IDENTIFYING SENSITIVITY THRESHOLDS IN ENVIRONMENTAL MODELS: WHEN DOES A MODEL BECOME INSENSITIVE TO CHANGE?

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ABSTRACT

Sensitivity of environmental models to changes in variable parameters can be measured in a variety of ways. One simple, yet effect way to judge model sensitivity is to calculate a sensitivity index (Hamby, 1994). Standard sensitivity indices compare the standardized percent change in a parameter threshold of interest and the model's state variable from the default model to an altered model run, resulting in a normalized dimensionless index value (Lenhart et al., 2002; Millington et al., 2009). Although traditional sensitivity indices are good at estimating a model's sensitivity to small changes above or below the default model parameter thresholds, they do a poor job of gauging model sensitivity with larger changes in parameter thresholds and indentifying thresholds at which models becomes insensitive to change. To better explore model sensitivity away from the default model parameter thresholds, and identify thresholds where a model becomes insensitive to changes in a particular variable, I have developed the relative sensitivity index. The relative sensitivity index is able to calculate a model's sensitivity relative to a previous model run, allowing the user to track changes in model sensitivity away from the default model run. To demonstrate the ability of the relative sensitivity index in exploring model sensitivity, the Tsetse Ecological Distribution (TED) Model's (a spatially explicit dynamic model that predicts tsetse fly distributions in Kenya) sensitivity to three parameters (NDVI, maximum temperature, and minimum temperature) was analyzed using two standard sensitivity indices and the relative sensitivity index.

INTRODUCTION

A sensitivity analysis is performed on an environmental model to identify the relative importance of the input variables in relation to the output state variable (Cariboni et al., 2006). A model is said to be sensitive to a particular variable when small changes to said variable's parameter threshold results in significant changes to the model output (Hamby, 1994). However, often the sensitivity of a spatially explicit model that uses remotely sensed continuous landscape variables (e.g., temperature, precipitation, vegetation indices, elevation, etc.) varies in a non-linear manner the further one altars parameter thresholds. This variability in model sensitivity away from the default model run represents an unknown to the model user, and should be explored to not only judge overall model sensitivity to a particular variable, but also identify when a model becomes insensitive to changes a variable.

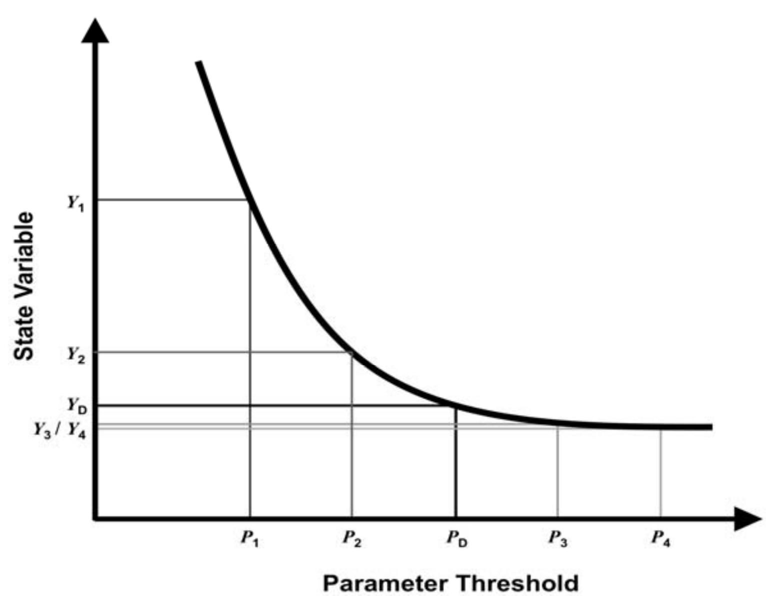

Figure 1. Schematic of the relationship between a parameter threshold (P) and the output state variable (Y) adapted from Lenhart et al. (2002). P_D and Y_D are the default model run.

