Niche theory

Key concepts

- Potential distribution
- Fundamental niche
- Realized niche

Climate change and the future distribution of Anopheles?

Malaria is a severe disease in many parts of Africa and Asia. Hundreds of millions of cases annually result in around one million deaths, a large portion of which are children. Human malaria is caused by infection with protozoans in the genus *Plasmodium*, primarily obtained from the bite of an infected mosquito belonging to the genus *Anopheles.*

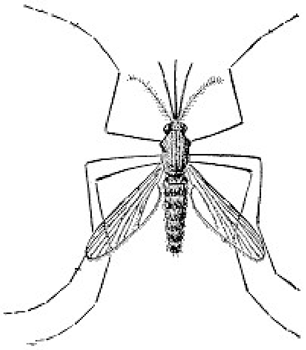

Figure 1: Mosquitoes in the genus *Anopheles* are the primary vector of *Plasmodium*, the cause of human malaria.

Malaria in sub-Saharan Africa has recently been in decline, largely due to anti-malarial interventions including the distribution of insecticide-treated nets, artemisinin-combination treatments, and indoor residual spraying for mosquitoes. However, these cannot account for all observed reductions in malaria incidence. For instance, malaria was observed to decline from near ubiquity to prevalence of 30% to 50% on the island of Pemba, Tanzania prior to the onset of vector control activities. Studies of rural communities in a nearby region indicated that these declines are most likely due to declines in the abundance of *Anopheles gambiae* and *An. funestus* mosquitoes, which in turn have responded to declining precipitation and interruptions in annual (periodic) rainfall patterns [1]. These studies suggest that changes in climate and weather may be as responsible as human interventions for declines in African malaria, at least in some regions.

This is important for several reasons. First, despite decelerations in the emission of greenhouse gases, changes in the global climate system are still widely expected to continue to 2100 and beyond. How will these changes affect the future distribution of the mosquitoes that transmit malaria? Second, it also seems probable that future human

[1] Dan W Meyrowitsch, Erling M Pedersen, Michael Alifrangis, Thomas H Scheike, Mwelecele N Malecela, Stephen M Magesa, Yahya A Derua, Rwehumbiza T Rwegoshora, Edwin Michael, and Paul E Simonsen. Is the current decline in malaria burden in sub-Saharan Africa due to a decrease in vector population? *Malaria Journal*, 10(1):188, January 2011

cases of malaria in Africa will be disproportionately due to the vector *Anopheles arabiensis* compared with historical patterns because the historically dominant vectors, *An. gambiae* and *An. funestus*, are selectively targeted by indoor interventions and in many cases are declining in relative abundance. *An. arabiensis*, by contrast, exhibits greater behavioral plasticity, is more associated with outdoor habitats, and is more likely to bite susceptible persons out of doors (exophagy) where protections are less likely to be in place [2]. Particularly, *An. arabiensis* is well known to favor dry (savannah) disturbed habitats while larval habitats are primarily small, temporary, freshwater pools and other built features of the landscape such as rice fields and fish ponds [3]. Thus, interventions with ITNs are less effective against *An. arabiensis* than *An. gambiae* and *An. funestus*. Further, because *An. arabiensis* executes its life cycle outside the built environment, it serves as a transmission route more likely to be subject to climate fluctuations. Taken together, these observations suggest that even as the transmission of malaria may be expected to continue to decline (because of aggressive interventions) that portion of transmission that remains will be disproportionately due to *An. arabiensis* and disproportionately subject to environmental conditions.

These observations give rise to several questions. How has past climate shaped the current distribution (and recent declines) of malaria in sub-Saharan Africa? What will be the future distribution of *An. arabiensis*? Can the effects of weather on the distribution of mosquitoes be harnessed as part of a program to eliminate malaria?

The ecological niche

Answering these questions requires mapping the future *potential distribution* of *An. arabiensis*. The potential distribution is the set of all locations at which the persistence of a species is probable in the absence of human interventions or historical contingencies such as stochastic extinction or introduction failure. That is, the potential distribution concerns not only the most conducive environmental conditions, but also the conditions at its environmental margins. The potential distribution, in turn, depends on the ecological *niche*, the set of environmental conditions under which a population of the species may persist. Mapping the probable effects of climate change on the distribution of *An. arabiensis* therefore requires first estimating its niche.

