

Review for PCI Ecology

Title: Environmental heterogeneity drives tsetse fly population dynamics

Authors: Helene Cecilia, et al.

Summary: The manuscript reviewed herein presents an interesting and substantial body of work which is largely technically sound, to the best of my understanding. In addition to a number of, I believe, small technical questions, the bulk of my comments are aimed at helping guide improvements to the writing for clarity. The work has potentially important implications for vector (and disease) control strategies. While the model is very specific to this case, as was the goal, the approach could be followed to investigate the role of environmental heterogeneity on population dynamics and control strategies in other systems.

The only major comment I have is that there needs to be a bit more information and clarity included in the manuscript. There are also technical questions that may or may not require additional work, but I prefer to include these in the order in which they appear. It is most likely they simply require clarification.

1. Abstract: "...patches with the lowest mean temperatures and lowest variations..." should say something like "smallest variations in temperature" or "lowest variation in mean temperatures".

2. Abstract: delete "to maximize its efficiency" from the last sentence. Unless I've missed something and "efficiency" was explicitly tested.?

3. L 14-15: I'm not completely convinced that this is true (maybe distribution, but dynamics?) and the modeling paper cited (which is definitely a great paper to cite elsewhere in this manuscript!) Hartemink et al. 2015 does not appear to be an appropriate citation to support this claim.

4. L 21-22: Not sure what this means. "elaborated" is not a logical word in this sentence, but I'm not sure what the point is except to say simply that population dynamics vary across space and time but control strategies are typically carried out in a uniform fashion, "potentially impairing management".

5. L 25: Should be "cause both"

6. The paper is generally well-written, though there are some vocabulary and grammatical errors typical of non-native English. I've only pointed out a few easy fixes or problems that impair understanding.

7. L 41-46. I totally agree, and can't wait to quote this whole paragraph in a lecture.

8. L 45: except, remove the word "easily".

9. L 47: should probably be "...entomologists have developed a number of models (refs), and encouraged..."

10. L 51. "ineffective" would be a better word choice than "misleading" as there isn't likely to be such a nefarious or neglectful intent (which is what "misleading" implies)!

11. L 52: Not sure what "area-wide principles" are. Is this jargon?

12. L 53: "imputed" should be "due"?

13. L56 - 65. There's a lot of repetitiveness and filler phrases here, plus some grammatical errors. I suggest: Remove "To address such an issue..." and simply write "Spatial complexity of the environment has been shown to considerably influence predictions (refs). Indeed, population dynamics are expected to vary locally among patches of variable suitability, possibly affecting population dynamics at the larger metapopulation scale."

To assess whether spatial and temporal heterogeneity drives tsetse fly population dynamics at the metapopulation scale, we developed..."

14. L 69: "harbor" is a bit anthropomorphic. I suggest "tsetse flies are highly structured across the metapopulation"

15. The final paragraph of the introduction should also include the goal of assessing control methods (increasing adult mortality), as this forms the basis for the manuscript's most interesting result.

16. L 76: should be "influential"

17. L 77-78: I suggest "However, its influence compared to, or combined with, demographic processes [is poorly understood/has not been shown or explored]."

18. 80-81 & 86: Be more precise about the temperatures at/over which these things occur.

19. At this point, the reader does not know what a "teneral" is.

20. L 92: should be "models" and "in the savannah group"

21. 98: should be "associated with human [irrigation?] activities."

22. 100: "Hence..." Actually, it is not clear how this differs from previous models because it's not clear how savannah flies differ in behavior and distribution. Need more information.

23. L 113: hold should be "held"

24. L 124: specify what the names are referring to: "was monitored in four areas: Hann, ...". Also, they are not labelled in Figure 1, but probably should be.

25. L 145: temperature largely increases or decreases?

26. Figure 1 should be two separate figures. This would give more space to also label the four sites. Also, "30x30 [m? km? cell?] simulated area..." It is not clear what scale the maps are showing. There should also be more clear legends in all figures. Here, the color scale should be labelled as number of individuals.

27. L 155: "predict" from here on out, it is not clear what conditions are being used to project a prediction onto. A table with the starting conditions/parameter values and those used for the various "scenarios" is needed.

28. L 158: There really should be a section on fly development, and maybe also a life-cycle diagram to accompany the model in Figure 1. It's just really difficult to follow for a non-specialist without this basic knowledge. Also, what is a "parity"? Is this jargon or a translation error? The word does not appear in Hargrove & Ackley 2015. Perhaps the authors mean "stages"? If so, this should be fixed throughout.

