

Modeling freshwater snail habitat suitability and areas of potential snail-borne disease transmission in Uganda

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Abstract. Geographic information system (GIS)-based modeling of an intermediate host snail species' environmental requirements using known occurrence records can provide estimates of its spatial distribution. When other data are lacking, this can be used as a rough spatial prediction of potential snail-borne disease transmission areas. Furthermore, knowledge of abiotic factors affecting intra-molluscan parasitic development can be used to make "masks" based on remotely sensed climatic data, and these can in turn be used to refine these predictions. We used data from a recent freshwater snail survey from Uganda, environmental data and the genetic algorithm for rule-set prediction (GARP) to map the potential distribution of snail species known to act as intermediate hosts of several human and animal parasites. The results suggest that large areas of Uganda are suitable habitats for many of these snail species, indicating a large potential for disease transmission. The lack of parasitological data still makes it difficult to determine the magnitude of actual disease transmission, but the predicted snail distributions might be used as indicators of potential present and future risk areas. Some of the predicted snail distribution maps were furthermore combined with temperature masks delineating suitable temperature regimes of the parasites they host. This revealed the coinciding suitable areas for snail and parasite, but also areas suitable for host snails, but apparently not for the parasites. Assuming that the developed models correctly reflect areas suitable for transmission, the applied approach could prove useful for targeting control interventions.

Keywords: snails, parasites, schistosomiasis, distribution, habitat modeling, remote sensing, geographic information system.

Introduction

In a recent malacological survey in Uganda, several freshwater snail species known to be important intermediate hosts of human and animal parasites were collected (Jørgensen, 2003). These included several *Bulinus* and *Biomphalaria* snail species known to act as intermediate hosts for the parasite *Schistosoma* sp., the cause of schistosomiasis in humans and other mammals. Also com-

monly encountered was *Lymnaea natalensis*, the intermediate host of *Fasciola gigantica* the cause of fascioliasis in wildlife, livestock and humans. Several of these snails also have the potential to host a number of amphistome species (stomach flukes), that cause serious infections in domestic livestock and wild grazing animals in Africa (Dinnik, 1964). However, like many other vector-borne diseases in the tropics and sub-tropics, parasitological survey data are scarce, rendering it difficult to assess the extent and magnitude of disease transmission. In general, the distributions of the snail-borne diseases depend largely on the spatial distribution of suitable intermediate host snails. However, it can be difficult to establish where transmission is likely to occur, based solely on the presence of suitable water bodies and intermediate host snails. There are areas where intermediate

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host snails occur, but there is no disease. Besides of course from human occupational and other socio-economic related factors, the absence of disease in these areas could be due to unfavorable environmental conditions for parasite development. Such conditions could include too low or too high temperatures, which affect the metabolic processes of both the snail host and the parasite, thus interfering with parasite reproduction within the snail, snail growth and snail survival rate (Appleton, 1978). Thus, studies of such abiotic factors are useful because they give an indication of the suitability of the habitat as a potential transmission site. Temperature has been pointed to as the most important factor (Appleton, 1978) besides factors such as rainfall (water availability), water velocity, geomorphology and habitat stability (Appleton, 1978).

Recently, several approaches to predictive modeling of species' geographic distributions based on biotic and abiotic factors have been developed within a geographic information system (GIS) framework. Such modeling tools have been applied within a variety of fields such as biogeography, conservation, evolutionary ecology, invasive-species management and disease ecology (e.g. Carpenter et al., 1993; Jarvis and Robertson, 1999; Hay et al., 2000; Peterson et al., 2002; James and McCulloch, 2002; Estrada-Peña, 2002; Arriaga et al., 2004). One approach is ecologic niche modeling of primary occurrence data (data placing a particular species in a particular site) (Stockwell and Noble, 1992; Stockwell and Peters, 1999; Peterson and Vieglais, 2001). The approach involves a machine-learning algorithm for discovering associations between point occurrence data and remotely sensed maps summarizing environmental dimensions that may or may not be important in limiting species' distributions. These associations constitute an approximation of species' fundamental ecologic niches (MacArthur, 1972) and provide a basis for understanding ecologic and geographic phenomena related to species distributions.

