

Comment on Capdevila et al. (2021) “Global patterns of resilience decline in vertebrate populations”

Mark D. Scheuerell^{1,*}

¹ U.S. Geological Survey Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA

* Correspondence: Mark D. Scheuerell <scheuerl@uw.edu>

This is version 0.21.11.17.

Background

Capdevila *et al.* (2021) use data from the Living Planet Database (Loh *et al.* 2005), to evaluate temporal trends in what they refer to as resistance and recovery. Given a time series of counts, Capdevila et al. (2021) first calculate the change in population size from one time step to another as

$$r_t = \log \left(\frac{N_{t+1}}{N_t} \right), \quad (1)$$

such that r indicates whether a population is increasing ($r > 0$), decreasing ($r < 0$) or stable ($r = 0$). They then refer to times when $r > 0$ as instances of recovery, and those when $r < 0$ as periods of resistance. Once the estimates of r have been calculated, Capdevila et al. create two different time series of recovery and resistance.

To estimate possible trends in recovery and resistance over time, Capdevila et al. use a state-space model for a biased random walk observed with error, whereby the true underlying change in population size is given by

$$r_t = r_{t-1} + \mu + E_t, \quad (2)$$

where μ is the upward or downward bias over time and $E_t \sim N(0, \sigma^2)$. The observed (estimated) change in population size (Y_t) is then given by

$$Y_t = r_t + F_t, \quad (3)$$

where $F_t \sim N(0, \tau^2)$ ¹. Capdevila then claim that they can rearrange equation (3) and substitute it into equation (2), as apparently Daskalova *et al.* (2020) did, to arrive at

$$Y_t = Y_{t-1} + \mu + E_t + F_t. \quad (4)$$

However, their algebra is incorrect and the combined equations should instead be

$$Y_t = Y_{t-1} + \mu + E_t + F_t - F_{t-1}. \quad (5)$$

Here I show that this approach fails to recover the true changes in the log of population size from time step to another, and offer a different, but related, approach to do so.

Estimating population size

There is a long history of estimating changes in population size from time series of count data, much of which is based upon a stochastic, discrete-time Gompertz model (Dennis & Taper 1994; Holmes 2001). Beginning with the deterministic version of the model,

$$n_t = n_{t-1} \exp[a + (b - 1) \log(n_{t-1})], \quad (6)$$

where n_t is the population size at time t , a is the intrinsic rate of population growth, and b is the strength of density dependence. When $b = 1$ the change in population size is density independent, and the strength of density dependence increased as $b \rightarrow 0$. On a log scale where $x_t = \log(n_t)$,

$$\begin{aligned} x_t &= x_{t-1} + a + (b - 1)x_{t-1} \\ &= a + bx_{t-1}. \end{aligned} \quad (7)$$

Here the equilibrium population size is given by $a/(1 - b)$ for $b \neq 1$. The stochastic version of this model is a simple, first-order autoregressive process, AR(1), given by

$$x_t = a + bx_{t-1} + e_t, \quad (8)$$

and $e_t \sim N(0, \sigma^2)$.

¹I note here that Capdevila et al. incorrectly refer to Y_t as the true change in population size, rather than r_t .

It is well known that sampling or observation errors will lead to an estimate of b that is biased low, suggesting the population is under greater density dependence than it is in reality. Thus, equation (8) is often combined with an explicit observation model to form a state-space model, whereby the observed log-counts (y_t) are a function of the true population size plus some error, such that

$$y_t = x_t + v_t, \quad (9)$$

and $v_t \sim N(0, \tau^2)$. Thus, rather than estimate the changes in population size from one time step to another from the observed counts, as Capdevila did with equation (1), the correct way to do so would be to fit the state-space model given by equations (8) and (9), and then use the estimates of x_t to examine changes population size over time, where

$$r_t^* = \left(\frac{x_{t+1}}{x_t} \right). \quad (10)$$

Other issues to consider

- length of time series (Capdevila claim 5 years is enough)

