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Temporal variability and flooding influence the ecological niche of *Biomphalaria* intermediate hosts for *Schistosoma mansoni* in rural Uganda

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Understanding the niches of intermediate hosts and vectors for environmentally transmitted pathogens is crucial for identifying endemic areas, assessing habitat suitability and targeting interventions. This study focuses on intermediate hosts of intestinal schistosomes, with over 700 million people at risk of lifelong infection. We compared habitat suitability and species interactions across 674 sites in 52 villages in rural Uganda between 2022 and 2024, capturing a severe flooding event. Spatiotemporal models incorporating a polygon-based method to account for space with time as a fixed effect were developed to analyse snail abundance for *Biomphalaria sudanica* and *B. stanleyi*. *B. sudanica* was associated with marshy sites near lake shorelines and presence of hyacinths, while *B. stanleyi* was more likely to be found in deeper waters with *Vallisneria* plants. However, cohabitation was common for both species. Habitat suitability for each species fluctuated temporally, and more starkly with extreme flooding, resulting in switching of species dominance. Our study suggests that events consistent with climate change may influence habitat suitability without necessitating an expansion of environmental areas. Our models enable tracking of dynamic ecological niches that, if replicated elsewhere and for other intermediate hosts or vectors, can be used to better target environmental and community interventions as environmental conditions change.

1. Introduction

Schistosomiasis is a neglected tropical disease caused by *Schistosoma* trematode flukes [1] with at least 700 million people at risk of infection, and most infected cases in sub-Saharan Africa [2]. Infections can lead to lifelong morbidities, including irreversible fibrosis of the bladder, spleen and liver, depending on the schistosome species [1]. Transmission relies on freshwater snails acting as intermediate hosts. Yet, schistosomiasis control efforts focus on mass drug administration (MDA) with implementations based on administrative units of endemic countries that neglect the complex spatiotemporal distributions of snails and their impact on human infection prevalence. Recent World Health Organization guidelines strongly recommend environmental interventions in the form of water treatment and snail control [3]. Integrated approaches thus far have focused on precision mapping of snail habitats [4–6]. However, key questions remain about the ecological niches of different snail species; defined here using the Hutchinsonian framework as the *n*-dimensional hyper-volume of environmental and resource conditions that permit a species to persist [7]. We also aim to understand the variability of these niches under changing climatic conditions and the best approaches for spatiotemporal modelling. Here, we focus on *Biomphalaria* snails, a common genus in sub-Saharan Africa, to assess habitat suitability across four timepoints that captured a severe flooding event and other distinct hydrological conditions.

Biomphalaria snails act as intermediate hosts for *S. mansoni*, facilitating its asexual reproduction and the release of thousands of infectious cercariae from a single miracidium and single snail [1]. This prolific reproduction enables a few hosts to infect entire communities, thereby complicating efforts to map and control infection risks, especially combined with the microgeographical focus of snail habitats that can vary on the basis of a few metres [8]. Snail distributions are made even more difficult to predict due to seasonal ecological variability such as rainfall, temperature and changes in conditions specific to freshwater sites such as vegetation type and growth [9]. Climate change and extreme weather events can further destabilize these habitats, altering snail populations and shifting transmission dynamics [10–13]. However, it remains an open question as to how such destabilization affects habitat suitability, including whether (i) ecological niches are simply expanding spatially with stable characteristics under fluctuating environmental conditions or (ii) ecological niche concepts need to be revisited and there are alternatives to simple habitat expansion.

Several studies have concluded that different *Biomphalaria* species are found in distinct ecological niches, which has led to a pattern of species dominance across different water sites. However, the specific environmental characteristics defining these niches have been inconsistently reported. It has been found that certain species occupy habitats along the shoreline, such as *B. sudanica* and *B. pfeifferi*, whereas other species occupy deeper waters, such as *B. stanleyi* and *B. choanomphala* [9,14]. Snail abundance has been linked with certain vegetation (e.g. *B. sudanica* with hyacinth plants and *B. stanleyi* with *Vallisneria* plants [9,15]) and physicochemical water parameters, such as water pH and water temperature, though there is disagreement regarding positive or negative associations for these climate-sensitive parameters [9,14,16]. For these proposed ecological niches, spatiotemporal models are lacking for studying how they respond to varying environmental conditions and complex events like severe flooding, which are becoming more common due to climate change.

Malacological studies use methods such as association tests [9,16,17], maximum entropy models [12,13] and regression analyses [4,14,15,18,19], but often overlook spatial factors. In large-scale studies, it is often unspecified whether and how sites were tracked across timepoints, which is particularly problematic in the context of flooding [13,18]. Simple aggregation of spatial data can mask important microhabitat patterns. Some models treat sites as random effects [14,15,19], which may not capture meaningful spatial variation, or report spatial autocorrelation without addressing it explicitly [15]. New approaches are needed to account for space in models seeking to assess ecological niches or habitat suitability over time.

We propose a generalizable spatiotemporal modelling pipeline designed to analyse the presence and stability of distinct ecological niches for different snail species. In three rural districts of Uganda, we collected data from a total of 674 water sites across four timepoints from 2022 to 2024, capturing a severe flooding event, two dry season annual timepoints and one seasonal timepoint during the rainy season. Our aims were to determine whether *B. sudanica* and *B. stanleyi* have distinct ecological niches and to evaluate the stability of these niches across changing climatic conditions, particularly in the context of flooding.

2. Methods

(a) Study context

The study was conducted within the prospective cohort SchistoTrack [20]. This community-based cohort was established in Buliisa and Pakwach in western Uganda and Mayuge in eastern Uganda, starting with 38 villages in 2022 and expanding to 52 villages as of 2024. The three districts feature distinct ecologies as Buliisa is situated along Lake Albert, Pakwach along the outlet of the Nile River from Lake Albert, and Mayuge along Lake Victoria. The communities in these rural districts heavily rely on water sourced from these water bodies and thus come into frequent contact with them. Malacology data are collected at least annually. Here, we examined all timepoints from 2022 (study baseline) to 2024. There were four malacology surveys: three annual collections in Jan–Feb of 2022, 2023 and 2024, and an additional seasonal collection in October–November 2023. To avoid confusion between the annual and seasonal collections in 2023, we henceforth refer to them as '2023a' and '2023b', respectively. Typically, January and February fall in the dry season, whereas October and November fall in the rainy season. However, the baseline timepoint (2022) exhibited a severe flooding event altering the water site conditions, especially in the western districts of Buliisa and Pakwach. The other timepoints exhibited conditions that are more typical of their respective months.

