1: Department of Biology
3: Conservation Biology Program

Making the Most of Mechanistic Models

Leslie Ries[1,2], Jessica Turner[3], Thomas Mueller[1], Lisa Crozier[4]

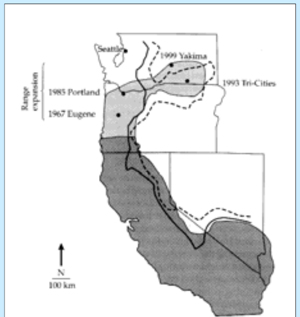
2: Socio-environmental Synthesis Center

4 Northwest Fisheries Science Center

INTRODUCTION: Mechanistic models of species distributions have been the subject of increased testing, but recent comparisons with correlative approaches have not shown their putative benefits, which include strengthened inference due to *a priori* predictions based on specific mechanisms and the ability to tease apart different dynamics. Through a new implementation of a butterfly distribution model subjected to past comparisons, we show the value of this approach by testing the model using abundance data, a metric more amenable to a model that predicts performance. We show that abundances have a positive relationship to predicted growth rates, but only in the cooler parts of this butterfly's range, suggesting an unidentified mortality source in warmer regions. This points to specific mechanisms that could be tested to improve the model. We also show how matching the year ranges of the environmental to distributional data provides a more robust test and suggests this species may not be in equilibrium with the recent climate. By testing the model in a way that takes advantage of the strengths of this approach, we were able to highlight the benefits of taking a mechanistic approach to species distribution models.

A SPECIES DISTRIBUTION MODEL BASED ON COLD TEMPERATURE TOLERANCE FOR THE COMMON SACHEM SKIPPER

The sachem butterfly is a common open-area skipper that uses a variety of common host grasses (e.g., Bermuda and crab grass). Starting in the 1960s, the sachem began experiencing a northern range expansion along the west coast (Box 1). Several experiments identified winter temperatures as a primary factor limiting growth (Box 2). Based on this work, a species distribution model was developed based on growing degree day model for summer recruitment and minimum January temperatures for overwinter survival (Box 3). We tested this mechanistic model across the sachems US range (below).

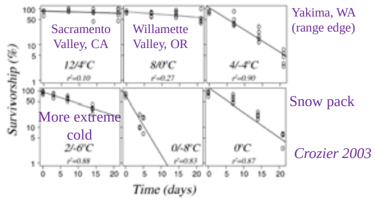


Box 1: The historic range of the sachem (dark grey) began to expand northward in the 1960s and by the 1990s had reached central Washington (light grey). One hypothesized cause was warming winters.

Box 2: Mechanistic experiments to test cold tolerance

Laboratory experiments

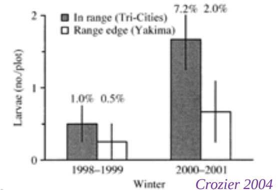
Exposed larvae to environment mimicking January high/low temps in different parts of their expanding range and under different conditions and measured overwinter survival.

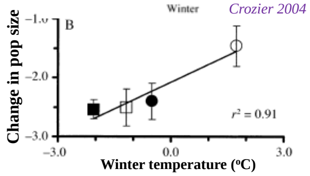


Observational field studies: In addition, field studies measured abundances from year to year showed a relationship with winter temperature.

Field experiments (transplants)

Overwinter survival measured for larvae collected in the Tri-cities and transplanted to both Tri-cities and Yakima (range edge).





Crozier, L. (2003). Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia*, 135(4), 648-656.
Crozier, L. (2004). Warmer Winters Drive Butterfly Range Expansion by Increasing Survivorship. *Ecology*, 85(1), 231-241.

Box 3: Crozier and Dwyer (2006) developed a mechanistic SDM that, when compared to a correlative SDM, did no better despite its increased mechanistic underpinnings (Buckley et al. 2010).

$$\lambda = \varphi[T_w(L,t)]R[T_s(L,t)].$$

Annual growth — Winter survivorship — Summer Recruitment

Winter survivorship is a function of mean January temperature. Summer recruitment is based on growing degree days.

Correlative (GLM): Mechanistic (C&D 2006):

Predicted range in grey (projected 3o expansion in dark grey) with recorded presences (filled circles) and absences (x's) showing model fit. Percent false + and – was similar between models

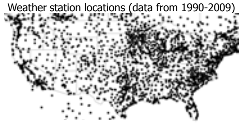
Buckley, L. B., et al. (2010). Can mechanism inform species' distribution models? *Ecology Letters*, 13(8), 1041-1054.
Crozier, L., & Dwyer, G. (2006). Combining Population-Dynamic and Ecophysiological Models to Predict Climate-Induced Insect Range Shifts. *The American Naturalist*, 168(1).