What are the conditions for persistence (non-extinction)? Roughly speaking, a population will persist when there exists some size of the population at which the growth rate of the population is greater than 0. That is if the growth rate of the population is given by $dn/dt =$

[2] Marianne E Sinka, Michael J Bangs, Sylvie Manguin, Maureen Coetzee, Charles M Mbogo, Janet Hemingway, Anand P Patil, Will H Temperley, Peter W Gething, Caroline W Kabaria, Robi M Okara, Thomas Van Boeckel, H Charles J Godfray, Ralph E Harbach, and Simon I Hay. The dominant Anopheles vectors of human malaria in Africa, Europe and the Middle East: occurrence data, distribution maps and bionomic précis. *Parasites & vectors*, 3(1):117, January 2010

[3] Marianne E Sinka, Michael J Bangs, Sylvie Manguin, Maureen Coetzee, Charles M Mbogo, Janet Hemingway, Anand P Patil, Will H Temperley, Peter W Gething, Caroline W Kabaria, Robi M Okara, Thomas Van Boeckel, H Charles J Godfray, Ralph E Harbach, and Simon I Hay. The dominant Anopheles vectors of human malaria in Africa, Europe and the Middle East: occurrence data, distribution maps and bionomic précis. *Parasites & vectors*, 3(1):117, January 2010

$f(n, \theta)$, showing the dependence of population growth both on population size (n) and some properties of the environment (θ), then the *fundamental niche* is the set of all values of θ such there there is some size n at which $f(n, \theta) > 0$.[4] Since such a value of n exists if and only if the maximum of $f(n, \theta)$ is greater than zero, we can define the fundamental niche formally using set builder notation as follows.

$$F = \{\theta : max(f(n, \theta) > 0)\} \tag{1}$$

In general, θ may be a vector of numbers representing multiple environmental dimensions such as average annual precipitation, number of frost free days, or annual mean temperature. If these environmental dimensions are represented by real numbers (that is, defined on a continuum somewhere between negative infinity and positive infinity), then the niche corresponds to one or more regions in *environmental space* (Figure 2). In general, not all environments in the fundamental niche will be occupied. For instance, some of these possible environments may not anywhere be realized in nature, many of these environmental conditions will be marginal so that the species is absent from many places where they are realized (although it could persist), or because interactions with other species prevent persistence (competitive exclusion) despite the fact that the environment is favorable. The subset of the fundamental niche at which the species is actually found is the *realized niche*.

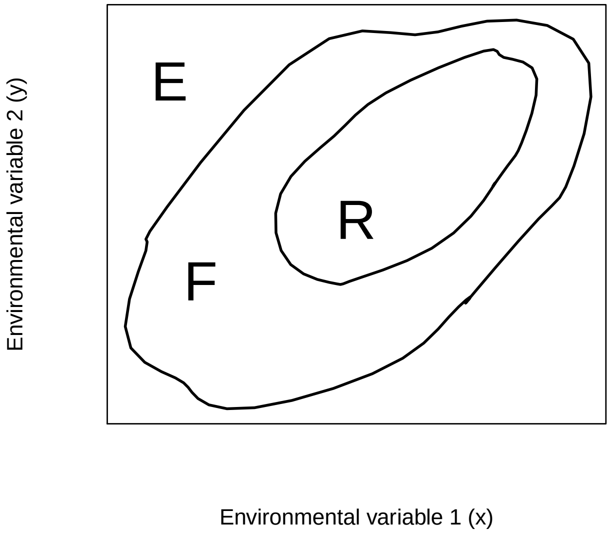

Figure 2: Two variables (x and y) define a space of possible environmental conditions (E), possibly not all realized in nature. A subset of this space, the fundamental niche F, consists of all combinations of x and y such that the species may persist. The realized niche R is the subset of F in which the species actually occurs in nature.

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[4] G.E. Hutchinson. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22:415–427, 1957

The niche boundary

How does one go about identifying the fundamental niche? First, because the boundaries of the niche are never directly observed they must be estimated from data. That is, observations are points within the space E, not smooth curves or regions. The boundary must be estimated from these points. How should this boundary be estimated? One possibility is to fit a model that gives the *probability* that a species will be present in a location given a particular set of environmental conditions. This model would assign a value between 0 and 1 to all environments and a cutoff, say 0.1 or 0.5, could be assigned. That is, a convention would be established such that an environment $\theta_1 = (x_1, y_1)$ would be considered to be in the niche if the probability of occurrence given θ_1 is greater then 0.1. An alternative approach is to fit a classifier – a statistical model that seeks to maximally classify observed environments into those occupied by the species and those where the species has not been observed. A final approach focuses on the *extreme observations*, i.e., the environmental *tolerances* of the species. Any of these approaches may be used so long as it is kept in mind that the fundamental niche is an inclusive concept – it contains all environments in which a species may persist, even those where it often does not. Only the last approach, which places the greatest value on extreme observations, identifies the boundary of the fundamental niche.

