**The Regime Shift Detector: a model to identify changes in dynamic rules governing populations**

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**Abstract**

1: Environmental factors may interact with internal rules of population regulation, sometimes perturbing systems to alternate dynamic states. Yet, pinpointing when sustained state changes occur in naturally fluctuating populations is difficult. An analytical approach that can identify the timing and magnitude of such changes, or “regime shifts”, would advance understanding of abrupt ecological transitions with potential to inform management of species of economic or conservation concern.

2: We develop a generalizable model, the “Regime Shift Detector” for detecting changes in the parameters of a simple density dependent model governing the temporal fluctuations of a population. The model is designed as a generalizable tool comprised of a suite of functions for examining population time series data for the presence, location, and magnitude of shifts. The model uses an iterative approach to fitting subsets of time series data, and then ranks the fit of a particular break point combination using model selection. We examined the performance of this model with simulated data and two real-world case studies involving >20-year population time series datasets documenting species of conservation and economic concern.

3: We found that under low error conditions, the regime shift detector model accurately identified no shift scenarios in approximately 60% of cases, and identified 1 break scenarios in 80% of cases and identified 2 or more break scenarios with >90% accuracy; yet, the model’s performance declined as sampling error increased. In our case study examining the invasion process of Multicolored Asian Ladybeetle (*Harmonia axyridis*), the regime shift detector identified shifts in population cycling associated with known variation in prey availability. However, in the case study examining the eastern population of Monarch butterflies (*Danaus plexippus*), the regime shift detector tool’s results were more ambiguous, suggesting that multiple super-imposed processes are likely involved in the decline of this species.

4: When interpreted in the context of known species biology, the regime shift detector has the potential to aid management decisions and identify critical drivers of change in species’ dynamics. In an era of rapid global change, it is critical to use tools which allow for understanding of population changes to internal regulators.

**Introduction**

Population dynamics are governed by internal, biotic rules and also abiotic factors, often leading to both 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 (Hare and Mantua 2000, Carpenter et al. 2008). Understanding how and when external environmental factors interact with internal density dependent regulation remains a fundamental challenge in population ecology (Sutherland et al. 2013, Eason et al. 2016).

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 models, which were initially developed for fisheries management (Ricker 1954, Beverton and Holt 1957) and describe the expected population size in year t as a function of the population size in year t-1. The accuracy of these simple density dependent models is generally highest for populations fluctuating around their carrying capacity (Sabo et al. 2004), with over-compensatory density dependence, and a short development period to minimize the effect of stage-structured lags (Bjørnstad and Grenfell 2001). 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, Barraquand et al. 2017, Boettiger 2018), these models remain useful, in large part due to their simplicity and ecologically meaningful interpretations (Gadrich and Katriel 2016). When parameter estimates differ between populations, or change in a single population, it suggests a difference in environmental constraints govern the population, providing a quantitative measure of an effect of environmental changes (Forchhammer and Asferg 2000, Berryman and Lima 2006, Zipkin et al. 2009, Bahlai, vander Werf, et al. 2015).

Although theoretically well-described, identifying abrupt transitions in ecological systems is challenging using real-world data due to a lack of a systematic approach that can be adapted across a variety of responses (Bestelmeyer et al. 2011). In many cases, transition points are applied to time series data *ad hoc*, based on data visualization or specific hypotheses surrounding factors affecting population fluctuations (Hare and Mantua 2000, Judith D. Toms and Mary L. Lesperance 2003, Weimerskirch et al. 2003, Berryman and Lima 2006, Knapp et al. 2012), creating the potential for observer biases in selecting break points. Break point analysis tools eliminate this bias by locating change points with a variety of optimization strategies, including linear and moving average methods (Braun and Muller 1998, Zeileis et al. 2001, Killick and Eckley 2014, Priyadarshana and Sofronov 2015). However, these methods are not optimal for data with internal, density dependent structure inherent to population time series data. Density-dependence within populations has the potential to mask transition points. For example, chaotic dynamics occurring immediately after a temporary disturbance can result in a change in population size, but not necessarily in the rules governing population fluctuations. As such, standard time series break point approaches do not accommodate changes in the driving dynamic between sequential data points, just the resultant data’s absolute value. Wavelet analysis has been applied to population time series to address changes in cycling patterns (Jenouvrier et al. 2005) but this method also does not account for density-dependence internal to the process as an explicit mechanism governing the fluctuations (Cazelles et al. 2008). A robust, unbiased tool for identifying regime shifts would simultaneously allow us to identify when shifts in population cycling processes occur and further quantify the specific changes to the underlying dynamic driving population size changes.

