

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

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Principle Investigators:

Edmund M. Hart

Beaty Biodiversity

Department of zoology

University of British Columbia

Vancouver, B.C. V6T 1Z4

ehart@zoology.ubc.ca

Scott A. Chamberlain

Biology Department

Simon Fraser University

Burnaby, B.C. V5A 1S6

scott.sfu@gmail.com

Project Summary: Species range shifts are 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. These models are statistical correlations between a species realized niche and abiotic variables, because they ignore ecological theory there is often a difference between predictions and a species' actual distribution (error). One potential source of error is that these models ignore differing rates of adaptation to novel climates. Our group will seek to understand the source of this error using meta-analysis, and integrate adaptation into range shift theory. However, much of the data from these models is locked in the form of published figures and maps. Therefore a second outcome of our working group will be a web-based data extraction tool. This will allow anyone to upload a figure and extract data from it and store it in DataONE. Beyond producing manuscripts, we will contribute tools for meta-analysis beyond the life of our working group.

Start date December 2012

End date December 2013

Data release December 2013

Resubmission? 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). Understanding range shifts is a pressing issue because as warming increases, species are exhibiting rapid distributional changes (Chen *et al.*, 2011). Since the late 1990's ecologists have been using species' distribution models (SDMs) to try and predict how those ranges will shift over the next century (Davis *et al.*, 1998; Iversen & 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). Early models ignored physiology, biotic interactions and rapid local adaptation, relying solely on correlations between current distribution and climate variables (Davis *et al.*, 1998; Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Helmuth *et al.*, 2005). Aside from variance due to lack of ecological theory (Elith & Leathwick, 2009), SDMs can show great variance in their predictive abilities (Elith *et al.*, 2006; Kearney & Porter, 2009; Elith *et al.*, 2010). More recent SDMs have begun to incorporate mechanisms such as physiology (Crozier & Dwyer, 2006; Buckley *et al.*, 2010, 2012) 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.*, 2012) but still only explain small percentage of variance. Other factors may be important in explaining the error in species actual ranges and their predicted distribution such as biotic interaction and adaptation.

Adaptation is important to understanding how species will respond to climate change (Visser, 2008; Lavergne *et al.*, 2010; Hoffmann & Sgrò, 2011), but is difficult to accurately measure in the field (Hansen *et al.*, 2012). Here we define adaptation as evolution of traits that increase fitness in novel environments (Reznick & Ghalambor, 2001), as opposed to phenotypically plastic adaptations that will not allow species to persist in the long term (Hoffmann & Sgrò, 2011). 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 SDMs (Hoffmann & Sgrò, 2011) (but see Kearney *et al.* (2009)). Shorter generation times allow for a more rapid adaptive response to strong selective pressures (Berteaux *et al.*, 2004; Somero, 2010; Hoffmann & Sgrò, 2011; Reed *et al.*, 2011; Shaw & Etterson, 2012; Walters *et al.*, 2012). The first reason is that species with shorter generation times can make use of standing additive genetic variation (Figure 1). Models of population persistence have demonstrated that shorter generation times can allow populations to persist by novel adaptation (Gomulkiewicz &

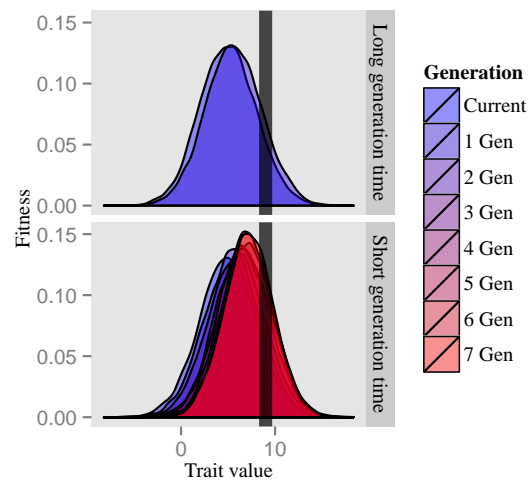


Figure 1: A species with a long generation time can only complete 1 generation in a fixed time, but a short generation time can complete 7 in the same time period, rapidly advancing towards the new fitness optimum (black line)