Sensitivity of environmental models can be measured in a variety of ways. One simple, yet effect way to judge model sensitivity is to calculate a sensitivity index (SI) (Hamby, 1994; Saltelli et al., 2004). Traditional SI compare the change in a parameter of interest (P), to the change in a model's state variable (Y), standardized by the default baseline model values (P_D and Y_D) (Figure 1), resulting in a normalized dimensionless index value (Lenhart et al., 2002; Millington et al., 2009). Although traditional SI are good at estimating a model's sensitivity to small changes above or below the default model parameter thresholds, they do a poor job of gauging model sensitivity with larger changes in parameter thresholds and indentifying thresholds at which a model becomes insensitive to change. To better explore model sensitivity, I have developed the relative sensitivity index (RSI). The RSI analyzes the change in the sensitivity between two distinct model runs with varying parameter values, thus comparing a model's sensitivity relative to the previous model run. By using the RSI, parameter thresholds can be decreased or increased to identify thresholds of interest and the point at which a model becomes insensitive to change.

METHODS

Sensitivity Indices

Three different SI equations were analyzed in this study. The first SI equation examined was presented in Lenhart et al. (2002) ($SI_{\text{Lenhart et al.}}$) and varies the input variable parameter threshold by a fixed amount both above and below the default parameter threshold, measures the change in the state variable that results from varying the parameter threshold, standardizes the change in the parameter threshold and state variable by the default values, and divides the standardized change in the state variable by the standardized change in the parameter (Equation 1).

$$SI_{Lenhart\,et\,al.} = \frac{\Delta Y_{\pm i} / Y_D}{2\Delta P_{D\,\&\,i} / P_D} \tag{1}$$

where Y is the dependant output state variable, P is the parameter threshold of the input variable being analyzed, i is the amount the parameter is varied above and below the default model, and D is the value associated with the default baseline model. Thus the $SI_{\text{Lenhart et al.}}$ equation analyzes model sensitivity of an equal positive (P_2) and negative parameter (P_3) change (Figure 1) into one standardized index.

The second SI equation is from Millington et al. (2009) ($SI_{\text{Millington et al.}}$) and was adapted from the SI equation presented in Hamby (1994) (J.D.A. Millington, personal communication). The $SI_{\text{Millington et al.}}$ equation varies the input variable parameter from the default model, measures the change in the state variable, standardizes change in the parameter threshold and state variable by the default values, and divides the standardized change in the state variable by the standardized change in the parameter (Equation 2).

$$SI_{Millington\,et\,al.} = \frac{\Delta Y_{D\,\&\,i} / Y_D}{\Delta P_{D\,\&\,i} / P_D} \tag{2}$$

where Y is the dependant output state variable, P is the parameter threshold of the input variable being analyzed, i is the amount the parameter is varied from the default model, and D is the value associated with the default baseline model. Thus the $SI_{\text{Millington et al.}}$ equation calculates model sensitivity of any parameter threshold change (P_i) and the resulting model state variable (Y_i) in relation to the default model values (P_D and Y_D) (Figure 1).

The third SI equation is the relative sensitivity index (RSI). The RSI equation calculates the change in parameter thresholds between two separate model runs, measures the change in the state variable between said model runs, standardizes change in the parameter threshold and state variable by the default values, and divides the standardized change in the state variable by the standardized change in the parameter (Equation 3).

$$RSI = \frac{\Delta Y_{i_1\,\&\,i_2} / Y_D}{\Delta P_{i_1\,\&\,i_2} / P_D} \tag{3}$$

where Y is the dependant output state variable, P is the parameter threshold of the input variable being analyzed, i_1 and i_2 are the model runs being compared, and D is the value associated with the default baseline model. Thus the RSI equation calculates model sensitivity relative to any two model runs (e.g., P_1 and P_2 [Figure 1]), rather than just comparing two model runs of equal parameter change above and below the default parameter threshold (i.e., $SI_{Lenhart\ et\ al.}$), or comparing an altered model run only to the default model values (i.e., $SI_{Millington\ et\ al.}$).

The comparison of the resulting SI values was facilitated by classifying each SI value into one of four categories described in Lenhart et al. (2002) (Table 1). A parameter was deemed insensitive if the SI value was between 0.00 and 0.05, implying that a change in the parameter resulted in little to no change in the state variable. Moderate and high sensitivity were assigned to SI values between 0.05 to 0.20 and 0.20 to 1.00, respectively. SI values greater than 1.00 imply a change in the state variable greater than the change in the parameter, thus indicating extreme sensitivity.

