Targeted elimination of species-rich larval habitats can rapidly collapse arbovirus vector mosquito populations at hotel compounds in Zanzibar

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Abstract. Understanding the dynamics of larval habitat utilization by mosquito communities is crucial for the design of efficient environmental control strategies. The authors investigated the structure of mosquito communities found at hotel compounds in Zanzibar, networks of mosquito interactions with larval habitats and robustness of mosquito communities to elimination of larval habitats. A total of 23 698 mosquitoes comprising 26 species in six genera were found. *Aedes aegypti* ($n = 16\,207$), *Aedes bromeliae/Aedes lillie* ($n = 1340$), *Culex quinquefasciatus* ($n = 1300$) and *Eretmapodites quinquevitattus* ($n = 659$) were the most dominant species. Ecological network analyses revealed the presence of dominant, larval habitat generalist species (e.g., *A. aegypti*), exploiting virtually all types of water holding containers and few larval habitat specialist species (e.g., *Aedes natalensis*, *Orthopodomyia* spp). Simulations of mosquito community robustness to systematic elimination of larval habitats indicate that mosquito populations are highly sensitive to elimination of larval habitats sustaining higher mosquito species diversity. This study provides insights on potential foci of future mosquito-borne arboviral disease outbreaks in Zanzibar and underscores the need for detailed knowledge on the ecological function of larval habitats for effective mosquito control by larval sources management.

Key words. community robustness, interaction networks, larval habitats, mosquito community, Zanzibar Island.

Introduction

Mosquitoes are the most important vectors of deadly pathogens affecting more than half of the world population (WHO, 2017). Vector control is the most cost-effective approach for reducing the transmission of mosquito-borne diseases (MBDs) and, for some diseases, is the only available tool to do so (Wilson *et al.*, 2020). Despite significant advances in achieving MBD control targets, residual outdoor malaria transmission still persists in endemic regions, particularly in the Zanzibar archipelago

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(Bjorkman *et al.*, 2019). Concurrently, the emergence and widespread resistance against all approved classes of insecticides in vector populations have persistently postponed the prospect of MBD elimination in the region (Jones *et al.*, 2012; Haji *et al.*, 2013), emphasizing the urgent need for novel and adaptable non-chemical environmental vector control practices. Spatiotemporal distribution of mosquito populations and pathogens is greatly affected by variations in climate and environmental factors (Campbell-Lendrum *et al.*, 2015). However, persistence of vector populations over the landscape is largely determined by availability of hosts and larval habitats (Chaves *et al.*, 2010; Franklinos *et al.*, 2019). Therefore, rigorous monitoring of mosquito community assemblages and modulating factors is critical for the design of integrated vector management approaches (Fouet & Kamdem, 2019). Notably, quantitative understanding of the structure and dynamics of mosquito–larval habitat interaction networks are crucial to identify functionally important larval habitats that can be efficiently targeted by environmental control interventions. Moreover, it can be used to predict the magnitude of the impact of larval source management strategies on a mosquito community.

The tourism industry, dominated by hotels, resorts and lodges (henceforth hotels), is the third most important economic sector in Zanzibar, accounting for nearly 27% of gross domestic product, 80% of foreign revenue and 72 000 jobs (The Revolutionary Government of Zanzibar, 2015). However, hotels in Zanzibar generate large quantities of solid waste (UNICEF, 2018) reported to be associated with higher risk of *Aedes*-borne disease outbreaks in Stone Town, the capital city of Zanzibar (Saleh *et al.*, 2018). The contribution of hotels in creating conditions for the establishment and proliferation of residual vector communities in Tanzania remains unknown. However, the relatively undisturbed environment inside hotel compounds may provide refuges for mosquito taxa of public concern, particularly during unfavourable times when periodic vector control campaigns have been implemented in surrounding communities. This might limit the efficacy of any control measures, as hotels have not been covered by community-wide mosquito control interventions. As circumstantial evidence for the hypothesis that hotels provide 'refuges' for mosquitoes, reports of mosquito bites by visitors have been increasing on these properties. This has been noted as one of the main reasons for negative reviews received by hotels, and a main cause for low interest in returning to the islands (Zanzibar Association of Tourism Investors, *personal communication*, May 2016). Moreover, tourists staying at hotels can import new variants of pathogens from endemic regions around the world. If these new pathogens infect the local mosquito community, it increases the risk of epidemics, with devastating impacts on the tourism-dependent economy of Zanzibar. Therefore, understanding the contribution of hotels to maintenance of residual hotspots of mosquito vector assemblages is crucial for devising effective and ecologically sound control practices. Our main goal was to investigate hotel mosquito community dynamics and local environmental drivers of mosquito assemblages. The authors also determined the network of larval habitat utilization and predicted mosquito population extinction cascades through larval habitat elimination. The authors tested the general hypothesis that there are certain types of larval habitats at studied sites

that maintain the stability of mosquito communities. Therefore, targeted elimination of these keystone mosquito sources can dramatically impair mosquito community robustness and cause rapid extinction of mosquito populations. Implications of our findings for the design of non-chemical environmental control interventions in Zanzibar are discussed.

