Challenges in predicting the effects of climate change on *Schistosoma mansoni* and *Schistosoma haematobium* transmission potential

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Abstract

Climate change will inevitably influence both the distribution of *Schistosoma mansoni* and *Schistosoma haematobium* and the incidence of schistosomiasis in areas where it is currently endemic, and impact on the feasibility of schistosomiasis control and elimination goals. There are a number of limitations of current models of climate and schistosome transmission, and substantial gaps in empirical data that impair model development. In this article we consider how temperature, precipitation, heat-waves, drought, and flooding could impact on snail and schistosome population dynamics. We discuss how widely-used degree-day models of schistosome development may not be accurate at lower temperatures, and highlight the need for further research to improve our understanding of the relationship between air and water temperature and schistosome and snail development.

Is climate change the elephant in the room for schistosomiasis control?

The 2012 'London Declaration' on neglected tropical diseases (NTDs) (see Glossary) put schistosome parasites on the list of ten NTDs that can expect to be eliminated, eradicated, or controlled by 2020 (See http://unitingtocombatntds.org/downloads/press/ntd_event_london_declaration_on_ntds.pdf). In recognising that the ecology of schistosomes is more complex than some other parasites, the targets for this infection are more geared towards control rather than eradication. Nonetheless, the 2012 World Health Organization report 'Accelerating work to overcome the global impact of neglected tropical diseases – a roadmap for implementation' sets a goal of schistosomiasis elimination in many areas by 2020 [1].

Climate change can be considered to act in the short, medium, and long-term. Within the climate change community, predicting changes over the short and medium term are considered more challenging than long-term changes due to the impact of weather variability. Given that schistosomiasis is unlikely to be eliminated or eradicated by 2020 (the short term), there is a pressing need to consider if and how the future climate will impact on the transmission of the parasite in the medium to long-term. There is, in fact, just one empirical published study that suggests schistosome transmission potential is increasing as a result of climate change [2]. The observation that schistosome infections are being transmitted up to 1682 m above sea level in Uganda suggests that the environment has become suitable above a previously defined limit of 1400 m [3].

Only a handful of studies have attempted to predict the effect of climate change on the distribution or transmission intensity of schistosomiasis using dynamical modelling [4-9]. These studies focused mainly on the effect of increasing mean temperature, with only one including changes in rainfall [6], and none considering the effects of extreme weather events. Here, we highlight the major gaps in current models of climate change and schistosomes and suggest areas of research that will help inform the next generation of mathematical models of schistosome transmission in relation to climate change. This Review focuses primarily on *Schistosoma mansoni* and *Schistosoma haematobium* (Box 1) because there are many differences between the issues involved in modelling the amphibious snail hosts of *Schistosoma japonicum* and the aquatic snail hosts of the two more widespread human schistosome species (Box 2). Papers cited in this review were identified using the search strategy described in Box 3.

Temperature

The global average surface temperature is predicted to be 1.8-4.0°C higher in 2090-2099, relative to 1980-1999 [10]. In areas currently at risk for schistosomiasis, warming is predicted to be between 2°C and 5°C. The increases in the daily minimum night time temperatures are predicted to be greater than the increases in the daily maximum temperatures, leading to a decrease in diurnal temperature range over most land areas [11].

Temperature is an important determinant of the limits of snail distribution and population size, as egg production, hatching, and death rates; juvenile maturation and death rates; and adult death rates all affected by temperature [12]. The rate of cercarial maturation inside infected snails is also affected by temperature, increasing as temperature increases [13]. At low temperatures, cercarial development is slow or suspended, and the probability of cercariae maturing before the snails die is low [3, 14].

Given these sensitivities, it is apparent that we need to understand comprehensively how snail ecology and schistosome development will be affected by temperature changes associated with climate change (Figure 1). Existing models agree that temperature is a key factor in determining schistosome transmission potential [4, 7, 8], but they do not account for a number of important modifiers. In the following sections of the paper we highlight how the complex relationship between climate and both schistosome and snail natural history will need to be considered in future modelling exercises.