Table 1. Sensitivity classes adapted from Lenhart et al. (2002).

Sensitivity Index	Class	Sensitivity
$0.00 \leq SI < 0.05$	I	Insensitive
$0.05 \leq SI < 0.20$	II	Moderate
$0.20 \leq SI < 1.00$	III	Highly
$SI \geq 1.00$	IV	Extremely

The Tsetse Ecological Distribution (TED) Model

To demonstrate the differences between the three SI a sensitivity analysis was performed on the Tsetse Ecological Distribution Model (TED Model). The TED Model is a 250m spatial resolution, raster-based, spatially explicit dynamic model that predicts tsetse fly (the vector for African trypanosomiasis, otherwise known as sleeping sickness in humans) distributions based on habitat suitability and fly movement rates. Individual binary presence / absence maps are produced at 16 day intervals, from 1/1/2001 to the acquisition date of the most recently available Moderate Resolution Imaging Spectroradiometer (MODIS) remotely sensed data products that are inputs to the model. At its simplest, the TED Model can be described in two separate parts: 1) a spatially explicit model that identifies suitable tsetse habitat and 2) a fly movement model that integrates tsetse distributions and fly movement rates (Figure 2).

The habitat suitability model uses four MODIS remotely sensed data sets: 1) the MODIS Terra NDVI Vegetation Indices 250m V005 (MOD13Q1) product as a surrogate for available moisture (see Williams et al., 1992), 2) the MODIS Terra Day Land Surface Temperature (LST) 1km V005 product (MOD11A2), 3) the MODIS Terra Night LST 1km V005 product (MOD11A2), and 4) the 1km MODIS type 1 Global Land Cover product (see DeVisser & Messina, 2009). Each of the four data sets was recoded to a binary suitable (1) vs. unsuitable (0) habitat classification scheme. These four binary habitat suitability maps are then combined to create an overall suitable tsetse habitat map for each 16-day epoch.

Although the first part of the model determines the location of suitable tsetse habitat, the expansion of suitable habitat might be greater than tsetse

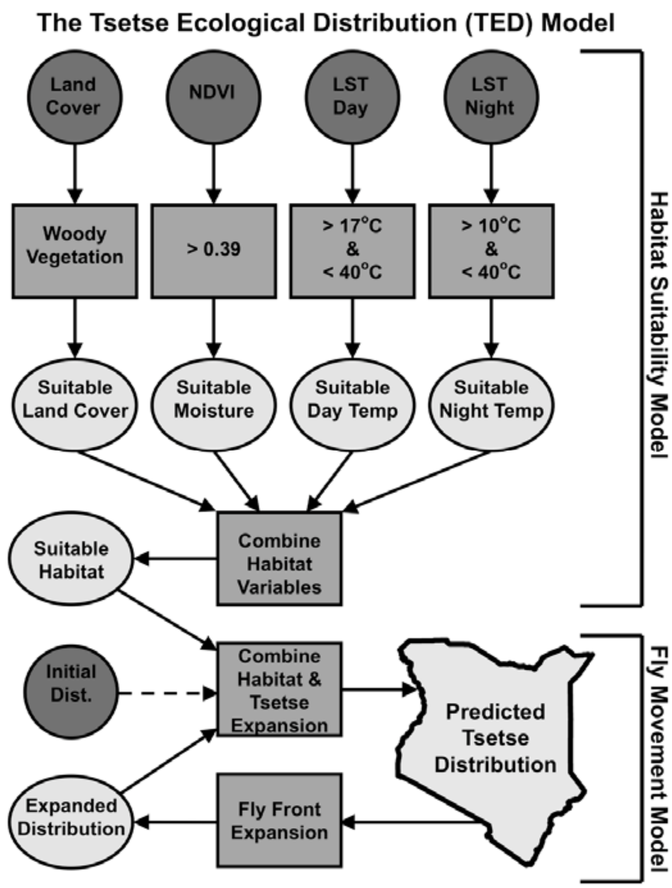

Figure 2. The Tsetse Ecological Distribution (TED) Model Flow Chart; dark grey circles are input variables, grey squares are conversions / calculations, light grey ovals are derived auxiliary variables, and model output for each scene is the Kenyan shaped Predicted Tsetse Distribution.

movement rates. To identify the location of tsetse distributions a fly movement model, which expands the previous tsetse distributions by an assigned fly movement rate, was coupled to the habitat suitability model. Thus the TED Model produces a unique tsetse distribution map every 16 days, and is able to predict tsetse distributions over time and space.