In this paper, we develop a generalizable tool for adapting a simple density dependent model to detect shifts in dynamic regimes within population time series data. We illustrate our approach using the Ricker model because of its simplicity and high performance under a variety of realistic environmental scenarios. Yet, the techniques described in our paper can be readily adapted for other population model structures, including more complicated processes such as seasonal periodicity or lag effects. We describe the basic structure of our model and how it can be used to evaluate the presence, location, and magnitude of shifts in dynamic regimes using population size time series data. We demonstrate the utility our model through a series of simulations and apply the model to real-world case studies of two populations of conservation and economic concern. First, we examine the invasion process of *Harmonia axyridis*, a cosmopolitan invasive lady beetle, including a biotic facilitation event, in the two decades following its arrival in Midwestern US agricultural ecosystems. Then, we examine the density of overwintering *Danaus plexippus,* the monarch butterfly, as the species has endured numerous threats throughout its migratory range over a similar two decade period.

**The Regime Shift Detector model**

We assume that the population of interest follows a Ricker model structure such that the population size in time t+1, , is dependent on the population size in time t, , the carrying capacity of the system, , and the per-capita annual growth rate, (Turchin 2003):

The population size in year t+1 is assumed to have stochastic variation, which is modeled using an error term , which follows a normal distribution centered around zero with a variance of . The parameters K, r, and are estimated from the population data (N1, N2, … N*t*). We selected the Ricker model because 1) it does not rely on any external information, other than population data over time; 2) only three parameters need to be estimated, and those parameters have ecologically meaningful interpretations; and 3) it is an extremely flexible distribution, taking a variety of forms, from linear to compensatory to over-compensatory, and thus has a wide range of applications across a wide variety of taxa (Ricker 1954, Brook and Bradshaw 2006).

To build the Regime Shift Detector model, we use 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, we first fit the Ricker model to the entire time series of available data, then the population time series is subdivided into all possible combinations of 2, 3, …, n subsets of sequential data points (hereafter, ‘break point combination’) and the Ricker model is fitted to each of the subsets produced for each break point combination. We constrain break point combinations to only include subsets with at least four sequential data points to avoid over-fitting.

After fitting each subset for a given break point combination, we evaluated the model’s Akaike Information Criteria for small sample sizes (AICc). To do this, we calculate AIC for each segment and sum them together to estimate one value for the model, and then compute the penalty term associated with the dimensionality of the model to compute AICc (Hall et al. 2013). 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, models were considered equivalent (Burnham and Anderson 2002).

The ‘regime shift detector’ is implemented as a series of R functions to enable a user to quickly generate a report on the fit of the model and the location of break points with their own data. Users provide the model with a data frame of population observations at standard time intervals. The model (and all subsequent simulations and case studies) were scripted and run in R Version 3.3.3 (R Development Core Team 2017) . 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>. We summarize the role of each function in S1, but readers can download the script file directly for implementation details.