A NEW IMPLEMENTATION OF THE MECHANISTIC MODEL SHOWS THE VALUE OF THIS APPROACH

Mechanistic models require species-specific data on factors that impact their performance and thus require much more advance work to implement than traditional correlative (or niche) models that rely only on widely available distribution data. Previous work (Box 3) suggested that the mechanistic approach did no better when looking at predictions of presence and absence throughout their range. We suggest that to get the most out of these mechanistic models, we should use the *a priori* predictions of the mechanistic approach to examine specifically where the model did well or poorly to identify knowledge gaps for future research. We also examine the benefits of using abundance rather than occurrence data and also matching year-spans of climate data to distribution data for better results.

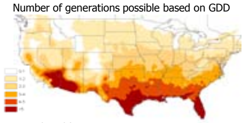
Box 4: Model implementation

Weather station locations (data from 1990-2009)

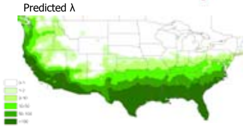


Probability of overwinter survival, Φ

Number of generations possible based on GDD



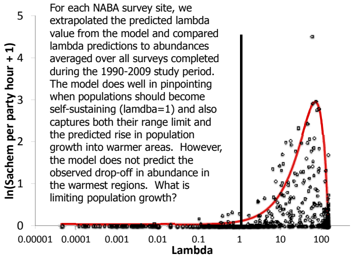
Predicted λ



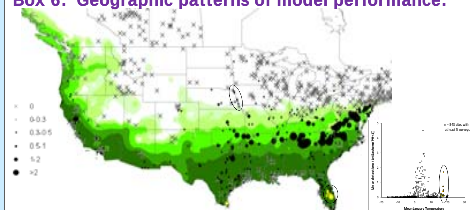
Data from the North American Butterfly Association's Count Program were used to test the model. Volunteers record every butterfly they observe at ~450 sites each year during one day. Started in 1975, 90% of surveys have occurred since 1990 so we used data from 1990-2009. For a model that predicts population growth, we suggest that the best test for the model is comparing lambda to mean abundances.

Box 5: Testing the model

For each NABA survey site, we extrapolated the predicted lambda value from the model and compared lambda predictions to abundances averaged over all surveys completed during the 1990-2009 study period. The model does well in pinpointing when populations should become self-sustaining (lamdba=1) and also captures both their range limit and the predicted rise in population growth into warmer areas. However, the model does not predict the observed drop-off in abundance in the warmest regions. What is limiting population growth?



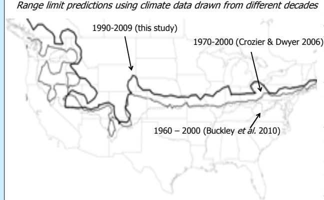
Box 6: Geographic patterns of model performance:



This map illustrates how the northern boundary is well-predicted along with the rise in abundance, but also shows the unexpected drop-off in the south where abundances are predicted to be at their highest. The map also highlights areas where abundances are higher than predicted – another result that is worthy of attention.

Box 7: Matching climate to distribution data

Range limit predictions using climate data drawn from different decades



Our implementation and test of this model is actually the third one to date and all three have used different climate data to implement the model. Crozier and Dwyer (2006) used climate data from 1970-2000 while Buckley et al. (2010) used data from 1960-2000. Our study uses a later date range (1990-2009) that matches the dates the distribution data are drawn from. Interestingly, current range limits are more congruent with predictions using 1970-2000 climate data. This could mean sachem are not in equilibrium with the current climate.

CONCLUSIONS

A recent comparison between Crozier and Dwyer's 2006 mechanistic model of sachem distributions was shown to do no better at predicting presence and absence than a simple niche model (Buckley et al. 2010). However:

- Presence/absence is a test more suited to niche models whereas mechanistic models predict performance and are best compared to abundance metrics when they are available
- *A priori* predictions allow for tests of model strengths and weaknesses and point to specific hypotheses to be explored:
  - What underlies lower performance in warmer areas of the range. Are they intolerant of too much heat (note that all the experiments in Box 2 focused on cold tolerance)? Do they experience increased predation or parasitism in warmer regions?
  - Are sachem in equilibrium with the current climate, or is their potential for range expansion?
  - Are the two identified areas of higher abundance (Box 6) statistical flukes, or have those local populations adapted to different temperature regimes, which could be easily tested in the lab?

Although comparisons between different modeling approaches can be informative, it is also important to implement and evaluate models in ways that take advantage of their putative benefits.

ACKNOWLEDGEMENTS

Funding for LR was provided by NSF (Award #1147049, Advancements in Biological Informatics) and the National Socio-environmental Synthesis Center (www.SESYNC.org)