Holt, 1995; Hoffmann & Sgrò, 2011). 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 Antarctic species with short generation times (Forcada *et al.*, 2008). One consequence of strong directional selection is the loss of additive genetic variance necessary for adaptation (Lande & Shannon, 1996; Hoffmann & Sgrò, 2011). However, species with shorter generation times also have higher rates of molecular evolution due to increased mutation rates (Thomas *et al.*, 2010) adding to the total additive genetic variance. The expectation is species with short generation times will track their climate on the expanding front of the range, but not necessarily go extinct at the trailing edge, instead adapting to novel climate conditions. Therefore one of the fundamental assumptions of SDMs, that species will track their current climate conditions as they shift latitudinally, can be violated by species with short generation times.

Our goal is to (1) quantify SDM error across a range of taxa, (2) investigate how rates of adaptation introduce error model prediction, and (3) build tools to automatically extract data from figures in the published literature.

Proposed Activities

Despite more than a decade of publications on SDMs, adaptation is still absent from almost all models (Kearney & Porter, 2009). We want to analyze the large number of existing SDMs and attempt to integrate adaptation into range shift theory. By calculating a standard metric of error it is possible to construct models of that unexplained deviance from actual distributions. 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. Using a combination of JavaScript and Python, we want to develop a web based tool for the extraction of data from a variety of figure types in existing publications. Furthermore once we collect data on error rates in SDM prediction we can test other hypotheses such as the influence of biotic interactions or the breakdown of mutualistic networks.

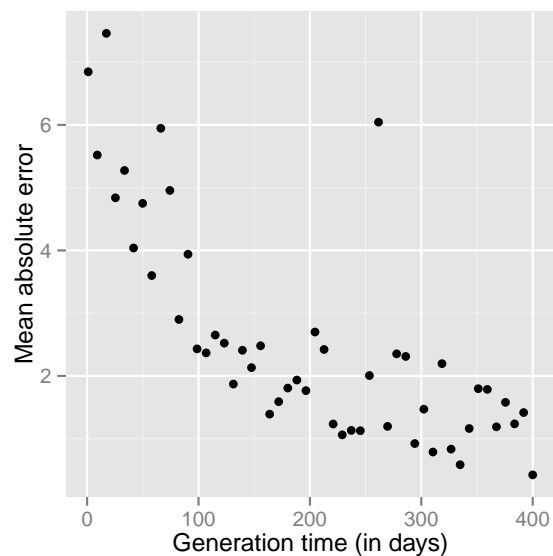


Figure 2: A potential hypothesis of how we expect model error to vary with generation time.

1. *Question 1: How much error is there in current SDM's between predictions and actual distributions?*
 - We will quantify the amount of error in published SDMs by comparing model predictions to original data sources. We will store this in a publicly accessible database on DataONE. This will serve as data for a review of the accuracy of SDM's over the last 10 years.

2. *Question 2: Does rate of adaptation (generation time) vary amounts of error in SDMs?*

- We hypothesize that SDMs 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 (Figure 2). Therefore they are less likely to track their current shifting climate. We will test this hypothesis by constructing mixed-effects models of SDM error.