*Simulation study*

We conducted a series of simulations to test the accuracy for the regime shift detector under a variety of scenarios. Given known input conditions, we evaluated the accuracy of the model output. The regime shift detector produces both a top break point combination, and a set of equally performing break point combinations for cases in which model fits produce equivalent AICc values (i.e. within 2 units of the best-performing fit). The impact of error was tested by simulation. For the purpose of scaling our findings to multiple population sizes, this error was simulated as a percentage of the population mean, rather than an absolute value. For each data point, a random value was selected from a normal curve of mean 0 and standard deviation of *.* To scale the standard deviation to the population size used in the simulations, and the expected value of N(t+1) was multiplied by this value to simulate error σ. Error intervals used = 1, 5, 10%, and every 10% thereafter to 90%. Each of these scenarios was run on 1000 simulated datasets for breakpoint combinations with 0, 1, 2 and 3, respectively. We also conducted simulations examining the performance of the model under varying sizes of shift, by altering the constants in the model to simulate changes in dynamic rules. To achieve this, we modified *r* and *K* individually by 10% intervals from their starting values (0%, 10%,…,90%) while holding all other parameters constant. We also tested the impact of time series length by modifying length of the simulated time series at two year intervals while holding other parameters constant. We further examined what errors occurred when the top selected break point combination did not match with the data generation process (described in more detail in Appendix S2).

We examined the regime shift detector’s performance from two perspectives. Firstly, we examined how frequently were the input conditions identified by the top ranked, and within the set of equivalently performing break point combinations (Fig. 1) (and conversely, a false negative rate; given a time series with a known set of break points, how likely is the regime shift detector to miss these break points in its output set?) Secondly, given an output of a particular type for the top ranked break point combination, what is the likelihood that the output has correctly identified input conditions (Fig. 2) (and conversely, a false positive rate: given an output from the regime shift detector, used on a data set with unknown break points, how likely is the top model identified to be ‘incorrect’)?

In general, scenarios with more breakpoints were more frequently identified correctly within the regime shift detector’s outputs (Fig. 1). Simulation conditions were detected in the break point combination sets in >90% of scenarios initiated with two or more break points under low noise conditions and in ~80% of scenarios initiated with one break point, and in the majority of those cases, the top-ranked break point combination was identical to input conditions (Fig. 1 A), although accuracy decreased with increasing experimental noise. Zero break scenarios were identified within the set of equivalent break points produced by the model in approximately 60-80% of input scenarios, increasing in accuracy with increasing experimental noise. The regime shift detector correctly identified shifts most frequently in cases with moderate changes to *K* (30-60%; Fig. 1 B), and smaller changes to *r* (<25%; Fig. 1 C). This result was somewhat counter-intuitive, as we would generally expect larger shifts to be more easily detected. However, because the Ricker model produces chaotic dynamics when a population is farther from its equilibrium state, a larger shift could potentially result in a situation where multiple break point fits would perform equivalently. Finally, as scenario length increased, the likelihood that the regime shift detector would accurately detect scenario conditions decreased, likely because of the factorial increase in potential break point combinations with each additional point in the time series (Fig. 1 D).

Conversely, when we examined regime shift detector model’s top outputs for accuracy by output type (i.e. the number of breaks found in the top-ranked breakpoint combination), we found that we could be most confident in model results which found no breakpoints, and those that found 3 or more breaks at low sample error rates (<10% of the sample mean; Fig. 2). When the regime shift detector found no breaks, it reflected a simulation scenario with no breaks in virtually all cases (Fig. 2 A). When the model identified scenarios with one or two breaks as the top model, this reflected the scenario conditions ~65% of the time, and decreasing with simulated error (Figs. 2 B, C). A similar pattern was observed for scenarios identified to have three breaks, however, accuracy was generally quite high with this output, with ~90% accuracy observed (Fig. 2 D).

**Applications**

We tested the performance of the regime shift detector model with two case studies using population time series data produced from field observations. Both case studies involve approximately two decades of observations of economically or culturally important insect species: one case examines an invasion process and the other examines a population decline, both occurring over the same time period in recent history.

