

# Stability concerns in random matrices

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## Background on the key question

Recently, Patel et al. (2018) demonstrated the stability criteria for eco-evolutionary systems. A key result was that an unstable (stable) ecological community could be stabilised (destabilised) by fast eco-evolutionary feedback, assuming the evolutionary system was itself stable. Likewise, Patel et al. (2018) showed that an unstable (stable) evolutionary system could be stabilised (destabilised) by fast ecological feedback, assuming the ecological community was itself stable. **Here I am going to show why the stability criteria for eco-evolutionary systems is such that stable ecological systems are *increasingly* likely to be destabilised, and unstable ecological systems are *decreasingly* likely to be stabilised, at higher numbers of species traits.** I will use a random matrix approach similar to that of Allesina and colleagues (Allesina and Levine 2011; Allesina and Tang 2012, 2015). The mathematical concept of what I describe below is not new, and is a similar point to what May (1971) explained nearly half a century ago (that increasing species number decreases stability). Still, this point was not, that I can find, noticed or acknowledged by Patel et al. (2018) when coming up with their stability criteria.

Additionally, I want to look at random ecological matrices from the context of varying generation time, as partly inspired by the use of  $\varepsilon$  by Patel et al. (2018) and partly by Jirsa and Ding (2004) to separate generation time of different species in a community. Species generation time varies by orders of magnitude within communities, potentially affecting the rate at which the density of one species affects the population growth rate of the other. Yet I've not been able to find anything on this in the literature in a random matrix context. I want to **determine if the effects of varying generation time among community members is stabilising or destabilising in an ecological system.** Hence, the goals here are twofold.

1. Demonstrate the inherent destabilising effect of rapid evolution, which can also be interpreted as plasticity (Patel et al. 2018), on ecological communities.
2. Determine if variance in generation time stabilises or destabilises random matrices.

I'm not sure if either would make a publication, or perhaps just a blog post, and whether they would need to be completely separated. I will present one a time.

## The destabilising effect of rapid evolution

Assume a community of  $n$  species, each with the same evolving trait (e.g., body size). Each species  $i$  therefore has its own associated trait  $m_i$  (originally I was thinking about parental investment – I thought that I had come up with something really interesting, then realised that Parker and Begon (1986) got there first). We can describe the dynamics of a system with two species  $i$  and  $j$  using the Jacobian matrix  $\mathbf{J}$  below (Patel et al. 2018),

$$\mathbf{J} = \begin{bmatrix} \mathbf{A} & \mathbf{B} \\ \mathbf{C} & \mathbf{D} \end{bmatrix} = \begin{bmatrix} \frac{\partial N_i W_i}{\partial N_i} & \frac{\partial N_i W_i}{\partial N_j} & \frac{\partial N_i W_i}{\partial m_i} & \frac{\partial N_i W_i}{\partial m_j} \\ \frac{\partial N_j W_j}{\partial N_i} & \frac{\partial N_j W_j}{\partial N_j} & \frac{\partial N_j W_j}{\partial m_i} & \frac{\partial N_j W_j}{\partial m_j} \\ \varepsilon \frac{\partial m_i}{\partial N_i} & \varepsilon \frac{\partial m_i}{\partial N_j} & \varepsilon \frac{\partial m_i}{\partial m_i} & \varepsilon \frac{\partial m_i}{\partial m_j} \\ \varepsilon \frac{\partial m_j}{\partial N_i} & \varepsilon \frac{\partial m_j}{\partial N_j} & \varepsilon \frac{\partial m_j}{\partial m_i} & \varepsilon \frac{\partial m_j}{\partial m_j} \end{bmatrix}.$$

Note that the matrix  $\mathbf{J}$  can be separated into four separate submatrices. The submatrix  $\mathbf{A}$  describes the effects that the density of one species has on its own population growth (diagonal) or that of another species (off-diagonal). The submatrix  $\mathbf{B}$  describes the effect the trait  $m$  of each species has on the population growth of itself or another species. The submatrix  $\mathbf{C}$  describes the effect that the density of a species has on a

species' changing  $m$ , and  $\mathbf{D}$  describes the effect that traits have on traits. The value of  $\varepsilon$  defines the rate of evolutionary change relative to ecological change; here I will just assume a high value of  $\varepsilon$ , but the conclusions regarding an increasing number of traits' effect on a relatively slowly changing ecological system will be equally applicable to an increasing number of species in a relatively slowly evolving system. I will therefore only assume a high value of  $\varepsilon$  for now.