Material and methods

Description of study sites

This study was carried out at four selected hotels in the south-east coastal region of Zanzibar Island (Fig. 1). Hotels were selected according to compound size (total residential and non-residential area not less than 1 hectare), accessibility during lower and higher tourism seasons, willingness to share data and willingness to accept publication of findings. Consent was obtained from hotel management to conduct the study on their properties. For anonymity purposes, hotel names are omitted in this article and, therefore, they are referred to as Hotel A, B, C and D. On this part of the island, the landscape is dominated by moderate forests, open grassland and some wetlands (Mwalusepo *et al.*, 2017). The largest hotel (Hotel B) occupied an area of approximately 28.06 hectares, and the remaining hotels encompass an approximate area of 6.6 hectares (Hotel A), 3.6 hectares (Hotel D) and 2 hectares (Hotel C). The climate of Zanzibar Island is heavily influenced by both south-west monsoon (*Kusi*) and north-east monsoon winds (*Kaskazi*), usually observed from April to October and November to March, respectively. The rainfall regime is divided into two main rainy seasons, the long rainy season (*Masika*) usually starts from mid-March to June, whereas the short rainy season (*Vuli*) occurs from November to December. The average monthly precipitation ranges from 30 mm in the winter (July) to 320 mm in the summer (December) and accumulated annual rainfall can reach 1600 mm (Forum, 2019a). Some scattered rain showers can also occur during winter. Daily average temperature oscillates from 22 °C in July to 32 °C in December (Forum, 2019a). The relative humidity is usually high, with a monthly average ranging from 87% during the long rainy season (March–June) to 76% in November and December (during the short rainy season), and reaches a minimum of 60% during the dry season (January–March and July–October) (Forum, 2019a). The eastern coastal region of Zanzibar Island is relatively arid, making it attractive and ideal for fishing villages, and tourist and recreational industries (Forum, 2019b).

Sampling of immature mosquitoes

Mosquito immature stages were monitored for a period of 10 months from September 2018 to October 2019. At each hotel, mosquitoes were surveyed over 4 to 6 days each month. The following sampling strategy, adapted from Tun-Lin *et al.* (1994) and Manrique-Saide *et al.* (2011), was adopted according to larval habitat size and water volume. (a) For containers with less than 20 litres of water, all the larvae and pupae were collected by sieving the water directly through a mesh net or
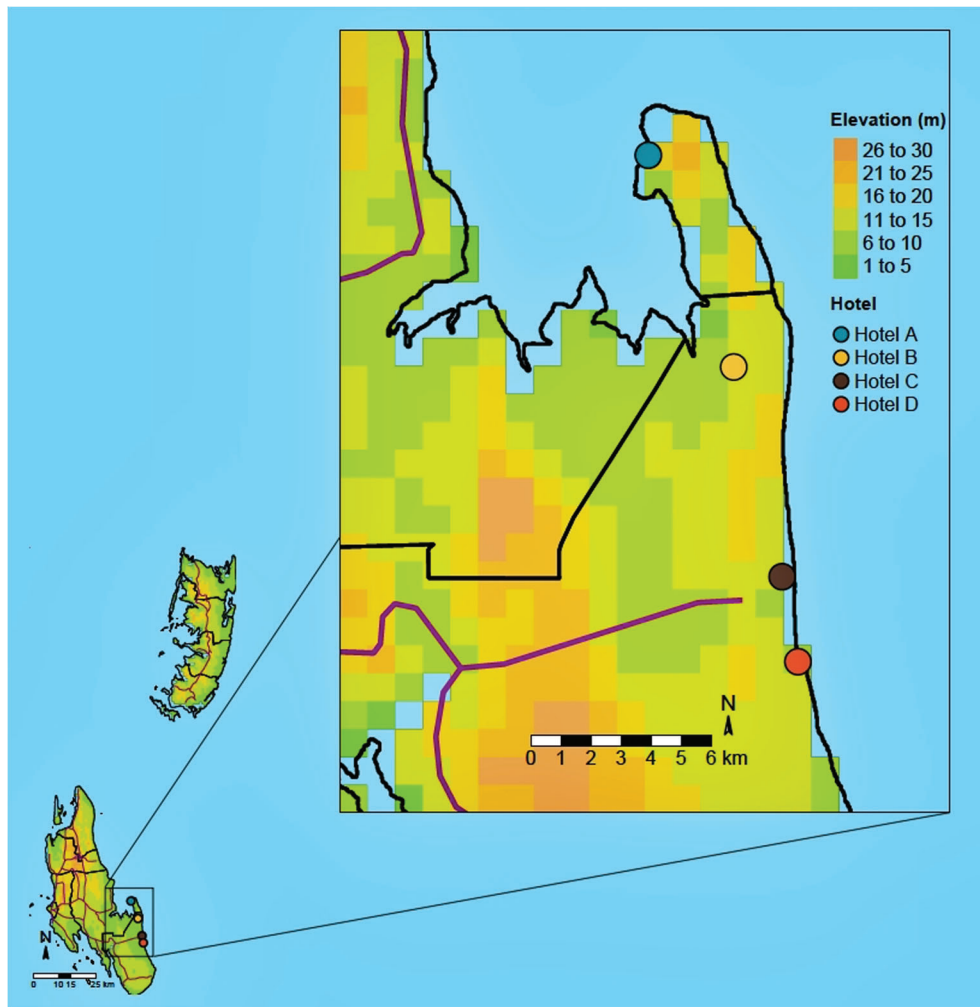
Fig. 1. Map of Zanzibar Island showing the geographical location of the four hotels on the coast of the Southeast region. Zanzibar Island is the largest and most southern of the two major islands of the Zanzibar archipelago. Dark magenta lines depict main roads.