29. L 161: Please cite the reference for this.

30. L 163: Should be "The model was implemented in Python..."?

31. Equations: given the mixed use of cases and super- and sub-scripting in these equations, I suggest a font that helps to distinguish them more clearly, if possible.

32. L 181-183. Why are Males not included in X (adults and teneral) here?

33. L 191-192: What does this mean, both mathematically and biologically?

34. L 196: Ref should be Lloyd-Smith.

35. L 205: I am not familiar with this type of spatially-explicit model. It seems similar to a cellular automata model, but the authors do not call it that. In a cellular automata framework, the edges must be treated in a pre-determined way (reflective, hard, wrap-around), and that can affect the results. Perhaps this framework does not need this specified, but I am at least personally curious how the "neighborhoods" are treated at the edges of the grid.

36. L 207: very cool!

37. L 212 & 218: again, the model scenario parameters should be in a table in the main text. The reader does not have a clear idea what these scenarios are because they have not been explicitly laid out. For sensitivity analyses, the authors could specify these ranges in the same table using brackets, etc. This would help the reader understand their methods and help with interpreting the results.

38. L 215: "old" is a bit crude. "mature" ?

39. L 216: fine to give this mathematical expression but it needs to be referred to (also) in words in the sentence.

40. L 224: preserve model hypotheses? what does that mean?

41. L 224: Is the weighting coefficient already given in the equations? if so, reference it here. If not, it should be.

42. L 235 & 236: again, these expressions should be given names in words within the sentence.

43. L 237-238: how was this assessed?

44. L 245: "female mortality"

45. L 246: "followed a logistic [function/ distribution]"

46. Figure 2: This figure is barely legible. I completely understand it can be difficult to show data from multiple sources, but better labelling could help. Two minor notes: dots --> "points" and the first panel should say "adult female daily mortality rate" instead of just daily mortality rate (right?). Also, in all figures, the A) B) C) panel labels should be outside of the figures and much larger.

47. L 251-253. The presentation of these data are confusing here because the authors present them in terms of properties of the "cells" or "grid" rather than "sites" or "landscape" or something real-world. Instead, it sounds like they are reporting a set of parameters rather than results. The authors could present the findings, then simply say the cell and grid properties were defined according to these empirical conditions.

48. L 256: "were seasonal"

49. L 257: female population was stable? was it not also seasonal? perhaps "consistent" across years would be a better term? Where do we see these data?

50. L 260: the figure does not (at least, clearly) capture this statement.

51. Figure 4: both panels need legends for the line types and colors. Also, ΔX : should it not be "time to development" ? be consistent.

52. L 270: How were interactions assessed? Is this result simply due to the low variance?

53. L 272: "to levels"

54. L 278: I am not convinced by simply looking at these two figures. Too much going on in each to understand what the authors are pointing to.

55. L 278-283: This whole section is really not clear. Revise.

56. Figure 5: I do not understand why/how the 60% increase in adult mortality in scenario 3 leads to complete loss of the entire female population in time step #1 for shorter-lived flies. How does it crash this fast (in a single time step)?

57. L 290-291: really? Could there simply not be enough power?

58. L 297: "can be" : has this been shown (in Vreysen et al 2011), or are the authors speculating? L 299: does Vreysen et al 2011 refer to this case in Zanzibar? If so, please clarify, and if not, please reference.

59. L 305-306: I completely agree, but have the authors sufficiently demonstrated this? It would be nice to see population dips then resurgences in population numbers over time. This I think is crucial.

60. L 313-316: this sentence is a bit confusing, re-word?

61. L 320-321: how are "realistic patterns" different from "knowledge-driven ones" ??

62. L 330: "complementary"

63. L 333: This sounds like the authors tested control targeting reproduction, which was not the case (unless I've missed something) rather than referring to the sensitivity analysis. If so, the language should be a bit more careful, as sensitivity depends on the range and variance of the parameter values used and response variables chosen. This may be nit-picking, but perhaps using the term "sensitive" in the sentence could resolve the ambiguity.

64. L 334: "willing to avoid mortality at all costs" is way too anthropomorphized. Please rephrase to better explain the phenomenon or cost in a biologically-meaningful way.

65. L 340-347: It's not clear what point this paragraph is meant to make. Also, "species' ecological strategy"

66. L 378-379: This sentence starts out clear, then falls apart. Maybe revise and break into two after "disappear"?