A novel approach to detecting changes in dynamic rules governing population fluctuations

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**Abstract**

**Introduction**

It is well-established that the dynamics of populations are governed both by internal, biotic rules, and abiotic (or external biotic) influences, leading to roughly equal weighting of stochastic and deterministic forces governing population fluctuation patterns (Bjørnstad and Grenfell 2001). External perturbations of dynamic population processes can lead to population or trophic regime shifts, where the internal rules that govern a population’s fluctuations transition to another state (Carpenter et al. 2008). However, understanding precisely how and when environmental factors interact with density dependent internal population regulation remains a fundamental question in ecology (Sutherland et al. 2013). The practical challenge of pinpointing when sustained state changes occur in naturally fluctuating populations has, to date, remained unresolved. Yet, an analytical approach which allows the identification of timing and magnitude of such changes would advance our understanding and have the potential to direct the management of species of economic or conservation concern.

Simple density dependent tools for modelling population time series were developed and championed during the 1950s and 60s. Examples of these models include the Ricker and Beverton-Holt stock and recruitment models, which were initially developed for fisheries management (Ricker 1954, Beverton and Holt 1957). Although this deterministic approach to population modelling has largely fallen out of favor for more complex strategies involving nonlinear stochastic elements (May 1976, Bjørnstad and Grenfell 2001), these models remain useful, in large part due to their simplicity and ecologically meaningful interpretations. When parameter estimates produced by fitting these models differ between populations, or change in a single population, it suggests differing environmental constraints are occurring on the population, providing a quantitative measure of environmental change (Bahlai, vander Werf, et al. 2015). The accuracy of these simple density dependent models is regarded highest for populations fluctuating around their carrying capacity (Sabo et al. 2004), with strong over-compensatory density dependence, and a short development period to minimize the effect of stage-structured lags (Bjørnstad and Grenfell 2001) .

Other ways of identifying when an ecological system is changing state

Changes to the internal rules represent state changes- ie regime shifts in the population. Need decision rules to identify when sustained changes have occurred.

Implications for species management

In this paper, we develop a generalizable tool for adapting a simple density dependent model to detecting shifts in dynamic regime in population time series data. The regime shift model is based on a script initially developed in (Bahlai, vander Werf, et al. 2015) to understand changes governing the internal dynamics of population regulation in the invasion process of *Harmonia axyridis* in the two decades following their arrival in southwestern Michigan. This model was able to detect the precise timing external factors affecting the internal drivers of population cycling (namely, the invasion and then subsequent pesticidal control of a preferred prey item), suggesting that the model itself may have broader applicability in understanding drivers of population dynamics for other species important in conservation and ecosystem management.

This paper describes how this tool was developed as a suite of functions for examining population time series data for the presence, location, and magnitude of shifts in dynamic regime, and examines the performance of this tool with simulated data and real-world case studies of two populations of conservation and economic concern.

**Methods**

A model script, simulations, and two case studies using population data from insect population monitoring were scripted and run in R Version 3.3.3 “Another Canoe” (R Development Core Team 2017) run within the RStudio Integrated development environment 1.0.136 (RStudio Team 2015). All data manipulations, analyses and figure scripts, including the complete development history, are publicly available in a Github repository at <https://github.com/cbahlai/monarch_regime>.

*The model*

For our purposes, we use the Ricker model to describe the dynamics within a system (Turchin 2003).

The Ricker model is a single-variable discrete time model in which N(t+1), the population at time t+1, is a function of N(t), where N(t) is the measure of population size in year t, and the parameters K and r (the carrying capacity and per capita yearly rate of increase respectively) are estimated for the population during the time period modeled. The Ricker model was selected for our purposes because 1) it does not rely on any external information, other than population data over time, to be fit; 2) only two parameters need to be estimated, and those parameters have ecologically meaningful interpretations, and 3) in our experience, the model simply fits insect population data well.

We used an iterative, model-selection based process to determine if, and when, shifts in dynamic regime had occurred within a given time series. To achieve this, first, the Ricker model was fit to the entire population time series, then the population time series was subdivided into all possible combinations of 2, 3, …, n subsets of sequential data points (hereafter, ‘break point combination’, for example, a twelve year series with a break point combination of 4, 8 would be broken into subset 1 = 1, , 2, 3, 4; subset 2 = 5, 6, 7, 8; subset 3 = 9, 10, 11, 12) and the Ricker model was fitted to each of the subsets produced for each break point combination. Break point combinations were constrained to only include subsets with more than three sequential data points to avoid over-fitting.