collecting them by pipettes. (b) If water volume was more than 20 L and emptying the container was not feasible (due to its size or nature), but there was good visibility and relatively low larval and pupal density (less than 100 individuals), then all the specimens were sampled using dippers and sweep nets or bowls. (c) Otherwise, only 10–15 dips/sweeps were randomly carried out to collect the specimens. (d) If containers were too deep (e.g., wells), samples were collected using small buckets (approx. 5 L) suspended by a rope. Ten buckets full of water collected from different sites inside the well were obtained. While in the field, mosquito larvae of well-known predacious species, such as *Toxorhynchites* species, *Culex tigripes* and *Eretmapodites* species were separated into different vials to avoid predation on other mosquito larvae. Extra samples of non-predacious mosquito larvae were collected to feed the predacious ones. Containers without mosquito larvae or pupae were considered as potential larval habitats for any local mosquito species only if it had water and physical integrity capable of retaining collected water for at least three consecutive days, which

corresponds with the average time required for larvae of several Afrotropical mosquito species to hatch from eggs in the wild (Service, 1990).

Sampling of adult mosquitoes

Host-seeking mosquitoes were sampled from 18.00 to 06.00 hours over 3 days a week using CO_2 unbaited CDC light traps (John W. Hock Company, Gainesville, FL, U.S.A.), due to challenges with acquisition of dry ice locally. This likely reduced our capacity to catch adults, but it is worth noting that the benefit of adding CO_2 to CDC light traps is species-specific, e.g., Sriwichai *et al.* (2015), and even baited CDC light traps are not particularly effective for diurnally active *Aedes* species (Li *et al.*, 2016). Light traps were hung up inside occupied bedrooms or set up in shaded places outside the same rooms (WHO, 1975). Resting mosquitoes were sampled by Prokopack aspirators (John W. Hock Company, Gainesville, FL, U.S.A.).

Resting collections were performed outdoors for 30 min, early in the morning (06.00–08.00 hours), whereas indoor collections were undertaken inside rooms for 15 min. Both outdoor and indoor collections were performed when conditions permitted (e.g., weather conditions, accessibility).

Sample processing and identification

Samples of immature mosquitoes were reared at insectary environmental conditions of temperature ($27 \pm 2\,°C$) and relative humidity ($75 \pm 10\%$) until they emerged as adults (WHO, 2016). Adult mosquitoes were identified morphologically down to species or genus levels using taxonomic keys for Afrotropical mosquito fauna (Service, 1990; Edwards, 1941; Jupp, 1986; Huang, 2004; Coetzee, 2020).

Environmental data

The environmental variable considered in this study was the normalized difference vegetation index (NDVI), a metric that reflects successional changes of local vegetation cover, and which correlates with fluctuations of mosquito incidence and abundance (Jamison *et al.*, 2015). Daily NDVI records were retrieved from NASA's Terra and Aqua satellites carrying moderate-resolution imaging spectroradiometer sensors (MODIS), via the R package MODISTools (Tuck *et al.*, 2014). NDVI data were obtained using the geographical coordinates of each hotel via MODIS product MOD13Q1, which provides global 16-day images at 250-m spatial resolution. Daily variation of NDVI was sampled in the function of the size of studied sites. NDVI ranges from 0 (no vegetation) to 1 (full vegetation growth) (Jamison *et al.*, 2015).

Data analysis

Mosquito community structure

Mosquito community structure was characterized in terms of mosquito abundance, expressed as the total number of specimens collected at each location per month, and mosquito diversity quantified in term of Hill numbers (^qD), which convert diversity indices into the effective number of species (ENS) (Chao *et al.*, 2014). The authors focused on three measures of Hill numbers of order q, that is, $q = 0$ (diversity of order 0, ^0D) quantifies species richness, the total number of observed species in the assemblage, $q = 1$ is the exponential of Shannon diversity and quantifies the effective number of abundant or equally common species (^1D), and $q = 2$ is the inverse of Gini–Simpson index, which quantifies the effective number of highly abundant species (^2D) (Chao *et al.*, 2014). The true number of mosquito species (actual richness) occurring at each study site was estimated by Chao1 bias corrected (Chao1 bc) richness estimator using the R package iNEXT (Hsieh *et al.*, 2016).

Exploratory analysis indicated that the composition of adult mosquito catches closely approximated nested subsets of larval collection samples (Tables S1 and S2). Additionally, some mosquito species were exclusively detected by one type of collection method and *vice versa*. As such, the authors pooled both adult and immature mosquito catches to overcome the problem of differential detectability between sampling methods, achieve more representative samples of mosquito species and, ultimately, obtain relatively accurate descriptions of mosquito species composition, estimation of the true mosquito richness and other aforementioned diversity indices. A similar approach has been applied with other insect communities (Colwell & Coddington, 1994). No further inferential analysis was performed on adult mosquito catches due to a very small number of individuals caught. Therefore, subsequent analyses were concentrated only on immature mosquito samples. The completeness and coverage of our sampling design were verified by species-accumulation curves (Chao *et al.*, 2014), see Figure S1.

