Understanding range shift model error: The influence of generation time and rate of adaptation on species distribution model predictions.

Working group proposal

Short title: Range shifts and rates of adaptation Submitted to NCEAS on August 31, 2012

Principle Investigator

Edmund M. Hart
Beaty Biodiversity Center
Dept. of zoology
University of British Columbia
4200-6270 University Blvd
Vancouver, B.C. V6T 1Z4
ehart@zoology.ubc.ca

Project Summary: Species range shifts is one of the most well documented responses of species to climate change and have been modeled using correlative niche models (species distribution models, SDMs) for more than a decade. Because these models are based on stastical correlations between a species realized niche and abiotic variables, there is often a deviance between predictions and a species' actual distribution. Our group will seek to understand the source of this deviance using meta-analysis. The first goal will be to test how rates of adaptation may constrain or enhance species' ability to match climate predictions. Further exploration of patterns in model deviance can be explored once data on range predictions and extant ranges has been assembled such as model artifacts and mutualistic networks. Currently much of the data from these models is locked in the form of published figures and maps though. Therefore a second product of our working group will be the development of a web-based data extraction tool. This will allow anyone to upload a figure and extract data from it and store that data in DataONE and other open source data sites. This will result in a data product with a usefulness that will outlast our working group, and enable future meta-analysis.

Start date December 2012End date December 2013Data release December 2013Resubmission? No

Problem Statement

Species' range shifts was one of the earliest documented ecological responses to climate change (Parmesan, 1996; Parmesan et al., 1999; Parmesan & Yohe, 2003). Since the late 1990's ecologist's have been using species' distribution models (SDM's) to try and predict how those ranges will shift over the next century (Davis et al., 1998; Iverson & Prasad, 1998; Guisan & Zimmermann, 2000; Peterson, 2001). These models assume that the realized niche of a species is primarily determined by climate variables (Austin, 2002; Dormann, 2007). Ignoring physiology, biotic interactions and rapid local adaptation has long been a source of criticisms for these models (Davis et al., 1998; Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Helmuth et al., 2005). Aside from ignoring ecological theory (Elith & Leathwick, 2009), SDM's can show great variance in their predictive abilities (Elith et al., 2006; Kearney & Porter, 2009; Elith et al., 2010). More recent SDM's have begun to incorporate mechanisms such as physiology (Crozier & Dwyer, 2006; Buckley et al., 2010, 2011) and life history traits (Midgley et al., 2006; Kearney & Porter, 2009; Pöyry et al., 2009; Angert et al., 2011) to improve fit. Including traits and physiology offers a significant improvement in model predictions (Angert et al., 2011; Buckley et al., 2011) but is nonetheless only a small percentage of unexplained variance. Other factors may be important in explaining the error in species actual ranges and their predicted distribution.

Adaptation (and microevolution) to climate change is often cited as being an important facet in understanding how species will respond to climate change (Visser, 2008; Lavergne et al., 2010; Hoffmann & Sgrò, 2011), but it is difficult to accurately measure in the field (Hansen et al., 2012). Despite adaptation playing an important role in species range shifts to both current (Thomas et al., 2001; Bridle & Vines, 2007) and historical climate change (Davis & Shaw, 2001) it is conspicuously absent from SDM's. One way of integrating adaptation into prexisting range shift predictions is by examining the deviance between SDM predictions at the current time and the current range of species and comparing it to generation time. Shorter generation times allow for a more rapid adaptive response to strong selective pressures (Berteaux et al., 2004; Somero, 2010; Reed et al., 2011; Shaw & Etterson, 2012; Walters et al., 2012). The first reason is that species with shorter