3. *Develop a program for data extraction from digitized figures with a web-interface.*

- We will develop an open source tool that allows anyone to extract data from digital figures including: scatter plots, bar charts and georeferencable 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. Because the trailing edge is of the most interest, it can be inferred from total area of occupancy. Species with less shift in the trailing edge will have a larger total area of occupancy. All these can 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. Using this framework we can add other covariates into our models to control for modeling artifacts, for instance it's known that different SDM construction methods have differences in performance (Elith *et al.*, 2006, 2010). Furthermore we will have assembled a database of residual model error. Our primary goal will be to analyze error in terms of generation time, but this does not exclude considering biotic interactions. Our group has three experts in networks: mutualistic networks (Chamberlain) and food webs (Poisot, Hart). Therefore we will also consider mutualistic pairs of species and examine if range shifts are limited by lack of co-expanding mutualists (Hellmann *et al.*, 2008; Pardini *et al.*, 2010) or enhanced by freedom from competitive interactions (Hellmann *et al.*, 2012). We have already begun assembling a database of papers from which we can extract data with taxa ranging from lichens to mammals (Table 3)

Data extraction from figures

Data from SDMs is often presented in the form of distribution maps or scatter plots (Figure 3). Current extraction tools (ImageJ, GraphClick) keep data locked on personal computers. Our goal is to create a resource for all scientists post-working group and facilitate future meta-analysis with open access data. Our data extraction tool lives in the web and be more powerful and beneficial to science and will be cross-platform (Windows, Linux, OSX, etc.), which is extremely important for wide adoption. In addition, it will allow for automatic data retrieval to a database on the backend, presentation of figures called via APIs from various publishers or user uploaded figures, automatic updating of the user interface (UI), authentication of users in order to track user statistics, and other features as needed.

We will build this data extraction tool using a combination of the JavaScript and Python programming languages. Users will be able to automate data extraction (for an example, see Figure 3). A JavaScript web interface will collect reference points on figure axes. Python is a powerful tool for image analysis with widespread use in other biological disciplines (Hanke *et al.*, 2009), and with its powerful machine learning packages (Pedregosa *et al.*, 2011) it

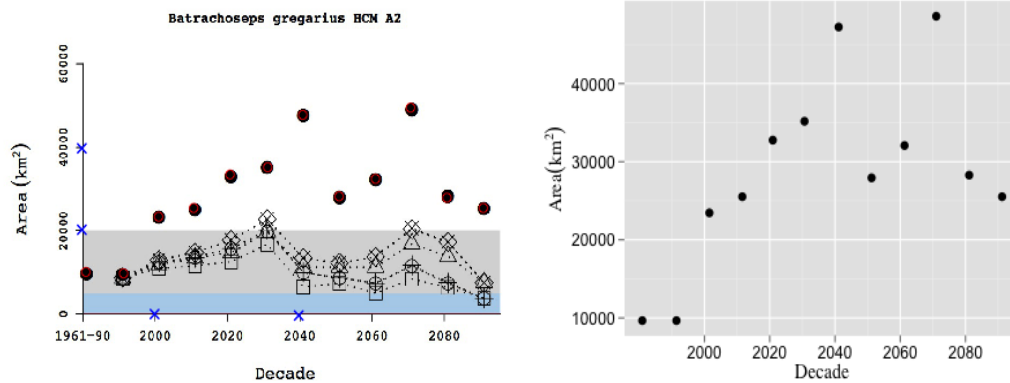


Figure 3: Left panel: Range shift predictions from Early & Sax (2011) of *Batrachoseps gregarius* with calibration points marked Right panel: Extracted data points using the digitize package for R (Poisot, 2011)

can learn to detect points in scatter automatically. Map data can be extracted in a similar fashion with users georeferencing points on maps such as cities and borders. Python's image tools can analyze pixel color and calculate the geographic size of each pixel. All the extracted data will all go to a central database stored on servers in the cloud and KNB/DataONE.

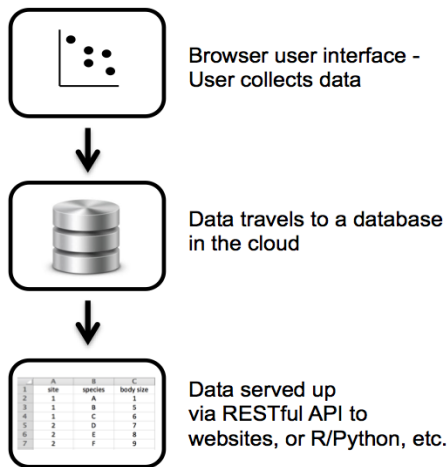


Figure 4: Figure extraction work flow moving from extraction to storage to sharing.