Spatiotemporal variation in mosquito composition

Multivariate abundance generalized linear models (manyGLM) (Wang *et al.*, 2012) were applied on immature mosquito catches to determine the magnitude of variations in mosquito composition between hotels, season and relationship with local variation in vegetation cover. Multivariate abundance models were fitted using the package mvabund (Wang *et al.*, 2012). The manyGLM fits a global multivariate model and several separate univariate GLMs according to the number of taxa in the community matrix. Inference is made by summation of all univariate model likelihood ratio (LR) statistics (Wang *et al.*, 2012). Therefore, the percentage each taxon contributes to global community response can be derived by comparisons between the LR from the deviance of the univariate model and the global deviance (*sum-of-LR*) (Wang *et al.*, 2012). A cubic spline smoothing function was applied to capture the possible non-linear effect NDVI on mosquito counts. Mosquito counts were assumed to follow a negative binomial (NB) distribution with log-link function to account for possible over-dispersion. Model compliance to distributional assumptions was assessed by visual investigation of scatter plots of observed residuals against the fitted residuals (Wang *et al.*, 2012).

Mosquito–larval habitat interaction networks

Ecological network analyses were applied to determine the structure and dynamics of mosquito–larval habitat interaction networks, and also to investigate the response of mosquito populations to induced elimination of larval habitats resulting from environmental control interventions. The followings standard network metrics were calculated: (a) network-level specialization index (H_2'); (b) species-level specialization index (d') (Blüthgen *et al.*, 2006); (c) species degrees index (d); network strength (Bascompte *et al.*, 2006) (e) and network robustness (R) (Memmott *et al.*, 2004). For further details on interpretation of network metrics see Table 1. Envisaging future mosquito control interventions by larval source management at studied sites, the authors simulated three potentially realistic tactics of systematic extinction of larval habitats and evaluated the probable impact

Table 1. Network metrics used to describe the structure and dynamics of mosquito community and larval site interaction networks.

Network metric	Definition/interpretation
Network-level specialization (H_2')	Applied to quantify the overall degree of mosquito community specialization in utilization of larval habitats. $H_2' = 0$ suggests generalist community and $H_2' = 1$ indicates specialist (selective) community
Species-level specialization (d')	Applied to quantify the degree of mosquito species specialization in use of larval habitat relative to other species in the network. $d' = 0$ indicates unselective/generalist population and $d' = 1$ indicates selective/specialist species
Species degrees	Indicates the number of interactions with other species in the network. Applied here to determine the number of mosquito species interactions with larval habitats
Species strength	Quantifies the importance of a resource for the entire network. Here it was applied to quantify the importance of a larva habitat to mosquito community stability
Robustness (R)	Applied to determine the tolerance of mosquito community to elimination of larval habitats. $R = 0$ indicates higher susceptibility to loss of larval habitats and $R = 1$ indicates higher resistance to loss of larval habitats

on mosquito community. The first tactic the authors examined (denoted here as $R0$) was random removal of larval habitats irrespective of frequency or number of links (i.e., total number of mosquito species that frequently exploit the resources as larval sites). This strategy was considered as the 'null model' with which to contrast other possible types of systematic elimination (Memmott *et al.*, 2004). The second tactic ($R1$) involved targeted extinction of larval habitats according to their prevalence in the environment, starting from the most prevalent to the least prevalent larval habitats. For the third strategy ($R2$), the authors simulated targeted removal of larval sites based on the number of species depending on them to breed (i.e., number of links), starting from the most connected to the least connected ones. Network robustness (R) was calculated as the area below the attack tolerance curve representing the proportion of mosquito species persisting as a function of eliminated larval habitats (Memmott *et al.*, 2004; Burgos *et al.*, 2007). The significance of observed network metrics was determined by comparison against expectations generated by null model algorithms proposed by Patefield (1981) and Vázques *et al.* (2007). As such, 1000 random network matrices were generated using the null model algorithms. To allow direct comparisons, observed network metrics were converted into *z*-scores determined as (Observed$_{metric}$ − Null$_{metric}$ mean)/Null$_{metric}$ standard deviation. Z-score values higher than or equal to 2 denote observed metrics significantly higher than expected by chance (Dormann *et al.*, 2009). Ecological interaction network metrics were estimated using the package bipartite (Dormann *et al.*, 2009). All the data processing tasks and statistical analyses were implemented with R software version 4.0.2 (R Core Team, 2020).

Results

Mosquito community structure and composition dynamics

In total, 23 698 mosquitoes were collected from both immature and adult mosquito surveys. Larval collections yielded the highest number of specimens, accounting for nearly 94.1% (22 307/23 698) of all specimens sampled, followed by samples using the Prokopack aspirator and CDC light trap, which contributed 4.69% (1112/23 698) and 1.14% (269/23 698), respectively. Twenty-six mosquito species were identified from