*Harmonia axyridis* in southwestern Michigan

The 1994 invasion of multicolored Asian ladybeetle *Harmonia axyridis* to southwestern Michigan, United States was documented in monitoring data collected on agriculturally-important Coccinellidae (ladybeetles) in landscapes dominated by field crops. Population density of ladybeetles is monitored in 10 plant communities weekly over the growing season using yellow sticky card glue traps starting in 1989 at the Kellogg Biological Station at Michigan State University. We used data on the captures of adult *H. axyridis* at the site from 1994-2017, culled at day of year 222 (August 10) to minimize the effect of year-to-year variation in the sampling period. We then calculated the average number of *H. axyridis* adults captured per trap, across all traps deployed within a sampling year, and used this value as the dependent variable in the Regime Shift Detector Model. Detailed sampling methodology is available in previous work (Bahlai et al. 2013, Bahlai, Colunga-Garcia, et al. 2015, Bahlai, vander Werf, et al. 2015).

Two break points- one occurring after 2000, and one occurring after 2005 were observed in the best break point combination model (Fig. 3 A). The shift from ‘phase A’ to ‘phase B’ in 2000 was characterized by substantial increases in the fitted values for K and r, with increases of ~75% and ~40% over their initial estimates, respectively (Table 1), followed by a return in ‘phase C’ to parameter estimates nearly identical to those observed for ‘phase A’ in the post-2005 shift (Table 1, Fig. 3 B). Although the regime shift detector ranked several break-point combinations similarly by AICc, the equivalently performing break point combinations were consistent with each other (a zero break fit, a one break fit with a break at 2000), the top-ranked break point combination (2000, 2005) was also selected by AIC.

Monarch butterflies in Mexican overwintering grounds

The eastern population of the North American monarch butterfly (*Danaus plexippus*) is migratory, with the majority of individuals overwintering in large aggregations in Oyamel fir forests within the transvolcanic mountains in the central region of Mexico (Urquhart and Urquhart 1978, Wassenaar and Hobson 1998). Monarchs are highly dispersed over their breeding season, occupying landscapes throughout the agricultural belt in central and eastern United States and southern Canada (Flockhart et al. 2017). As such, estimates of the overwintering population size can provide a convenient and inclusive annual metric of the eastern migratory population (Prysby and Oberhauser 2004). The total area occupied by overwintering monarch colonies is recorded each season as a proxy for population size. We used data documenting observations of area occupied from 1995 to 2017 (based on early winter, December-January surveys), compiled by the World Wildlife Fund Mexico (available at MonarchWatch; Lovett 2017).

The regime shift detector model indicated that the best break point combination fit was single break that occurred after 2003 in the monarch overwintering density data. (Fig. 4). The shift was characterized by a dramatic decrease in absolute area occupied by overwintering monarchs between 2004 and 2005 winter seasons (Fig. 4 A), corresponding with a >50% reduction in K and a 15% reduction in r (Table 2) and a shift to a smoother and overall less abundant dynamic in their second phase (Fig. 4 B). However, the model selection results were somewhat ambiguous, (i.e. the top ranked break point combination had an AICc of 120.2), and ranked two additional models functionally equivalent: one with a break after 2003 and an additional break after 2008, and another one-break model with an intermediate break in 2006. The regime shift detector model ranked these three break point combinations of different structures similarly by AICc (the latter two models with identical values of AICc to the third decimal place, at 121.864 and 121.867 repsectively), but varied in rank when using AIC. By AIC, the two-break combination of 2003, 2008 was strongly favored (AIC=106.9), followed in rank by the one-break fit at 2003 (AIC=114.6) and the one break fit at 2006 (AIC=116.3).

