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

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**Abstract**

1: Environmental factors may interact with internal rules of density dependent population regulation, sometimes perturbing systems to alternate dynamic states. Yet, pinpointing when sustained state changes occur in naturally fluctuating populations has remained unresolved. An analytical approach which allows the identification of timing and magnitude of such changes, or “regime shifts”, would advance our understanding and have the potential to direct the management of species of economic or conservation concern.

2: We develop a generalizable model, the “Regime Shift Detector” for adapting a simple density dependent model to detecting shifts in the dynamic regime observed in population time series data. This model was developed to be used 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 the Ricker model on subsets of time series data, and ranking the fit of the 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 sampling error conditions, the regime shift detector model accurately identified no shift scenarios in approximately 90% of cases, and identified 1 and 2 break scenarios in ≥70% of cases and identified 3 or more break scenarios with >80% accuracy, although its 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 examine population cycling in Monarch butterflies (*Danaus plexippus*), the regime shift detector tool’s results were more ambiguous, suggesting that multiple super-imposed processes are 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 aide management decisions and identify and rank critical drivers of change in a species’ 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.

**Introduction**

Population dynamics are governed both by internal, biotic rules, and abiotic influences, often leading to similar 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 (Hare and Mantua 2000, Carpenter et al. 2008). Understanding precisely how and when environmental factors interact with density dependent internal population regulation remains a fundamental challenge in ecology (Sutherland et al. 2013, Eason et al. 2016). An analytical approach which allows identification of timing and magnitude of regime shifts in populations would have the potential to direct the management of species of economic or conservation concern (Bestelmeyer et al. 2011).

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). The accuracy of these simple density dependent models is regarded as 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). 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 (Gadrich and Katriel 2016). 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 an effect of environmental changes (Forchhammer and Asferg 2000, Berryman and Lima 2006, Zipkin et al. 2009, Bahlai, vander Werf, et al. 2015).

Although well described in theory, characterization of abrupt transitions in ecological systems has generally lacked a common approach when identifying these shifts in real-world data (Bestelmeyer et al. 2011). In many cases, transition points are applied to the time series *ad hoc*, based on data visualization or specific hypotheses surrounding factors affecting population fluctuations (Hare and Mantua 2000, Weimerskirch et al. 2003, Berryman and Lima 2006, Knapp et al. 2012), creating the potential for observer bias in selecting the break points themselves. Break point tools have been developed eliminate this bias by approaching 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), but for data series without the internal, density dependent structure inherent to population time series. Wavelet analysis has been applied to population time series to determine changes in cycling pattern, (Jenouvrier et al. 2005), but this method also does not explicitly account for density-dependence. A robust, unbiased tool for identifying these shifts prior to explicitly quantify changes occurring in shifts between phases is warranted.

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 describe the basic structure of our model and how it can be used to examine population time series data for the presence, location, and magnitude of shifts in dynamic regimes, and examine the performance of this tool with simulated data and real-world case studies of two populations of conservation and economic concern.

**Methods**

*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, and is the error. 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 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, we first fit the Ricker model 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. 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 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. The model, simulations, and case studies 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>. We summarize the role of each function in S1, but we encourage the reader to download the script file directly for the details of implementation, included as line-by-line comments in the script.

*Simulations*

We conducted a series of simulations to test the accuracy for the regime shift detector under a variety of scenarios. In this manuscript, we focus on our ‘outcome-based ‘ scenarios, i.e. given the model’s output, what is the probability of correctly identifying the input scenario? The impact of sampling error was tested by simulating random noise as a percentage of the dependent variable. For each data point, a value on a continuous interval from -*%noise* to +*%noise* was selected randomly, and the expected value of N(t+1) was multiplied by this value to simulate error σ. Noise intervals used *%noise* = 1, 5, 10%, and every 10% 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. Additional simulations examining the performance of the model under varying sizes of shift and length of time series are described in Appendix S2.

*Case studies*

We used two case studies to test the performance of the regime shift detector script on population time series produced by field observations. 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 multicolored Asian ladybeetle *Harmonia axyridis* to southwestern Michigan, United States was captured as part of 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. 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* inspired the need for a regime shift detector (Bahlai, vander Werf, et al. 2015).

We used data documenting 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.

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 (citation). The total area occupied by overwintering monarch colonies is recorded 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 December of 1995 to December of 2016, compiled by MonarchWatch.org . Data are available directly from MonarchWatch (Lovett 2017).