Air temperature as a proxy for water temperature

All temperature-sensitive stages of the life cycles of *S. mansoni* and *S. haematobium* occur within water, as do all life stages of their intermediate hosts. Data on water temperature is rarely routinely collected, however, and climate predictions do not estimate future freshwater temperatures. Air temperature has therefore been used as a proxy for water temperature in most models (e.g., [4, 7]). The justification given is that the temperature of shallow water is similar to ambient air temperature. But is this justified? Comparisons between air temperature and water temperature in a variety of water bodies suggest that unadjusted air temperature is often not a reliable proxy, with surface water temperatures more than 2°C higher in many cases [15, 16].

Does this matter?

A warning on the potential impact of neglecting this issue in mathematical models comes from work on the malaria vector *Anopheles gambiae* in Kenya. Paaijmans *et al.* [17] demonstrated that using air temperature instead of water temperature resulted in an increase in mosquito numbers with increasing temperature being greatly overestimated. It is probable that the bias caused by modelling air temperature as a proxy for water temperature will be even greater in dynamical models of schistosome transmission because the majority of the stages of the life cycles of the schistosome parasites and intermediate host snails occur in water.

Temperature gradients within water bodies

The use of air temperature as a proxy for water temperature is further complicated by the fact that intermediate host snails are not confined to the shallows of deeper ponds and lakes. In some bodies of water, surface water temperatures are considerably higher than water temperatures at greater depths [18, 19]. Snails may exploit these temperature gradients to potentiate their own survival. Snails have been found in water at depths of 4.3 m for *Biomphalaria smithi*, 12.2 m for *Biomphalaria choanomphala*, 4-5 m for *Biomphalaria glabrata*, and 4.5 m for *Biomphalaria pfeifferi* [20]. Snails are capable of surviving for extended periods at these depths; for example, *Bi. glabrata* [21] and *Bi. pfeifferi* [22] have been shown to survive for 24 and 31 days when submerged in boxes at depths of 10 m and 15.25 m, respectively. For snails in deep bodies of water, spending time at depths of several meters could therefore be a way of avoiding above-optimum temperatures. Burying in mud at the bottom of the water could further decrease the maximum temperature to which snails are exposed [23]. These behaviours will be particularly important during heat waves when the high temperatures found at the surface would greatly reduce snail survival. There is also some evidence that the reverse occurs, with snails in a South African pond spending less time in deeper water in winter when water temperatures are below optimal [18]. Miracidia may follow the snails to shallower and deeper water, as they are negatively phototactic at high temperatures, but move towards light and warmer temperatures as overall temperatures decrease [24].

Does this matter?

If the potential for snails to move to greater depths is not considered, predictions of the effect of climate change on schistosomiasis distribution may overestimate the reductions in schistosomiasis risk in areas with large water bodies and where temperatures are above the optimum for snail development. To improve model predictions, further studies are needed on the ability of each snail species to live and reproduce at different depths, and the tendency of snails to increase the depth at which they live in response to high surface temperatures.

Water temperature and schistosome development in snails

Studies of vector-borne parasite transmission and temperature often use a 'growing degree-day' approach to parameterise models [25]. The approach can be applied both to the development of the intermediate host as well as the schistosome within the intermediate host. It is based on the idea that the organisms in question require a certain number of heat units to complete their development. These heat units are measured in growing degree-days and are calculated as the difference between the mean daily temperature and the development threshold temperature of the organism, which is the temperature below which the organism will not develop [26]. The number of growing degree-days are taken to be zero for a day if the mean daily temperature is below the development threshold temperature. For this calculation to be valid, after adjustment for time spent below the development threshold temperature, the decrease in development rate when the temperature is below average must be exactly balanced by the increase in rate when the temperature is above average. This assumption is valid only if, above the development threshold temperature, there is a linear relationship between temperature and rate of development. Experimental work suggests the relationship is linear for *S. mansoni* development when temperatures do not fluctuate outside of 16-35°C [27]. Models that assume a linear relationship over a greater range will either over-estimate or under-estimate the rate of schistosome development.