The aims of the present study were: (i) to produce

habitat suitability maps for snail species known to act as intermediate hosts for parasites in Uganda, and (ii) to identify suitable/unsuitable areas of disease transmission overlapping these host snail distribution ranges, based on knowledge of optimal temperature regimes for parasitic development in the snail.

Distribution maps indicating levels of habitat suitability for the snails were developed using the desktop version of the genetic algorithm for rule-set prediction (GARP) (Stockwell and Noble, 1992; Stockwell and Peters, 1999). The distribution maps are, where possible, discussed in the context of known parasite occurrence and distributions. If successful, the applied approach could prove a valuable tool to identify on a large scale, suitable areas for intermediate host and parasite species (for which detailed information is not available), and for planning the operational aspects of disease control interventions.

Materials and methods

Snail occurrence point data

Snail sampling was conducted in the period 2000 to 2003. Approximately 20,000 freshwater snail specimens were collected from 89 different sampling sites across Uganda. In addition to the larger lakes, a number of inland habitats were sampled, including swamps, temporal ponds, small lakes, rivers and streams. All sampling localities were geo-referenced using a hand-held global positioning system (GPS) (Trimble GeoExplorer II; Trimble Navigation Ltd., Sunnyvale, CA, U.S.A.). Other than *Biomphalaria* species (the intermediate host snail of *Schistosoma mansoni*), at least three other freshwater snail species groups and genera that are also intermediate hosts of parasites were identified. These were members of the *Bulinus truncatus/tropicus* species complex and the *Bulinus africanus* group (intermediate hosts of, among others, *S. haematobium* that cause urinary schistosomiasis), and the *Bulinus forskalii*

group, intermediate hosts of *S. intercalatum* (Wright et al., 1972) and *S. bovis* (Southgate and Knowles, 1975). The gastropod species *L. natalensis*, the intermediate host of the liver fluke *F. gigantica*, that causes fascioliasis in both humans and animals throughout Africa (Mas-Coma et al., 1999), were also among frequently encountered snail species. A list of the snail species found in Uganda and the parasites they potentially host can be seen in Table 1.

Due to unresolved taxonomic problems and difficulties with species determination, species belonging to the *Bu. truncatus/tropicus* complex are referred to the species complex and not the individual species throughout this paper. Snail species “*Biomphalaria* cf. *pfeifferi*” and *Biomphalaria sudanica* suggested to be responsible for inland transmission of intestinal schistosomiasis in Uganda are modeled together due to cur-

rent taxonomical problems with the separation of the species. “*Bi.cf. pfeifferi*”, conchologically looks like *Bi. pfeifferi* but are molecularly closely related to *Bi. sudanica* (Jørgensen, 2003). They are referred to in this paper as *Bi. “pfeifferi”/sudanica* (see also Stensgaard et al., 2005), and are represented by a total of 44 individual point records. The distribution of species belonging to the *Bu. truncatus/tropicus* complex were modeled together, due to difficulties with morphological species identification and unresolved taxonomic issues within these groups, (Jørgensen, 2003). Members of the *Bu. africanus* group were included as well, as they are important *S. haematobium* hosts. Together, they made up a total of 42 species records. The *Bu. forskalii* group was represented with 19 individual point records, *L. natalensis* with 54 point records and *Bi. choanomphala* with 17 point records. Other

Table 1. Naturally infected intermediate snail hosts present in Uganda, and the parasites they potentially host (after Brown, 1994). Records of widespread parasite presence is indicated with (++), reported individual cases with (+). No presence confirmed or presence unknown is indicated with (-).