**Results**

*Simulations*

The regime shift detector model’s outputs were very accurate in detecting input conditions of simulated datasets in low noise (<25%) conditions (Fig. obs\_outcomes). When the regime shift detector model indicated that it had found no breaks in the data, this result reflected input scenarios with nearly 90% accuracy when sampling error was below 50% (Fig. obs\_outcomes A). When the script identified scenarios with one or two breaks, sampling error affected the accuracy of outcomes more negatively, with accuracy dropping to just over 70% 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 regime shift detector model produced identical results to the previous implementation, even with the inclusion of four subsequent years of data (Bahlai, vander Werf, et al. 2015). 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). 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).  
  
*Case study- Monarch butterflies*

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 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 is, 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 model provides an objective tool for examining population regulation pattern shifts in natural populations. 253

The regime shift detector tool, as is, represents a compromise between sensitivity and simplicity. We illustrated through case studies 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 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 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. As we have demonstrated herein, alternate dynamics should be considered, and compared to outputs, for a holistic interpretation.

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 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.

**References**

**Bahlai, C. A., M. Colunga-Garcia, S. H. Gage, and D. A. Landis**. **2013**. Long term functional dynamics of an aphidophagous coccinellid community are unchanged in response to repeated invasion. PLoS One. 8: e83407.

**Bahlai, C. A., and M. K. Sears**. **2009**. Population dynamics of Harmonia axyridis and Aphis glycines in Niagara Peninsula soybean fields and vineyards. Journal of the Entomological Society of Ontario. 140: 27–39.

**Bahlai, C. A., W. vander Werf, M. O’Neal, L. Hemerik, and D. A. Landis**. **2015**. Shifts in dynamic regime of an invasive lady beetle are linked to the invasion and insecticidal management of its prey. Ecological Applications.

**Bahlai, C., M. Colunga-Garcia, S. Gage, and D. Landis**. **2015**. The role of exotic ladybeetles in the decline of native ladybeetle populations: evidence from long-term monitoring. Biol Invasions. 17: 1005–1024.

**Baker, N. T.** **2017**. Estimated annual agricultural pesticide use by crop group for states of the conterminous United States, 1992-2014. National Water Quality Assessment Program.

**Batalden, R. V., K. Oberhauser, and A. T. Peterson**. **2007**. Ecological Niches in Sequential Generations of Eastern North American Monarch Butterflies (Lepidoptera: Danaidae): The Ecology of Migration and Likely Climate Change Implications. Environmental Entomology. 36: 1365–1373.

**Berryman, A., and M. Lima**. **2006**. Deciphering the effects of climate on animal populations: diagnostic analysis provides new interpretation of Soay sheep dynamics. The American Naturalist. 168: 784–795.

**Bestelmeyer, B. T., A. M. Ellison, W. R. Fraser, K. B. Gorman, S. J. Holbrook, C. M. Laney, M. D. Ohman, D. P. C. Peters, F. C. Pillsbury, A. Rassweiler, R. J. Schmitt, and S. Sharma**. **2011**. Analysis of abrupt transitions in ecological systems. Ecosphere. 2: art129.

**Beverton, R. J., and S. J. Holt**. **1957**. On the dynamics of exploited fish populations. Springer Science & Business Media.

**Bjørnstad, O. N., and B. T. Grenfell**. **2001**. Noisy Clockwork: Time Series Analysis of Population Fluctuations in Animals. Science. 293: 638.

**Braun, J. V., and H.-G. Muller**. **1998**. Statistical Methods for DNA Sequence Segmentation. Statistical Science. 13: 142–162.

**Brower, L. P., L. S. Fink, R. J. Kiphart, V. Pocius, R. R. Zubieta, and M. I. Ramírez**. **2015**. Effect of the 2010–2011 drought on the lipid content of monarchs migrating through Texas to overwintering sites in Mexico, pp. 117–129. *In* Monarchs in a Changing World: Biology and Conservation of an Iconic Butterfly. Cornell University Press.

**Brower, L. P., D. R. Kust, E. Rendon-Salinas, E. G. Serrano, K. R. Kust, J. Miller, C. Fernandez del Rey, and K. Pape**. **2004**. Catastrophic winter storm mortality of monarch butterflies in Mexico during January 2002. The Monarch butterfly: biology and conservation. 151–166.

**Brower, L. P., D. A. Slayback, P. Jaramillo-López, I. Ramirez, K. S. Oberhauser, E. H. Williams, and L. S. Fink**. **2016**. Illegal logging of 10 hectares of forest in the Sierra Chincua monarch butterfly overwintering area in Mexico. American Entomologist. 62: 92–97.

**Burnham, K. P., and D. R. Anderson**. **2002**. Model selection and multimodal inference: a practical information-theoretic approach, 2nd ed. Springer Science + Business Media, LLC, New York.