pooled immature and adult mosquito catches (Tables S1 and S2). Both larval and adult mosquito samples contained important vector species (Table S3). *Aedes aegypti* was by far the most abundant species collected as larvae from all four hotels and, together with *Aedes bromeliae/Aedes lillie*, *Aedes metallicus* and *C. quinquefasciatus*, represented 88.77% (19 801/22 307) of all mosquitoes collected (Table S1). *Culex quinquefasciatus* was the most common species among the adult catches, accounting for 88% (1224/1391) of all specimens (Table S2). Thirteen mosquito species were detected at Hotel C, 14 species (Hotel B) and 17 species (Hotel A and Hotel D) from pooled immature and adult samples. The observed number of species is within the range of the estimated richness (^0D) predicted using the Chao1 richness estimator (Table S4). The highest mosquito diversity was observed at Hotel D, followed by Hotel A, D and C (Table S4). The sample-size-based rarefaction curves fitted on each hotel mosquito community reached an asymptote after a minimum sample size of 2000 individuals, indicating that our sampling design was able to detect all possible mosquito taxa occurring at each studied site (Figure S1). The results also indicate that mosquito abundance peaks during the long rainy season (around May and June), whereas mosquito species diversity (^0D, ^1D and ^2D) peaks around 1–3 months later after the end of the long rainy season (July–August) (Fig. 2). Consistent with this, there was a strong 1-month delayed dependence of richness on mosquito abundance (Spearman correlation: $r = 0.61$, $P < 0.001$). The manyGLM showed significant variability in mosquito composition (species turnover) between hotels and season, and a significant non-linear effect of NDVI (Table 2). However, the magnitude of covariate effects on mosquito assemblages was species-specific (Table 2). Additionally, mosquito abundance and richness also increased non-linearly with NDVI index. However, NDVI values above 0.55 did not significantly explain variability in abundance and richness (Figure S2).

Structure and dynamics of mosquito–larval habitat interaction networks

The architectures and seasonal dynamics of mosquito–larval habitat interaction networks are shown in Fig. 3. The rainy season interaction network comprised 18 mosquito species and 11 types/groups of larval habitats (Fig. 3), whereas in the dry
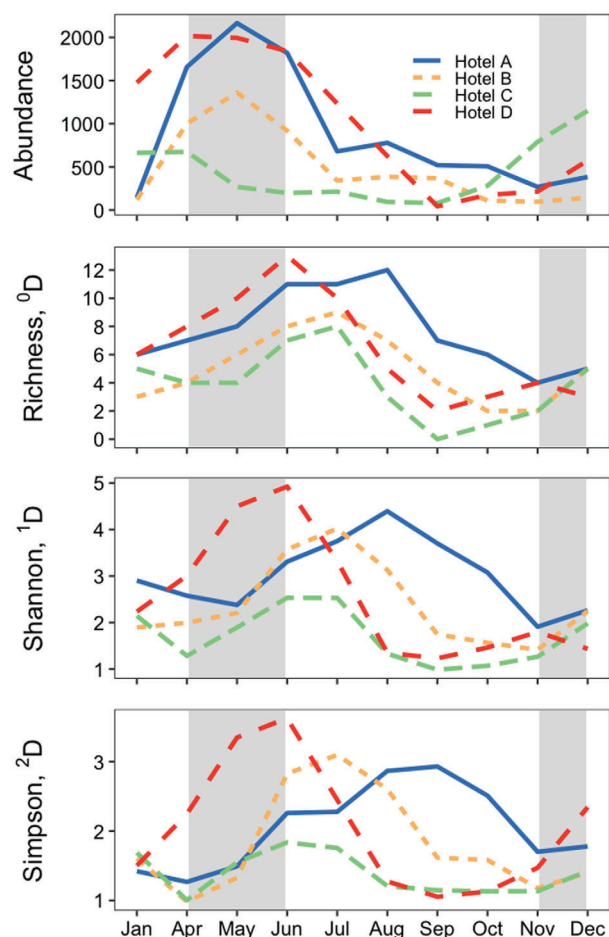
Fig. 2. Temporal dynamics of mosquito community abundance and diversity expressed as net mosquito richness (^0D), Shannon (^1D) and Simpson (^2D) diversities, expressed as the effective number of species (Hill's number). Mosquito abundance erupts and peaks in the long rainy season whereas diversity peaks usually occur after the end of the long rainy season and can remain high throughout the first 2 months at the beginning of the dry season. Shaded rectangles indicate the long (April–Jun) and short (November–December) rainy season periods.

season the network comprised 19 mosquito species sharing 12 types of larval habitats (Fig. 3). Interaction networks were dominated by abundant larval habitat generalist species, which can exploit virtually all types of larval habitats, and less abundant larval habitat specialist species (Fig. 3, Tables S5 and S6). There was a higher tendency for specialization in larval habitat use both at species-level and network levels (Fig. 3, Tables S5 and S6). Observed network-level specialization indices were $H_2' = 0.115$ ($P < 0.001$) and $H_2' = 0.276$ ($P < 0.001$) in the rainy season and dry season, respectively. *Aedes aegypti* was the most prominent larval habitat generalist irrespective of the season. This vector species was found associated with all 11 types/groups of larval habitats identified in the rainy season, and in 83% of all habitats identified in the dry season.

Mosquito community robustness to elimination of larval habitats

Network analyses indicated that plastic containers were the most important resource on which mosquito communities depended for breeding (Table S7). Other resources such as three holes and concrete tanks were also significant for mosquito community stability, particularly in the dry season (Table S7). Simulations of network robustness to induced elimination of larval habitats indicated that the mosquito communities were less tolerant to the elimination of highly connected larval habitats (e.g., plastic containers). Eradication of such types of resources sustaining higher mosquito diversity in the community would cause significant disruption of mosquito community structure leading to more rapid extinction of mosquito species at studied sites than removing larval habitats randomly or prioritizing only the most abundant ones (Fig. 4). The highest impact of larval habitat elimination was predicted in the dry season (Fig. 4).