Mapping niches

Finally, once a model of the fundamental niche has been obtained, identifying a species potential distribution consists primarily in classifying geographic locations with respect to their position in environmental space. That is, there is a many-to-one mapping between locations in geographic space and locations in environmental space. Once this mapping is established a map may be colored to represent those locations that belong to the niche and those that do not (Figure 3)

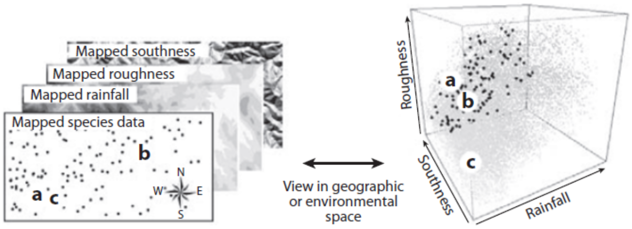


Image: Elith & Leathwick (2009)

Figure 3: The many-to-one mapping between geographic space and environmental space enables mapping the potential distribution of a species from a model of its fundamental niche.

The potential distribution of Anopheles arabiensis

Locations at which *Anopheles arabiensis* was collected in Africa during the twentieth century are shown as yellow points in Figure 4. For comparison the same number of points sampled randomly over the African landmass are shown in grey. From these two sets of points it would appear that *Anopheles arabiensis* is selective about the environments it inhabits.

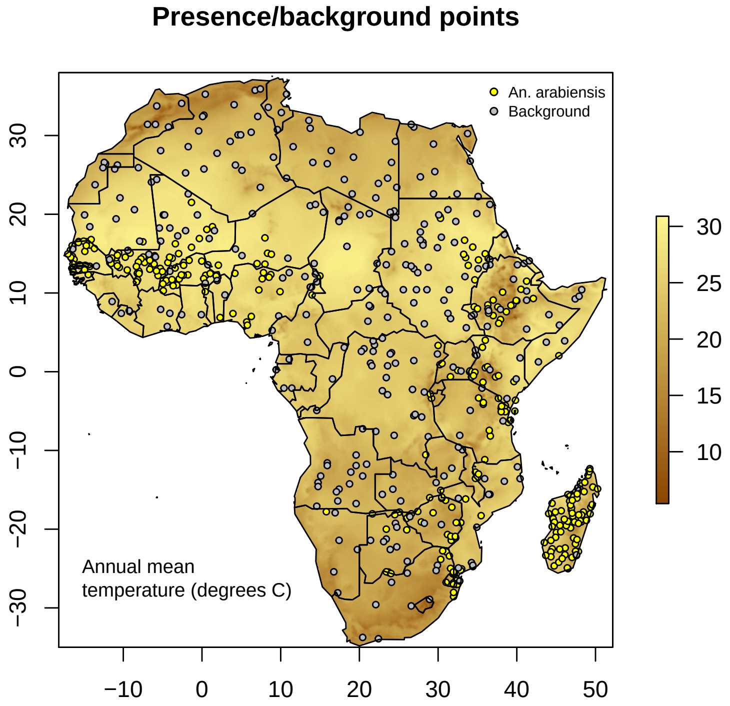


Figure 4: Distribution of sampling points for all *Anopheles arabiensis* and a balanced random sample of background points.

Eighty-six different environmental variables that could be obtained at the spatial resolution of 0.1 decimal degree were chosen for niche modeling. These variables represented such things as annual and monthly temperature, precipitation, and the seasonal amplitude in climate fluctuations. However, statistical analysis showed that most of the information contained in these eighty-six variables could be compressed into two new variables using a multivariate technique called *principal components analysis* that uses linear operations to transform a large number of correlated observations into a smaller number of uncorrelated observations. A plot of the *An. arabiensis* occurrence points and the random sample shows that *An. arabiensis* is a climate generalist in the sense that it tolerates a wide range of environmental conditions (Figure 5).