**Carpenter, S. R., W. A. Brock, J. J. Cole, J. F. Kitchell, and M. L. Pace**. **2008**. Leading indicators of trophic cascades. Ecology Letters. 11: 128–138.

**Eason, T., A. S. Garmestani, C. A. Stow, C. Rojo, M. Alvarez-Cobelas, and H. Cabezas**. **2016**. Managing for resilience: an information theory-based approach to assessing ecosystems. J Appl Ecol. 53: 656–665.

**Flockhart, D. T. T., L. P. Brower, M. I. Ramirez, K. A. Hobson, L. I. Wassenaar, S. Altizer, and D. R. Norris**. **2017**. Regional climate on the breeding grounds predicts variation in the natal origin of monarch butterflies overwintering in Mexico over 38 years. Glob Change Biol. 23: 2565–2576.

**Forchhammer, M. C., and T. Asferg**. **2000**. Invading parasites cause a structural shift in red fox dynamics. Proceedings of the Royal Society of London B: Biological Sciences. 267: 779–786.

**Gadrich, T., and G. Katriel**. **2016**. A Mechanistic Stochastic Ricker Model: Analytical and Numerical Investigations. Int. J. Bifurcation Chaos. 26: 1650067.

**Goulson, D.** **2013**. An overview of the environmental risks posed by neonicotinoid insecticides. J Appl Ecol. 50: 977–987.

**Hare, S. R., and N. J. Mantua**. **2000**. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography. 47: 103–145.

**Heimpel, G., L. Frelich, D. Landis, K. Hopper, K. Hoelmer, Z. Sezen, M. Asplen, and K. Wu**. **2010**. European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America. Biological Invasions. 12: 2913–2931.

**Herron, G. A., and L. J. Wilson**. **2011**. Neonicotinoid resistance in Aphis gossypii Glover (Aphididae: Hemiptera) from Australian cotton. Australian Journal of Entomology. 50: 93–98.

**Jenouvrier, S., H. Weimerskirch, C. Barbraud, Y.-H. Park, and B. Cazelles**. **2005**. Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. Proceedings of the Royal Society B: Biological Sciences. 272: 887–895.

**Killick, R., and I. Eckley**. **2014**. changepoint: An R package for changepoint analysis. Journal of Statistical Software. 58: 1–19.

**Knapp, A. K., M. D. Smith, S. E. Hobbie, S. L. Collins, T. J. Fahey, G. J. A. Hansen, D. A. Landis, K. J. La Pierre, J. M. Melillo, T. R. Seastedt, G. R. Shaver, and J. R. Webster**. **2012**. Past, present, and future roles of long-term experiments in the LTER Network. Bioscience. 62: 377–389.

**Lovett, J.** **2017**. Monarch Population Status.

**May, R. M.** **1976**. Simple mathematical models with very complicated dynamics. Nature. 261: 459–467.

**Mueller, E. K., and K. A. Baum**. **2014**. Monarch-parasite interactions in managed and roadside prairies. Journal of insect conservation. 18: 847.

**Nauen, R., and I. Denholm**. **2005**. Resistance of insect pests to neonicotinoid insecticides: Current status and future prospects. Arch. Insect Biochem. Physiol. 58: 200–215.

**Pleasants, J. M., and K. S. Oberhauser**. **2013**. Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. Insect Conservation and Diversity. 6: 135–144.

**Powles, S. O. D. S. B.** **2010**. Glyphosate-resistant crops and weeds: now and in the future.

**Priyadarshana, W., and G. Sofronov**. **2015**. Multiple break-points detection in array CGH data via the cross-entropy method. IEEE/ACM Transactions on Computational Biology and Bioinformatics (TCBB). 12: 487–498.

**Puinean, A. M., S. P. Foster, L. Oliphant, I. Denholm, L. M. Field, N. S. Millar, M. S. Williamson, and C. Bass**. **2010**. Amplification of a Cytochrome P450 Gene Is Associated with Resistance to Neonicotinoid Insecticides in the Aphid Myzus persicae. PLOS Genetics. 6: e1000999.

**R Development Core Team**. **2017**. R: A Language and Environment for Statistical Computing 3.3.3. R Foundation for Statistical Computing.

**Rhainds, M., H. J. S. Yoo, P. Kindlmann, D. Voegtlin, D. Castillo, C. Rutledge, C. Sadof, S. Yaninek, and R. J. O’Neil**. **2010**. Two-year oscillation cycle in abundance of soybean aphid in Indiana. Agricultural and Forest Entomology. 12: 251–257.