The TED Model produced 204 unique tsetse distribution maps that predict the spatial distribution of tsetse within Kenya at a 16-day temporal resolution between 1/1/2001 and 12/19/2009 (the last scene acquisition date for data used in this paper). A one-year initialization period (1/1/2001 to 12/31/2001) is used to lessen the impact of the starting tsetse distribution on the TED Model's predicted tsetse distributions, leaving 184 scenes between 1/1/2002 to 12/19/2009 for analysis. The individual scenes are then summed and divided by 184 (the total number of scenes) to create a percent probability map of tsetse presence (Figure 3).

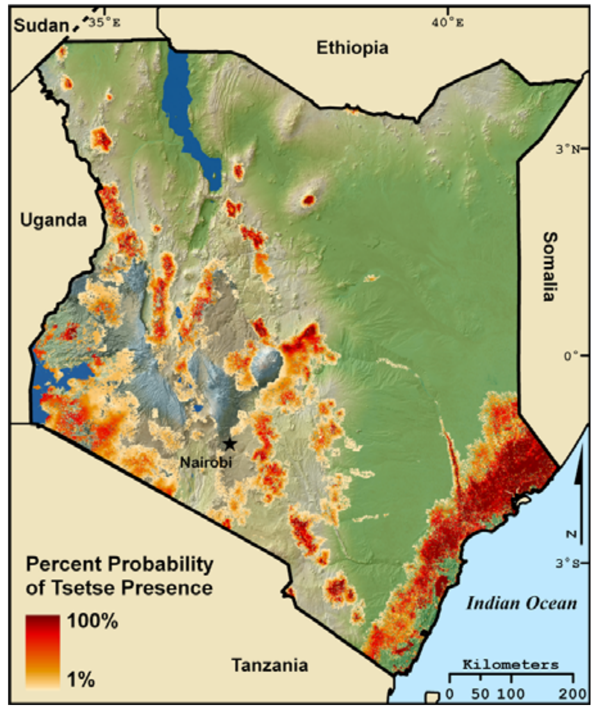

Figure 3. The TED Model percent probability map overlaid on a physiographic map of Kenya to show the location of predicted tsetse distributions. The surface area ≥ 50% was used as the state variable in the sensitivity analysis.

The TED Model Sensitivity Analysis

The state variable in the TED Model sensitivity analysis was the surface area of the percent probability map above 50%. The three variables examined were moisture (i.e., NDVI), maximum temperature, and minimum temperature. Land cover and fly movement rates were excluded from the sensitivity analysis since land cover is a nominal variable and can not be incrementally increased or decreased, and fly movement rates could only be increase by relatively large increments of 250m due to the spatial resolution of the TED Model. The NDVI parameter threshold of 0.39 (see Williams et al., 1992) was varied by 0.02 (~5%) to a minimum threshold value of 0.00 and a maximum threshold value of 0.80. The maximum temperature parameter threshold of 40°C was varied by 1°C to a minimum value of 25°C and a maximum value of 80°C. The minimum temperature parameter threshold of 10°C for night LST and 17°C for day LST was also varied by 1°C. However, since minimum temperature has two different threshold values for day and night LST (due to the diurnal nature of tsetse), the standardization of the SI was performed using only the night time parameter threshold considering that 10°C is a lethal threshold (Terblanche et al., 2008) and 17°C is a mobility threshold (Mellanby, 1936 / 1939).