Surveys for data collection were created using Open Data Kit (ODK) Collect (versions 2022.4.2, 2023.2.4 and 2024.1), and data were entered in the ODK surveys on Android devices (software version Android 9 and 10). ODK Central (versions 2022.3.1, 2023.2.1 and 2024.2.1) was used for data management and quality control. Further data and statistical analyses were performed using R (version 4.2.1) [21].

(b) Water sites and covariates

Surveys were conducted by eight malacologists working in pairs and assisted by local auxiliary workers. Sites within the catchment of the study that were reported to be frequented by village inhabitants by the local assistants were identified. Information was collected for all water sites, irrespective of the presence of snails. Long beaches and shorelines were divided into multiple sites, with each site defined as a 15 m segment. This approach was used to capture potential variations in snail abundance associated with microhabitats [8]. Ephemeral ponds, defined here as water bodies that dry up in less than 2 months, were excluded from the surveys.

The information collected at each site included: GPS coordinates (taken while the surveyor was standing in the water); water depths (shallowest and deepest parts); human activities frequently performed there; number of boats present; site landform; water speed; occurrence of environmental modifications; ground substrate; types of vegetation, livestock and fish present; water turbidity, temperature and pH; total dissolved solids; conductivity; and start time of snail sampling. These were chosen based on theoretical importance from the literature. In addition, several photographs were taken of the water sites. During the collection period (2022–2024), the malacologists aimed to visit the same water sites based on the GPS coordinates and the previously taken photographs. Any additional water sites indicated by the local workers were visited as well. However, it proved challenging to match water sites over the years due to significant environmental changes (such as shoreline shifting) and other obstacles (e.g. presence of wild animals). Therefore, we analysed the data as a series of repeated cross-sectional surveys.

A set of 44 covariates was assembled to be used in variable selection based on the data collected at the water sites. The covariates were split into five broader categories: spatiotemporal information, general site characteristics, physicochemical parameters, environmental and ecological attributes, and human activities. Detailed descriptions of covariates along with collection procedures can be found in electronic supplementary material, text S1. The numerical variables were scaled to have a mean of zero and a s.d. of one across the entire time frame using the `scale` function in R.

(c) Snail outcomes

Snail sampling was performed by two malacologists at all sites. Snail identification to species level was performed based on external morphological characteristics with the aid of a dissecting microscope (Olympus SZ61 stereo microscope). Morphological characteristics as per species were as indicated in well-established taxonomic keys by the Danish Bilharziasis Laboratory [22]. Species of the genus *Biomphalaria* collected included *B. sudanica*, *B. stanleyi*, *B. pfeifferi* and *B. choanomphala*. Further details on snail sampling can be found in electronic supplementary material, text S2. We focused on the two most common species in our study, *B. sudanica* and *B. stanleyi*, with their abundance (counts of snails at each site) as our primary outcomes. The purpose was to identify whether each species occupies a distinct ecological niche, and to determine the environmental and ecological conditions that are key determinants of its presence and abundance in water habitats. This analysis extended to investigating species cohabitation, defined as the presence of both species at a given water site. This was further extended to species dominance, defined as the species with the highest absolute count of snails within a site, further examining whether dominance was stable or switched over time. The other two species commonly found in Uganda, *B. pfeifferi* and *B. choanomphala*, were not modelled due to their low numbers. We believe *B. pfeifferi* was present due to extreme flooding, which displaced them from their usual seasonal pond habitats. Furthermore, shedding snails were also only discussed descriptively due to their low numbers, and because the focus of this article is on ecological niches related to presence and abundance.

(d) Spatial analysis

To understand the extent to which the snail counts of each of the two species at a given water site were similar or dissimilar to the counts in nearby locations, we calculated spatial autocorrelation for each outcome. Using the `spdep` package [23], we first identified neighbouring observations by applying the `dnearneigh` function, setting a distance threshold equal to the maximum distance between any two sites within the same district. This ensured that sites from different districts were not considered as neighbours. We then computed Moran's *I* [24], which quantifies spatial autocorrelation, using the `moran.test` function. We constructed static spatial units in the form of polygons that included the water sites to allow for comparison across timepoints. These were subsequently used as a random effect in our statistical models to account for any spatial autocorrelation. Using conventional administrative units [4], such as villages, would have been an unsuitable proxy for spatial relationships, as water sites were not always geographically located within their assigned villages. To accurately reflect this, we considered the households involved in the study and created a tessellation of polygons for each district separately based on the location of the households. This method was chosen because our ecological framework is centred on the human–environment interface of transmission. Previous research has demonstrated that water contact activity declines rapidly with household distance from water sites [25]; therefore, our polygons were defined using household locations to create a spatial unit that accurately reflects the proximity of the human population to the water sites they likely use. Two approaches were explored for generating these polygons: (i) household clustering to capture spatial groupings independent of village boundaries (cluster-based polygons), and (ii) household grouping based on self-reported village affiliations (village polygons). The cluster-based polygons were chosen for subsequent statistical modelling as they better aligned with the spatial focus of the study. Details of the alternative village-based approach are provided in electronic supplementary material, text S3.

Constructing polygons based on household clustering was purely spatial and did not take into consideration the villages as defined by local residents or by the national government. To do this, we first applied a clustering algorithm to identify household clusters. Hierarchical clustering was chosen as it does not require any predefined number of clusters and does not allow for any points (households) to be treated as noise [26], unlike density-based clustering [27]. A distance matrix between all the households in the district was calculated using the Vincenty (ellipsoid) method [28]. To determine the optimal number of clusters (k), the gap statistic was considered as a goodness of clustering measure [29]. The gap statistic compares the within-cluster variation for different values of k in the actual data to that of a null reference distribution, which assumes no cluster structure. The optimal number of clusters is the k that maximizes the gap statistic, indicating that the clustering structure in the data is significantly better than what would be expected by random chance. Using the factoextra and cluster packages [30,31], we computed the gap statistic (with 500 simulations) and applied a hierarchical clustering algorithm with both the complete and average linkage methods [32], which ultimately gave us the same clusters. The polygons were constructed using the household locations; Voronoi polygons were generated for each household [33], and subsequently these polygons were merged according to the cluster they belonged in. We identified which polygon each water site lay within for each timepoint and created the polygons variable. For the construction of the tessellations, we used the following packages: deldir [34], sp [35], sf [36] and maptools [37].