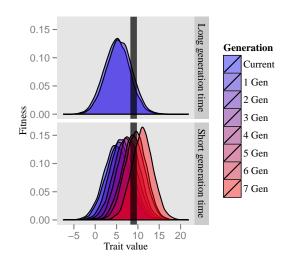


Figure 1: A species with a long generation time can only complete 1 generation in a fixed time, but a short generation time can complete 7 in the same time period, rapidly advancing towards the new fitness optimum (black line)

generation times are can make use of standing additive genetic variation (Figure 1). For instance fur seals are predicted to be unable to adapt to rapid climate change because of long generation times, but this is not the case for other antartic species with short generation times (Forcada et al., 2008). Species with shorter generation times also have higher rates of molecular evolution due to increased mutation rates (Thomas et al., 2010). This contributes

to the amount of additive genetic variance necessary for adaptive responses to a changing environment (Lande & Shannon, 1996). Our goal is to measure SDM error and investigate how rates of adaptation introduce error model prediction

Despite more than a decade of publications on SDM's, adaptation is still absent from most models (Kearney & Porter, 2009). Is there a way to analyze the vast number of existing SDM's to make inferences about the sources of error? By calculating a standard metric of error it is possible to construct models of that unexplained deviance. The challenge is that much of the data for these models is locked in the form of published figures. Methods already exist for data extraction such as the *digitize* package (Poisot, 2011) for R (Figure 2). Using a combination of JavaScript and Python, we can implement a web based interface for digitization of figure data available to anyone.

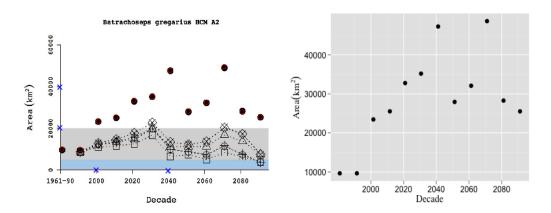


Figure 2: Left panel: Range shift predictions fram Early & Sax (2011) of Batrachoseps gregarius with calibration points marked Right panel: Extracted data points using the digitize package for R (Poisot, 2011)

Proposed Activities

Our goal is to understand how rates of adaptation can cause error in SDM predictions and construct web-based tools for data collection that can be stored in open access databases for other researchers to use. Furthermore once we collect data on error rates in SDM prediction we can test other hypotheses.

- Question: Can residual error in SDM predictive models be explained by rates of adaptation?
 - Hypothesis: SDM's for species with shorter generation times should have greater error rates because they can rapidly adapt to new invaders and novel climate scenarios at the trailing edge of their distribution. Therefore they are less likely to track their current shifting climate
- Software product: A web-based interface for data extraction of digitized figures.
 - An open source tool that will allow anyone to extract data from digital figures including: scatter plots, bar charts and georeferenceable maps. The interface will store the data at DataONE which can then be used for any future meta-analysis.

Error analysis

Error can be calculated in three ways: difference in area of occupancy, difference in expanding front, and difference in trailing edge. The first two are the most common and we will have the largest sample from these. All these can be theoretically be compared by converting them to Z-scores and calculating a standard error statistic such as root-mean squared error. Once we have quantified error, we can construct mixed effects models with error as the response variable. The predictor of interest will be generation time. Other variables will also be included, for instance it's known that different SDM contstruction methods have differences in performance (Elith et al., 2006, 2010). Using this framework we can add other covariates into our models to control for modeling artifacts.