*Application summaries*

Our case studies represent 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. 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 (neonicotinoid insecticide use) (Bahlai, vander Werf, et al. 2015)- leading to relatively simple pulsed changes in dynamics. The first shift in the dynamics of *H. axyridis*, after 2000, corresponds to the well documented arrival and establishment of a preferred prey item from its native range, soybean aphid, to North America (Ragsdale et al. 2004, Wu et al. 2004). The invasion of this aphid dramatically increased resources available to *H.axyridis* in habitats that the beetles were already well-established in (Bahlai et al. 2013), supporting both a higher carrying capacity and a greater intrinsic rate of increase. The second shift we observed, after 2005, is more difficult to directly explain, as the prey item still persists in the landscapes where *H. axyridis* occurs (albeit in lower numbers). However, this shift thought to be linked to landscape-scale use of neonicotinoid insecticides through prey numbers, because these insecticides affect the prey most when colonizing new hosts in spring, limiting the early season reproduction of *H. axyridis* (Bahlai, vander Werf, et al. 2015)*.*

The findings of the regime shift detector script on the Monarch overwintering population is, as expected, more ambiguous than that for *H. axyridis*. 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), weather events (Brower et al. 2004), changing land use and habitat availability on wintering grounds (Vidal and Rendón-Salinas 2014), and loss of hostplants due to changing agricultural practices on breeding grounds (Hartzler 2010, Pleasants and Oberhauser 2013) as factors influencing monarch population dynamics. With many super-imposed drivers, changing dynamics are likely to be driven by both press and pulsed processes, making the detection of discrete break points associated with regime shifts more difficult.

Although we observed a shift in dynamic after the 2003 overwintering season, conclusions about best models depended highly on the information criterion used to rank them (Table 2). For example, if AIC was used instead of AICc to rank break point combinations, the regime shift detector model was more sensitive to apparent shifts in dynamics, and in this case, a two-break model with shifts after 2003 and 2008 was best ranked, with stepwise declines in carrying capacity at these points and roughly consistent. 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. For example, several extreme climate events affecting monarch overwintering survival have been documented in the past decades (Brower et al. 2004, 2015, Zalucki et al. 2015). Similarly, changing herbicide use practices in central North America 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 (Duke and Powles 2009), 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). In each crop, use of the herbicide largely plateaued thereafter, which may account for the signal of changing dynamics in Monarchs we observed after 2003 and after 2008 (Duke and Powles 2009, Pleasants and Oberhauser 2013, Baker 2017).

The regime shift detector model has limited ability to detect gradual changes in environmental conditions resulting in smooth shifts in population dynamics. A smooth, rather than abrupt, decline in carrying capacity for monarchs could be driven by a variety of known factors: increasing deforestation in their overwintering grounds or changes to temperature and precipitation from climate change could likely leave this particular signature on the overwintering data because these drivers are progressive. Indeed, 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 and loss of habitat from winter storms at the winter colonies continues to occur (Brower et al. 2016). 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 smooth shift in population processes.

**Discussion**

The regime shift detector model provides a novel and objective tool for examining population regulation pattern shifts in natural populations. Moreover, the analytical framework presented by the regime shift detector model provides a tool for comparing population processes over time and between ecosystems. As we illustrated with our case studies, the results produced by our model not only identify and quantify the parameters changes, but can also provide comparative insight into the potential drivers in the systems under study. The regime shift detector model thus provides a basis for future work examining dynamic shifts across taxa with different generation times and lags between external drivers and population responses.

The regime shift detector model, as is, represents a compromise between sensitivity and simplicity. Our case studies show how the information criteria used and decision rules for cutoff have a dramatic impact on the results of the model, and thus should be considered critically before drawing conclusions from model results. Similarly, we recommend users 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 model, 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. For instance, we use the discrete form of the Ricker model, with a yearly time step, but encourage end users to apply regime shift detector approaches to both a model structure and temporal resolution appropriate to their systems. As we have demonstrated herein, alternate dynamics should be considered, and compared to outputs, for a holistic interpretation.