Data in the database will be exposed via a RESTful API, which will allow anyone to search and retrieve data. Eventually we will make the tool public to anyone. A long term goal is to allow for crowdsourcing of data extraction from figures at large scales, similar to Galaxy Zoo, Citizen Sky, and FoldIt. The massive scale at which this tool will operate can transform quantitative meta-analysis studies. Currently, researchers extract data once from a figure, and someone else may proof their data. However, with our tool, we can potentially get 10 different users to click on each and every point in a single figure, providing for greater accuracy and a measure of precision. To make this happen we need a tool that lives in the web and can take advantage of the massive scale at which science can be done.

Participants

Table 1: *Participant list. I have organized a group of ecologists, evolutionary biologists and programmers representing a diversity career stages, institutions and NCEAS experience (* represents new NCEAS visitors.). In particular all of the programmers are biologists that have experience building computational tools for ecological questions. All listed participants are confirmed.*

Participant	Affiliation	Expertise / Notes
Jessica Hellmann	University of Notre Dame	Climate change, range shifts, adaptation
Lauren Buckley	University of North Carolina Chapel Hill	Climate change, range shifts, SDM development.
Amy Angert	University of British Columbia	Climate change, range shifts, SDM development
Jessica Blois*	University California Merced	Climate change, range shifts SDM development
Scott Chamberlain*	Simon Fraser University	Evolution, software development, <i>NCEAS technical liaison</i>
Karthik Ram	Univeristy of California Berkeley	Climaet change, GIS, software development
Tim Poisot	Universit du Qubec Rimouski	Network theory, evolution, software development
Rich FitzJohn*	The University of New South Wales	Evolution, software development
Jens Stevens*	The University of California Davis	Climate change, range shifts, <i>Graduate student</i>
Mark Hahnel*	Digital Science UK, Figshare	Software development, data management
Edmund Hart*	University of British Columbia	Climate change, software development, <i>In charge of data policy requirements</i>

Proposed timeline

Table 2: *Proposed timeline. We plan to have three meetings over the course of our working group, each time simultaneously developing our software product and writing manuscripts.*

Meeting	Objectives
Prior to meeting	<ul style="list-style-type: none"> • Develop web backend for data extraction from figures, have beta version working. • Create complete list of all relevant SDM papers to extract data from (approx. 400 found down to approx. 150, see Table 3). • Download data for all species in SDM papers and assemble base range sizes and boundaries.
I. December 2012	<ul style="list-style-type: none"> • Beta test figure extraction software, develop web front end and work with NCEAS to set-up databases to store extract data. Begin working on web front-end • Begin extracting data from figures and assembling figure database • Develop models of SDM error. • Create outline for potential manuscripts.
II. Summer 2013	<ul style="list-style-type: none"> • Complete web front end, and beta user interface for figure extraction. Work with NCEAS to finalize data storage • Finalize initial manuscripts for submission. • Develop ideas for other uses of the error data extracted from SDMs.
III. Winter 2013	<ul style="list-style-type: none"> • Publicly release website after any final tweaks. • Revise submitted manuscripts. • Outline and/or make revisions on further manuscripts using our existing data.

Anticipated Results and Benefits

Accurate prediction of species range shifts is of theoretical and conservation importance (Thomas *et al.*, 2006), and can have important economic implications (such as pest management (Thomson *et al.*, 2010)). Integrating adaptation into range shift theory also has direct conservation value because it can be used in efforts to save biodiversity (Heller & Zavaleta, 2009; Sgrò *et al.*, 2011). By examining what factors impact SDM prediction error, we can identify what factors are of greatest importance in future SDM models, and perhaps which factors are less relevant for immediate implementation. We will produce manuscripts and tools that will be of broad interest to other researchers and conservation managers. We expect a minimum of 3 publications and 1 software tool and potentially other papers.