(e) Statistical modelling

We fitted generalized linear mixed models (GLMMs) [38] with a zero-inflated negative binomial (ZINB) distribution to the snail counts for *B. sudanica* and *B. stanleyi* using the glmmTMB package in R [39]. A log link function was used for the count component to ensure no negative values are predicted, and a logit link function for the zero-inflation component to ensure the probability of an excess zero is between zero and one. While the distribution of counts is often modelled with a negative binomial distribution, we accounted for excess zeros by incorporating zero inflation, which considers structural zeros in addition to the zeros arising from the count process [40]. For instance, zeros in our snail counts may arise from the true absence of snails due to unsuitable habitats or other environmental conditions (structural/true zeros), measurement error such as the inability to collect snails on a given day (sampling/false zeros), or sampling variability, e.g. snails could have been present but, perhaps due to microenvironmental changes on the day of sampling, they are not (random/true zeros). Odds ratios (ORs) from the zero-inflation component of these models represent the odds of an observation being a structural zero. Thus, an OR > 1 indicates higher odds of a site being unsuitable for snails, while an OR < 1 indicates lower odds. This contrasts with traditional logistic regression, where ORs reflect the odds of presence.

We constructed a minimally adjusted model including the timepoint and district covariates as fixed effects and the polygons covariate as a random effect (in both the conditional and zero-inflation parts of the GLMM). We then performed variable selection on the 41 remaining variables, separately for each species, to determine the final fixed effects. We selected variables for the zero-inflation part by adding them individually and using likelihood ratio tests (LRTs) to assess significance (p-value < 0.05) [41], using the lrtest function from the lmtest package [42]. Significant variables were included in the zero-inflation part of the minimally adjusted model, and the same process was applied to the conditional part of the now-updated model. This resulted in two GLMMs, one per species, with the district of Mayuge excluded for *B. stanleyi* given its absence from Lake Victoria. We used variance inflation factors (VIFs) to investigate multicollinearity in the fully adjusted models [43] using the multicollinearity function from the performance package [44], and variables (that were not part of the minimally adjusted model) with VIF > 5 were removed one by one until no multicollinearity was detected. ORs and rate ratios (RRs) were calculated by exponentiating coefficient estimates for the zero-inflation and conditional parts, respectively.

The DHARMa package was used to perform goodness-of-fit tests on simulated residuals [45]. We measured spatial autocorrelation in the residuals of the fully adjusted models using Moran's I, as before, to determine whether any unaccounted-for autocorrelation remained. Additionally, we computed the corrected Akaike information criterion (AICc) for the minimally and fully adjusted models to estimate the relative quality of each.

We applied multiple cross-validation methods to evaluate model generalizability and predictive capacity. Stratified five-fold cross-validation preserved temporal or spatial structures by sampling from each timepoint, district, or polygon, accounting for distinct climate profiles or ecological differences and local variations in snail habitats. Leave-one-out cross-validation (LOOCV), training on all polygons except one, tested model sensitivity to individual polygons. Model performance was evaluated using receiver operating characteristic (ROC) curves (for the probability of a site having zero snails) and area under the curve (AUC) values, using the caret package for training and cross-validation [46], and the pROC package for ROC/AUC computation [47].

A summary of the methods and generalizable spatiotemporal modelling pipeline is presented in electronic supplementary material, figure S4.

3. Results

(a) Summary of water sites and snails

We observed 674 water sites across four timepoints (2022–2024). In the flooded season (2022), we surveyed 143 sites across 38 villages, with two villages reporting no water sites. The number of villages increased to 52 in subsequent timepoints, where we surveyed 177 sites in 2023a, with seven site-free villages; 175 sites in 2023b, with five site-free villages; and 179 sites in 2024, with five site-free villages. Four of the villages that were added to the study after the 2022 survey remained site-free throughout. A breakdown of sites by timepoint and district is shown in electronic supplementary material, table S5. Among the original 38 villages, the number of sites was highest in 2022 (143), attributed to the severe flooding event. The rest of the timepoints had fewer sites (138, 134 and 141, respectively). Site characteristics differed significantly over districts and timepoints (electronic supplementary material, table S6), particularly for altitude, water depth, water pH, water temperature, conductivity and site landform (electronic supplementary material, figure S7).

Across all timepoints and sites, 61 459 snails were collected: 62.7% (38 505/61 459) *B. sudanica*, 31.8% (19 516/61 459) *B. stanleyi*, 3.7% (2253/61 459) *B. pfeifferi* and 1.9% (1185/61 459) *B. choanomphala*. A total of 618/61 459 snails were observed to be shedding human cercariae, resulting in an infection rate of 1%. From the 618 shedding snails, the species breakdown is as follows: 20.7%

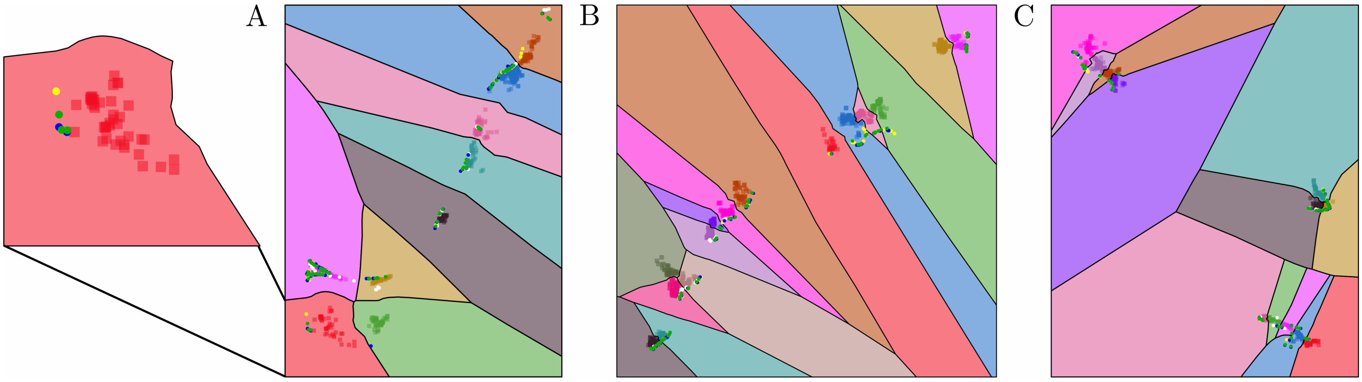

Figure 1. District tessellations including water sites. **(A)** Buliisa, (B) Pakwach, (C) Mayuge. Squares represent individual households and dots represent water sites. The site colours correspond to the four timepoints: white—2022; yellow—2023a; blue—2023b; green—2024. On the left, we show an example of a zoomed-in polygon.

(128/618) *B. sudanica*, 75.1% (464/618) *B. stanleyi*, 2.9% (18/618) *B. pfeifferi* and 1.3% (8/618) *B. choanomphala*. Breakdowns by district and timepoint are presented in electronic supplementary material, table S8 and figure S9.