After fitting each subset for a given break point combination, the Akaike Information Criteria for each subset were summed together, providing an overall AIC for the fit. To further account for the effect of small series sizes, we calculated AICc (AIC correction for small samples) by using the total number of parameters estimated for the fit (where nparameters = 3 (nbreaks + 1), because for each fit, r, K and error were estimated), and this factor was added to the total AIC for each break point combination. Then, AICc values were used to rank fits for each break point combination, and fits for break point combinations with lower AICc values were considered to have better performance. When AICc values differed by two units or less, model performance was considered equivalent (Burnham and Anderson 2002), so when models were found with equivalent performance, the simplest model (ie: the one with fewest parameters and break points) was selected for further analysis. If the top-ranked models had the same number of parameters, the one with the numerically lowest AICc was considered best-ranked for the purpose of further analysis.

*Technical implementation*

The ‘regime shift detector’ was implemented as a series of R functions to enable a user starting with a standard data frame of population observations at a standard time intervals to quickly generate a report on the fit of the model described above to their own data. Herein we summarize the role of each function, but we encourage the reader to download the script file directly from <https://github.com/cbahlai/monarch_regime/blob/master/regime_shift_detector.R> for the details of implementation, included as line-by-line comments in the script.

addNt1- takes a raw data frame with columns for year, population abundance measure, and converts it to a three column data frame with year, population in year, population in the next year, and gives the data consistent column names for use in downstream functions. Most of the functions described below require this function to be used to transform data prior to use, unless otherwise specified.

AICcorrection- takes a data series and the number of breaks used in a given fit to calculate the AICc correction factor to be added to the total AIC for the fit

rickerfit- fits the Ricker model using the Levenberg-Marquart nonlinear least squares method for nonlinear model fitting to a given data frame. This function calls the nlsLM function from minpack.lm (Elzhov et al. 2016). To aide in model convergence, the function also computes a realistic starting value for K by calculating the mean of the population (based on the assumption that a population being fit to the Ricker model is likely fluctuating around its carrying capacity). The starting value for r was set at 1.5. The function outputs a vector containing the AIC, the estimate for r, its standard error, and the estimate for K and its standard error.

splitnfit- takes a given data fame, fits the complete data series with the rickerfit function, then subsets it in two by creating a break point three years after the start of the series, calls the rickerfit function to fit the data from each subset produced there. Then the function walks through the data, increasing the break point by one time step each iteration, and compiles the AICs and break points used for each fit, resulting in a data frame of break point combinations and respective AICs.

findbreakable- examines the output from the splitnfit function to determine if any of the break point combinations produced might be further subdivided (ie: has enough points to not violate the rule we set to only fit series with four or greater points).

subsequentsplit- used output from findbreakable function to identify cases where data can further be subsetted using the splitnfit function, feeds those cases in, and compiles results together with that produced by simpler break point combinations produced by splitnfit.

nbreaker- uses splitnfit, findbreakable, and subsequentsplit, combined with input data, to create a data frame consisting of a column of all possible break point combinations, and the respective AICs of the resultant fits. This function uses an iterative approach to allow simpler functions that break a data into two parts to be used to find an unlimited number of break points (within constraints of series length).

AICtally- takes data in, subjects it to nbreaker, pulls out the AICs produced by nbreaker, adds them together and counts the number of fits performed, number of breaks in the data, computes the corrected AICc using AICcorrection, and returns these values as a data frame.

allfits- appends the results of nbreaker and AICtally together into a single data frame, resulting in summary statistics for all possible break point combination fits for the input data series.

equivalentfit- takes in data, feeds it to allfits, and uses the output from allfits to pull out the subset of all equivalently-performing breakpoint combination fits (here, within 2 units of AICc), and outputs these fits as a data frame.

bestfit- feeds data to the equivalentfit function to get a data frame describing equivalent fits, and uses our decision rules (in this case, select the break point combination requiring the fewest parameter estimates from the list of equivalent models, and if there are multiple equivalent models still, select the one with the numerically lowest AICc) to output the specifics of that break point combination as a data frame.

bestmodel- feeds data to the bestfit function to identify the best break point combination, and then use that information to create a data frame describing the parameter estimates (r, K and standard error for each) for fitting the Ricker model to each of the subsets of timeseries, allowing a user to quantify the dynamic rule changes found by fitting the model changes at each break point.

modelspecification- in case a user wishes to investigate specification of similarly ranked models, this function takes data in the format produced by the bestfit function and produced a data frame describing the model specification of the given break point combination.