The two different threshold values of minimum and maximum temperature present another issue since a 1°C change at 10°C represents a 10% change in the parameter threshold, while at 40°C a 1°C change represents a 2.5% change. This difference in the percent change is a result of 0°C being associated with the freezing point of water, which in the case of environmental modeling has the potential to be a contrived minimum value. However, converting temperatures from Celsius to Kelvin, normally a logical choice to avoid such issues, causes a 1°C parameter threshold change to only represent ~0.37% change, which greatly inflates all calculated SI values. To avoid this predicament, a 1°C change in both minimum and maximum temperature was standardized to a 4% change, the equivalent of a 1°C change if both default parameter thresholds were set at 25°C (i.e., halfway between the two original threshold values). Thus minimum and maximum temperature $SI_{\text{Lenhart et al.}}$, $SI_{\text{Millington et al.}}$, and RSI values were calculated using Equation 4, Equation 5, and Equation 6 respectively:

$$SI_{Lenhart\,et\,al.} = \frac{\Delta Y_{\pm i} / Y_D}{2\Delta P_{D\&i} * 0.04} \quad (4)$$

$$SI_{Millington\,et\,al.} = \frac{\Delta Y_{D\&i} / Y_D}{\Delta P_{D\&i} * 0.04} \quad (5)$$

$$RSI = \frac{\Delta Y_{i_1 \& i_2} / Y_D}{\Delta P_{i_1 \& i_2} * 0.04} \tag{6}$$

where *Y* is the dependant output state variable, *P* is the parameter threshold of the input variable being analyzed, *i* is the model run being analyzed, and *D* is the value associated with the default baseline model.

RESULTS

The results of the sensitivity analysis performed on NDVI and minimum temperature variables showed a synchronistic relationship with predicted tsetse distributions (i.e., an increase in parameter thresholds resulted in an increase in predicted tsetse distributions) (Figure 4; Table 2 & 3). The results of the sensitivity analysis performed on the maximum temperature variable showed an inverse relationship with predicted tsetse distributions (i.e., an increase in the parameter threshold resulted in a decrease in predicted tsetse distributions) (Figure 4; Table 4).

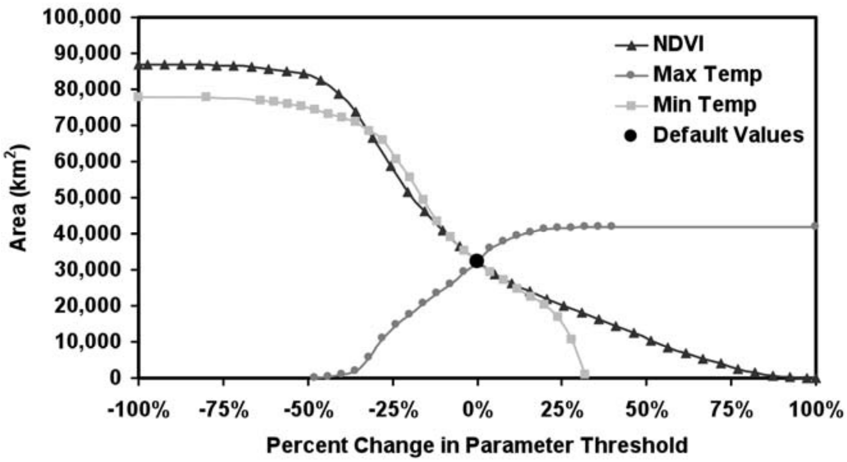

Figure 4. Combined and standardized parameter threshold values and the corresponding surface area state variable used in the sensitivity analysis.

DISCUSSION

A comparison of the three SI shows that the $SI_{Lenhart\ et\ al.}$ equation produced the least amount of variation in SI values, with a combined range of 0.66 (NDVI) to 1.63 (minimum temperature). However, after binning SI values into one of the four sensitivity classes (Table 1), it was observed that the $SI_{Millington\ et\ al.}$ equation produced the least amount of variation in classes, with 94.4% of all SI values classified as class IV (i.e., SI ≥ 1.00) (Table 5). The low amount of variation of SI values produced by the $SI_{Lenhart\ et\ al.}$ and $SI_{Millington\ et\ al.}$ equations likely stems from the change in parameter and state variable values always being tied to the default baseline model.

In the case of the $SI_{Millington\ et\ al.}$ equation the SI value is directly linked to the default baseline model values since ΔP and ΔY are the change in the model run being analyzed from the default baseline model. Thus the further the altered model run is from the default model parameter values, the less reliable the $SI_{Millington\ et\ al.}$ equation is at gauging model sensitivity. An example of this can be viewed in the sensitivity analysis of maximum temperature with a 5°C increase in the parameter threshold. The $SI_{Millington\ et\ al.}$ equation produced SI values that remain quite high, despite predicted distributions no longer markedly increasing in surface area. This occurs because the high degree of change that occurred with 1°C to 4°C increase in parameter thresholds inflates SI values calculated with further parameter threshold increases, resulting in less variation of SI values overall.