(b) Spatial autocorrelation and spatial unit

Moran's I indicated spatial autocorrelation prior to model building (*B. sudanica*: $I = 0.131$, p-value < 0.001; *B. stanleyi*: $I = 0.010$, p-value < 0.001). Cluster- and village-based polygons were compared. For the polygons reliant on household clustering, the optimal number of clusters, k, for each district was computed as 9, 15 and 12 for Buliisa, Pakwach and Mayuge, respectively (electronic supplementary material, figure S10). The number of spatial units was reduced by 30.8% when moving from self-reported administrative villages (52) to cluster-based polygons (36; figure 1). As village-based polygons required manual, subjective household reassignment (electronic supplementary material, figure S11), cluster-based polygons were used in all models as a random effect to account for spatial autocorrelation.

(c) Ecological niche of *B. sudanica*

B. sudanica snails were present in 63.8% (430/674) of all water sites across the four sampling timepoints (electronic supplementary material, figure S12). Figure 2 presents OR and RR plots of the fully adjusted model for *B. sudanica*, and the model without Mayuge is shown in electronic supplementary material, figure S13.

Water sites in Buliisa and Pakwach had 4.50 (95% CI: 1.69–12.02) and 5.27 (95% CI: 1.96–14.12) times higher odds of being unsuitable for snails compared to sites in Mayuge. Sites with no observed snails may have arisen due to unsuitable ecological conditions or sampling challenges. Temporal variation was observed, with sites in 2023 a and 2023b having 2.45 (95% CI: 1.13–5.29) and 3.38 (95% CI: 1.45–7.91) times higher odds of being unsuitable for snails compared to 2022. Collecting snails in the afternoon had 2.60 (95% CI: 1.03–6.55) times higher odds of sites being unsuitable for snails compared to early morning collection. Lake beach was the reference category as it was the most common site landform. Lake sites with marshy landforms had lower odds of being unsuitable for snails compared to beachy landforms (OR = 0.27, 95% CI: 0.13–0.58), while no other landforms showed significant differences to the reference category. The presence of hyacinth was associated with lower odds of a site being unsuitable for snails (OR = 0.39, 95% CI: 0.20–0.76), while *Vallisneria* plants were associated with 2.44 (95% CI: 1.37–4.34) times higher odds. The presence of chickens was associated with 3.43 (95% CI: 1.65–7.13) times higher odds of a site being unsuitable for snails, whereas both the presence of goats and plastic (or other waste) was associated with lower odds (OR = 0.50, 95% CI: 0.26–0.97 and OR = 0.47, 95% CI: 0.27–0.82, respectively). Finally, medium turbidity also had lower odds of a site being unsuitable for snails (OR = 0.58, 94% CI: 0.33–0.99) relative to low turbidity.

Among sites that were suitable for snails, the expected snail abundance showed a 55% decrease in the western district of Buliisa (RR = 0.45, 95% CI: 0.34–0.59) and a 66% decrease in the western district of Pakwach (RR = 0.34, 95% CI: 0.26–0.44) compared to the eastern district of Mayuge (right section of figure 2). The expected count was lower during the flooding event in 2022, with counts in 2023a and 2023b showing a 47% (RR = 1.47, 95% CI: 1.06–2.03) and 55% (RR = 1.55, 95% CI: 1.11–2.16) increase, respectively, while counts in 2024 showed no significant difference. The presence of *Ceratophyllum* and hyacinth plants was associated with a 43% (RR = 1.43, 95% CI: 1.11–1.84) and a 36% (RR = 1.36, 95% CI: 1.01–1.85) increase in expected abundance on average, respectively. Sites with clay as ground substrate had a 33% decrease in snail abundance (RR = 0.67, 95% CI: 0.48–0.94). Snail abundance also decreased with higher water pH, where each one s.d. (≈ 0.8 pH) increase was associated with a 17% decrease in expected abundance (RR = 0.83, 95% CI: 0.71–0.97). Similarly, each one s.d. (≈ 1.4°C) increase in water temperature was associated with an 18% decrease in expected snail abundance (RR = 0.82, 95% CI: 0.74–0.91).

(d) Ecological niche of *B. stanleyi*

B. stanleyi snails were observed in 40.7% (196/482) of the sites, excluding sites in Mayuge (electronic supplementary material, figure S14). Figure 3 presents the OR and RR plots of the fully adjusted model for *B. stanleyi*.