RSdetector- uses the raw time series data to produce a report, calling all the previous functions, either directly, or through other functions, with short explanatory text preceding each result. First, a simple plot of population over time is produced (N(t) by t), then data is fed to the addNt1 function, and the resultant N(t), N(t+1) data is plotted to visualize the potential for the data to conform to a Ricker curve. Then, the data is fed through the allfits function, producing a complete list of all break point combinations tested and their respective fit statistics. The data is subsequently fed through the equivalentfit and bestfit functions so that a user can assess how the decision rules specified impacted the selection of the best model. Finally, the data is fed through the bestmodel function to produce the set of regression parameters for each time series subset produced by the best break point combination found.

*Simulations*

A function was created to simulate time series data following Ricker dynamics under set break point combination conditions. The function takes values for of start year, number of years to simulate, % noise, a starting population N, starting values for K and r, a break point combination, a % change in K and a % change in r to be simulated for each break point. Percent noise was included as a means to simulate sampling error that would be observed in a real sampling plan, and was simulated by creating a continuous interval from 100% minus noise to 100% plus noise, randomly sampling from within that interval, and multiplying the predicted observation N(t+1) by the resultant value. Change of K and r at each break point were randomly selected by the script to either increase or decrease by the given % change.

The simulated data were fed into a function that tested if the regime shift detector model was able to identify the breaks as set for the simulation by comparing the input conditions to those output by the bestmodel function in the regime shift detector script file. Results of comparing the input to the output were encoded as follows:

1. script was successful at detecting all break points and simulation conditions
2. script identified all simulated breaks, but also found one or more ‘extra’ breaks
3. script missed one of the simulated breaks, but all others found were correct
4. script identified the correct number of breaks, but one or more breaks were mismatched
5. no correct breaks were identified by the script, or breaks were identified in a no-break scenario

A base scenario was constructed, with start year =1, number of years = 25, a starting population of 3000, a sampling error of up to 5%, a starting value for K = 2000, a starting value for r =2, a % change at each break point of 40 and 20% for K and r respectively, and a set of 0, 1, 2, or 3 break points randomly selected from within the possible values defined by start year and number of years.  
  
This script was used to test the frequency of a given result under a variety of different scenarios by changing the value of one parameter at a time from the base scenario. Specifically, the impact of different sizes of regime shift was tested by creating scenarios where the % change in r and K were individually modified at 10% intervals from 0 to 90%, the impact of length of time series was examined by extending the length of the time series by 2 year intervals from 25 to 33, and the impact of sampling error was tested at 1, 5, 10%, and every 10% interval thereafter to 90%. Each of these scenarios was run on simulated data with 0, 1, 2 and 3 break point combinations, and each scenario by break point combination was iterated 500 times with newly simulated data. Results from the simulations were compiled at intervals of 50 iterations and stored as csv files within the project repository for further analysis. The complete script which simulates the data, applies the regime shift detector, and compiles the results is available at: <https://github.com/cbahlai/monarch_regime/blob/master/simulations.R>

*Case studies*

We used two case studies to test the performance of the regime shift detector script on population time series data produced under natural conditions as parts of observational experiments. Both case studies involve approximately two decades of observations of economically or culturally important insect species, however, one case examines an invasion process, and another examines a population decline, both occurring over the same time period in recent history.

*Harmonia axyridis* in southwestern Michigan

The 1994 invasion of *Harmonia axyridis* to Michigan State University’s Kellogg Biological Station in southwestern Michigan, United States was captured as part of an observational experiment to monitor agriculturally-important Coccinellidae (ladybeetles) in landscapes dominated by field crops. The coccinellid monitoring experiment was initiated in 1989 as part of the Long Term Ecological Research project, a National Science Foundation funded network of sites devoted to the maintenance of similar experiments. Population density of ladybeetles is monitored in 10 plant communities weekly over the growing season using yellow sticky card glue traps: detailed sampling methodology is available in previous work (Bahlai et al. 2013, Bahlai, Colunga-Garcia, et al. 2015, Bahlai, vander Werf, et al. 2015). The invasion process observed for *H. axyridis* initially inspired the need for a regime shift detector (Bahlai, vander Werf, et al. 2015); herein, we revisit these data with a refined tool and two years of additional observations of this population (1994-2015).

Raw sampling data documenting the captures of adult *H. axyridis* at each sampling point, during each sampling week were extracted from the database, and these raw data are available here: <https://github.com/cbahlai/monarch_regime/blob/master/casestudydata/kbs_harmonia94-15.csv>. Dates were converted to day-of-year format, and then data were culled at day-of-year 240 to minimize the effect of variation in sampling period between sampling years (Bahlai, vander Werf, et al. 2015). From these data, the average number of *H. axyridis* adults captured per trap, across all traps deployed within a sampling year were computed, providing a data frame in the format required by the RSdetector function. The RSdetector function was then used on this 1994-2015 data frame, and then the analysis was repeated using data culled at 1994-2013, to allow for direct comparison with the outputs from the original conception of the regime shift detector model.