Does this matter?

The experiments described above indicate that current growing degree-day models of schistosomiasis distribution and climate change [5, 26] could greatly underestimate the potential for schistosomiasis to spread to areas currently too cold for transmission. To improve the parameterisation of future models, similar experiments could be conducted with *S. haematobium*, and the use of nonlinear relationships between temperature and rate of development in growing degree-day models should be explored.

An additional complicating factor is that snails may move to greater depths to improve survival following exposure to and/or infection with schistosomes. This phenomenon was demonstrated over 20 years ago in an experiment, which observed that *Bi. glabrata* exposed to schistosome cercariae preferred water temperatures 1.9±0.5°C cooler than non-exposed snails five weeks after exposure [28]. To our knowledge, it has not been investigated whether this behaviour is found in wild snails.

Multiple species of intermediate host snail

Snails of the genera *Biomphalaria* and *Bulinus* act as intermediate hosts for *S. mansoni* and *S. haematobium*, respectively (Box 2). Within each genus, there are several species of snail capable of acting as an intermediate host, and multiple species of snail hosts can be found at any one site [29]. Each species of snail has slightly different requirements for development, such as a preference in habitat for shallow or deep water [30]. Temperature needs vary as well; *Biomphalaria alexandria* eggs require temperatures between 15°C and 30°C to hatch, whereas *Bulinus truncatus* eggs will hatch at temperatures as low as 12.5°C and as high as 35°C [12]. Additionally, there is a range of susceptibility to schistosome infection among species [31].

A recent geographical risk model clearly demonstrates the need to consider multiple snail species in any modelling exercise [6]. The model was parameterised separately to each of five African species of *Biomphalaria*, and highlighted diverse potential ranges. *Bi. alexandrina* is limited to small areas of north and west Africa, whereas *Bi. pfeifferi* is found in much of sub-Saharan Africa. Models will therefore be unreliable if the diverse requirements of snail species are not taken into consideration and if, in the case of statistical models, the model is applied over an inappropriately large geographic area. Evidence of this phenomenon is found by examining a statistical model of environmental data and *S. haematobium* risk parameterised using data from one area of coastal Tanzania. The model performed well in other coastal areas of Tanzania, but not elsewhere in the country [32]. This was thought to be because the snails that inhabit the coastal area of Tanzania are distinct from those found elsewhere in the country. Each species will respond differently to a specific environmental factor, resulting in the poor fit of models that are not fitted separately for multiple snail species.

Further complications are added by the need to consider subspecies and geographical strains of snails, which can have slightly different characteristics and requirements [33], and by the fact that snail species cannot always be accurately identified using morphology. A study comparing the molecular and morphological classification of *Biomphalaria* specimens found a number of discrepancies [34]. Many of the data that are currently available for parameterising models come from snail species identified using morphological methods only, and the geographical source of the snails used is not always given [33].

Does this matter?

In the absence of experimental data on many snail species and sufficient field-based data on wild snail populations, current dynamical models of *S. mansoni* and *S. haematobium* transmission have been necessarily limited in terms of their scope for addressing the potential impact of climate change [4, 7, 8]. In some models, it has been necessary to fill the gaps in empirical data by mixing up information from different snail species for each stage of the life cycle [4, 7, 8]. Models such as this allow some reflection of the relationship between temperature and transmission, but cannot estimate schistosomiasis transmission potential in any one location. They will also not be able to reliably predict any expansion in the geographic distribution of schistosomiasis due to climate change. Many areas could become suitable for the survival of one or more snail species, but geographic scale needs to be considered because snail populations are unlikely to become established unless the areas become suitable for species of snails already found nearby.

At present, many of the data needed to parameterise models to single snail species are not available. Experiments are needed to determine the effect of temperature on each stage of the life cycles of all important intermediate snail hosts, identified using both morphological and molecular methods and from a known location. A better knowledge of the current distribution of each species will also enable improved predictions to be made of areas where new snail colonies could become established.