The SI values produced by the $SI_{Lenhart\ et\ al.}$ equation are indirectly related to the default baseline model, since the ΔP is always calculated from parameter thresholds of an equal amount below and above the default baseline model. By examining twice the spread in parameters values the $SI_{Lenhart\ et\ al.}$ equation further exacerbates the problem of gauging model sensitivity away from the default model run, resulting in decreased SI value variation. The linking of both negative and positive parameter changes has the added potential to allow one particular directional parameter change to unduly influence the calculation of a SI value without the users knowledge (e.g., maximum temperature). In the case of maximum temperature, SI values calculated by the $SI_{Lenhart\ et\ al.}$ equation show little variation with a ± 7°C change in the parameter threshold, despite the only slight positive change and substantial negative change in the state variable from the model run using a ± 6°C parameter change.

Table 2. Results of the sensitivity analysis performed on NDVI. The default model run (parameter threshold 0.39) is highlighted in bold

NDVI Parameter Threshold	State Variable (km^2)	$SI_{Lenhart\ et\ al.}$	$SI_{Millington\ et\ al.}$	RSI
-0.01	86,800	0.66	1.65	0.00
0.01	86,795	0.69	1.73	0.01
0.03	86,785	0.73	1.83	0.01
0.05	86,766	0.76	1.94	0.02
0.07	86,731	0.80	2.06	0.04
0.09	86,659	0.85	2.19	0.10
0.11	86,501	0.89	2.34	0.18
0.13	86,207	0.94	2.51	0.35
0.15	85,627	0.99	2.69	0.33
0.17	85,088	1.05	2.90	0.49
0.19	84,280	1.12	3.14	1.05
0.21	82,548	1.18	3.38	2.28
0.23	78,771	1.22	3.51	3.05
0.25	73,716	1.24	3.58	4.31
0.27	66,581	1.22	3.45	4.75
0.29	58,713	1.17	3.20	4.26
0.31	51,669	1.12	2.93	3.33
0.33	46,164	1.12	2.80	3.14
0.35	40,974	1.12	2.63	2.65
0.37	36,596	1.19	2.61	2.61
0.39	**32,273**	—	—	—
0.41	28,711	1.19	2.15	2.15
0.43	26,095	1.12	1.87	1.58
0.45	23,957	1.12	1.67	1.29
0.47	22,030	1.12	1.55	1.16
0.49	20,010	1.17	1.48	1.22
0.51	18,168	1.22	1.42	1.11
0.53	16,251	1.24	1.38	1.16
0.55	14,305	1.22	1.36	1.18
0.57	12,370	1.18	1.34	1.17
0.59	10,369	1.12	1.32	1.21
0.61	8,555	1.05	1.30	1.10
0.63	6,776	0.99	1.28	1.08
0.65	5,254	0.94	1.26	0.92
0.67	3,907	0.89	1.22	0.81
0.69	2,536	0.85	1.20	0.83
0.71	1,579	0.80	1.16	0.58
0.73	710	0.76	1.12	0.52
0.75	364	0.73	1.07	0.21
0.77	72	0.69	1.02	0.18
0.79	29	0.66	0.97	0.03
Minimum		0.66	0.97	0.00
Maximum		1.24	3.58	4.75
Mean		1.00	2.01	1.31

Table 3. Results of the sensitivity analysis performed on minimum temperature. The default model run (parameter threshold of 10°C) is highlighted in bold