1. A review paper of the existing SDMs and their error rates. (*Question 1*, Target journals: Review in Global change biology, Concepts and Synthesis in Ecology)
2. Meta-analysis of SDM error and generation time exploring how rates of adaptation influence the predictability of range shifts. (*Question 2* Target high impact journals: Science, Nature, Ecology Letters, PNAS)
3. A methods paper detailing the algorithms and procedures used to automatically extract data from figures (*Goal 3* Target journals: Methods in Ecology and Evolution, PLoS ONE, Ecological Informatics)
4. A software tool that will be a website where people can extract figure data from any paper they want. We will work closely with the NCEAS KNB staff on how best to manage and store data at KNB and DataONE. This tool will have lasting usefulness for meta-analysis well past the lifespan of our working group.

Rational to conduct work at NCEAS

NCEAS is an ideal place to conduct our work because it is the perfect place to combine deep ecological knowledge and computational expertise in data management. The KNB and the expertise of NCEAS computational staff will be important to successfully managing the data we hope to collect, as well as their collaborating with software engineers (such as Ben Leinfelder) in developing our figure extraction tool. Several of our participants (Buckley and Angert) were members of an earlier working group (NCEAS Project 12054: Mechanistic distribution models: Energetics, fitness, and population dynamics) which improved species distribution models by including traits and physiology. This project builds off that initial working group by trying integrating adaptation into SDM theory.

How you heard about NCEAS Call for proposals: Twitter

Table 3. Sample of published SDMs that we can extract data from and their original data sources

Organism	Figure Type	Reference	Original Data Source
Cracidae (bird)	Scatter plot, map	Peterson (2001)	Other publication
Protaceae (Angiosperm)	Map	Bomhard <i>et al.</i> (2005)	Protea Atlas Project
<i>Salix herbacea</i> (dwarf willow)	Map	Alsos <i>et al.</i> (2009)	Global Biodiversity Information Facility (GBIF)
<i>Ochotona princeps</i> (American pika)	Map	Calkins <i>et al.</i> (2012)	Global Biodiversity Information Facility (GBIF)
<i>Leiopelma hochstetteri</i> (Frog)	Map	Fouquet <i>et al.</i> (2010)	New Zealand Atlas of the Amphibians and Reptiles (public)
<i>Trachemys scripta</i>	Map	Rödder <i>et al.</i> (2009)	Global Biodiversity Information Facility (GBIF)
Lizards	Frequency plot	Buckley <i>et al.</i> (2010)	Global Biodiversity Information Facility (GBIF)
conifers	Map	Maiorano <i>et al.</i> (2012)	European Pollen Database and literature
Mammals	Scatter plot, map	Lawler <i>et al.</i> (2006)	Digital Distribution Maps of the Mammals of the Western Hemisphere
<i>Atalopedes campestris</i> (insect)	Scatter plot, map	Peterson (2001)	Other publication
<i>Pararge aegeria</i> (butterfly)	Map	Willis <i>et al.</i> (2009)	Biological Records Centre and Butterfly Conservation
<i>Ortalis poliocephala</i> (Bird)	Map	Peterson <i>et al.</i> (2002)	CONABIO
<i>Dracaena cinnabari</i> (tree)	Map	Attorre <i>et al.</i> (2007)	Private, contact authors
<i>Uroplatus</i> (Lizard)	Map	Pearson <i>et al.</i> (2007)	Private, contact authors
European mammals	Map	Levinsky <i>et al.</i> (2007)	Published data set
<i>Contarinia nasturtii</i> (insect)	Scatter plot, bar chart	Mika <i>et al.</i> (2008)	Published data set
North American trees	Bar chart, Map	McKenney <i>et al.</i> (2007)	Canadian Tree Hardiness DB
British lichens	Map	Ellis <i>et al.</i> (2007)	British Lichen Society

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