There is considerable uncertainty in many of the estimates of the parameter values used in dynamical models, and the effects of this are not always made clear. A recent study investigated the sensitivity of *Oncomelania hupensis* range predictions in Sichuan province, People's Republic of China, to uncertainty in two key degree-day model parameters: (i) the lower temperature threshold for development and (ii) the total number of degree-days necessary for the completion of development [25]. The study found that estimates of snail densities, the seasonality of population dynamics, and range predictions were all highly sensitive to changes in the parameters, even to levels of parametric uncertainty that are common in disease models. This was particularly the case along the edges of the range of the snail population, and therefore studies attempting to predict the effect of climate change on the potential range of schistosomiasis will be particularly sensitive to this cause of inaccuracy. In many cases, experiments are needed to improve estimates of parameter values and reduce uncertainty.

Precipitation

The Intergovernmental Panel on Climate Change (IPCC) predict that climate change will cause overall increases in the amount of precipitation in high latitudes and overall decreases in most subtropical land regions [10]. The frequency of heavy precipitation events, and the proportion of total rainfall from heavy falls, will increase over most areas.

The relationship between precipitation and schistosome transmission is difficult to characterise. Large-scale statistical models can show no effect [6], but patterns of precipitation may be important on a smaller scale. Changes in the amount of precipitation in an area could be associated with increased or decreased range of infection, but other factors could be more important than the amount of precipitation itself, such as the length of the dry season [35]. In general, it seems probable that increased rainfall would increase schistosome transmission, but in some cases it could reduce it, for example by creating fast-flowing water that is unsuitable for cercaria [36] or snail survival [37].

The relationship between changes in precipitation and snail numbers may be further complicated by changes in rates of evaporation. In general, evaporation is predicted to increase in areas where rainfall is predicted to increase and decrease in areas where rainfall is predicted to decrease [38]. Changes to established rainfall patterns will therefore not necessarily lead to corresponding changes in the size and permanence of water bodies.

In addition to affecting snail populations, changes in rainfall could affect the proportion of schistosome eggs that enter a water body. Because of this, Liang *et al.* [39] included seasonal variation in rainfall in their mathematical model of *S. japonicum* transmission in the People's Republic of China, with the amount of rainfall determining the proportion of schistosome eggs that entered the aquatic component of the model.

Does this matter?

The lack of a strong Africa-wide relationship in statistical models suggests that the relationship between rainfall and snail abundance changes by habitat. For instance, the amount and seasonality of rainfall could be more important for snails living in temporary water bodies than for snails living in permanent lakes. Both this and the geographical variation and uncertainty in predictions of future precipitation are likely to impede the development of any large-scale models of precipitation change and schistosomiasis. The difficulties are further increased by the gaps in our knowledge of the different ecological requirement of snail host species.

Seasonality

Human schistosome intermediate host snail populations exhibit large seasonal fluctuations in many areas, but the direction of effect varies by region. Snails in highland regions can experience lower growth rates during the cold season [40], whereas snails in lower areas, for example along the coast, can benefit from cooler temperatures [41]. The diverse environments associated with the type of water body, such as streams and ponds, could also be influential [42].

In general, seasonality in snail numbers and schistosome transmission can be attributed largely to seasonal patterns of rainfall in tropical areas, and seasonal changes in temperature in sub-tropical and temperate areas [43]. The permanence of the water bodies responsible for transmission in an area also affects seasonality [44], however, seasonal fluctuations in rainfall have a larger effect on temporary versus permanent water bodies.

Does this matter?

It is probable that climate change will result in a longer period of high transmission in areas where transmission largely occurs in permanent water bodies and where transmission is currently lower in cooler seasons. In other areas, changes in temperature and patterns of rainfall will have more variable effects on the seasonality of schistosome transmission. Neglecting the issue of seasonality in dynamic models will lead to unreliable estimates of the relationship between environment and disease transmission.