Discussion

Entomological surveillance and mosquito control interventions have traditionally targeted households and peri-domestic environments (WHO, 2017). Therefore, interventions have not covered the private sector or non-government managed properties, such as hotels, resorts, lodges and others. This has perpetuated the gap in our knowledge regarding the potential of these micromanaged non-public infrastructures to initiate MBD outbreaks of public health concern. The authors found that hotels in Zanzibar sustain diverse assemblages of both vector and nuisance mosquito species. This is important because consistent

Table 2. Summary of the effects of hotel, season and vegetation cover (NDVI) on mosquito assemblage abundance and species composition from larval collections.

| Variable	Residual *df*	*df*	Deviance	*P-values*	Species with significant contribution to total deviance*
Hotel	27	3	208.69	0.001	*Aedes aegypti* (16.51%), *Aedes simpsoni* (14.02%), *Aedes metallicus* (23.07%), *Aedes bromeliae* (17.55%), *Eretmapodites quinquevittatus* (17.90%), *Eretmapodites subsimplicipes* (13.61%), *Culex tigripes* (8.39%)
Season	26	1	40.61	0.04	*A. bromelia/Aedes lillie* (5.36%); *Eretmapodites chrysogaster* (4.78%)
Hotel:Season	23	3	73.80	0.018	*E. subsimplicipes* (6.39%), *Culex quinquefasciatus* (22.70%)
NDVI	24	4	195.34	0.001	*A. aegypti* (9.58%), *A. bromeliae/A. lillie* (14.66%), *E. subsimplicipes* (13.01%), *Eretmapodites conchobius* (16.93%)
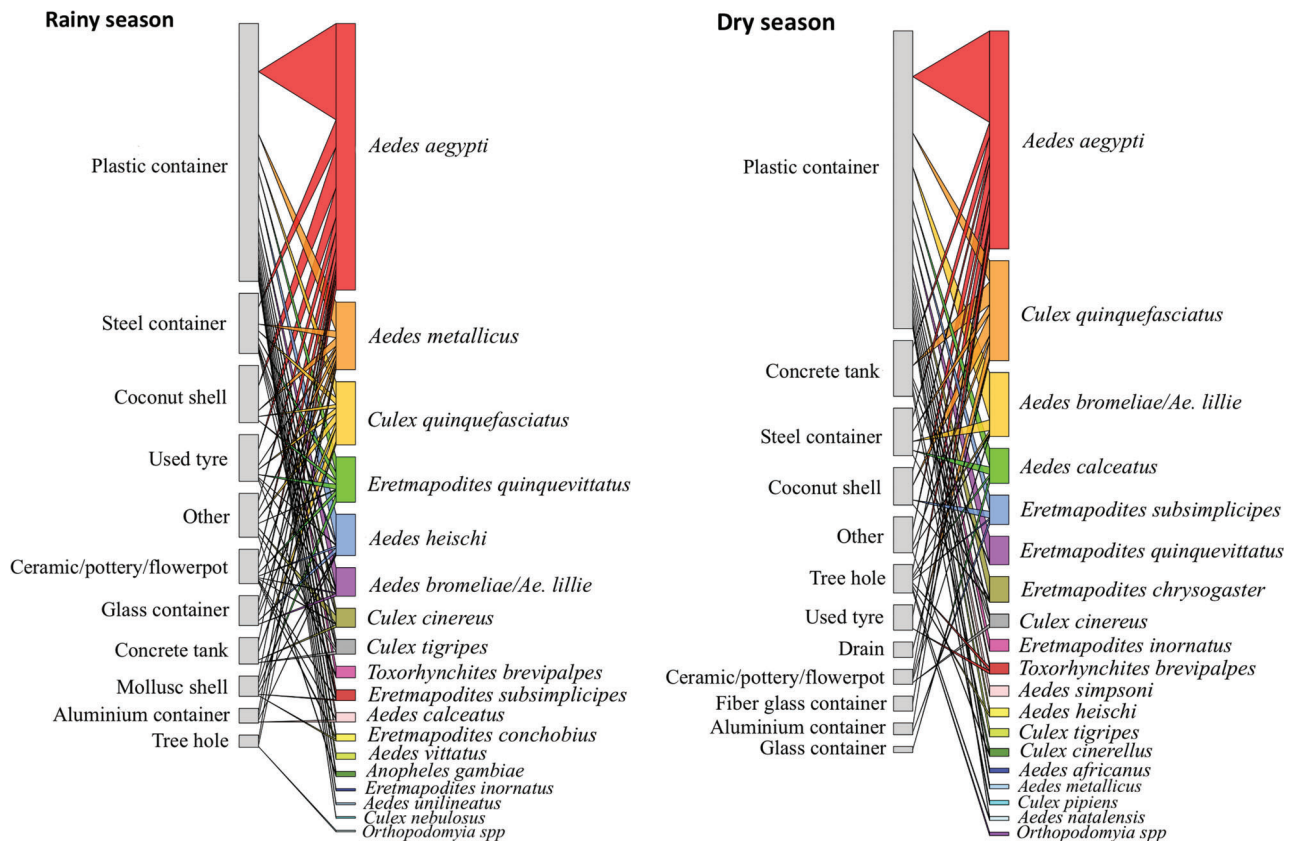
Fig. 3. Quantitative bipartite interaction networks involving mosquito populations and larval habitats identified at studied hotel compounds during rainy and dry seasons. Each rectangle size represents proportional abundance of larval habitats (left) and mosquito species (right). The triangles represent interactions and triangle size is proportional to the frequency of interactions. The rectangles of species nodes and interactions triangles were assigned the same colour to highlight the number of links of each species (higher node) to larval habitats (lower nodes).