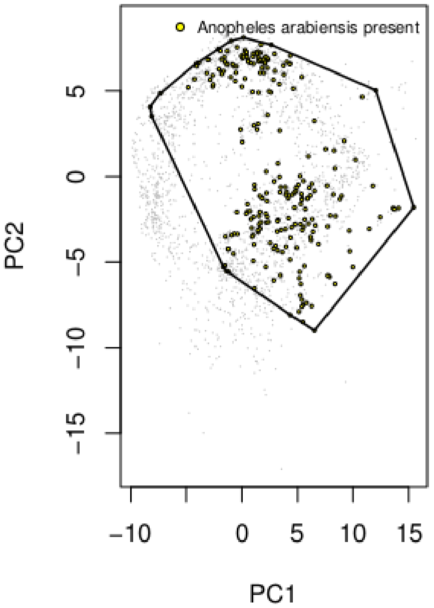


Figure 5: Occurrences of *Anopheles arabiensis* and a random sample of locations in Africa are shown in the space of the first two principal components. Despite the spatial clustering in Figure 4 this plot shows that *An. aranbiensis* is a climate generalist in the sense that it occupies almost the entire space of African environments. This result is underscored by the curve connecting the outermost points (convex hull) in this space.

(LOBAG-OC) is a recently developed extreme value method for ecological niche modeling. An ecological niche model obtained using LOBAG-OC accurately depicts the historic range of of *An. araniensis* in Africa (Figure 6A).

What is more interesting is that under three plausible climate change scenarios, the future distribution of *An. arabiensis* is expected to be considerably reduced (Figure 6B-D). Figure 7 shows the total geographic area (sq. km) inhabitable by *An. arabiensis* under both baseline and forecasted future climate conditions and relative to the area of the entire African land mass. These results suggest that even in the absence of vector control and land conversion, the spatial distribution and total exposure of the African population to malaria transmitted by *An. arabiensis* is expected to change dramatically. Indeed, while the estimated effect of projected climate change is relatively large (reductions in area of 48%-61%), the differences among climate change scenarios are relatively small (Figure 6B-D). Map differences between baseline and projected climate models suggest that reductions of habitat will be especially extensive in Western and Central Africa; portions of Botswana, Namibia, and Angola in Southern Africa; and portions of Sudan, South Sudan, Somalia, and Kenya in East Africa (Figure 8). The East African Rift Valley and Eastern Coast of Africa, where *An. arabiensis* is most abundant today, are expected to remain habitable.

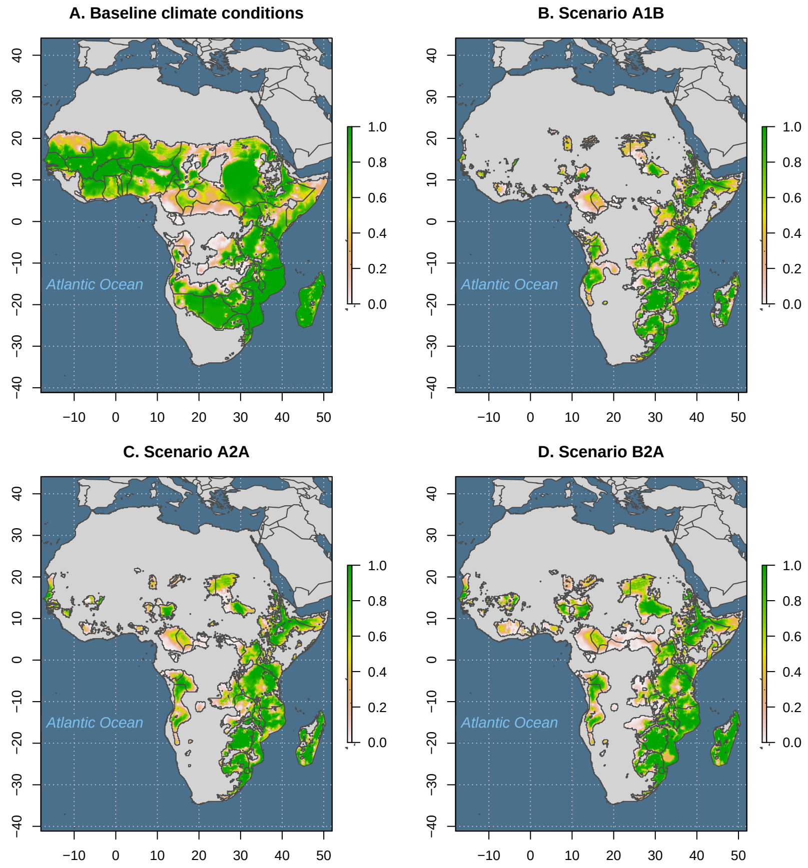


Figure 6: A. Modeled potential distribution of *Anopheles arabiensis* habitat in Africa given the current global climate. B. Future potential distribution of *Anopheles arabiensis* in Africa under IPCC Scenario A1B. C. Future potential distribution of *Anopheles arabiensis* in Africa under IPCC Scenario A2A. D. Future potential distribution of *Anopheles arabiensis* in Africa under IPCC Scenario B2A.