Extreme events

Heat waves

The frequency, duration, and intensity of heat waves are predicted to increase over coming decades [38]. The effect of heat waves on schistosome transmission in an area will depend on typical maximum water temperatures in relation to the optimum temperatures for the snail hosts. In areas that are normally well above the optimum temperature, schistosomiasis incidence may be greatly reduced both while the heat wave is on-going and for some time afterwards. Sufficiently long or hot heat waves could even temporarily or permanently eliminate the intermediate host snails from an area, particularly if additional snail control measures are implemented while the snail population is vulnerable.

In colder areas, heat waves could potentially increase the transmission potential of schistosomes and the incidence of schistosomiasis, resulting in outbreaks occurring in areas that normally experience little transmission. In areas that are typically too cold for schistosomes to develop, but where suitable intermediate host snails are found, transmission may occur if miracidia are introduced into water bodies where the snails are found.

Drought

More intense and longer lasting droughts have occurred in many areas of the world since the 1970s, particularly in the tropics and subtropics. It is projected that the proportion of the world that is affected by droughts will continue to increase over coming decades [10].

Biomphalaria and *Bulinus* snails are aquatic and will only reproduce in water (Box 2). Some or all species are able to aestivate, which enables them to survive short-term drying up of water bodies [33]. This is a common occurrence for species that live in temporary ponds and streams, which can regularly dry up for several months at a time [33]. Droughts can both lengthen the time that temporary water bodies are empty and dry up permanent water bodies. The abilities of snail species to survive different lengths and severities of desiccation in natural conditions are not well understood. Survival rates will depend on many factors, including the species of snail, whether habitats dry up gradually or rapidly, soil moisture, and relative humidity [44]. Survival may be lower for snail populations with little history of previous desiccation [44].

Regardless of the snail species and environmental conditions, the extended drying up of water bodies will inevitably be harmful to the survival of any resident snail populations [45]. Lack of rain over multiple years will be particularly detrimental if the snail populations are unable to fully recover their numbers between each dry season [46]. Droughts of a sufficient length and severity may even lead to the temporary or permanent elimination of the snail population from a site. This is particularly likely in areas that are currently marginal for snail survival [47].

Flooding

The Intergovernmental Panel on Climate Change (IPCC) predicts that rainfall events will become more intense over coming decades, leading to an increase in flooding in many parts of the world [11].

In general, the species of snail that act as intermediate hosts for human schistosomes are unable to tolerate water flows over approximately 0.3 ms^{-1} [48]. Intense rainfall and flooding could therefore greatly reduce the number of snails found at a transmission site [40].

While the majority of snails that are washed away by fast flowing water will not survive, some snails may end up in favourable habitats and could potentially establish new colonies, as observed in the People's Republic of China [49]. This could both reintroduce snails and schistosomes to areas from which they had previously been eliminated, and facilitate the spread of snails, including infected snails, to areas that are newly suitable for snail populations and/or schistosome development. Flooding may therefore play a large role in determining the actual range of schistosomiasis, as opposed to its potential range, over coming decades.

Does this matter?

The effect of extreme weather events on schistosome transmission may well be influential in the future, but capturing these events within dynamic models will be challenging due to the difficulty in predicting their occurrence and severity over the decadal time scales over which models are expected to operate. The effects of an extreme event could have only short term effects or wipe out snail populations entirely for longer periods or even permanently. Floods could potentially also act as seeds to establish transmission in new areas. The solution to this issue will include stochastic models combined with more intense surveillance efforts following flooding.

Concluding remarks

As of yet, we do not have a firm idea of how climate change will affect the transmission of schistosomiasis, and the effects of changes in temperature, rainfall, and extreme events may be differ between areas (Figure 1). Carefully designed and parameterised models of climate and schistosomiasis can provide a useful guide to areas that will become newly suitable for schistosomiasis transmission in future years. They can also indicate which areas within the current range of schistosomiasis may be at risk of increased transmission. Dynamical models will benefit from being parameterised separately for each individual intermediate host snail species, and from including changes in patterns of rainfall and extreme events, in addition to changes in temperature. Geographical scale is important when developing statistical models, and they should ideally be fitted separately for different snail species and water body types. We consider that there are several crucial areas of research in the area of snail ecology, which would greatly improve future models. This includes measuring the effect of water temperature on each stage of the life cycle of each intermediate host snail species and estimating survival over time during aestivation of different snail species in a variety of conditions. Finally, there are a number of other questions that need to be considered when interpreting the results of models of climate change and schistosomiasis (Box 4), as changes other than climate change will also affect the future distribution and intensity of schistosomiasis.