Monarch butterflies in Mexican overwintering grounds

North American Monarch butterflies (*Danaus plexippus*) are migratory, with the majority of their population overwintering in the Mexican highlands in large aggregations on Oyamel fir trees within the transvolcanic mountains in the central region of the country (Urquhart and Urquhart 1978, Wassenaar and Hobson 1998). Monarchs are highly dispersed over their breeding season, occupying landscapes throughout south and central North America (Flockhart et al. 2017), so overwintering population measures provide a convenient integration of total population size in a large portion of the species’ North American range. Since the 1995 overwintering season, various groups have monitored the total area occupied by overwintering monarch colonies each season as a proxy for raw population counts, to minimize disturbance to the butterfly aggregations themselves. We used data documenting observations of area occupied from the winter of 1995 to the winter of 2017, compiled from these surveys by MonarchWatch.org (note that the northern hemisphere overwintering season overlaps two calendar years, in this study we have used the year in which the winter started, i.e. 1995 from the winter of 1995-1996, to define the year of observation). As these data are proprietary, they are not reproduced here, but are available directly from MonarchWatch (Lovett 2017).

Monarch overwintering population data were subjected to the RSdetector function. Because the time series data also suggested the possibility of a simple linear decline in K (i.e. a linear decline in the mean population) data were also modelled this way, and the information criteria produced from this simpler model was used to compare to the performance of the RS detector.

**Results**

*Simulations*

Simulations were conducted by modifying one critical parameter at a time from a base scenario to determine how modifying each parameter affected the findings of the RSdetector model. When varied sampling error was simulated as ‘noise’ (Fig. noise\_sim), the script’s ability to detect starting conditions generally dropped as percent noise increased, with the exception of no-break scenarios, which were generally correctly identified at a rate of approximately 60%, regardless of simulated sampling error (Fig. noise\_sim A). Outcomes involving the script finding extra breaks were most common in scenarios initiated with only one break (Fig. noise\_sim B), while outcomes where one break was missed by the script only occurred in scenarios initiated with three breaks, increasing with sampling error, and then plateauing at about 20% of outcomes above 30% sampling error (Fig. noise\_sim C). Outcomes identifying the correct number of breaks but misidentifying one break’s location peaked at around 20% sampling error in scenarios initiated with three break points, and at approximately 40% sampling error in scenarios initiated with two break points (Fig. noise\_sim D), and total failure to identify initial conditions generally increased with sampling error, with the exception of scenarios intiated with no break points (Fig. noise\_sim E).

Modifying the length of time series that a scenario was initiated with affected the ability of the script to identify the starting conditions (Fig. Nyears), with model performance decreasing slightly with length of time series (Fig. Nyears A). In general, increasing time series length increased the probability that the script would correctly identify the break points from the initial conditions, but also ‘find’ an additional break points (Fig. Nyears B) or find a break in a scenario that was not initiated with any breaks (Fig. Nyears E). Other erroneous results were rare (Figs. Nyears C, D).

The effect of modifying regime shift size on the script’s ability to detect conditions with which the scenarios were initiated was examined by modifying the % change in r and K at the given break point combination (Figs. changeK, changeR). The script was best able to identify initial conditions when the value for K was shifted by approximately 40% (Fig. changeK A) with extra breaks more frequently detected in scenarios initiated with larger changes of K at break points (Fig. changeK B). Complete failure to identify break points was most common in scenarios with small shifts in K (Fig. changeK E); missed breaks occurred rarely in 3 break scenarios regardless of the shift in K (Fig. changeK C) and misidentified breaks occurred occasionally in scenarios with 2 or 3 breaks and very large or very small shifts in K (Fig. changeK D.) The efficiency of the script responded differently to modifications of the size of shifts in r: instead of an intermediate optimum shift as observed for K, smaller shifts involving changes in r were most easily detected by the script (Fig. changeR A). The script was more likely to erroneously find additional breaks, miss breaks, or misidentify breaks as shifts in r increased (Fig. changeR B, C,D). Complete failure to identify correct break combinations increased slightly with increases in r for scenarios initiated with 1, 2, or 3 break points, but error rates remained constant regardless of shift in r in the zero-break scenarios (Fig. changeR E)

