on modeling the effects of control interventions on \( \psi \), looking both at interventions that took place in the same month as sampling (denoted \( \text{control}_{\text{same-lag}} \)) and during the preceding month (lagged effect, \( \text{control}_{\text{lagged-lag}} \)). These models also consider meteorological and dwelling conditions. Since two teams were involved in vector monitoring, we also modeled detection probability (\( \psi \)) as a function of the observer team to account for possible differences in team performance [39,40].

On the second stage, we set aside control interventions and focused on estimating time-dependent occupancy for the whole
Table 2. Meteorological covariate effects on dwelling infestation rates by Aedes aegypti and Ae. albopictus: dynamic site-occupancy models fitted to a 38-month dataset.

| Species/model                  | AICc  | Covariate                    | β    | SE  | CI-lower | CI-upper |
|--------------------------------|-------|------------------------------|------|-----|----------|----------|
| Aedes aegypti, 38 months       |       | t_{max-2-week-lag} \(\beta\) | -0.63| 0.14| -0.90    | -0.35    |
|                                | 0.98  | t_{max-2-week-lag} \(\beta\) | -0.57| 0.12| -0.81    | -0.33    |
|                                | 6.29  | t_{max-2-week-lag} \(\beta\) | 0.50 | 0.14| 0.23     | 0.77     |
| Aedes albopictus, 38 months    |       | t_{max-2-week-lag} \(\beta\) | -0.59| 0.09| -0.77    | -0.41    |
|                                | 21.4  | t_{max-2-week-lag} \(\beta\) | 0.46 | 0.09| 0.28     | 0.64     |

“\(\beta\)” denotes that no covariates entered this part of the model; see text for further details. AICc: variation of Akaike information criterion (corrected for small sample size) values with respect to the first-ranking model in each set; \(\beta\), slope coefficient estimated for each covariate in the corresponding model; SE, standard error; CI-lower and CI-upper, limits of the 95% confidence interval; \(t_{max-2-week-lag}\), standardized mean of maximum daily temperatures during sampling and the previous 15 days; \(t_{max-1-week-lag}\), standardized mean of maximum daily temperatures during sampling days and the previous week; \(t_{min-1-week-lag}\), standardized mean of minimum daily temperatures during sampling days and the previous week; \(t_{max-1-week-lag}\), standardized mean of daily rainfall over the month before sampling; trap, trap-type covariate; observer, observer team covariate; see main text for further details on covariates.

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38-month dataset, including the final 13 months of control-intervention monitoring. This second set of models also considered the effects of meteorological covariates on occupancy, albeit with a larger amount of data. Since we used two trapping devices during the first phase of monitoring, detection probabilities were modeled as a function of trap type, and, once again, as a function of the observer team. We also assessed the amount of bias present in naive vs. model-derived infestation rate estimates (bias = 1 − [naïve/model-derived values]).

Ethics Statement

Sampling was carried out with permission from dwelling owners, and did not involve endangered or protected species. SLBL holds a permanent license (27733-1) from the Brazilian Institute for Environment and Natural Resources (IBAMA) for sampling insect vectors such as the Aedes species we studied.

Results

Descriptive Results: Observed Infestation

Both vector species were detected in a high proportion of dwellings throughout the study period (Figure 2), with harmonic mean values of 0.60 for Aedes aegypti (range, 0.50–0.91) and 0.61 for Aedes albopictus (range, 0.28–0.96). There was an apparent relationship between site-occupancy and weather (Figures 2 and 3). The particularly hot and dry period of June-September 2009 coincided with a sharp decrease of Aedes albopictus infestation: observed values fell from ~0.70–0.80 to ~0.30–0.50. A less marked decline was also apparent for Aedes aegypti. Both species, however, quickly recovered with the onset of the rainy season. Dwelling infestation indices (the World Health Organization ‘house index’) reported by routine municipal surveillance for our study neighborhood, based on 15 ‘rapid larval surveys’ [20] carried out between October 2005 and October 2011 (Figures 3 and 4), yielded a harmonic mean of just 0.033 (range, 0.015–0.089). These descriptive results rely on the assumption that vectors were absent from sites where they were not observed; however, no perfect vector-detection method is available. The modeling results summarized in the next section address this key limitation.