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Figure 1. Potential effects of climate change on schistosomiasis and on intermediate host snail species. The flow chart summarises projected climate changes such as increasing temperatures, changes in precipitation, and increasing frequencies and intensities of heat waves, droughts and flooding, on the ecology of intermediate host snails and schistosome transmission. The central column lists climate change events. The left and right hand columns relate each climate event to the natural history of schistosomiasis. The left hand column corresponds to increased transmission potential, and the right hand column to decreased transmission potential.

Glossary

Aestivation: A period of dormancy that allows snails to survive for extended periods out of water. Some species of *Biomphalaria* and *Bulinus* snails can live in temporary water bodies by aestivating during the dry season(s), although mortality during aestivation is high.

Control: "Reduction of disease incidence, prevalence, morbidity or mortality to a locally acceptable level as a result of deliberate efforts. Continued intervention measures are required to maintain the reduction [50]."

Elimination: "Reduction to zero of the incidence of infection or disease caused by a specified agent in a defined geographical area as a result of deliberate efforts. Continued measures to prevent re-establishment of transmission are required [50]."

Empirical: Data or knowledge acquired through observation or experimentation, as opposed to data or knowledge obtained through statistical or dynamical modelling.

Eradication: "Permanent reduction to zero of the worldwide incidence of infection caused by a specific agent as a result of deliberate efforts. Intervention measures are no longer needed [50]."

London Declaration on Neglected Tropical Diseases: A collaborative disease eradication programme launched in January 2012 in London, UK, that provides goals for the eradication or elimination of 10 neglected tropical diseases, including schistosomiasis, by 2020.

Mathematical/dynamical modelling: Dynamical models are simplified representations of complex systems, such as the schistosome lifecycle, that can be used to explore questions about the overall system that cannot be explored using empirical methods. They are parameterised with, or informed by, empirical data.

Statistical modelling: Statistical models look for correlations between explanatory variables, such as mean annual temperature, and outcome variables, such as the incidence of schistosomiasis. They can use data from a range of different locations, different time points, or both.

Box 1. The lifecycles of human schistosomes

The vast majority of human schistosomiasis is caused by infection with *S. mansoni*, *S. haematobium*, or *S. japonicum*. *S. mansoni* is found in South America and the Caribbean, Africa, and the Middle East; *S. haematobium* in Africa and the Middle East; and *S. japonicum* in the Far East. All of the species reproduce sexually in humans (and, in the case of *S. japonicum*, other mammals), and asexually in aquatic snails.

Pairs of adult worms are found in humans in the veins of the bladder, ureters, and kidneys (*S. haematobium*) or the veins of the small intestine (all other species). The worms reproduce sexually, producing around 20-3500 eggs a day [51]. These eggs pass through the vein wall and tissues to the lumen of the gut or bladder, from where they are excreted in urine (*S. haematobium*) or faeces (all other species). Upon reaching fresh water, the eggs hatch releasing miracidia.

To progress to the next stage of their lifecycle miracidia must find and infect a suitable snail host before their food stores are exhausted [52]. Upon locating a snail, the miracidia penetrate it and start to develop into primary sporocysts. These primary sporocysts produce secondary sporocysts, which in turn produce cercariae which are shed from the snail.