Snail	Parasites	Main mammalian host	Uganda
<i>Biomphalaria</i> spp.:	<i>S. mansoni</i>	Man	(++)
<i>Bi. “pfeifferi”/sudanica</i> ,	<i>S. rodhaini</i>	Rodents	(+)
<i>Bi. choanomphala</i> ,	<i>Paramphistomum</i>	Livestock and wild grazing animals	(-)
<i>Bi. stanleyi</i>	<i>sukari</i>		
<i>Bulinus</i> spp.:			
<i>Bu. africanus</i> group	<i>S. haematobium</i>	Man	(+)
	<i>S. bovis</i>	Cattle	(+)
	<i>S. mattheei</i>	Cattle, sheep	(-)
	<i>S. curassoni</i>	Cattle, sheep	(-)
	<i>S. intercalatum</i>	Man	(-)
	<i>S. leiperi</i>	Antelopes, cattle	(-)
	<i>Echinostome</i> spp.		
<i>Bu. truncatus/tropicus</i>	<i>S. bovis</i>	Cattle	(+)
complex	<i>S. haematobium</i>	Man	
	<i>S. margrebowiei</i>	Antelopes, cattle	(-)
	<i>Calicophoron</i>	Livestock and wild grazing animals	(-)
	<i>microbotrium</i>		
<i>Bu. forskalii</i> group	<i>S. intercalatum</i>	Man	(-)
	<i>S. bovis</i>	Man	(+)
	<i>S. margrebowiei</i>	Antelopes, cattle	(-)
	<i>Carmyerius</i> sp.	Livestock and wild grazing animals	(-)
	<i>P. phillerouxi</i>	Livestock and wild grazing animals	(-)
<i>Lymnaea</i> spp.:			
<i>L. natalensis</i>	<i>F. gigantica</i>	Cattle, sheep	(+)

known intermediate host snail species (e.g. *Bi. stanleyi* and *Bi. smithi*) were not modeled due to lack of sufficient point records.

Parasitological data

The only currently available parasitological survey data from Uganda, comes from a recent epidemiological study of *S. mansoni*, conducted by the Vector Control Division, Ministry of Health Uganda in the period 1998-2002. Data is available from 201 georeferenced schools from across Uganda, including a total of 13,798 schoolchildren (Kabatereine et al., 2004). The dataset was divided into presence/absence data for endemic disease transmission at a particular site, using a cut-off value of 5% prevalence. This data set is used to validate the specificity and sensitivity of the final map of predicted suitable transmission areas for *S. mansoni*. No such data exist for any of the other parasites in Uganda.

Snail distribution model development

As environmental input data for ecological niche modeling in the present study, we chose environmental and climatic variables, suggested to be important for freshwater snail distributions. This included temperature and water availability proxies from satellite sensor land surface temperature (LST) products (day- and night-time) and normalized difference vegetation index (NDVI) (annual mean, wet and dry season) from the MODIS satellite sensor. A climate surface grid of monthly long-term climate data for the climatic normal period 1931-1960 (IGAD/Nile Minimum Medical Database (MMBd) (Malone et al., 2001) was also utilized. Furthermore, landscape characteristics such as altitude and slope (from a digital elevation model), distances from streams, major rivers, wetlands and lakes, and a vegetation map from the National Biomass Study Project (Ministry of Natural Resources, Kampala, Uganda, 1995) were included.

GARP utilizes presence data only, rather than

both presence and absence, which is the more general case. Hence, variability among GARP models (which is typical of genetic algorithms) and complications in interpreting results based on presence only input data make model selection critical (Anderson et al., 2003). The procedure for choosing the most optimal models in this paper thus follows the recommendations of Anderson et al. (2003). The 10 best models for each species were selected following these recommendations and criteria. The models were then summed in ArcGIS® version 8.3 (ESRI, Redlands, CA) creating a composite prediction in which the value for each map pixel corresponds to the number of models (1-10) predicting a species presence in that cell. The resultant composite map represents a density surface related to the probability of suitable environmental conditions for that particular species. GARP was set to run 100 times with a convergence limit of 0.01 and 200 maximum iterations. Besides from the internal evaluation procedures of the modeling programme itself, the performance (accuracy) of the snail distribution models was evaluated using Cohen's kappa (Cook, 1998), which includes absence records.