Simulation study

```
## load libraries
library("MARSS")

## set random seed for reproducibility
set.seed(123)

##
tt <- 20

qq <- 0.6

rr <- 0.3

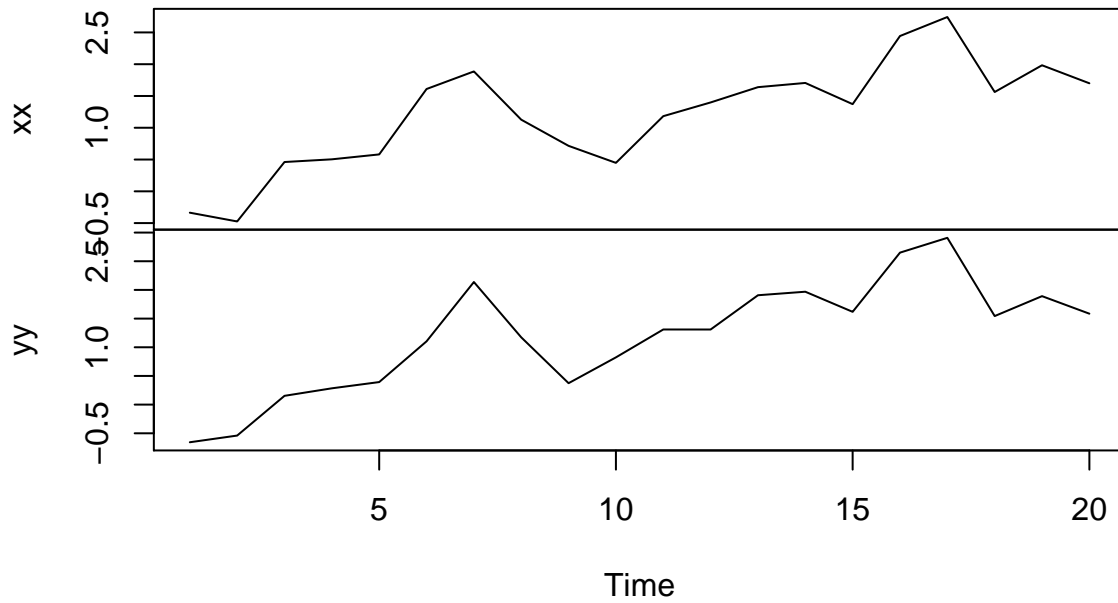
ww <- rnorm(tt, 0, qq)

xx <- cumsum(ww)
```

```
yy <- rnorm(tt, xx, rr)
```

```
plot.ts(cbind(xx, yy))
```

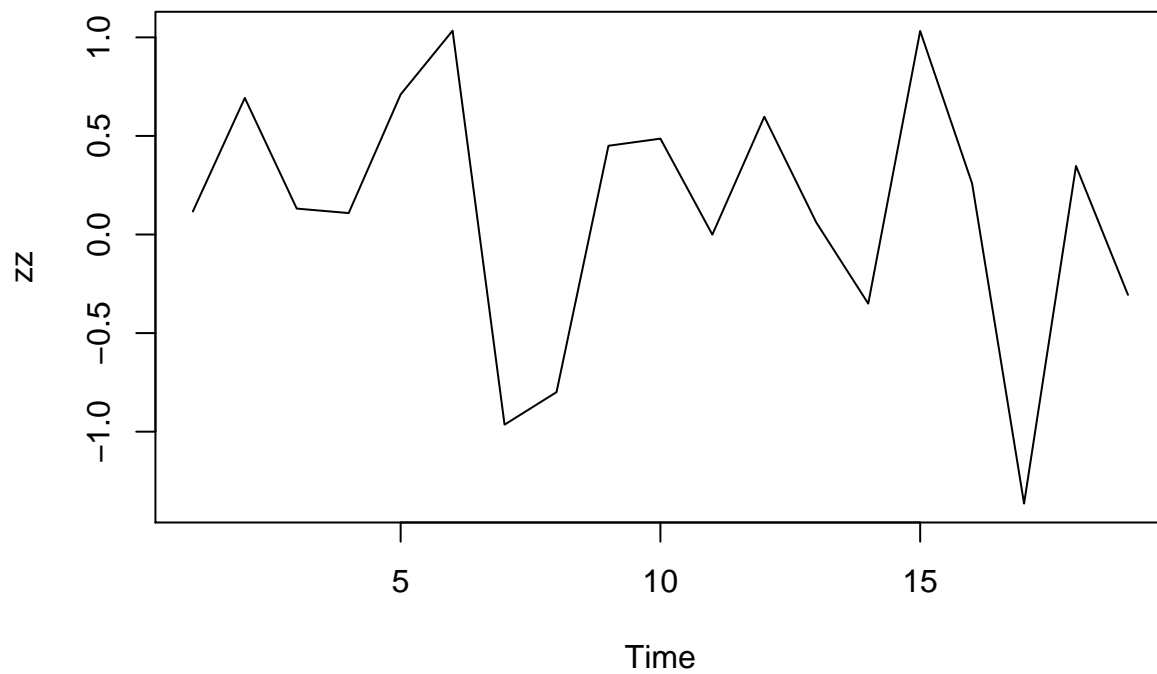
cbind(xx, yy)