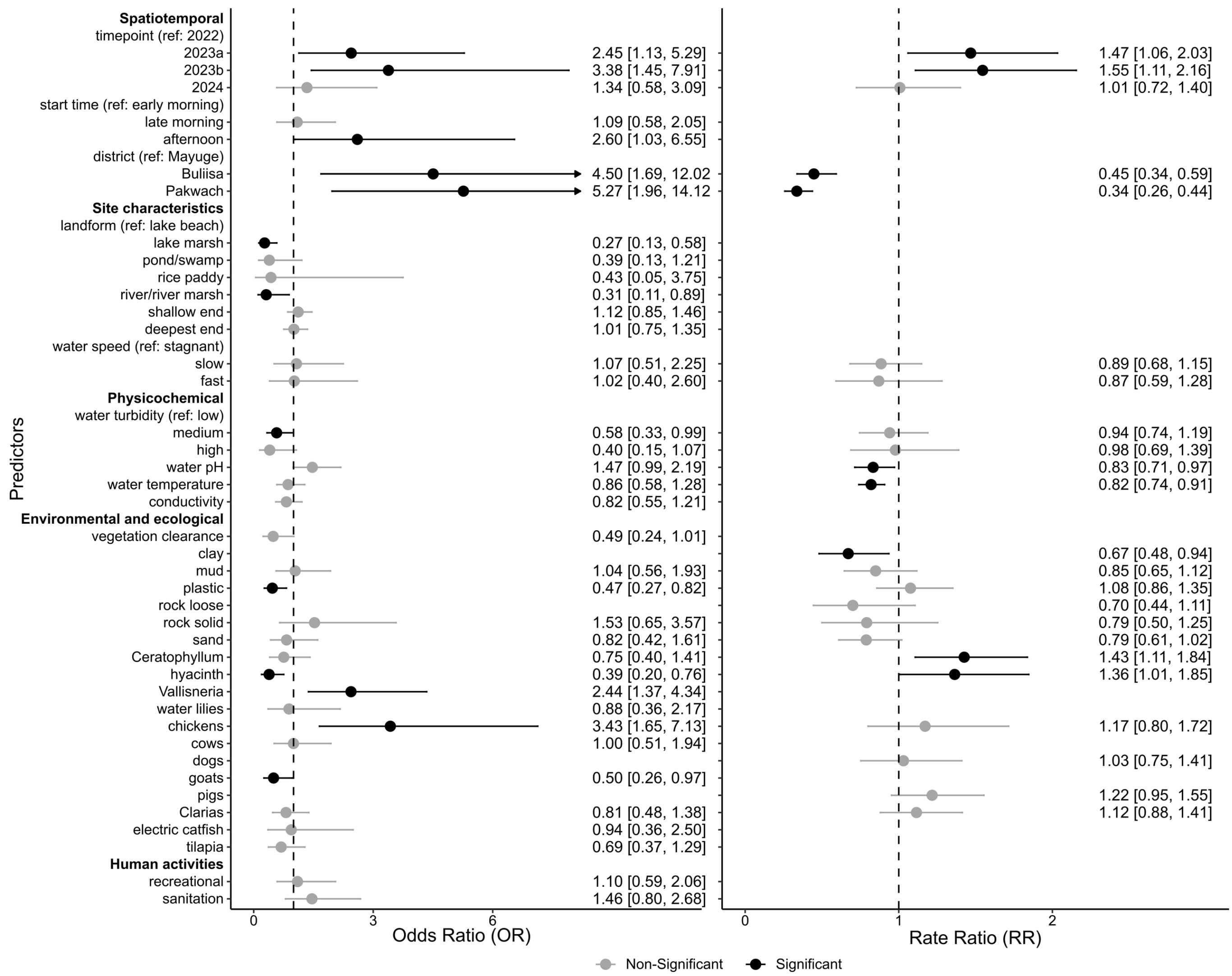

Figure 2. Fully adjusted *B. sudanica* model**.** Odds ratios (left) and rate ratios (right) for the zero-inflation and conditional components of the model, respectively. Dots correspond to the exponentiated coefficient estimates and lines correspond to the 95% CIs. Arrows indicate that the CI continues off the plot.

Comparing the likelihood of sites in Buliisa and Pakwach being unsuitable for snails, we observed no significant difference between the districts (p-value = 0.085). Temporal variation in unsuitability for snails was noticed; compared to the 2022 timepoint, the odds of a site being unsuitable for snails were 2.65 (95% CI: 1.11–6.34) times higher in the 2023b and 6.50 (95% CI: 2.15–19.64) times higher in 2024, while, in 2023a, the odds were lower (OR = 0.38, 95% CI: 0.17–0.82). Lake sites with marshy landforms had lower odds of being unsuitable for snails compared to lake sites with beachy landforms (OR = 0.40, 95% CI: 0.18–0.91). The presence of *Clarias* fish was associated with 2.96 (95% CI: 1.61–5.45) times higher odds of a site being unsuitable for snails, while the presence of *Vallisneria* plants and plastic (or other waste) was associated with lower odds (OR = 0.23, 95% CI: 0.12–0.44 and OR = 0.40, 95% CI: 0.21–0.75, respectively). Finally, each one s.d. (≈ 12.1cm) increase in water depth at the shallow end of the site led to lower odds of a site being unsuitable for snails (OR = 0.76, 95% CI: 0.57–1.00).

Among sites that were suitable for snails, there was no significant difference in the expected number of snails between the two districts (p-value = 0.562). However, temporal differences were observed. Compared to 2022, the expected number of snails showed a 167% increase (RR = 2.67. 95% CI: 1.62–4.40) in 2023a and 107% increase (RR = 2.07, 95% CI: 1.01–4.25) in 2023b. Conversely, 2024 exhibited a 71% decrease in snail abundance (RR = 0.29, 95% CI: 0.11–0.79) compared to 2022. The presence of *Vallisneria* plants was associated with a 106% increase (RR = 2.06, 95% CI: 1.25–3.40) in expected snail abundance, while vegetation clearance led to a 283% increase (RR = 3.83, 95% CI: 1.96–7.48) in the expected number of snails compared to sites where this environmental modification had not occurred. Lastly, snail abundance was associated with a 30% decrease for each one s.d. (≈41 m) increase in altitude (RR = 0.70, 95% CI: 0.60–0.82).

(e) Species cohabitation and dominance switching

The two species had many overlapping ecological dimensions, yet their ecological niches were distinct. In the zero-inflated component, overlapping selected variables included landform, shallow end depth, water speed, water pH, plastic and sand ground substrates, *Vallisneria* plants, chickens, *Clarias* fish and recreational activities, whereas only water speed, water pH, mud and plastic substrates overlapped for the conditional components. Plastic and *Vallisneria* had significant coefficients for both models (in the