Deriving transmission suitability maps based on temperature and snail distributions

The intra-molluscan stages of transmission for many snail-borne parasitic diseases are often identified as the weakest link and most sensitive to the effects of temperature. Thus, after developing distribution maps for the host snail species, these were superimposed with temperature masks for the parasite species they host, to produce maps of suitable transmission areas. The temperature masks were developed using GIS query procedures on the MODIS LST layers based on experimentally established thermal maximum and minimum limits of the intra-molluscan development for *S. mansoni*, *S. haematobium* and *F. gigantica*. Areas that were found to be below the theoretical developmental null point for the parasite in the snail

were identified from annual mean night-time (minimum) LST for both dry season and wet season, and excluded. These optimal temperature regime maps were then combined to produce one final temperature mask for each parasite species. The temperature regime used to create the *S. mansoni* temperature mask were 16-35°C with a developmental null point of 14.2°C (Pflüger, 1980, Joubert et al., 1986). A temperature regime of 18-32°C and a developmental null point of 15.3°C were used to mask out areas unsuitable for *S. haematobium* transmission (Pflüger et al., 1984). For *F. gigantica* a base life cycle development temperature of 16°C (Dinnik and Dinnik, 1963) and a thermal tolerance limit of > 36°C (Dinnik and Dinnik, 1963; Malone, 2005) was used to create the temperature mask.

Results

Snail distribution models

Distribution models were developed for five different snail species or species groups: *Bi. "pfeifferi"/sudanica"*, *Bi. choanomphala*, *Bu. truncatus/tropicus* (and *Bu. africanus*), *Bu. forskalii* and *L. natalensis*. The resultant distributional maps can be seen in Fig. 1 (a-e).

The distribution maps produced by GARP indicate that *Bi. "pfeifferi"/sudanica*, (Fig. 1a), the main intermediate host snail of *S. mansoni* in inland areas in Uganda, and *L. natalensis*, (Fig. 1b) the first intermediate host of the liver fluke *F. gigantica* in Africa (Brown, 1994), have the widest distributions. The *Bu. truncatus/tropicus* and *Bu. africanus* (Fig. 1c) also show a wide distribution, although the concordance between the 10 superimposed models is not as strong as with the former two. Only about half of the predicted areas are chosen by 9-10 models. The modeled distribution for the *Bu. forskalii* group (Fig. 1d) is more moderate and concentrated in the central areas of Uganda, along the eastern coastal areas of Lake

Victoria, and scattered fragmental areas in the south-western region of the country. For another *S. mansoni* intermediate host in Uganda, *Bi. choanomphala* (Fig. 1e), suitable habitats were predicted at Lake Victoria margins, along the Victoria Nile, the Lake Kyoga margins, a few narrow strips at Lake Albert and some of the crater lakes in the south-western regions of Uganda. The GARP *Bi. choanomphala* model showed very good agreement between the model predictions and observed presence/absence data, with a kappa value of 0.76 (S.E. = 0.09). All other modeled freshwater gastropods showed a relatively poor agreement, with kappa values between 0.18 and 0.23 (S.E. = 0.05-0.06).

Transmission suitability maps

Superimposing the relevant snail distribution maps with the temperature masks for the parasites *S. mansoni*, *S. haematobium* and *F. gigantica*, revealed geographic areas where both snails and parasites are likely to co-exist, indicating the ecologically suitable transmission areas for each snail-borne disease. The resultant maps can be seen in Fig. 2.

In general, the snails appear to be restricted in their distribution in the northern parts of the country (dry and hot), whereas the parasites (based solely on temperature) seem to be restricted only in the south-western region which, according to the average annual LST maps, are too cold for their development.