50

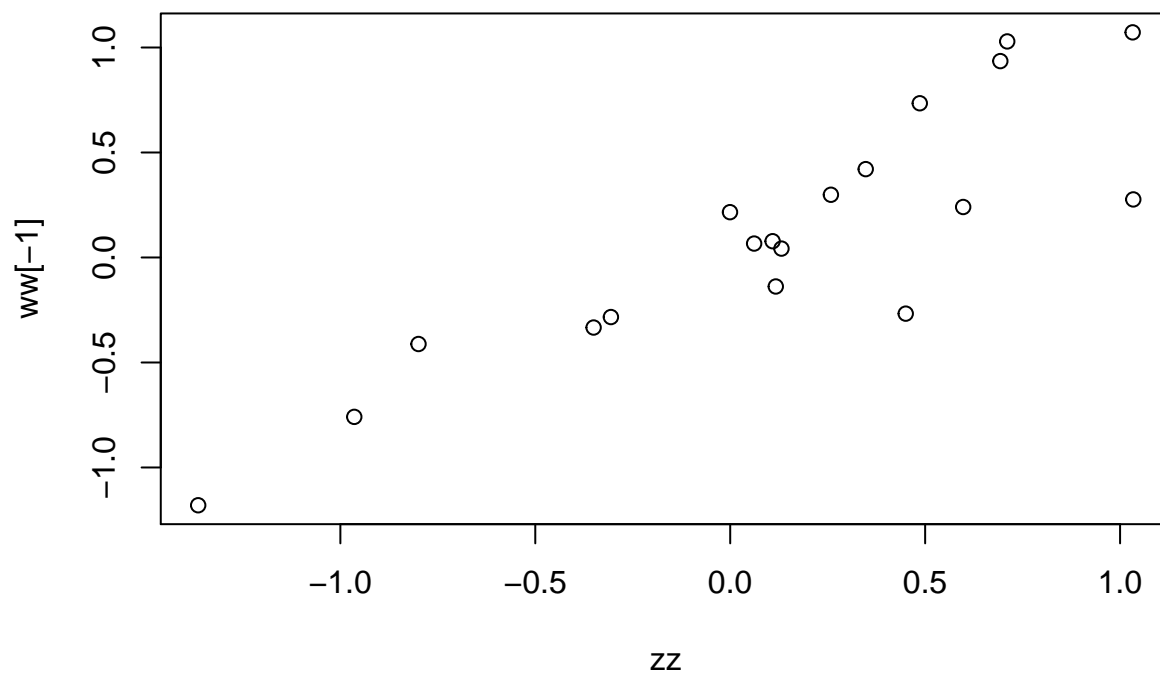
```
zz <- diff(yy)
```

```
plot.ts(zz)
```



51

```
plot(zz, ww[-1])
```



52

```
library(MARSS)

mod_list <- list(
  B = matrix("b"),
  U = matrix("u"),
```

```

Q = matrix("q"),
Z = matrix(1),
A = matrix(0),
R = matrix("r")
)

con_list <- list(maxit = 2000)

mod_fit <- MARSS(matrix(zz, nrow = 1), model = mod_list, control = con_list)

53 ## Success! abstol and log-log tests passed at 23 iterations.
54 ## Alert: conv.test.slope.tol is 0.5.
55 ## Test with smaller values (<0.1) to ensure convergence.
56 ##
57 ## MARSS fit is
58 ## Estimation method: kem
59 ## Convergence test: conv.test.slope.tol = 0.5, abstol = 0.001
60 ## Estimation converged in 23 iterations.
61 ## Log-likelihood: -18.14313
62 ## AIC: 46.28626    AICc: 50.90164
63 ##
64 ##      Estimate
65 ## R.r      0.286
66 ## B.b     -0.107
67 ## U.u      0.130
68 ## Q.q      0.108
69 ## x0.x0    0.516
70 ## Initial states (x0) defined at t=0
71 ##
72 ## Standard errors have not been calculated.
73 ## Use MARSSparamCIs to compute CIs and bias estimates.

cor(t(mod_fit$states), ww[-1])

74 ##      [,1]
75 ## X.Y1 0.869326

```

76 References

- 77 Capdevila, P., Noviello, N., McRae, L., Freeman, R. & Clements, C.F. (2021). Global
78 patterns of resilience decline in vertebrate populations. *Ecology Letters*.
- 79 Daskalova, G.N., Myers-Smith, I.H., Bjorkman, A.D., Blowes, S.A., Supp, S.R., Magurran,
80 A.E., *et al.* (2020). Landscape-scale forest loss as a catalyst of population and biodiver-
81 sity change. *Science*, 368, 1341–1347.
- 82 Dennis, B. & Taper, M.L. (1994). Density dependence in time series observations of natural
83 populations: Estimation and testing. *Ecological Monographs*, 64, 205–224.
- 84 Holmes, E.E. (2001). Estimating risks in declining populations with poor data. *Proceedings*
85 *of the National Academy of Sciences*, 98, 5072–5077.
- 86 Loh, J., Green, R.E., Ricketts, T., Lamoreux, J., Jenkins, M., Kapos, V., *et al.* (2005). The
87 living planet index: Using species population time series to track trends in biodiversity.
88 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360, 289–295.