The top break-point combination selected by the regime shift detector was more likely to over-estimate the number of breaks than to under-estimate at low and intermediate numbers of breaks in the time series: about a third of the scenarios identified as one break in the top-ranked break point combination were initiated under zero break conditions, a similar number of scenarios identified as two-break were initiated under one and two break conditions. However, break-point combinations with higher numbers of break points are subject to greater penalties in the calculation of AICc. Thus, a user can have high confidence in an accurate detection of break points if the regime shift detector model indicates either zero, or ≥3 breaks in a time series, because these scenarios must have very good fit to achieve this ranking. In the more intermediate scenarios where one or two breaks are identified, the set of similarly-ranked models should be considered when interpreting the results from the model, as illustrated by our case studies.

The method presented here could easily be adapted to population processes better described by other model structures or with the incorporation of covariates (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 future implementations by modifying the 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. AICc allows for a more conservative selection of break-point combinations while minimizing overfitting in higher sampling error scenarios as compared to AIC, by down weighting the selection criterion for models with many break points. However, this more conservative approach negatively affected the model’s ability to detect shifts in dynamic 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. The ambiguity and differences in system complexity we observed from our case studies allow us to illustrate the important impact of model selection criterion choice on the ultimate output of the Regime Shift Detector model, and how criteria optimize models for different outcomes (Burnham and Anderson 2002). AICc-based ranking of models produced sets of equivalently performing break point combinations in both of our case studies, presenting a practical problem. Thus, we used other information criteria, specifically AIC, to aide in the interpretation of the results set. If it is reasonable to assume that the population data being subjected to the regime shift detector 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 or resolve ambiguities in ranking within sets of very different break point combinations.

Because the model uses a single datum to represent the population in a given year, the regime shift detector model must be constrained to avoid over-fitting to short time series. This limitation means that shifts in dynamic regime occurring less than four time steps apart cannot not be detected with this modelling approach. Thus, the results of the model should be interpreted with caution in populations undergoing rapid change in their environments or internal dynamics. However, in these cases, a model relying on yearly time step data such as the Ricker may be insufficient to document change. If additional, within year or season data are available, the regime shift detector model can be adjusted to reflect their structure, potentially improving the temporal precision of results.

Regardless of the specific model structure used within the regime shift detector, 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 function that fits the Ricker model 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.

We used simulations to understand how changing various inputs affected the likelihood of the regime shift detector in identifying the conditions under which the data were produced. Simulations indicated that the performance of the regime shift detector model declined rapidly with increasing levels of error (Fig. 2), a behavior that is, in general, expected of any statistical tool. Nevertheless, whenever possible, the variability of the data should be quantified to help evaluate the model’s results in the context of variation within the data due to sampling error. The error rate of the regime shift detector in detecting initial conditions varies with output, but in low-sampling-error scenarios amongst top-ranked break point combinations, an output of zero or three or more break points by the script is generally greater than 90% accuracy, while outputs of one or two breaks have a lower rate of accurately detecting input conditions, at just under 70%. The lower accuracy in these one and two break top outputs is primarily explained by over-estimating the number of breaks (ie., the model assigning breaks where there are none). This may occur because of an insufficient penalty to ‘finding’ extra breaks for these intermediate scenarios, whereas when a break point combination with three breaks rises to the top rank despite substantial penalty for model complexity, it is indicative of an excellent fit. Nevertheless, in scenarios initiated with 1-2 breaks, the set of equivalent break point combinations indicated by the regime shift detector contained the initiation conditions of the scenario in >80% of cases (Fig. 1).

Other input conditions also impacted the performance of the regime shift detector model. The effect of changing the magnitude of the shift was dependent on which parameter was changed and by how much (Figs. 2 B, C). 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 results that were more error prone (Fig. 2 D). This 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 (i.e. AICc) would decrease as sample sizes grew, leading to increasing likelihood of identifying extra breaks.