**Ricker, W. E.** **1954**. Stock and Recruitment. J. Fish. Res. Bd. Can. 11: 559–623.

**RStudio Team**. **2015**. RStudio: Integrated Development for R (RStudio, Inc., Boston, MA, 2015). URL: https://www. rstudio. com/products/rstudio.

**Saunders, S. P., L. Ries, K. S. Oberhauser, W. E. Thogmartin, and E. F. Zipkin**. **2017**. Local and cross-seasonal associations of climate and land use with abundance of monarch butterflies Danaus plexippus. Ecography. n/a-n/a.

**Sutherland, W. J., R. P. Freckleton, H. C. J. Godfray, S. R. Beissinger, T. Benton, D. D. Cameron, Y. Carmel, D. A. Coomes, T. Coulson, M. C. Emmerson, R. S. Hails, G. C. Hays, D. J. Hodgson, M. J. Hutchings, D. Johnson, J. P. G. Jones, M. J. Keeling, H. Kokko, W. E. Kunin, X. Lambin, O. T. Lewis, Y. Malhi, N. Mieszkowska, E. J. Milner-Gulland, K. Norris, A. B. Phillimore, D. W. Purves, J. M. Reid, D. C. Reuman, K. Thompson, J. M. J. Travis, L. A. Turnbull, D. A. Wardle, and T. Wiegand**. **2013**. Identification of 100 fundamental ecological questions. J Ecol. 101: 58–67.

**Turchin, P.** **2003**. Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press.

**Urquhart, F. A., and N. R. Urquhart**. **1978**. Autumnal migration routes of the eastern population of the monarch butterfly (Danaus p. plexippus L.; Danaidae; Lepidoptera) in North America to the overwintering site in the Neovolcanic Plateau of Mexico. Can. J. Zool. 56: 1759–1764.

**Vidal, O., J. Lopez-Garcia, and E. Rendon-Salinas**. **2014**. Trends in Deforestation and Forest Degradation after a Decade of Monitoring in the Monarch Butterfly Biosphere Reserve in Mexico. Conservation Biology. 28: 177–186.

**Vidal, O., and E. Rendón-Salinas**. **2014**. Dynamics and trends of overwintering colonies of the monarch butterfly in Mexico. Biological Conservation. 180: 165–175.

**Wassenaar, L. I., and K. A. Hobson**. **1998**. Natal origins of migratory monarch butterflies at wintering colonies in Mexico: New isotopic evidence. Proceedings of the National Academy of Sciences. 95: 15436–15439.

**Weimerskirch, H., P. Inchausti, C. Guinet, and C. Barbraud**. **2003**. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. Antarctic Science. 15: 249–256.

**Zalucki, M. P., L. P. Brower, S. B. Malcolm, and B. H. Slager**. **2015**. Estimating the climate signal in monarch population decline. Monarchs in a changing world. Biology and conservation of an iconic butterfly.

**Zaya, D. N., I. S. Pearse, and G. Spyreas**. **2017**. Long-Term Trends in Midwestern Milkweed Abundances and Their Relevance to Monarch Butterfly Declines. BioScience. 67: 343–356.

**Zeileis, A., F. Leisch, K. Hornik, and C. Kleiber**. **2001**. strucchange. An R package for testing for structural change in linear regression models.

**Zipkin, E. F., C. E. Kraft, E. G. Cooch, and P. J. Sullivan**. **2009**. When can efforts to control nuisance and invasive species backfire? Ecological Applications. 19: 1585–1595.

**Zipkin, E. F., L. Ries, R. Reeves, J. Regetz, and K. S. Oberhauser**. **2012**. Tracking climate impacts on the migratory monarch butterfly. Glob Change Biol. 18: 3039–3049.

**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. 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.** 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. 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 obs\_outcomes: **Observed outcomes of Regime Shift Detector Script 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 sampling error (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 Harmonia: **Regime shift detector breaks and Ricker model fits for an invasive ladybeetle**. Population data documentis 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 pf apparent regime shifts as observed by Bahlai et al 2015. When data from 2014-2015 are included in the analysis (data following the black dashed line), the shift after 2005 is no longer detected by the model. B) Ricker fits of phases of population dynamics as determined by Bahlai et al 2015 (solid lines) and the new fit indicated by two additional years of sampling data (black dashed line).

Figure Monarch: **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, 1995-2016 A) Time series documenting raw data of estimated area occupied by overwintering monarchs by year. Vertical blue lines indicate timings of apparent regime shifts as indicated by the regime shift detector script. B) Ricker fits of phases of population dynamics as indicated by the regime shift detector script. Between each phase, the carrying capacity K decreased by about 50% from its former value, while r increased slightly in the transition from phase A to phase B. An alternate fit associated with a one break model that combine phases B and C, is given by the black dashed line.