Like miracidia, cercariae must find and infect a suitable host before their food reserves are depleted. Upon encountering a potential host, the cercariae penetrate its skin and transform into schistosomula. Over the course of several days, the schistosomula enter the venous system and are carried round the body. Schistosomula that are successful in reaching the liver start to feed and grow. Upon reaching sexual maturity they form pairs and travel together to their final locations in the perivesical venous plexus of the bladder, ureters, and kidneys (*S. haematobium*) or the mesenteric veins of the small intestine (all other species), where they start to produce eggs. In total, the time between infection and the first detectible excretion of eggs is around 35 days for *S. mansoni*, 70 days for *S. haematobium*, and 38 days for *S. japonicum* [52].

Water temperature has a substantial effect on the rate at which schistosomes progress through their lifecycles, cercaria and miracidium mortality and infection rates, and cercaria production rates [33].

Box 2. The lifecycles of *Biomphalaria* and *Bulinus* snails

Each of the three main human schistosome species reproduces asexually in a specific genus of snail: *S. mansoni* in *Biomphalaria* species, *S. haematobium* in *Bulinus* species, and *S. japonicum* in *Oncomelania hupensis*. Schistosomes are capable of infecting and developing in multiple species of *Biomphalaria* and *Bulinus* snails. The lifecycles and habitats of *Biomphalaria* and *Bulinus* snails are described here because this Review focuses on the transmission of *S. mansoni* and *S. haematobium*, and the lifecycle of amphibious *Oncomelania* snails differs in many respects.

Biomphalaria and *Bulinus* snails are aquatic and live in freshwater. Different species have varying habitat requirements ranging from large, permanent lakes, to slow moving areas of rivers and irrigation canals, to seasonal streams and ponds [33]. The snails are unable to tolerate water flows of over around 0.3 ms^{-1} [48]. Many species are able to aestivate to survive the temporary desiccation of their water bodies, although survival during aestivation tends to be low and varies greatly between species and populations [33].

The snails are hermaphroditic and can reproduce by self-fertilisation or outcrossing. They lay egg capsules containing multiple eggs on firm surfaces in water. These eggs hatch into juvenile snails, which develop into adult snails and produce eggs of their own. Egg production, development and hatching rates, juvenile development rates, and juvenile and adult snail mortality rates vary greatly with temperature [33].

Both juvenile and adult snails can be infected by miracidia and will go on to produce cercariae. The parasites are harmful to their snail hosts, increasing mortality substantially [13] and greatly reducing or preventing snail egg production [53].