Modeling Results I: Effects of Control Interventions

On the first stage of our analysis we modeled the effects of vector control interventions carried out by local health authorities on site-occupancy by Aedes aegypti and Aedes albopictus. These models used data from 55 dwellings monitored from October 2010 to October 2011 with up to three ovitraps per dwelling and month. Overall, the data encompass results from 1907 ovitraps, of which 849 detected Aedes aegypti and 828 detected Aedes albopictus.

Aedes aegypti detection/non-detection data are best explained by a model with just one covariate on \(\psi\), the average of maximum daily temperatures measured with a 2-week-lag (\(t_{max-2-week-lag}\)), which had a negative effect on site-occupancy (Table 1). The second-ranking model is also substantially supported by the data (\(\Delta\text{AICc} = 0.73\)); it includes the additive effects of \(t_{max-1-week-lag}\) and control interventions carried out during the same month (control\_lag) on \(\psi\). The effect of temperature was again negative; this model also yielded a negative point estimate of the control coefficient, but uncertainty about this estimate is large and the 95% confidence interval overlaps zero (Table 1). Among candidate models including dwelling covariates, the one with the lowest AICc estimates a weak, positive effect of poor house condition on infestation, but, again, the estimate of this effect is too uncertain to draw any strong conclusions (Table 1).

The top-ranking model for Aedes albopictus estimates a negative effect of 1-week-lagged minimum temperatures (\(t_{min-1-week-lag}\) on infestation; in addition, the model suggests that houses in poor condition might have been at a slightly higher risk of infestation, albeit the estimated coefficient’s 95% confidence interval includes zero (Table 1). Adding control interventions carried out the month before (control\_lag) resulted in a model that fits reasonably well (\(\Delta\text{AICc} < 1\)). For this second model, the negative coefficient of control\_lag on \(\psi\) is nevertheless small and imprecise, with
Figure 3. Observed and model-estimated dwelling infestation by *Aedes aegypti* (A) and *Ae. albopictus* (B). Monthly model-derived site-occupancy estimates (solid circles, with 95% confidence intervals); monthly observed infestation (empty circles); and *Ae. aegypti* infestation indices derived from 13 ‘rapid larval surveys’ [28] (red circles in panel A). On the x axis, grey boxes highlight the periods in which city-wide, massive *Aedes* control campaigns, called *Operação Impacto* [29,30], took place. Arrows indicate months in which control activities were performed in our study neighborhood (red arrows, interventions included as model covariates).

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Modeling Results II: Long-term Site-occupancy Dynamics

The results in the previous section show that modeling time-specific occupancy as a function of control interventions or dwelling-level covariates did not improve the ranking of the models. Therefore, we felt justified to extend modeling to the full dataset – focusing on the potential effects of meteorological variables on site-occupancy by Aedes species. The analyses make use of a 38-month dataset including individual results of 5799 trap-weeks, which detected Ae. aegypti on 2641 occasions and Ae. albopictus on 2538 occasions. In these models, colonization probability (denoted \( \gamma \)) was constrained to be constant across months, while monthly local (dwelling-level) extinction probabilities \( (c) \), of primary interest in the context of vector control, were derived from \( \psi \) and \( \gamma \) estimates as described in MacKenzie et al. [39,40].

The full Ae. aegypti data were best explained by a model including the 2-week-lagged average of daily maximum temperatures \( t_{\text{max},-2\text{-lag}} \), which had a negative effect on site-occupancy probabilities (Table 2). The model with \( t_{\text{max},-2\text{-lag}} \) as a covariate on \( \psi \) also fitted the data well, and estimated a similar effect to that of \( t_{\text{max},-2\text{-lag}} \) (Table 2). The remaining models that we examined, including a null model without any covariates, performed substantially worse than these two top-ranking models (see Table S1). Among models that included rainfall covariates, the best-performing one had a \( \Delta AICc = 6.29 \) and estimated a positive effect of total rainfall \( (r_{\text{1-week-lag}}) \) on \( \psi \) (Table 2).