Min Temp Parameter Threshold (C°)	State Variable (km^2)	$SI_{Lenhart\ et\ al.}$	$SI_{Millington\ et\ al.}$	RSI
-10	77,660	0.75	1.76	0.13
-6	76,986		2.16	0.39
-5	76,480		2.28	0.52
-4	75,812		2.41	0.44
-3	75,247		2.56	0.62
-2	74,447		2.72	0.93
-1	73,247		2.89	0.79
0	72,221		3.09	0.96
1	70,985		3.33	1.99
2	68,413	1.63	3.50	1.97
3	65,868	1.53	3.72	4.16
4	60,493	1.41	3.64	3.87
5	55,501	1.37	3.60	4.80
6	49,301	1.30	3.30	4.58
7	43,391	1.21	2.87	3.39
8	39,011	1.15	2.61	2.86
9	35,321	1.13	2.36	2.36
10	**32,273**	—	—	—
11	29,472	1.13	2.17	2.17
12	27,168	1.15	1.98	1.78
13	24,662	1.21	1.97	1.94
14	22,427	1.30	1.91	1.73
15	20,183	1.37	1.87	1.74
16	16,765	1.41	2.00	2.65
17	10,666	1.53	2.39	4.72
18	1,009	1.63	3.03	7.48
30	0	0.75	1.25	0.07
Minimum		0.75	1.25	0.07
Maximum		1.63	3.72	7.48
Mean		1.28	2.59	2.27

Unlike the $SI_{Lenhart\ et\ al.}$ and $SI_{Millington\ et\ al.}$ equations the RSI equation resulted in a higher degree of variability in both SI values (a combined range of 0.00 to 7.48) and class values (Table 5). In addition to the SI values produced by the RSI equation having a higher degree of variability, the RSI equation does not rely on the default model values to calculate ΔP and ΔY. Ergo, the RSI equation can analyze changes in model sensitivity relative to any two-model runs away from the default model values without suffering the previously discussed problems experienced by the $SI_{Lenhart\ et\ al.}$ and $SI_{Millington\ et\ al.}$ equations, provided that the parameter thresholds of the two model runs being compared are reasonably close (e.g., $\Delta P \leq \sim 10\%$). In essence the RSI equation can be used to track model sensitivity, providing the user more information on parameter thresholds of interest.

Parameter thresholds of interest may come in the form of a sudden increase in SI values (e.g., 15°C - 18°C minimum temperature parameter threshold), at which point the state variable drastically increase or decrease in value. Variables that produced such results may be of concern with regards to model uncertainty, potentially requiring more data to be collected, or in the case of the TED Model, data validation, to insure model uncertainty is minimized (Cariboni et al., 2007). Parameter thresholds where SI values suddenly decrease (e.g., 31°C - 30°C maximum temperature parameter threshold), at which point the percent change in the state variable is small, likely

Table 4. Results of the sensitivity analysis performed on maximum temperature. The default model run (parameter threshold of 40°C) is highlighted in bold

Max Temp Parameter Threshold (Cº)	State Variable (km^2)	$SI_{Lenhart\ et\ al.}$	$SI_{Millington\ et\ al.}$	RSI
28	21		2.08	0.21
29	297		2.25	0.48
30	921	0.79	2.43	0.66
31	1,770	0.86	2.63	3.04
32	5,694	0.87	2.57	3.96
33	10,809	0.85	2.38	3.05
34	14,751	0.86	2.26	2.19
35	17,584	0.91	2.28	2.30
36	20,556	0.96	2.27	2.14
37	23,315	1.03	2.31	2.05
38	25,962	1.15	2.44	2.55
39	29,254	1.28	2.34	2.34
40	**32,273**	—	—	—
41	35,843	1.28	2.76	2.76
42	37,827	1.15	2.15	1.54
43	39,290	1.03	1.81	1.13
44	40,413	0.96	1.58	0.87
45	41,105	0.91	1.37	0.54
46	41,472	0.86	1.19	0.28
47	41,676	0.85	1.04	0.16
48	41,797	0.87	0.92	0.09
49	41,831	0.86	0.82	0.03
50	41,857	0.79	0.74	0.02
80	41,878		0.19	0.00
Minimum		0.79	0.19	0.00
Maximum		1.28	2.76	3.96
Mean		0.96	1.86	1.41

indicate a critical threshold has been reached and the model is decreasing in sensitivity to said variable. In lieu of model parsimony, these critical thresholds should be examined to see if they have the potential to fall within the range of model / data uncertainty, and is so the variable may need to be removed.