Using the parasitological data on *S. mansoni* to evaluate the sensitivity of the developed transmission suitability map showed that 85.6% (95% confidence interval (CI) = 84.4-87.7%) of the positive disease data points were correctly identified by the predicted suitable transmission areas for intestinal schistosomiasis. The proportion of true negatives that were correctly identified by the model (negative disease points in unsuitable transmission areas) was 56.2% (95% CI = 55.1-58.5%). Thus the descriptive model for *S. mansoni* had a high sensitivity but only a moderate specificity.

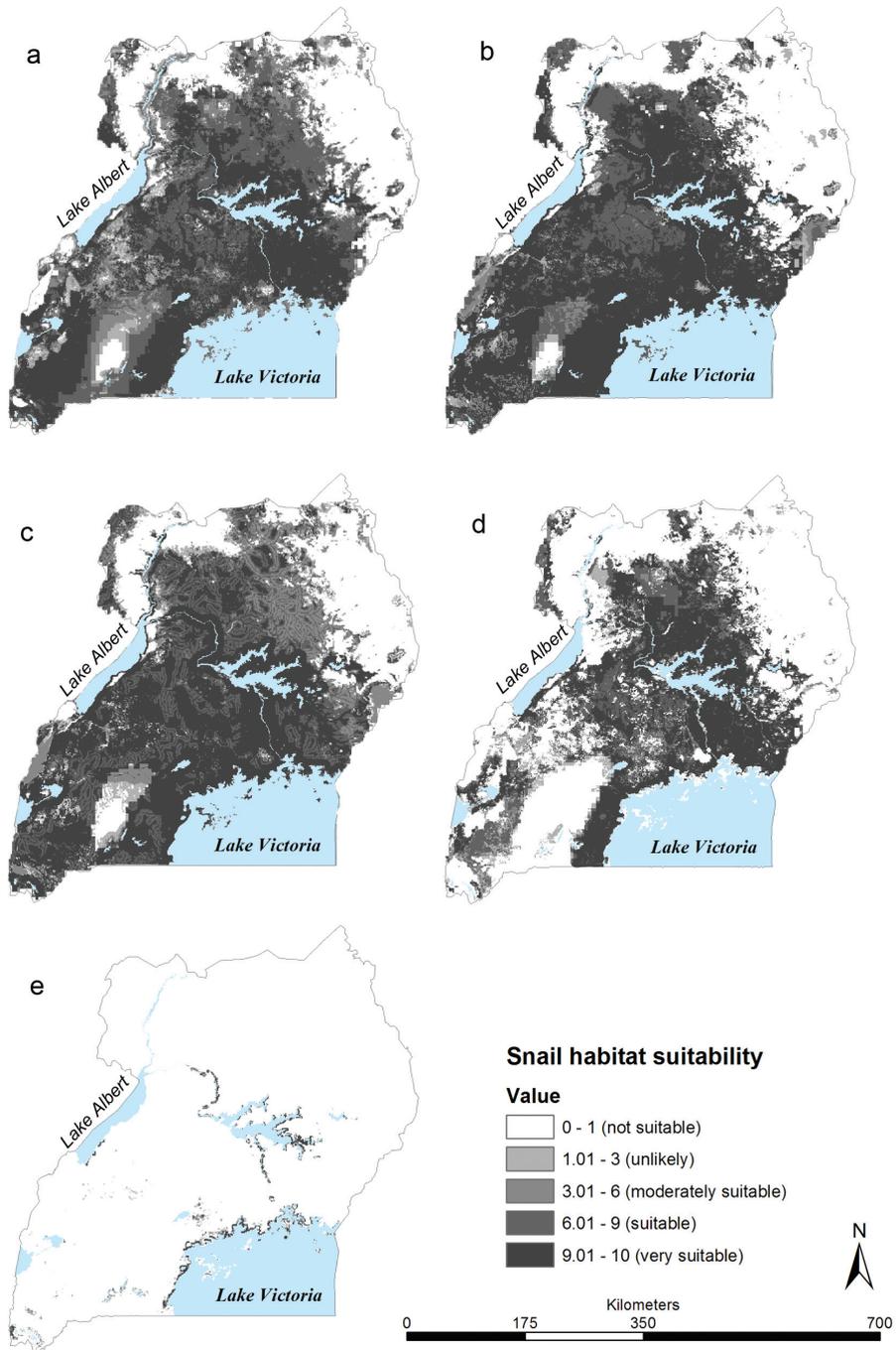


Fig. 1. Snail species distribution maps as modeled by GARP. a) *Biomphalaria* “pfeifferi”/sudanica, b) *Lymnaea natalensis*, c) *Bulinus truncatus/tropicus* complex including *B. africanus*, d) *Bulinus forskalii* group, e) *Biomphalaria choanomphala*. Numbers 1-10 indicate number of models, out of a total of 10 models, choosing a particular pixel as species presence. This is translated into an index of likely snail habitat suitability, with higher values indicating higher suitability.

Discussion

Nearly all the modeled snail distributions indicate that substantial areas of Uganda are suitable habitats for intermediate host snails and thus potential risk areas for the parasites that they host during the asexual stage of the life cycle. In general, the areas predicted to be unsuitable habitats are the dry and hot areas of northern and north-eastern Uganda and for some of the snail species, also scattered parts of the cooler southwestern Uganda with low precipitation. The