Figure 3A shows monthly site-occupancy estimates for Ae. aegypti derived from the lowest-AICc model. With few exceptions, point estimates were consistently >90% (harmonic mean 0.91; range, 0.79–0.97) and showed a weak seasonal pattern (Figure 3A). Model-based infestation estimates are about 30% higher than observed values based on ovitraps results (median bias, 0.29 (Figure 4). The estimated average sensitivity of ovitraps at detecting infestation by Ae. aegypti varied from \( p = 0.48 \) (95% confidence interval 0.45–0.51) to \( p = 0.65 \) (0.63–0.67), depending on which field team performed monitoring (details not shown); 1355 out of 4553 ovitraps-weeks and 450 out of 1246 Adulttrap-weeks did not detect Ae. aegypti in dwellings where other traps yielded evidence of infestation. Local extinction probability estimates were overall very low (harmonic mean \( \psi = 0.04 \); range, 0.01–0.18), reaching higher values in hotter months (Figure 5A); mean site-colonization probabilities were estimated as \( \gamma = 0.66 \) (95% confidence interval 0.54–0.76) over the study period. The best-ranking Ae. albopictus model included only one site-occupancy covariate, \( t_{\text{min},-1\text{-lag}} \), which had a negative effect on \( \psi \) (Table 2). The remaining models performed substantially worse (\( \Delta AICc > 20 \)), but several of the candidate specifications we tested had convergence problems. The only model with a rain covariate estimates a positive effect of 4-week-lagged rainfall on site-occupancy by Ae. albopictus (Table 2). Site-occupancy estimates derived from the best-ranking model are presented in Figure 3B. As with Ae. aegypti, monthly \( \psi \) values were always high (harmonic mean 0.83; range, 0.66–0.94), with minimum \( \psi = 0.66 \) (95% confidence interval 0.59–0.72) in October 2011. Monthly Ae. albopictus \( \psi \) estimates were more unstable than those of Ae. aegypti, with relatively strong fluctuations after the dry-hot summer of 2009 (Figure 3B). Observed infestation (based on ovitraps) was also biased downwards (by ~26%) in our Ae. albopictus data (Figure 4), yet ovitraps were fairly sensitive at detecting Ae. albopictus (\( p = 0.63 \), 95% confidence interval 0.62–0.65). Monthly local extinction probabilities were low: harmonic mean \( \psi = 0.07 \), range 0.02–0.32,
Mean dwelling colonization probability was estimated as $c = 0.59$ (95% confidence interval 0.51–0.66).

Discussion

Reliable dwelling infestation estimates are critical for decision-making in the context of dengue vector surveillance and control. The definition of programmatic goals, the management of resources, and the assessment of intervention effects all rely heavily upon such estimates. Using a large dataset and a sound...
analytical approach we have shown that routine vector surveillance and control are both performing poorly: at least in our study setting, (i) ‘rapid larval surveys’ yielded dwelling infestation indices that were markedly lower than the site-occupancy rates based on ovitrap data, and (ii) control campaigns had negligible effects on site-occupancy. Our results suggest that combining ovitrap-based surveillance (e.g., [43–45]) with analytical methods that account for imperfect detection (e.g., [21,22,35–40]) would help quantitatively assess, and likely enhance, dengue control programs. Moreover, from a disease transmission perspective, the presence of foraging gravid females in a dwelling, which ovitraps detect with reasonable sensitivity, is arguably more important than the presence of larvae, which is what ‘rapid larval surveys’ aim to detect.

Before discussing our findings any further, we identify several study limitations to keep in mind when interpreting the present results. First, we used detection/non-detection data, ignoring variations in vector abundance. However, presence-absence and abundance data seem to correlate well (e.g., refs. [46,47]), and, importantly, both empirical and modeling results suggest that Ae. aegypti abundance thresholds (above which dengue transmission is maintained) are typically very low, i.e., ~0.5–1 female per person or ~0.5–1.5 pupae per person [48,49]; therefore, the probability that at least one gravid female is present in a dwelling, which we modeled here, is clearly an epidemiologically relevant parameter.