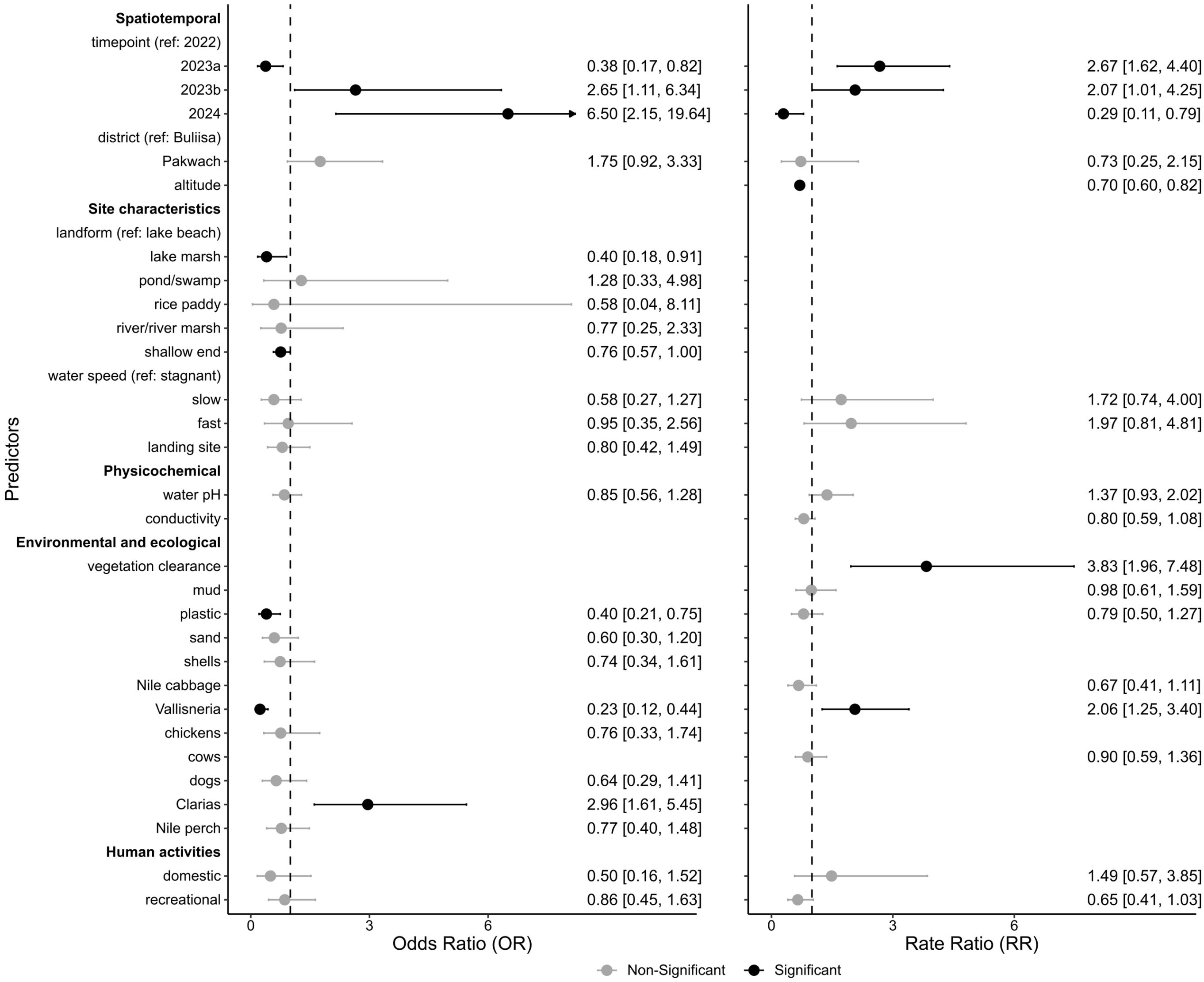

Figure 3. Fully adjusted *B. stanleyi* model**.** Odds ratios (left) and rate ratios (right) for the zero-inflation and conditional components of the model, respectively. Dots correspond to the exponentiated coefficient estimates and lines correspond to the 95% CIs. Arrows indicate that the CI continues off the plot.

zero-inflation part), with the effect of *Vallisneria* in opposite directions for each species. Despite distinct ecological niches, the two species cohabitated in 17.2% (83/482) of all sites across time (excluding Mayuge) with cohabitation peaking in 2022 (during the severe flooding event) at 30.3% (30/99) and subsequently varied: 17.3% (22/127) in 2023a, 10.3% (13/126) in 2023b and 13.8% (18/130) in 2024. Sites with cohabitation were largely clustered together within a few polygons. Spatiotemporal variations in species presence and cohabitation are shown in electronic supplementary material, figure S15. We also investigated dominance (differences in absolute abundance) to understand potential temporal dominance switching. Over 70% of cohabitated sites (59/83) had an absolute difference of more than 20 snails between species (median 51, IQR 131). Overall, 51.2% (247/482) of sites were dominated by *B. sudanica* and 29.5% (142/482) by *B. stanleyi*, with the remainder having no snails or equal abundance of both species (figure 4). Dominance switching was more evident in Buliisa, with somewhat balanced dominance (in terms of how many sites each species is dominant at) in 2022 and 2023b, but clear single-species dominance in 2023a and 2024.

(f) Model validation

Results from goodness-of-fit tests on simulated residuals are shown in electronic supplementary material, figure S16. There was no remaining spatial autocorrelation in either model, as indicated by Moran's I values close to zero for the models' residuals (−0.004, p-value = 0.8 for *B. sudanica* and −0.003, p-value = 0.6 for *B. stanleyi*). The selected predictors improved the fit of the minimally adjusted models, which already included key spatiotemporal features (timepoint, district and polygons), as shown by the AICc: *B. sudanica* AICc = 5426 (minimally adjusted model) and 5293 (fully adjusted model); *B. stanleyi* AICc = 2602 (minimally adjusted model) and 2489 (fully adjusted model).

For stratified five-fold cross-validation, when sampling within each polygon, district and timepoint, the average AUC values were 0.80, 0.80 and 0.80 for *B. sudanica* and 0.83, 0.82 and 0.78 for *B. stanleyi*. For LOOCV, AUC values ranged from 0.125 to 1 (median 0.67) for *B. sudanica* and from 0.20 to 0.96 (median 0.75) for *B. stanleyi*. The *B. sudanica* model's ability to predict snail absence was lower in polygons where hyacinth, goats and/or plastic (waste) were present. For *B. stanleyi*, predictive performance