next step towards identifying suitable transmission areas for snail-borne diseases in Uganda was to overlay the snail distribution maps with a mask of suitable temperature regimes for the intra-molluscan parasite development. This revealed that, while the snail distributions were restricted in the north and north-eastern parts of Uganda (high temperatures, low precipitation/moisture), the distribution of the parasite was instead restricted in the southern and cooler parts of the country. This is in agreement with earlier observations that, while parasites are more sensitive to low temperatures than they are to high temperatures, the opposite is true for many of their snail hosts which do not withstand high temperatures well (Appleton, 1978). Only *F. gigantica* and its intermediate host snail *L. natalensis* show potential for transmission also in the southern areas of Uganda. Not surprisingly, this parasite has the largest overall transmission area. *Fasciola* parasites cause fascioliasis in herbivores, principally sheep and cattle, but have also been shown to be a widespread health problem for humans as well (Mas-Coma and Bargues, 1997; Mas-Coma et al., 1999).

Today, based on estimates of up to 91 million infected humans globally (Keiser and Utzinger, 2005) fascioliasis must be considered an important human parasitic disease. Very few studies on the epidemiology of human and animal fascioliasis in Uganda exists, but according to an investigation of the potential distribution of *F. gigantica* in East Africa, emanating from Food and Agricultural Organization (FAO) databases, a large part of