surveillance and characterization of vector species dynamics and drivers of mosquito population persistence in the environment is critical for tailoring precise and context specific environmental control measures that can effectively target all fractions of known vector populations and nuisance species. Persistence of nuisance mosquitoes can potentially undermine public perception of control approaches, even if the most important vector species have been successfully eradicated (Killeen *et al.*, 2007). Our data also show consistent time lags of 1–3 months between the peak of mosquito abundance and mosquito diversity at each study site. The late peak in diversity (July–August) suggests that mosquito communities reach stability shortly after the end of the rainy season, probably favoured by reduced frequency of natural disturbance events (e.g., rainstorms), which can cause dramatic losses of mosquito immature stages (Paaijmans *et al.*, 2007). This hypothesis may hold in locations such as Zanzibar, where there are no surface rivers or large collections of permanent water bodies (Hardy *et al.*, 2015). Therefore, rainfall can either drive or limit the propagation of local mosquito populations, depending on the amount and frequency, as observed elsewhere (Shaman & Day, 2007). Our findings also suggest that the risk of MBD exposure can be consistently higher even 1–3 months after the end of the rainy

season. Quantitative understanding of the local dynamics of mosquito community composition can provide valuable information on environmental risks of emergent pathogen exposure, and the potential risks associated with the introduction of invasive vector species. The authors observed significant site-to-site and seasonal variability in mosquito composition, which may reflect differential response to local variations of microclimate and environmental characteristics. The authors also observed a significant non-linear effect of vegetation cover (reflected by variation of NDVI index) on mosquito community abundance and diversity. The NDVI index is an indicator of local vegetation productivity and spatiotemporal dynamics, with high values indicating higher vegetation cover (Pettorelli *et al.*, 2005). Vegetation cover may indirectly increase mosquito abundance and diversity by creating suitable conditions for establishment and survival of mosquito populations. Increasing vegetation cover may, for instance, reduce evaporation rate of standing water from rainfall, gardening or house-refuse and, thereby, contribute towards availability and persistence of potentially suitable larval habitats (Sauer *et al.*, 2021). Vegetation can also create suitable mosquito resting habitats and increase availability of key energetic resources such as nectar (Peach & Gries, 2020). Several studies have also reported a significant positive association
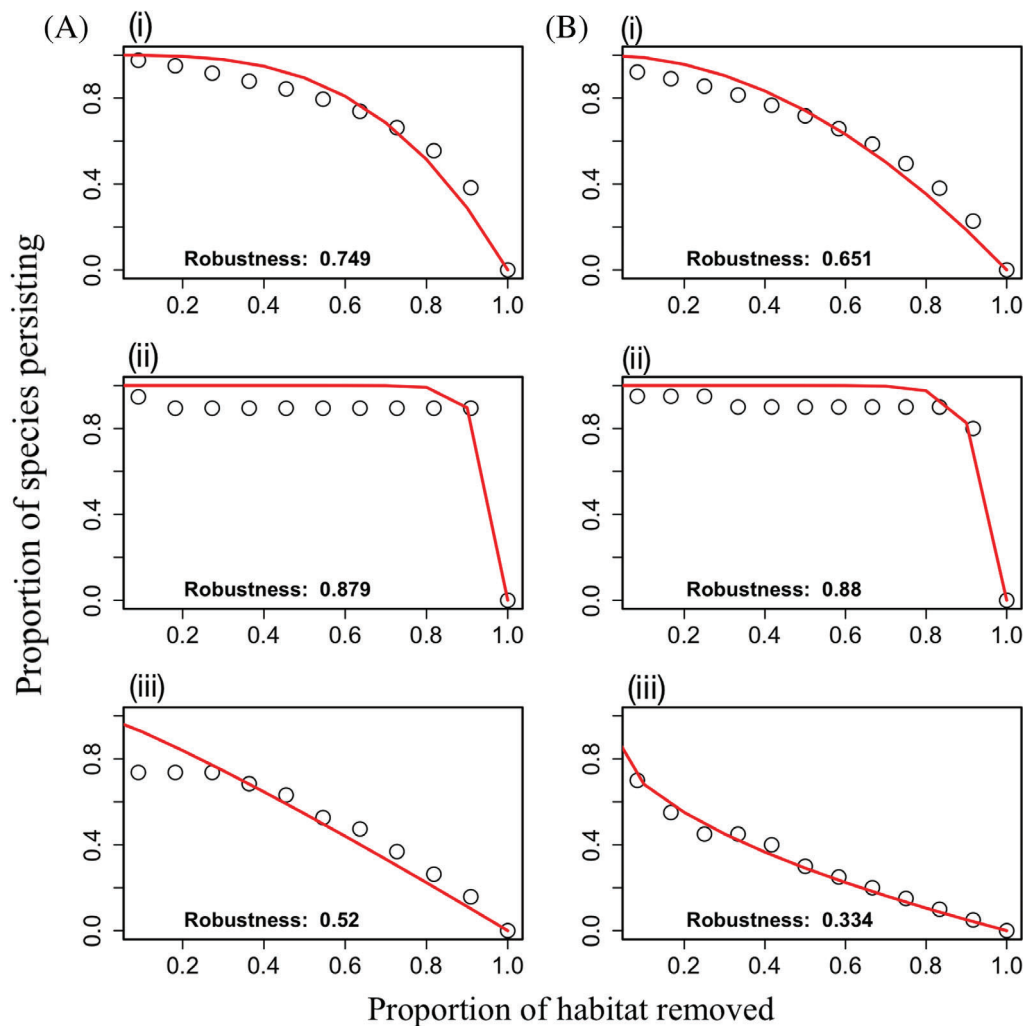
Fig. 4. Mosquito community robustness to induced elimination of larval habitats during rainy season (A) and dry season (B) considering three strategies of larval habitats removal. The three larval habitat removal strategies are: (i) random removal, ignoring larval habitat abundance and strength (species richness per *capita*) in the network; (ii) removal based on larval habitat abundance, and (iii) removal based on larval habitat strength, starting from the most to least connected larval habitat. Loss of higher linked (keystone) larval habitats tend to cause rapid collapse of the network when compared to random extinction and extinction strategy prioritizing most abundant larval sites.