References

- Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J. (2011). Do species' traits predict recent shifts at expanding range edges? *Ecology letters*, 14, 677–89.
- Austin, M. (2002). Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, 157, 101–118.
- Berteaux, D., Réale, D., McAdam, A.G. & Boutin, S. (2004). Keeping pace with fast climate change: can arctic life count on evolution? *Integrative and comparative biology*, 44, 140–151.
- Bridle, J.R. & Vines, T.H. (2007). Limits to evolution at range margins: when and why does adaptation fail? *Trends in ecology & evolution*, 22, 140–7.
- Buckley, J., Butlin, R.K. & Bridle, J.R. (2011). Evidence for evolutionary change associated with the recent range expansion of the British butterfly, Aricia agestis, in response to climate change. *Molecular Ecology*, 21, no–no.
- Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J. & Sears, M.W. (2010). Can mechanism inform species' distribution models? *Ecology letters*, 13, 1041–54.
- Crozier, L. & Dwyer, G. (2006). Combining Population-Dynamic and Ecophysiological Models to Predict Climate-Induced Insect Range Shifts. *The American naturalist*, 168.
- Davis, A.J., Jenkinson, L.S. & Lawton, J.H. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, 391, 783–786.
- Davis, M.B. & Shaw, R.G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science (New York, N.Y.)*, 292, 673–9.
- Dormann, C.F. (2007). Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, 8, 387–397.
- Early, R. & Sax, D.F. (2011). Analysis of climate paths reveals potential limitations on species range shifts. *Ecology Letters*, pp. no–no.
- Elith, J., Anderson, R.P., Ferrier, S., Guisan, A., Graham, C.H., Dudik, M., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T.,

- Phillips, S.J., Richardson, K., Scachetti-pereira, R., Schapire, R.E., Williams, S., Wisz, M.S. & Zimmermann, N.E. (2006). Novel methods improve prediction of species distributions from occurrence data. *Ecography*, 2, 129–151.
- Elith, J., Kearney, M. & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1, 330–342.
- Elith, J. & Leathwick, J.R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697.
- Forcada, J., Trathan, P.N. & Murphy, E.J. (2008). Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*, pp. 2473–2488.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993–1009.
- Guisan, A. & Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135, 147–186.
- Hansen, M.M., Olivieri, I., Waller, D.M. & Nielsen, E.E. (2012). Monitoring adaptive genetic responses to environmental change. *Molecular Ecology*, 21, 1311–1329.
- Helmuth, B., Kingsolver, J.G. & Carrington, E. (2005). Biophysics, physiological ecology, and climate change: does mechanism matter? *Annual review of physiology*, 67, 177–201.
- Hoffmann, A. & Sgrò, C. (2011). Climate change and evolutionary adaptation. Nature.
- Iverson, L. & Prasad, A. (1998). Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs*.
- Kearney, M. & Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology letters*, 12, 334–50.
- Lande, R. & Shannon, S. (1996). The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution*.
- Lavergne, S., Moquet, N., Ronce, O. & Thuiller, W. (2010). Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics*, 41.
- Midgley, G.F., Hughes, G.O., Thuiller, W. & Rebelo, a.G. (2006). Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Diversity and Distributions*, 12, 555–562.
- Parmesan, C. (1996). Climate and species' range. Nature, 382, 765–766.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T. & Others (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579–583.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.

- Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography, 12, 361–371 ST Predicting the impacts of climate ch.
- Peterson, A.T. (2001). Predicting species' geographic distributions based on ecological niche modeling. *The Condor*, 103, 599–605.
- Poisot, T. (2011). The digitize Package: Extracting Numerical Data from Scatterplots. *The R Journal*, 3, 25–26.
- Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009). Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, 15, 732–743.
- Reed, T., Schindler, D. & Waples, R. (2011). Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conservation Biology*.
- Shaw, R.G. & Etterson, J.R. (2012). Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. *The New phytologist*.
- Somero, G.N. (2010). The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. The Journal of experimental biology, 213, 912–20.
- Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, a.D., Davies, Z.G., Musche, M. & Conradt, L. (2001). Ecological and evolutionary processes at expanding range margins. *Nature*, 411, 577–81.
- Thomas, J.a., Welch, J.J., Lanfear, R. & Bromham, L. (2010). A generation time effect on the rate of molecular evolution in invertebrates. *Molecular biology and evolution*, 27, 1173–80.
- Visser, M.E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings. Biological sciences / The Royal Society*, 275, 649–59.
- Walters, R.J., Blanckenhorn, W.U. & Berger, D. (2012). Forecasting extinction risk of ectotherms under climate warming: an evolutionary perspective. *Functional Ecology*.