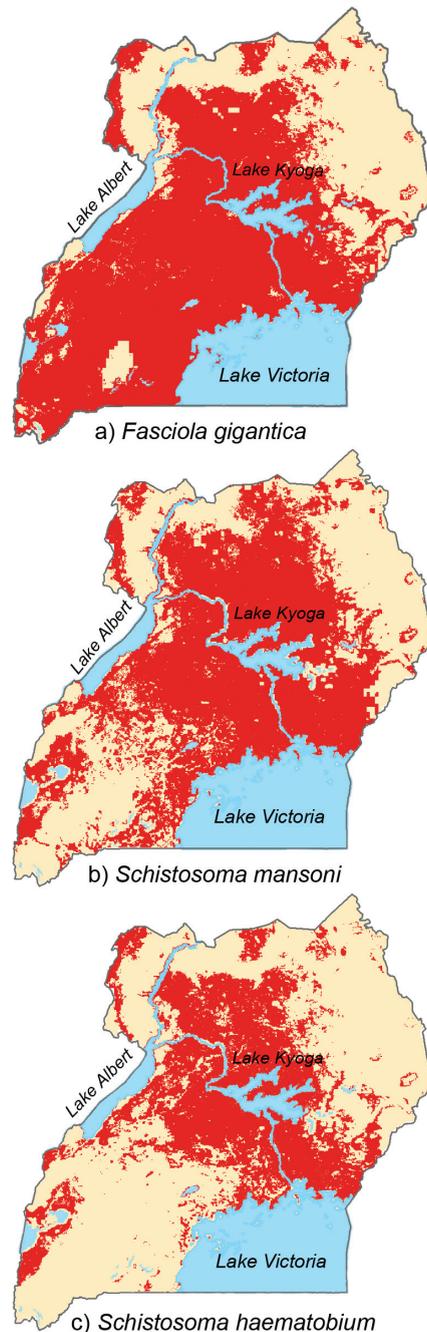


Fig. 2. Transmission suitability maps based on vector snail distributions and areas of suitable temperature regimes for parasite development in the host snail for a) *S. mansoni* (host snails *Bi. "pfeifferi"/sudanica* and *Bi. choanomphala*), b) *S. haematobium* (host snails *Bu. truncatus/tropicus* and *Bu. africanus* and c) *F. gigantica* (host snail *L. natalensis*).

Uganda is at potential risk of the disease (Malone et al., 1998). There are reports of fascioliasis prevalence rates of 53.7% in livestock in Uganda (Ogambo-Ongoma, 1972) and reports of *F. gigantica* in African buffaloes and antelopes in Uganda (Bindernagel, 1972). Furthermore, there has been speculation about the part possibly played by wild African ruminants in the epidemiology of fascioliasis, both in relation to infection of domestic livestock and out of concern for the potential damage that fascioliasis could cause to wildlife confined within reserves (Hammond, 1972; Brown, 1994). A recent investigation (Ocaido et al., 2004) has shown that *F. gigantica* is one of the most widespread helminths among wildlife in and around Lake Mburo National Park in Uganda, confirming earlier reports by Hammond and Sewell (1993) and Okao (1975), that in Uganda *F. gigantica* can be maintained in wildlife without the presence of domestic livestock. The reports on *Fasciola* in both wildlife and livestock, combined with the large geographical areas of suitable *L. natalensis* habitat modeled for Uganda, indicate a potential human and livestock health risk, especially in areas around national parks where mixed game and livestock production systems exist (Ocaido et al., 2004). To evaluate the magnitude of human risk to fascioliasis in Uganda, epidemiological studies in areas overlapping with modeled suitable habitats for *L. natalensis* should be undertaken.

The snail distribution map for *Bu. truncatus/tropicus* complex and *Bu. africanus* also show a wide distribution potential with similar ranges to those of *Bi. "pfeifferi"/sudanica*. However, the temperature masks indicate a larger suitable transmission area for *S. mansoni* than for *S. haematobium*. The latter is reported to be found in the areas surrounding Lake Kyoga in central Uganda, where it co-exists with *S. mansoni* (Bradley et al., 1967) an area that lies in the midst of the predicted suitable transmission area. Why the disease is not more widespread in Uganda, given the apparently wide distribution of some of its host snail, remains to be investigated through expanded

epidemiological surveys.

The distribution models, both for *S. mansoni* and its main intermediate host *Bi. "pfeifferi"/sudanica*, in inland Uganda showed a fairly wide potential distribution and was the only model that could be tested against readily available parasitological point data. It showed a high sensitivity in that the predicted suitable transmission areas were able to capture 85.6% of the schools in Uganda where the infection prevalence of *S. mansoni* was above 5%. The specificity was however low as there were several schools with lower infection prevalences found within the predicted transmission area. However, considering the multi-factorial nature of the disease, the lack of a highly accurate diagnostic approach and an ongoing chemotherapy-based morbidity control programme, this is not unexpected. In fact, large variation in schistosomiasis prevalence between closely situated schools and communities is a well known phenomenon.

The *Bu. forskalii* group, host to *S. bovis* among others, seems to have a more restricted distribution than the other *Bulinus* species. Not much is known about the epidemiology of the parasite in Uganda as no complete epidemiological survey has been conducted. The first substantiated report of *S. bovis* comes from Lake Albert, western Uganda (Stothard et al., 2004). This area overlaps with modeled suitable host snail habitats. Further epidemiological surveys are needed to clarify the extent of bovine schistosomiasis, particularly since the lakeside plain where *S. bovis* was isolated has been earmarked for a future game reserve (Stothard et al., 2004).