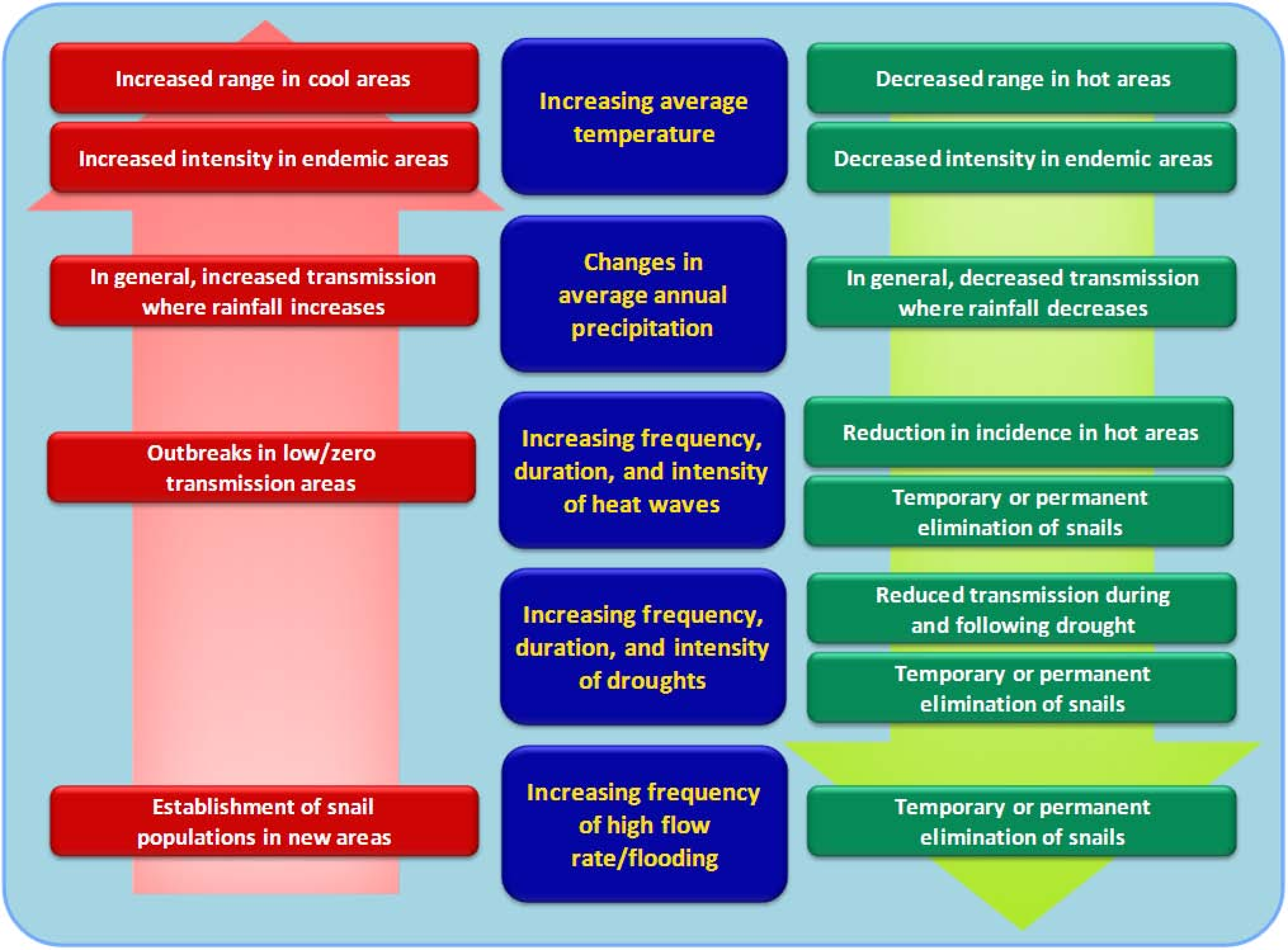
Box 3. Strategy of reviewing the literature

Articles were identified by searching Medline through PubMed and Google Scholar using various combinations of search terms including “schistosom*”, “*Biomphalaria*”, “*Bulinus*”, temperature”, “model*”, “predict*”, “precipitation”, “rain*”, “flood*”, “drought”, and “ecology”. Many older articles were found using reference lists in Brown (1992) [33]. Additional articles were obtained by citation tracking. Articles were selected for inclusion in the review if they identified or illustrated key issues that should be considered when attempting to predict the effects of climate change on *S. mansoni* and *S. haematobium* transmission.

Box 4. Outstanding questions

There are many gaps in the experimental and observational data needed to support modelling efforts. Current models do not explore sufficiently the impact of climate change. Many questions remain, including:

- Will intermediate host snail species and schistosomes adapt to climate change?
- How quickly will intermediate host snails spread to areas newly suitable for their survival?
- What effect will climate change have on the food sources, predators, and other parasites of intermediate host snails?
- What effect will current mass-treatment and other control strategies have on the long-term distribution and intensity of schistosomiasis?
- What will be the relative impact of climate change compared to other modifiers?


Increased range in cool areas
Increased intensity in endemic areas
Increasing average temperature
Decreased range in hot areas
Decreased intensity in endemic areas
In general, increased transmission where rainfall increases
Changes in average annual precipitation
In general, decreased transmission where rainfall decreases
Outbreaks in low/zero transmission areas
Increasing frequency, duration, and intensity of heat waves
Reduction in incidence in hot areas
Temporary or permanent elimination of snails
Increasing frequency, duration, and intensity of droughts
Reduced transmission during and following drought
Temporary or permanent elimination of snails
Establishment of snail populations in new areas
Increasing frequency of high flow rate/flooding
Temporary or permanent elimination of snails