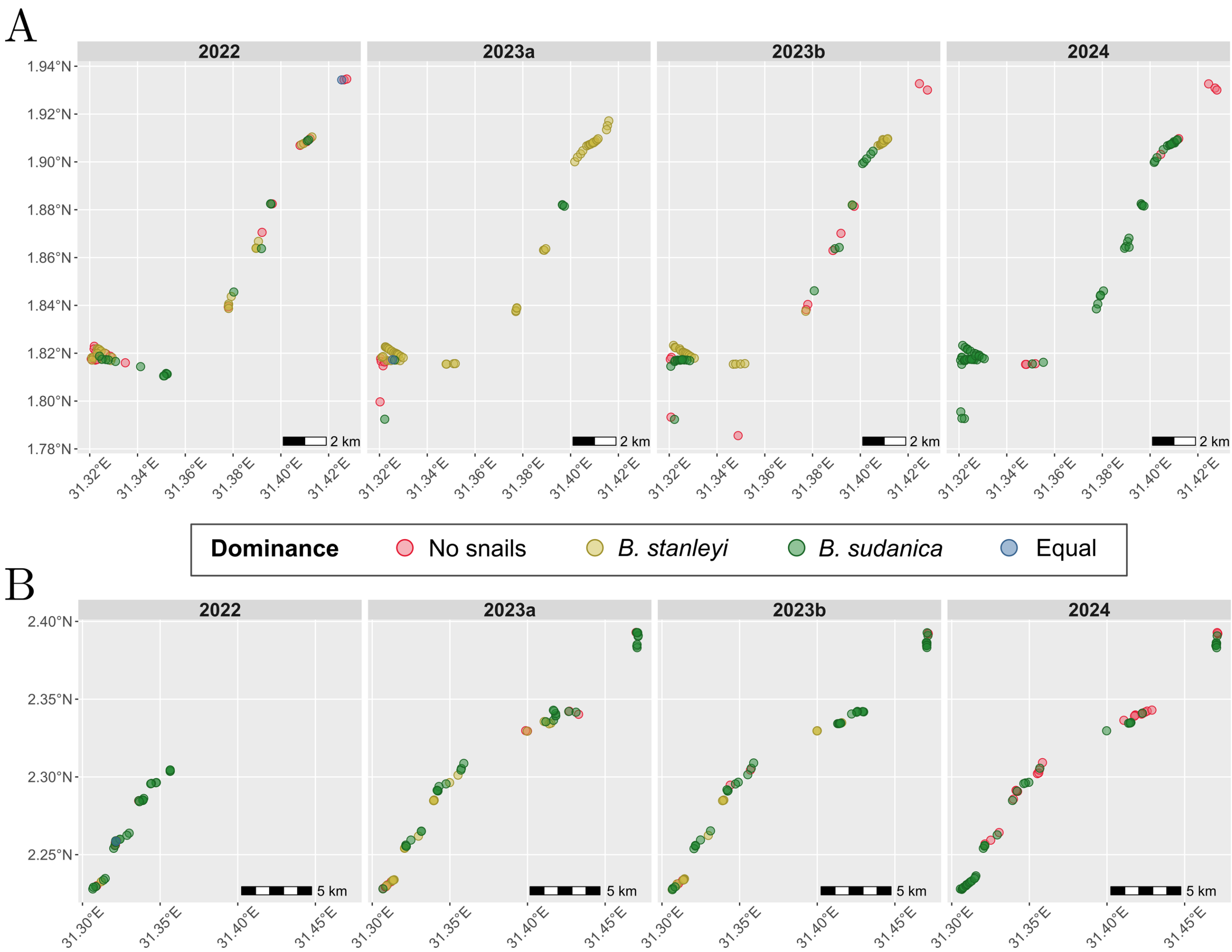

Figure 4. Within-site dominance of snail species. (A) Buliisa, (B) Pakwach. Each circle represents a water site. The site colours correspond to the dominance status: red—no snails at site; yellow—*B. stanleyi* dominant; green—*B. sudanica* dominant; blue—equal abundance of each species.

was lower in polygons where snails were absent despite the presence of *Vallisneria* plants and/or plastic, and where snails were present alongside *Clarias* fish.

4. Discussion

Extreme events and temporal trends influence habitat suitability of the snail intermediate hosts. Understanding these spatiotemporal influences is essential for identifying areas of ongoing transmission and adapting interventions to climate change. Here, we focused on the spatiotemporal distributions and ecological niches of *B. sudanica* and *B. stanleyi* snails, intermediate hosts of *S. mansoni*, in schistosome-endemic areas of rural Uganda. We surveyed 674 water sites from 2022 to 2024 across four ecologically distinct periods. We found that the snail distributions were strongly influenced by extreme flooding and other temporal variations, leading to species cohabitation, dominance switching and instability in the distinction of their ecological niches.

The ecological niches of *B. sudanica* and *B. stanleyi* were influenced by site characteristics, ecological factors and physicochemical water parameters. The presence of *B. sudanica* was associated with marshy sites with medium to high water turbidity and lower water pH and temperatures, as well as presence of waste, goats, hyacinth and *Ceratophyllum* plants. Conversely, the presence of chickens, *Vallisneria* plants, and clay substrates created unsuitable conditions. Afternoon snail collections (compared to early morning) showed an increase in snail absence, supporting the shedding patterns observed in the literature [48]. The presence of *B. stanleyi* was associated with marshy habitats with deeper shallow ends and presence of waste and *Vallisneria* plants, while the presence of *Clarias* fish was a limiting factor, possibly due to predation. A significant relationship with altitude was observed, with higher elevations being unsuitable for *B. Stanleyi*—perhaps an indicator for air temperature as lower altitudes are associated with higher temperatures. This may explain its absence in Mayuge, where the average altitude (1148 m) is higher than in Buliisa (621 m) and Pakwach (625 m). Our findings might suggest that increasing water temperature due to climate change can be detrimental to certain snail species like *B. sudanica*. While climate change can increase schistosome transmission in areas where temperatures lie within schistosomiasis' thermal optimum [49], our study shows that this is unlikely to be the case in our region, as our median water temperature per district were above the reported thermal optimum range (median water temperatures of 27.7°C in Buliisa, 29.2°C in Pakwach and 28.6°C in Mayuge, where the thermal optimum is reported as 23.1–27.3°C [49]). Furthermore, waste materials could provide microhabitats or resources that snails take advantage of, perhaps due to their potential implications on water quality, although the specific mechanisms remain unclear.

The two species often coexisted across seasons, with their seemingly distinct ecological niches reflecting flexible habitat use rather than fixed boundaries. Studies often portray habitat differentiation, rarely exploring the conditions that support both species (such as plastic or other waste and vegetation clearance) or the possibility of cohabitation [9,16]. However, our results show that the species not only coexist but also exhibit temporal shifts in species dominance within cohabitated sites, which underscores the dynamic role of temporal variations in shaping their ecological interactions. Patterns of temporal dominance were particularly evident in the district of Buliisa, where *B. stanleyi* dominated during the 2023a timepoint, which exhibited dry conditions, and *B. sudanica* became dominant during the 2024 timepoint, which also exhibited dry conditions, but followed an extended rainy season, as per reports from the malacologists and local residents. In the 2022 and 2023b timepoints, where the first captured an extreme flooding event and the second was during the typical rainy season, we saw a balance between species, blurring habitat distinctions, with clustered cohabitated sites. During 2023a and 2023b, sites were more likely to have no *B. sudanica* present; however, when they were present, their abundance was higher, suggesting that while many sites became unsuitable, those that remained suitable supported larger populations. This pattern implies that conditions during those timepoints may reduce overall habitat availability but create temporary niches for *B. sudanica* in the remaining habitats. This supports previous studies where normal water levels were more suitable for *B. sudanica* than flooded conditions [9,14]. In contrast, *B. stanleyi* habitat suitability increased during 2023a, compared to during the flooded event in 2022, consistent with the literature [9]. In 2023b, habitat suitability declined, but the remaining suitable sites supported larger snail populations. Extreme flooding, characterized by high water levels, may reduce light penetration to submerged vegetation, decreasing oxygen concentrations and influencing snail dynamics. These conditions can be exacerbated by decomposing plants such as *Vallisneria* and hyacinths, which are otherwise beneficial to *B. stanleyi* and *B. sudanica*, respectively. However, the interaction between flooded conditions and decomposing vegetation might create harmful environments for snails over time, highlighting the complex interplay between vegetation presence, water quality and seasonal effects shaping habitat suitability and snail abundance over time. Even established knowledge of species' climatic associations, once compared across species, provides evidence of otherwise overlooked shared snail habitats. While our findings of spatiotemporal cohabitation and shifts in species dominance provide insight into the mechanisms that may permit long-term coexistence, they are observational. Future experimental research is required to confirm the stability of this coexistence and its underlying ecological drivers.