For the whole system (ecology and evolution) to be stable when traits change quickly relative to population densities, evolution by itself  $\mathbf{D}$  must be stable. This is the case when all of the eigenvalues of  $\mathbf{D}$  are negative. Additionally, for the system  $\mathbf{J}$  as a whole to be stable, we need to consider the feedback between ecology and evolution. Patel et al. (2018) showed that the system as a whole is stable when the following is satisfied,

$$s(\mathbf{A} + \mathbf{B}\mathbf{D}^{-1}(-\mathbf{C})) < 0.$$

I am specifically interested in the case in which  $\mathbf{D}$  is known to be stable. Using random matrices containing element values that are real numbers uniformly distributed between  $-4$  and  $4$ , I will show that rapid evolution is almost never stabilising and almost always destabilising when over six species and their traits  $m$  are considered. To do this, I will use the following code, which finds a stable random matrix  $\mathbf{D}$  and assigns random element values (possibly, but not necessarily stable) to  $\mathbf{A}$ ,  $\mathbf{B}$ , and  $\mathbf{C}$ . I will do this for 20000 replicates of species numbers from  $n = 2$  to  $n = 8$ .

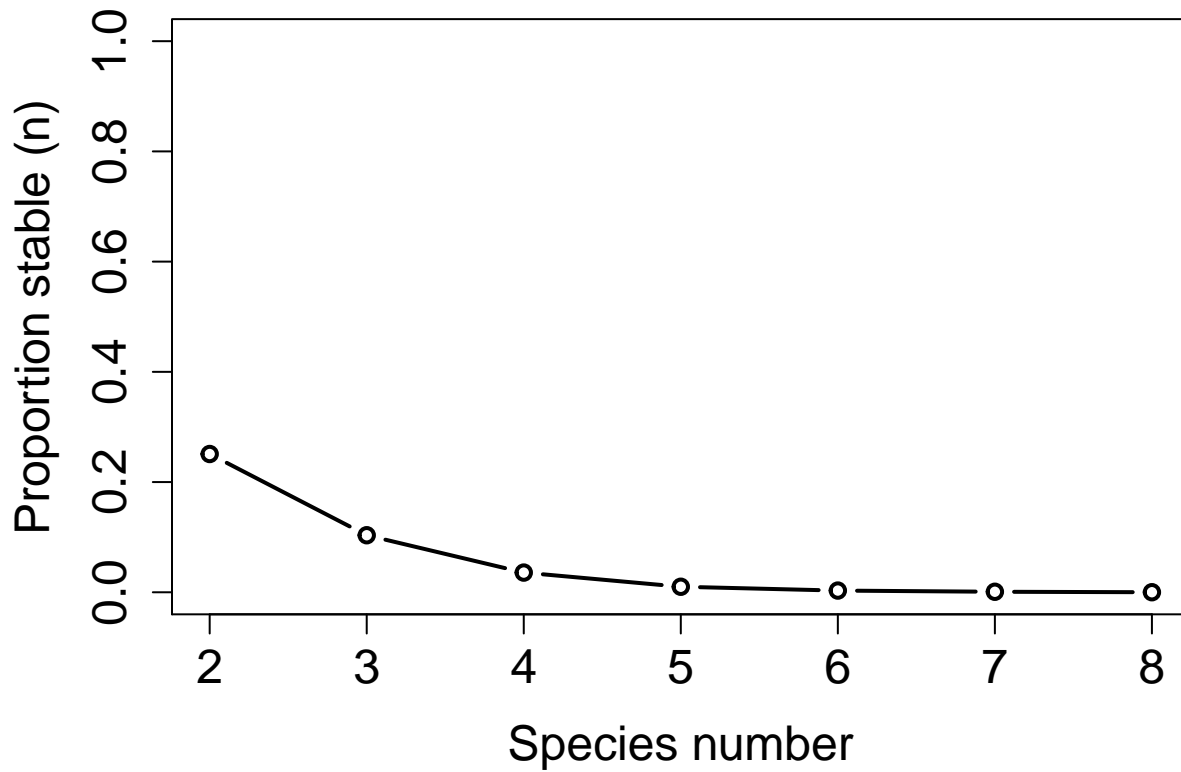
```
random_comm <- function(dm = 2, iter = 10000){
  stabilised_fastevo <- NULL;
  unstabled_fastevo <- NULL;
  nn <- dm * dm;
  tot_stabled <- 0;
  tot_unstabled <- 0;
  tot_eco_stab <- 0;
  stabilised_fastevo <- NULL;
  unstabled_fastevo <- NULL;
  while(iter > 0){
    stabilised <- 0;
    unstabilised <- 0;
    Adat <- runif(n = nn, min = -4, max = 4);
    Bdat <- runif(n = nn, min = -4, max = 4);
    Cdat <- runif(n = nn, min = -4, max = 4);
    A <- matrix(data = Adat, nrow = dm, ncol = dm);
    B <- matrix(data = Bdat, nrow = dm, ncol = dm);
    C <- matrix(data = Cdat, nrow = dm, ncol = dm);
    egD <- 1;
    while(egD >= 0){
      Ddat <- runif(n = nn, min = -4, max = 4);
      D <- matrix(data = Ddat, nrow = dm, ncol = dm);