To aide in the interpretation of regime shift detector script outputs in a situation where the conditions under which the data were produced are unknown (i.e. any ‘real’ population data) we also examined the scenarios where sampling error was varied in the converse way- by the proportion of input scenarios resulting in a given observed outcome (Fig. obs\_outcomes). When the regime shift detector script indicated that it had found no breaks in the data, this result generally reflected input scenarios with more than 80% accuracy when sampling error was below 50% (Fig. obs\_outcomes A). When the script identified scenarios with one two breaks, sampling error affected the accuracy of outcomes more negatively, with accuracy dropping to approximately 60% at levels of sampling error approaching 25% (Figs. obs\_outcomes B, C). A similar pattern was observed for scenarios identified to have three breaks, however, accuracy was generally higher with this output, with >80% accuracy observed even at a sampling error rate of 25%.

*Case study- Harmonia axyridis*

The sampling error (in the form of standard error of the mean) for population samples of *H. axyridis* was estimated at about 6% from the raw data.

When the regime shift detector script was run using the *H. axyridis* population data from 1994-2013, as was used in the previous study, the script produced identical results to the previous implementation (Bahlai, vander Werf, et al. 2015) when break point combinations were ranked by AICc and AIC. Only one break point combination was identified by the regime shift detector: no break point combinations with equivalent fit were identified. Two break points- one occurring after 2000, and one occurring after 2005 were observed in this ‘best’ break point combination model (Fig. harmonia\_fit A). In this truncated data, the shift from ‘phase A’ to ‘phase B’ at the year 2000 was characterized by substantial increases in the fitted values for K and r (Table 1, ‘original’ data structure), followed by a return to parameter estimates nearly identical to those observed for ‘phase A’ in the post-2005 shift from ‘phase B’ to ‘phase C’ (Table 1 ‘original’ data structure, Fig. harmonia\_fit B).  
  
However, when the regime shift detector was applied to updated *H. axyridis* population data, which included two additional sampling years, the results were strikingly different. The two new observations, but 2015 observation, in particular, broke from the trend in dynamics observed in 2006 and after (Fig. harmonia\_fit A, data to the left of black vertical dashed line), and the regime shift detector script only located the post-2000 break in these data (Table 1, ‘updated’ data structure, Fig. harmonia\_fit B). In this case, the resultant regression parameters estimated for the period combining all apparent phases from 2001 on were intermediate in value, with greater standard error, than those estimated for phases B and C from the fits resulting from the shorter time series (Table 1, ‘updated’ data structure , Fig. harmonia fit B, dashed curve).

*Case study- Monarch butterflies*

Sampling error could not be estimated for this population measure as it is only reported as a single value- total area occupied by overwintering monarchs.

The regime shift detector script found three different break point combinations that were deemed to have equivalent performance by their respective AICcs, two models with a single break after 2003 and 2006 respectively, and a third with breaks at 2003 and 2008. However, when ranked by AIC, the two-break model substantially out-ranked both of the single-break models. Similarly, the population dynamic was modelled as a linear decline in carrying capacity K produced a fit that was ranked best of all scenarios tested by AICc, but second best after the two break point model by AIC (Table 2). The break point combination as ranked by AIC, the two break model is represented graphically by the solid lines in Fig. monarch\_fit (A, B) but the fit of the one break model is also given by the dashed line in Fig. monarch\_fit B.

**Discussion**

*Regime shift model structure*

The implementation of the model described here used the Ricker function because it presented an ideal compromise of simplicity and fit for the populations we wished to model. However, the method presented here could easily be adapted to population processes better described by other models, and incorporating other dependent variables which may be available (for example, if a population had a known response to temperature or another environmental variable). Similarly, this approach is not necessarily limited to population processes: a regime shift detector script could be developed to identify changes in any ecological dynamic with a well-defined internal rule governing its fluctuations. The sensitivity and precision of the approach could also be adjusted in these future implementations by adjustment of decision rules regarding selecting models of equivalent and best fit.

AICc was the information criterion used to rank break-point combination models, with all models ranked within two units of the lowest AICc considered to have equivalent performance, however, just a single ‘best’ model from the set of equivalent models was used for comparison in the simulations. The decision to only include one ‘best’ fit represented a compromise between accuracy, simplicity of script outputs, and computational intensity when running many simulation iterations. Overall script performance would likely have a higher rate of detecting all initial conditions if the set of all equivalently fitting models, instead of just the top-ranked, had been considered when comparing the performance of the script to the input conditions. In response to this observation, we developed the ‘modelspecification’ function so that a user may manually produce regression statistics associated with similarly ranked fits and interpret those values in the context of the known biology of the species under evaluation.