Vegetation clearance has been proposed as a sustainable intervention to control snails and reduce human infection risk [50,51]. However, our findings indicate that it had a borderline significant effect on *B. sudanica* presence and increased *B. stanleyi* abundance. These results suggest that disturbances to vegetation structure or water conditions can sometimes create suitable environments for snails, contradicting previous studies that linked submerged vegetation removal to reduced *Biomphalaria* abundance [50,51]. These studies, conducted in West Africa along the Senegal River, focused on *B. pfeifferi* and *Bulinus* snails, and *Ceratophyllum* plants, suggesting that the findings may not be generalizable to other species, regions, or types of vegetation. Therefore, vegetation removal could yield mixed results, depending on species and ecological context. This raises the question: Can snail control interventions designed for one species be effective across multiple species, or would it require a detailed, species-specific strategy? The complexity increases in a multi-species approach, as different species have different ecological niches that need targeting, leading to infeasible or ineffective strategies. Additionally, such interventions may have unpredictable or mixed effects, as the relationship between vegetation structure, water quality and snail populations is often complex and context dependent. Therefore, a targeted, integrated approach, possibly incorporating multiple intervention strategies, may be necessary to address the challenges of snail control, and longer-term efforts to offset climate change cannot be ignored. Future large-scale studies are still needed to investigate the generalizability of environmental modifications across different species, regions and vegetation types.

B. stanleyi snails have been understudied not only for their interactions with coendemic snail species, but also importantly for human transmission. *B. stanleyi* snails are native to Lake Albert and closely related to *B. pfeifferi* [52]. While they have been previously reported in Lake Chad and Lake Cohoha [53], their current presence in these regions remains unclear. Despite studies exploring aspects of their phylogeny [54], morphology [55], ecology [9] and population dynamics [56], *B. stanleyi* is largely overlooked compared to other *S. mansoni* intermediate hosts such as *B. sudanica*, *B. pfeifferi* and *B. choanomphala*, which are more widespread. This is particularly concerning given that areas around Lake Albert are characterized by a high burden of life-threatening morbidity related to *S. mansoni*, such as portal hypertension and high infection prevalence [25,57], raising questions about the role of *B. stanleyi* in parasite virulence and transmission. Experiments have demonstrated that *B. stanleyi* can act as an efficient host for the *S. mansoni* isolates from Lake Victoria [58], performing even better than native Lake Victoria snails. Should this species migrate to other regions, such as Lake Victoria, or, even worse, cross borders to other countries, it could impact transmission dynamics and infection rates, potentially undermining ongoing control efforts, such as MDA. Further research is necessary to understand the potential migration of this species into other *S. mansoni*-endemic regions and its implications for schistosomiasis control.

A limitation of our study is its focus on only the two most common species found in our specific study sites, *B. sudanica* and *B. stanleyi*. While this provided a foundation for understanding the ecology of these species in our area, it is important to acknowledge the role of *B. pfeifferi* and *B. choanomphala* as important intermediate hosts in other *S. mansoni*-endemic regions [59–61]. The variable capacity of different snail species to serve as effective hosts is a key factor contributing to the highly spatially heterogeneous patterns of schistosomiasis [59,60,62,63]. Therefore, while our study provides a foundation for understanding the ecology of the species in our area, a more comprehensive understanding will require further research into the ecological niches and transmission potential of all four species across their respective geographical ranges.

In an ideal scenario, the identification of false zeros would be straightforward, allowing for their removal or direct modelling from the data. A limitation in our spatial approach is that it requires a spatial boundary to be defined, which in this case was the study catchment area to enable ground truth data collection. As a result, water sites could potentially be missing within the catchment of our tessellations. Another limitation arises from the treatment of districts and timepoints as fixed effects, which prevents the model from predicting unseen districts or timepoints as a whole, but this can be overcome in future studies applying our pipeline if there is a large number of districts or timepoints and each is incorporated as a random effect.

The spatial unit used for environmentally mediated pathogens, such as schistosomes, affects how we understand transmission and the effectiveness of interventions. We developed new methods to account for spatial autocorrelation in environmentally dependent models of infectious diseases with intermediate hosts or vectors that have limited mobility ranges. Especially for schistosomiasis, the need for a more relevant spatial unit has been evident and overlooked, with districts still acting as the implementation unit of interventions in many countries [64,65]. Flooding or dryness causes shorelines to move, leading to uncertainty as to which water sites are the same over time, especially in areas with extreme weather variations. By constructing spatial units based on households rather than water sites, we created a more stable and robust framework for tracking water site locations over time. This approach minimizes the risk of changes between surveys, making it a reliable tool for future work in identifying focal points of transmission. Additionally, it offers flexibility in linking with administrative boundaries if needed and improving the relevance of geographical clustering for interventions. The effectiveness of our method for dealing with spatial autocorrelation was evident when initial autocorrelation present in the outcomes was no longer present in the residuals of our models that incorporated the polygons as a random effect. This framework is suitable for future studies on intervention implementation, mobility matrix construction and other spatially explicit modelling. The variation observed in the LOOCV results underscores the importance of selecting appropriate spatial units. The models performed better when the spatial units matched consistent ecological conditions, highlighting the need for future studies that apply statistical models to report failure cases, as these emphasize the challenges of predicting species distribution in highly variable ecological landscapes, even within the same districts.

In this article, we challenge the hypothesis that *B. sudanica* and *B. stanleyi* have distinct, stable ecological niches, providing evidence of cohabitation driven by extreme flooding and temporal disturbances. Our findings and models, if replicated elsewhere, may help to define environmental control strategies and targeted community interventions, especially in the context of climate change.

Ethics. Data collection and use were reviewed and approved by Oxford Tropical Research Ethics Committee (OxTREC 509-21), Vector Control Division Research Ethics Committee of the Uganda Ministry of Health (VCDREC146) and Uganda National Council for Science and Technology (UNCST HS 1664ES).

Data accessibility. All relevant data and code are available on Dryad [66].

Supplementary material is available online [67].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.A.I.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; A.M.B.: data curation, writing—review and editing; F.B.: data curation, writing—review and editing; B.N.: data curation, writing—review and editing; N.B.K.: data curation, project administration, resources, writing—review and editing; G.F.C.: conceptualization, data curation, funding acquisition, methodology, project administration, resources, software, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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