There will be some modest gains in habitat, especially on the margins of the current range in South Sudan, South Africa, and Angola.

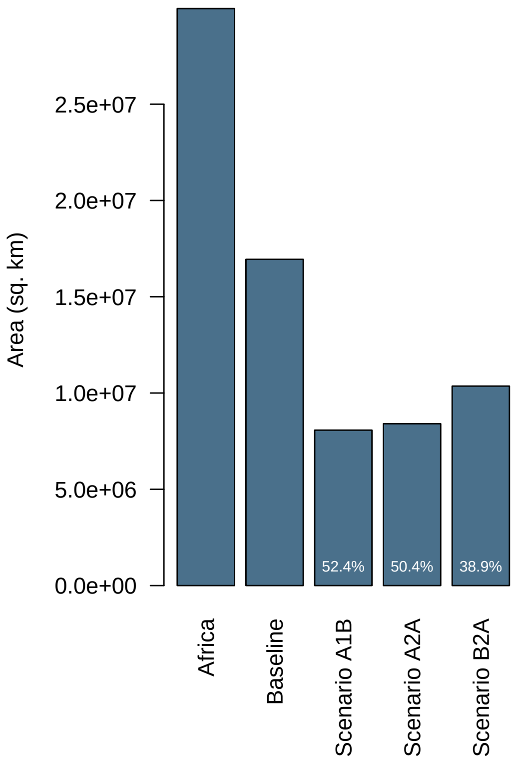
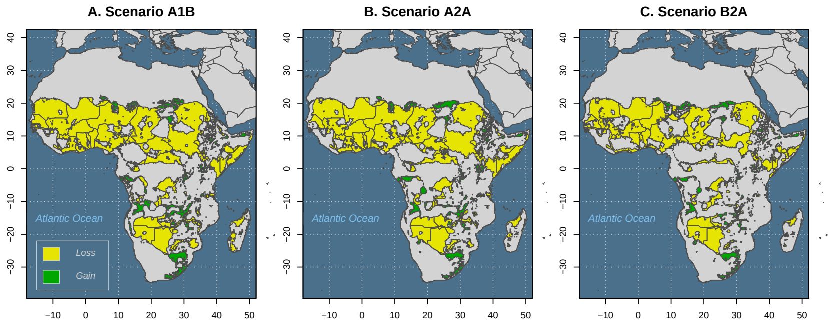


Figure 7: Current distribution of *Anopheles arabiensis* habitat in Africa compared with the total land mass area of Africa and potential distribution under three climate change scenarios. Overplotted quantities are percent habitat loss from baseline.

In conclusion, niche modeling has shown *An. arabiensis* to be a climate generalist with widespread potential distribution in Africa. That is, the fundamental niche of this species is large, even if the current and future geographic distributions are relatively smaller. An ecological niche model for *An. arabiensis* projected using data from global climate simulations predicts that despite these wide tolerances, the potential distribution of *An. arabiensis* is likely to be reduced by 48% - 61% by 2050.

Test yourself

- What is the potential distribution?
- What are the different concepts of “niche”?
- Describe the relationship between “environmental space” and “geographic space”.



A. Scenario A1B

B. Scenario A2A

C. Scenario B2A

Figure 8: A. Losses and gains of *Anopheles arabiensis* habitat in Africa under future climate scenario A1B compared with the current distribution. B. Losses and gains of *Anopheles arabiensis* habitat in Africa under future climate scenario A2A compared with the current distribution. C. Losses and gains of *Anopheles arabiensis* habitat in Africa under future climate scenario B2A compared with the current distribution.

Bibliography

[1] G.E. Hutchinson. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22:415–427, 1957.

[2] Dan W Meyrowitsch, Erling M Pedersen, Michael Alifrangis, Thomas H Scheike, Mwelecele N Malecela, Stephen M Magesa, Yahya A Derua, Rwehumbiza T Rwegoshora, Edwin Michael, and Paul E Simonsen. Is the current decline in malaria burden in sub-Saharan Africa due to a decrease in vector population? *Malaria Journal*, 10(1):188, January 2011.

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