Minimum and Maximum temperature posed a unique problem when calculating SI values since a 1°C change at the two different parameter thresholds represented drastically different percent changes, which ultimately would have influenced the calculated SI values. By standardizing to a parameter threshold halfway between the two original thresholds (i.e., 25°C) this problem was eliminated, however, it highlights an overarching issue of comparing two unrelated variable's SI values if the percent change in parameter values is not similar. For example, if the change in parameter thresholds was say 10% per altered model run, and another variable had changes of 1% in a parameter thresholds per altered model run, then the comparison of SI values calculated by any of the three methods examined in this study would be inappropriate due to the drastic difference in the scale of parameter change. The three variables assessed in the TED Model (i.e.,

Table 5. The percentage of SI values that fell within a given sensitivity class for each SI equation

	$SI_{Lenhart\ et\ al.}$	$SI_{Millington\ et\ al.}$	RSI
Class I	—	—	10.1%
Class II	—	—	7.9%
Class III	43.6%	5.6%	24.7%
Class IV	56.4%	94.4%	57.3%

NDVI, maximum temperature, and minimum temperature) had percent parameter thresholds of roughly 5%, 4%, and 4% respectively. Although the change was not exactly the same, it is similar enough to allow a comparison in variable sensitivity.

CONCLUSION

Sensitivity of environmental models to particular variables can be measured in a variety of ways. In this study two traditional SI equations (i.e, $SI_{\text{Lenhart et al.}}$ and $SI_{\text{Millington et al.}}$), and the new RSI equation were examined. The $SI_{\text{Lenhart et al.}}$ and $SI_{\text{Millington et al.}}$ equations were found to accurately gauge model sensitivity around the default model parameter thresholds, but were unreliable at exploring model sensitivity as the percent change from the default parameter thresholds increased. The RSI equation, which calculates model sensitivity relative to a previous model run rather than just the default model run, was able to track changes in model sensitivity and provided more information on changes in model sensitivity. Given that the goal of any model sensitivity analysis is to try and quantify relative importance of the input variables in relation to the output state variable (Cariboni et al., 2006), a SI that provides more information to the user should be preferred.

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REFERENCES

Cariboni, J., Gatelli, D., Liska, R., & Saltelli, A., 2007. The role of sensitivity analysis in ecological modeling, *Ecological Modelling*, *203*(1-2), 167–182.

DeVisser, M. H., & Messina, J. P., 2009. Optimum land cover products for use in a Glossina-morsitans habitat model of Kenya, *International Journal of Health Geographics*, *8*, 39.

Hamby, D. M., 1994. A review of techniques for parameter sensitivity analysis of environmental models, *Environmental Monitoring and Assessment*, *32*(2), 135-154.

Lenhart, T., Eckhardt, K., Fohrer, N., & Frede, H. G., 2002. Comparison of two different approaches of sensitivity analysis, *Physics and Chemistry of the Earth*, *27*(9-10), 645-654.

Mellanby, K., 1936. Experimental work with the tsetse-fly, Glossina palpalis, in Uganda, *Bulletin of Entomological Research*, *27*, 611-632.

Mellanby, K., 1939. Low temperature and insect activity, *Proceedings of the Royal Society of London, Series B, Biological Sciences (1934-1990)*, *127*(849), 473-487.

Millington, J., Wainwright, J., Perry, G. L., Romero-Calcerrada, R., & Malamud, B. D., 2009. Modelling Mediterranean landscape succession-disturbance dynamics: A landscape fire-succession model, *Environmental Modelling and Software*, *24*(10), 1196–1208.

Saltelli, A., Tarantola, S., Campolongo, F., & Ratto, M., 2004) *Sensitivity Analysis in Practice: A Guide to Assessing Scientific Models,* John Wiley & Sons Ltd., West Sussex, England, pp. 1-219.

Terblanche, J. S., Clusella-Trullas, S., Deere, J. A., & Chown, S. L., 2008. Thermal tolerance in a south-east African population of the tsetse fly Glossina pallidipes (Diptera, Glossinidae): Implications for forecasting climate change impacts, *Journal of Insect Physiology*, *54*(1), 114-127.

Williams, B., Rogers, D., Staton, G., Ripley, B., & Booth, T., 1992. Statistical modeling of georeferenced data: mapping tsetse distributions in Zimbabwe using climate and vegetation data, In *Modeling Vector-Borne and Other Parasitic Diseases* (pp. 267-280). Nairobi, Kenya: The International Laboratory for Research on Animal Diseases.