between NDVI and mosquito presence, abundance and diversity (Juri *et al.*, 2015; Roiz *et al.*, 2015; Ferraguti *et al.*, 2016), and MBD prevalence (Jamison *et al.*, 2015).

Ecological network analyses identified small groups of abundant larval habitat generalist vector species, such as *A. aegypti*, *A. bromeliae/A. lillie*, *Aedes simpsoni*, *A. metallicus* and *Eretmapodites quinquevittatus*, that can colonize virtually all types of available water holding artefacts as larval habitats. These observations concur with what is known about oviposition habits of some of these mosquito species, such as, e.g., *A. aegypti* group (Reiter, 2007) and *E. quinquevittatus* (Louni-bos, 1980). It has been argued that this opportunistic oviposition behaviour may be an evolutionary adaptation to maximize the survivorship and fitness of immature stages. It also facilitates propagation over the landscape in the presence of highly ephemeral larval habitats (Reiter, 2007). By contrast, there is

also a group of larval habitat specialist mosquito species, such as *Aedes natalensis* and *Ortopodomyia* spp, which in the present study were found strictly exploiting tree holes in co-occurrence with some generalist species. This type of ecological network topology has been observed in other insect taxa, and may be a co-evolutionary adaption for mosquito communities to resist extreme events, such as habitat disturbances (Vázques & Aizen, 2004; Bascompte *et al.*, 2006). The ability of generalist species to successfully colonize virtually all types of larval habitats implies that control of this species guild may require much more effort than control of specialist species. However, our results also show an increasing tendency for specialization in larval habitat use during the dry season compared to the rainy season, implying that larval habitat generalist populations, which are the most abundant, may be more vulnerable to control measures targeting mosquito sources in the dry season. What

drives phenological specialization in resource use remains poorly understood. However, we can tentatively hypothesize that factors such as competition for disproportionately available larval habitats and behavioural avoidance of predation might be potential drivers in our cases. The size, frequency and number of larval habitats are expected to decrease in the dry season, so that some mosquito-larval habitat ecological interactions may be lost due to natural extinction of larval habitats. Therefore, shortage of larval resources may increase the rate of inter-specific competition forcing some mosquito species to avoid oviposition in larval habitats with competitors or predator species (Schneider *et al.*, 2000; Kesavaraju & Juliano, 2004).

The impact of environmental control interventions by mosquito-larval sources have been traditionally evaluated for a restricted group of well-known vector species. Therefore, mosquito community-wide effects of such types of interventions remain poorly understood. Our simulations of mosquito community tolerance to induced elimination of larval habitats indicate that mosquito populations are most vulnerable to elimination of highly connected (i.e., species-rich) larval habitats (e.g., plastic containers, ceramic pots, coconut shells and tree holes). This is particularly the case in the dry season. Eradication of such sources of higher mosquito diversity can cause rapid extinction of mosquito populations at studied sites. This finding implies that mosquito control interventions by larval source management should prioritize targeted elimination of ecologically functional larval habitats, not just based on larval habitat prevalence. Our results also indicate that the impact of removing ecologically functional larval habitats will be higher in both the rainy and dry seasons compared to other simulated control strategies. However, it is worth mentioning that ecological interaction networks are dynamic systems, so the possibility of adaptive rewiring of lost interactions that have been broken by control measures cannot be ruled out, as observed in other insect taxa (CaraDonna *et al.*, 2017). Therefore, experimental trials to investigate the response of mosquito communities to induced disturbance by elimination of functionally important larval habitats is encouraged before area-wide implementation of larval source management interventions.

Concluding remarks

Our findings show that hotels in Zanzibar can sustain a high diversity of vectors and nuisance mosquito species showing predictable interactions with identified larval habitats. Therefore, coordinated mosquito control strategies between tourism and public health sectors on the island are encouraged. Mosquito communities are highly vulnerable to elimination of larval habitats sustaining higher mosquito species richness, making larval source management a potential candidate for future environmental control interventions. Our findings also highlight the need for further investigation on the ecological function of larval habitats for effective mosquito management by environmental control approaches. This study has focused on mosquito communities within hotel compounds, but future studies in other settings are encouraged.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supporting information.

Conflict of interest

The authors declare no potential conflict of interest.

Author contributions

AK, MA, KS and PF conceived the study; AK, FS, FK, CW, MA, KS and PF designed the study; AK, FS, KH and DLS performed and supervised field surveys and data collection; AK performed data analysis and wrote the first draft of the manuscript. All authors reviewed and approved the final manuscript.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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