With regards to selection of information criteria, AICc was used for decision-making in the regime shift detector script rather than AIC because it allowed for a more conservative selection of break-point combinations while minimizing overfitting in higher sampling error scenarios- essentially by down weighting the selection criterion for models with many break points. However, this more conservative approach negatively affected the script’s ability to detect higher break frequency in low sampling error scenarios, particularly for one and two break input scenarios, because the penalty term for increasing the complexity of the model dramatically increases with AICc. Thus, if it is reasonable to assume that the population data being subjected to the regime shift detector script has a low associated sampling error, a user may wish to use less conservative information criteria (i.e. AIC) to rank break point combination models.

Because the model uses a single datum to represent the population in a given year, the model had to be constrained to avoid over-fitting to short time series. Unfortunately, this limitation means that shifts in dynamic regime occurring less than four time steps apart will not be detected by this modelling approach. In populations undergoing rapid change in their environments or internal dynamics, thus, the results of the script should be interpreted with caution, because a single-variable discrete time step model like the Ricker may not fully leverage available information. In these cases, using a model that allows, for example, within season dynamics to be measured may be more useful.

Regardless of model used to form the basis of the regime shift detector script, it is important that the model’s fitting function is set with some understanding of the data’s structure to prevent fitting or convergence issues. For example in our case, the rickerfit function was set to have a starting value of r at 1.5. For populations with dynamics that are expected to deviate from this value dramatically, setting this value to one closer to the expected value will aide in model convergence.

*Simulations*

Using the decision rules as set, simulations were performed to understand how changing various inputs affected the likelihood of the regime shift detector script identifying the conditions under which the data were produced. Simulations indicated that the performance of the regime shift detector script declined rapidly with increasing levels of sampling error (Fig. noise\_sim), a behavior that is, in general, expected of any statistical tool. Nevertheless, whenever possible, the sampling error of the data subjected to the script should be quantified to help evaluate the script’s results in the context of variation within the data due to sampling error. The error rate in detecting initial conditions varies with output, but in low-sampling-error scenarios, an output of zero or three or more break points by the script is generally approaching 90% accuracy, while outputs of one or two breaks have a lower rate of accurately detecting input conditions, at just under 80%.

Other input conditions also effected the performance of the regime shift detector script. The effect of changing the magnitude of the shift was dependent on which parameter was changed and by how much (Figs. change, changeR). Although larger shifts in regression parameters would, intuitively, lead to a higher likelihood of detection, these larger shifts would also be more likely to induce chaotic dynamics in the years immediately following the shift, potentially making the timing of shifts more difficult to pinpoint. Similarly, longer time series yielded regime shift detector script results that were more error prone (Fig, Nyears A), likely because, firstly, there were simply more possible break-point combinations for the model to select from, and secondly, because the penalty for increasing parameterization (AICc) would decrease as sample sizes grew, leading to increasing likelihood of identifying extra breaks (Fig. Nyears B).

*Case studies*

Our case studies represent two different biological processes- invasion and a population decline, in two very well studied insect species, allowing us to interpret the outputs of the regime shift detector script in the context of known biology. The two species represent ideal test case studies because they also represent cases with differing complexity in population drivers. In the case of *H. axyridis*, dynamics of this predacious species is believed to be closely coupled with prey availability (Bahlai and Sears 2009, Heimpel et al. 2010, Rhainds et al. 2010, Bahlai, Colunga-Garcia, et al. 2015), which, in turn, is driven by documented pest management practices(Bahlai, vander Werf, et al. 2015)- leading to relatively simple pulsed changes in dynamics. With Monarch butterflies, drivers of population dynamics are complex and result from drivers at local and continental scales (Saunders et al. 2017): previous studies have implicated climate (Zipkin et al. 2012), specific weather events (Brower et al. 2004), changing land use and habitat availability (Vidal and Rendón-Salinas 2014), and management practice (Pleasants and Oberhauser 2013) in their population dynamics. With many super-imposed drivers, we would predict the changing dynamics of this species would be driven by both smooth and pulsed processes, making the detection of discrete break points associated with regime shifts more difficult.   
  