Second, some of our data may violate the assumption of independence of traps with regard to detection and of dwellings with regard to infestation: this may result in negatively biased estimates with overly narrow confidence intervals. The high values of infestation indices that do not account for imperfect detection suggest that this problem was, in practice, negligible – our conclusions would not change because of somewhat broader confidence intervals. In addition, we measured only, and coarsely, a small number of covariates, but these were selected because of their known importance for our target species (e.g., [33–36,50]). Our ‘control’ covariate included control interventions in just three out of 13 months of assessment, and this clearly lowered the precision of effect-size estimates: it seems possible that with more intervention data we might be able to detect a small effect whose 95% confidence interval could exclude zero. Yet, since ~70–90% of dwellings remained infested despite control interventions, ‘statistical significance’ would in this case be of no practical importance [49]. Acknowledging these caveats, we feel confident that our models adequately estimate infestation rates as well as some of the major determinants of those rates in our study area. The main difference between our approach and previous attempts to assess infestation by dengue vectors is that we go beyond measuring indirect indices of infestation (i.e., adult or larvae presence/absence or counts) to produce statistical estimates of the probability that our study units (dwellings) are occupied by the target vector species.

We found little evidence that dwelling infestation rates decreased measurably as a result of the vector control campaigns carried out by local health authorities in our study neighborhood. These campaigns involved the elimination/treatment of thousands of artificial breeding containers [29,30], and were expected to have larger effects on Ae. aegypti, which unlike Ae. albopictus rarely breeds in natural water collections [5,17]. Our results show, however, no measurable effect of control interventions on any of the two vectors (Table 1); indeed, females of both species consistently continued to lay eggs, and probably forage, in most of the dwellings we surveyed, irrespective of whether control interventions had or had not taken place in the neighborhood. Our models suggest that this lack of effect could be related to the fact that interventions are usually planned to coincide with the wet-cool season, which is when local extinction probabilities drop to their lowest values (Figure 5). Summer interventions might perhaps be more effective [51], since they could synergize the negative effects of high temperatures on Ae. albopictus and Ae. aegypti detected by our models and in previous studies (e.g., [50–53]). These negative effects of high temperature, however, have to be considered in the particular context of our study. First, the extrinsic incubation period of dengue virus and the vector’s gonotrophic cycle can both be shortened by warmer weather, increasing transmission risk; second, relatively high temperatures probably favor vector development in overall cooler climates [10].

One practical implication of our findings is that Ae. aegypti breeding sites appear to be often overlooked by vector control agents during active surveillance and, principally, in control campaigns. This suggests a key drawback to be addressed in the development of novel Ae. aegypti control strategies, which should not heavily depend on the ability of control agents to detect breeding sites while inspecting premises. Two major candidate strategies address this problem from very different, but complementary, perspectives: (i) the use of adult mosquitoes to transfer potent larvicidal particles from contaminated ‘dissemination stations’ to clean breeding sites [54], and (ii) the release of mosquitoes carrying transgenes [55,56] or specific Wolbachia strains [57] that impair reproduction and/or reduce competence to transmit dengue virus.

Conclusions

The reported bias of infestation indices that do not account for imperfect detection suggests that the findings of most dengue vector ecology studies must be interpreted with caution. Even ovitraps, which performed relatively well, yielded naïve infestation rates that were consistently biased downwards by about 30%. The analytical strategy we used here incorporates this sampling-process uncertainty, and could therefore substantially contribute to this field of inquiry.

Finally, our results suggest two promising avenues for the much-needed improvement of dengue vector surveillance [58]. First, simple hay infusion-baited ovitraps [32] should be preferred to ‘rapid larval surveys’: they are more sensitive and provide a measure of dwelling infestation by foraging gravid females (see also, e.g., refs. [43–45,59]). Second, the repeated-sampling approach we used considerably improves infestation rate estimates by explicitly taking imperfect detection into account. Enhanced entomological surveillance systems and data analyses that explicitly account for the detection process would, in turn, allow for reliably assessing the effects of control interventions, irrespective of the specific tactics employed. Without such an assessment, the grounds on which massive public spending is directed towards dengue vector control (e.g., [60]) remain questionable.

Supporting Information

Table S1 The complete sets of site-occupancy dynamic models.

(XLSX)

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Author Contributions

Contributed to the last version of the manuscript: FA-F SDP-T GF SLBL EZ-P. Conceived and designed the experiments: FA-F GF SDP-T SLBL.

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