When interpreted in the context of known species biology, the regime shift detector model has the potential to aide management decisions and identify, and rank critical drivers of change in internal dynamics of a population. Our modeling framework should be useful in this era of rapid global change affecting species dynamics, as it can help evaluate population changes relative to internal regulators.

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**Table 1:** 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. The ‘Phase’ column gives a shorthand for referring to the data subsetting structure indicated by the regime shift detector model.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Data**  **structure** | **Phase** | **Years in subset** | **r ( ± SE)** | **K ( ± SE)** |
| 1994-2017 | A | 1994-2000 | 1.3 ± 0.3 | 0.31 ± 0.02 |
|  | B | 2001-2005 | 2.3 ± 0.3 | 0.43 ± 0.03 |
|  | C | 2006-2013 | 1.6 ± 0.3 | 0.27 ± 0.03 |
|  |  |  |  |  |

**Table 2.** Ricker model fits for each phase between break points resulting from fitting population data documenting the area occupied by overwintering Monarch butterflies in their winter habitat in the Mexico, 1995-2016. Regression parameters r represent the per capita yearly intrinsic rate of increase and K the carrying capacity, in units of hectares occupied. The ‘Phase’ column gives a shorthand for referring to the data subsetting structure indicated by the regime shift detector model.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Data structure** | **Phase** | **Years in subset** | **r ( ± SE)** | **K ( ± SE)** |
| One break | A | 1995-2003 | 1.0 ± 0.5 | 10.1 ± 1.9 |
|  | B | 2001-2015 | 0.8 ± 0.3 | 4.1 ± 0.7 |
|  |  |  |  |  |

**Figure captions**

Figure 1: **Performance the regime shift detector model under varying conditions.** Proportion of results where initial conditions were detected by the top model (circles) or within the equivalent model set (squares) under A) varied noise (in the form of standard error) B) varied % changes in the K constant in the Ricker model C) varied % changes in r, the intrinsic rate of increase in the Ricker model and D) simulated time series length. Sets of 0, 1, 2 and 3 break points were randomly generated from within the set of possible values each scenario was iterated 1000 times. Lines joining points represent a third order polynomial GAM representing the best fit, with standard error.

Figure 2: **Observed outcomes of the regime shift detector model relative to simulation conditions.** Proportion of results with a given outcome under varied simulation length in years. Sets of 0, 1, 2 and 3 break points were randomly generated from within the set of possible values, and data were simulated with a 20% shift of r and a 40% shift of K at the given break point. Each series consisted of 25 years of simulated data and each scenario was iterated 500 times. Lines joining points represent a third order polynomial GAM representing the best fit, with standard error. Data are plotted here by output of the regime shift detector script under varied standard error as a proportion of the mean (i.e. % noise) and input break point combination conditions, where A) proportion of scenarios where zero breaks were detected; B) proportion of scenarios where one break was identified; C) scenarios with two break points identified; and D) scenarios where three breaks were identified by the regime shift detector script.

Figure 3: **Regime shift detector breaks and Ricker model fits for an invasive ladybeetle**. Population data documenting the invasion of *Harmonia axyridis*, a ladybeetle native to eastern Asia, to plots at the Kellogg Biological Station in southwestern Michigan, USA, 1994-2015 A) Time series documenting average number of adults captured, per trap, per year. Vertical blue lines indicate timings of shifts in dynamics, as indicated by the regime shift detector model. B) Ricker fits of phases of population dynamics as indicated by the regime shift detector model.

Figure 4: **Regime shift detector breaks and Ricker model fits for a species of conservation concern.** Population data documents the area occupied by overwintering Monarch butterflies in their winter habitat in the Mexico, 1995-2017. A) Time series documenting raw data of estimated area occupied by overwintering monarchs by year. Vertical blue line indicates timing of a shift in dynamics, as indicated by the regime shift detector model. B) Ricker fits of phases of population dynamics as indicated by the regime shift detector model.