In general, maps that reveal areas of both high probability of snail and parasite occurrence could be used to guide first-priority control interventions. In areas where snail habitat suitability apparently is low relative to disease transmission, other factors must play vital roles which should be taken into consideration when planning health interventions. Furthermore, seen in the context of limited resources for interventions, targeted snail control could focus on areas suitable for both par-

asite and snail. However, given the risk of future climate change, attention should be given to snail distribution areas where parasites might not exist presently, as described in another original research paper in this issue of *Geospatial Health*, with an emphasis on *Oncomelania hupensis*, the intermediate host for *S. japonicum* (Yang et al., 2006).

Ecological niche modeling has been shown to be an interesting tool also for epidemiology (Peterson et al., 2002; Levine et al., 2004). However, as all other modeling approaches, it cannot make up for lack of sufficient and relevant data. Some of the developed models showed a relatively poor performance as measured by the kappa statistic. This relatively poor performance can be caused by several different factors. One obvious reason for the poor performance could be that the set of snail data is insufficient, both in terms of numbers of point records and lack of coverage in some areas. In addition, freshwater gastropods are generally elusive species that can be difficult to detect during snail sampling surveys. An alternative explanation could be a poor identification of snail species-specific habitat suitability, due to the unresolved taxonomy with in some of the groups modeled together as one "species". Furthermore, distributional GARP predictions may often include areas that are not inhabited by the species in question, resulting in a focus on ecological niches and potential geographic distributions instead of on actual geographic distributions (the realized niches of species). This would result in commission (over-prediction) errors (Peterson and Vieglais, 2001). Errors in the prediction of species' distributional areas can also be due to algorithmic and biotic errors derived from model construction and data uncertainties (Fielding and Bell, 1997). Biotic errors are inevitable because the model is a simplification of reality and cannot include all of the environmental factors that influence the different species' distribution. Other environmental parameters, such as water temperature, oxygen content, pH, stream flow, etc., potentially have a greater influence. Finally, the spatial scale or resolution of

the model can also determine the patterns of association detected between the environmental variables and species presence/absence (Rahbek and Graves, 2000; Karl et al., 2000). Future studies should preferentially test the datasets with the newer but rarely used species distribution modeling methods, including machine-learning methods and community models which recently have been shown to outperform more established methods (Elith et al., 2006). Furthermore, Bayesian geostatistical analysis, incorporating uncertainty into the modeling process, has recently proven a powerful and statistically robust tool for identifying high schistosomiasis prevalence areas in a heterogeneous and imperfectly known environment, an approach that enables objective decisions to be taken as to the need for further data collection (Raso et al., 2005; Clements et al., 2006).

The approach employed in the current study provides quantitative, operational estimates of a species' geographic range that gives insight into the biology and ecology of both the snail and parasite species, and would primarily be primarily useful for intermediate host snail management. In addition the maps can be used to guide productive fieldwork, through identification of e.g. areas of low disease risk, but high probability of sustaining host snails. These areas might presently be unsuitable for the parasite, but could become important new transmission areas under environmental change scenarios, including global warming as articulated above.

Because of the numerous sources of uncertainty in the modeling process, it is vitally important to test the output predictions of any model but a meaningful validation can often be difficult to carry out due to lack of truly independent test datasets (Elith et al., 2006). One step towards improving the evaluation of model performance in predicting species' distribution is to use independent, well-structured presence/absence datasets for validation (Elith et al., 2006). However, as in the study presented here, this type of data set often does not exist. In the end, the choice of spatial

scale, environmental predictor variables (Guisan and Zimmerman, 2000) and the representation of environmental relationships within a model all reflect assumptions by the modeler. Regardless of the conceptual assumptions, the cost efficiency and rapid development of species predictive models make them useful for large-scale prediction. It should, however, be stressed that modeling never can provide a complete substitute for detailed, continued collection of field data.

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