In the *H. axyridis* case study, the regime shift detector script detected identical shifts to those observed in the previous study, when applied to the 1994-2013 data used in that study: specifically, shifts after 2000 and after 2005 corresponding to the invasion, and subsequent control of a prey item, with neonicotinoid insecticides (Bahlai, vander Werf, et al. 2015). However, when updated data, including observations from 2014-2015 were included in analysis, the post-2005 regime shift was no longer detected. Examination of the time series data suggests that a new dynamic emerging in these additional years of data may be the cause (Fig. harmonia\_fit). These two additional years deviate considerably from the population pattern observed in 2006-2013, in fact, they appear to be more similar to the dynamic observed during 2001-2005, when prey populations were uncontrolled by neonicotinoids. Because the regime shift detector script is unable to detect shifts with three or fewer years of data to minimize overfitting, these new data are constrained to be part of the previous, less explosive dynamic, so the script finds that the new, post 2006 phase integrating the 2014-2015 data does not differ from the explosive dynamics of 2001-2005. Thus, it seems probable that the script’s performance was compromised in this situation with the very earliest signs of a new shift in dynamic regime.

There are several possible biological explanations for *H. axyridis’* return to explosive population dynamics relating to prey availability. The resultant dynamic could be indicative of recent changing use patterns in neonicotinoids in central North America. Indeed, neonicotinoid insecticides are a subject of considerable controversy implicated with environmental impacts (Goulson 2013), so it is possible that farmers and land managers simply began using less of these insecticides in 2014 in response of this controversy. Alternately, extreme rainfall early in the growing season in the US Midwest in 2015 may have compromised the efficacy of neonicotinoid seed treatments. Finally, we may be observing the early signs of insecticide resistance among the field crop pests targeted by neonicotinoid seed treatments (Nauen and Denholm 2005, Puinean et al. 2010, Herron and Wilson 2011). Additional years of observation will be essential in determining if this apparent emerging shift is rooted in biological or management drivers, or simply represented a ‘blip’ in *H. axyridis’* dynamics.

The findings of the regime shift detector script on the Monarch overwintering population was, as expected, more ambiguous than that for *H. axyridis*, but still provides useful information in interpreting the timing of events effecting population density and cycling of the butterfly. Multiple models for describing the dynamics of monarchs were ranked similarly, and the conclusions reached about ‘best models’ depended highly on the information criterion used to rank them (Table 2). Using AICc, a more conservative decision rule down-ranking more complex models, a model assuming the carrying capacity was undergoing a linear decline was favored over all break-point models tested by the regime shift detector script, but only slightly so. Yet, using AIC allowed the script to be more sensitive to apparent shifts in dynamics, and in this case, a two-break model with shifts after 2003 and 2008 were observed, with stepwise declines in carrying capacity at these points and roughly consistent, although perhaps slight growth in the intrinsic rate of increase at the first shift. However, there is biological basis to support either of these favored models, and the reality faced by monarch butterflies is likely a super-imposition of both.

A smooth decline in carrying capacity for monarchs could be driven by a variety of factors which we know to have occurred: increasing deforestation in their overwintering grounds or loss of prairie breeding habitat in central North America would likely leave this particular signature on the overwintering data because these drivers are progressive and not reversible in the short term. Indeed, changes of these kinds are well-documented. Although the monarch’s overwintering habitat has been protected by various conservation strategies directed by the Mexican government dating back to 1980 (Vidal et al. 2014), illegal logging activity in the overwintering zone has occurred as recently as 2015 (Brower et al. 2016). Systematic prairie loss in the monarch’s breeding habitat has also been implicated with their decline (Mueller and Baum 2014), however, this loss has largely plateaued in recent decades (Zaya et al. 2017). Climate change, in the form of gradual shifts to less favorable conditions for overwintering, breeding, or feeding is also probable (Batalden et al. 2007), and could also manifest in an observed smooth decline.

Pulsed changes in carrying capacity would be observed due to specific climatic events and changing land management practices. Several extreme climate events affecting monarch overwintering survival have been documented in the past decades (Brower et al. 2004, 2015, Zalucki et al. 2015). However, assuming conditions largely return to previous averages after the climate event, we would not expect any one single extreme climate event to have lasting, multiple year impacts on the internal dynamic rule governing monarch population fluctuations. Indeed, we observe population densities at an outlying low density in 2013-2014 (as described in (Vidal and Rendón-Salinas 2014)) return to previous dynamics in subsequent years. Changing herbicide use practices in central North America, however, represent pulsed changes to new management states, and have largely eliminated milkweed from agricultural field crops (Zaya et al. 2017). This change in management, brought about by the introduction of glyphosate resistant soybeans and maize, has had the effect of dramatically reducing the density of agricultural weeds, including milkweed, within agricultural fields. Indeed, although glyphosate tolerant soybeans and maize were introduced to the US market in 1996 and 1998 respectively (Powles 2010), actual glyphosate use lagged behind, with dramatic increased in use of the pesticide in 1998- 2003 in soybean, and 2007-2008 in maize (Baker 2017). This pulsed increase in glyphosate use roughly correspond to shifts detected by our script, and glyphosate use in these crops has been implicated in monarch decline by multiple previous authors. Thus, findings from our regime shift detector tool could be used to pinpoint thresholds of herbicide use or critical areas of adoption in future investigations.  
  
**Conclusions**

The regime shift detector script provides a new objective tool for examining population regulation pattern shifts in natural populations. However, like most quantitative analytical methods, its use is not without caveats, and results produced by the script should be critically examined within the context of what is known about species biology and ecology.

The regime shift detector tool, as is, represents a compromise between sensitivity and simplicity. We have illustrated through case studies how the information criteria used and decision rules for cutoff have a dramatic impact on the results of the script, and thus should be considered critically before drawing any conclusions by the use of this tool. Similarly, we recommend a user carefully consider the limitations of the tool in the context of the raw data presented: if phases of change are too short to be detected by the script, its ability to detect these shifts will be limited, and the resultant variation may reduce the script’s sensitivity for detecting other shifts in the data. As we have demonstrated herein, alternate dynamics should be considered, and compared to script outputs, for a holistic interpretation.

When interpreted in the context of known species biology, the regime shift detector script has the potential to aide management decisions and identify, and rank critical drivers of change in a species internal dynamics. In an era of rapid global change affecting species dynamics, it is critical to use tools which allow better understanding of changes to internal regulators of population, and not base management decisions on population numbers alone.

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**Table 1:** Regression parameters Ricker model fits for each phase between break points resulting from fitting population data of *Harmonia axyridis* from Kellogg Biological Station, 1994-2015. Regression parameters r represent the per capita yearly intrinsic rate of increase and K the carrying capacity, based on population numbers expressed as average number of adult *H. axyridis* captured per trap, per year. Analyses were performed on a subset of the data, from 1994-2013 to compare to previous use of this approach (Bahlai, vander Werf, et al. 2015), and then again on the updated data including two additional sampling years. Note that the information criteria cannot be compared between the two data structures here, as they represent two different sets of independent variables; these criteria represent the ‘best’ of those that were used to rank competing break point combinations tested within the given data structures. The ‘Phase’ column gives a shorthand for referring to the data subsetting structure under the most complex scenario represented here.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Data**  **structure** | **AIC** | **AICc** | **Phase** | **Years in subset** | **r ( ± SE)** | **K ( ± SE)** |
| Original, to 2013 | -13.5 | -7.5 | A | 1994-2000 | 1.3 ± 0.3 | 0.33 ± 0.03 |
|  |  |  | B | 2001-2005 | 2.2 ± 0.2 | 0.46 ± 0.02 |
|  |  |  | C | 2006-2013 | 1.5 ± 0.2 | 0.29 ± 0.02 |
|  |  |  |  |  |  |  |
| Complete, to 2015 | -36.8 | -16.8 | A | 1994-2000 | 1.3 ± 0.3 | 0.33 ± 0.03 |
|  |  |  | B+C | 2001-2015 | 1.6 ± 0.4 | 0.43 ± 0.05 |
|  |  |  |  |  |  |  |

**Table 2.** Model performance of top-ranked models of differing structures fit to population data documenting the area occupied by overwintering Monarch butterflies in their winter habitat in the Mexico, 1995-2016. One break and two break models are for best break point combinations selected by regime shift detector script, while ‘linear K’ model assumes a linear decline of carrying capacity K and a single constant intrinsic rate of increase r. The ‘Phase’ column gives a shorthand for referring to the data subsetting structure under the most complex scenario represented here.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model structure** | **AIC** | **AICc** | **Phase** | **Years in subset** | **r ( ± SE)** | **K ( ± SE)** |
| One break | 114.6 | 120.2 | A | 1995-2003 | 1.0 ± 0.5 | 10.1 ± 1.9 |
|  |  |  | B+C | 2001-2015 | 0.8 ± 0.3 | 4.1 ± 0.7 |
|  |  |  |  |  |  |  |
| Two break | 106.9 | 121.9 | A | 1995-2003 | 1.0 ± 0.5 | 10.1 ± 1.9 |
|  |  |  | B | 2004-2008 | 1.6 ± 0.2 | 5.6 ± 0.3 |
|  |  |  | C | 2009-2016 | 1.2 ± 0.4 | 2.8 ± 0.5 |
|  |  |  |  |  |  |  |
| Linear K | 112.9 | 118.5 | A+B+C | 1995-2016 | 1.3 ± 0.3 | - |
|  |  |  |  |  |  |  |