      egD <- max(Re(eigen(D)$values))
    }
    eco_stable <- max(Re(eigen(A)$values)) < 0;
    slow_evo_maxE <- max(Re(eigen(A + B %*% solve(D) %*% (-C))$values));
    stable_fast_evo <- slow_evo_maxE < 0;
    if(eco_stable == FALSE & stable_fast_evo == TRUE){
      list_ele <- length(stabilised_fastevo$A) + 1;
      stabilised_fastevo$A[[list_ele]] <- A;
      stabilised_fastevo$B[[list_ele]] <- B;
      stabilised_fastevo$C[[list_ele]] <- C;
      stabilised_fastevo$D[[list_ele]] <- D;
      stabilised <- 1;
    }
  }
}
```

```

    }
    if(eco_stable == TRUE & stable_fast_evo == FALSE){
      list_ele <- length(unstabled_fastevo$A) + 1;
      unstabled_fastevo$A[[list_ele]] <- A;
      unstabled_fastevo$B[[list_ele]] <- B;
      unstabled_fastevo$C[[list_ele]] <- C;
      unstabled_fastevo$D[[list_ele]] <- D;
      unstabilised <- 1;
    }
    if(stabilised == 1){
      tot_stabled <- tot_stabled + 1;
    }
    if(unstabilised == 1){
      tot_ustabled <- tot_ustabled + 1;
    }
    if(eco_stable == TRUE){
      tot_eco_stab <- tot_eco_stab + 1;
    }
    iter <- iter - 1;
  }
  results <- list(ecologically_stable = tot_eco_stab,
                 stabilised = tot_stabled, destabilised = tot_ustabled,
                 stabilised_all = stabilised_fastevo,
                 destabilised_all = unstabled_fastevo);
  return(results);
}

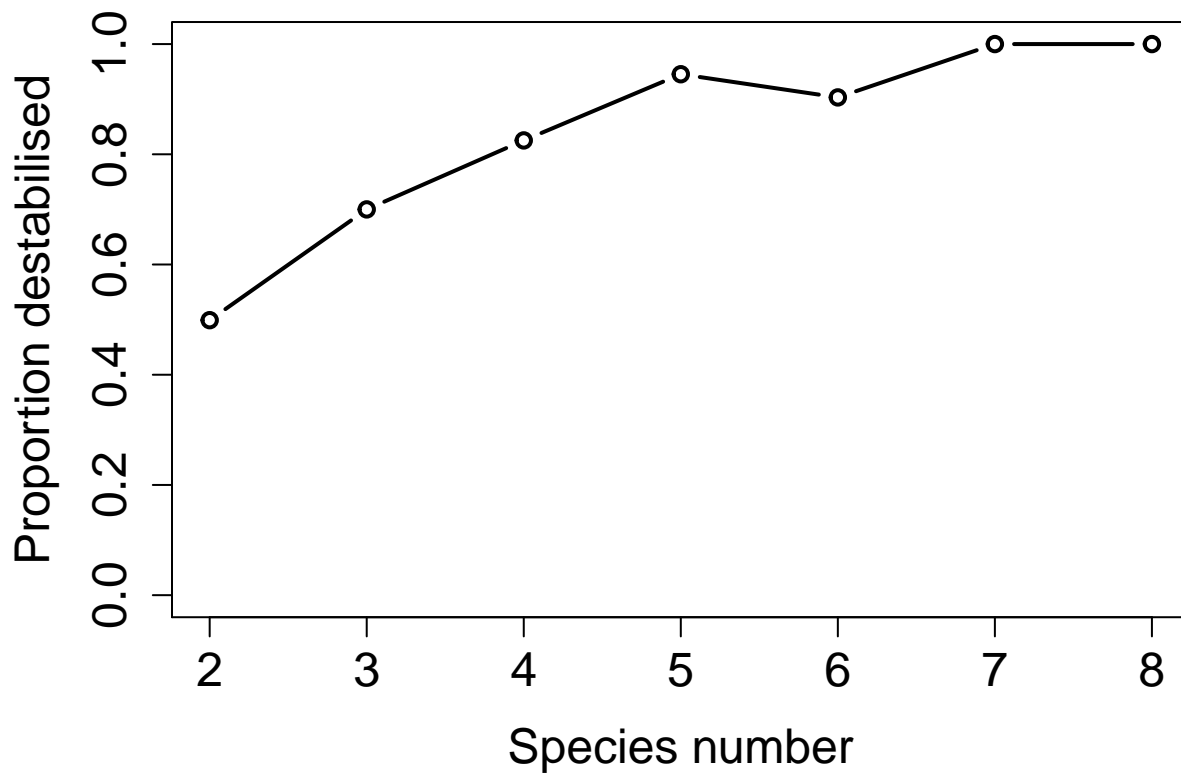
```

53 Note that the code above takes a while to run for a large number of species, and this is mostly caused by  
 54 having to find a random matrix  $D$  that is stable. The code first checks whether  $A$  is stable, and if it is stable,  
 55 whether or not eco-evolutionary dynamics destabilise the stable ecological community. If it is not stable, then  
 56 the code checks whether eco-evolutionary dynamics stabilise the unstable ecological community. As expected  
 57 (May 1971), ecological stability decreases with an increasing number of species.



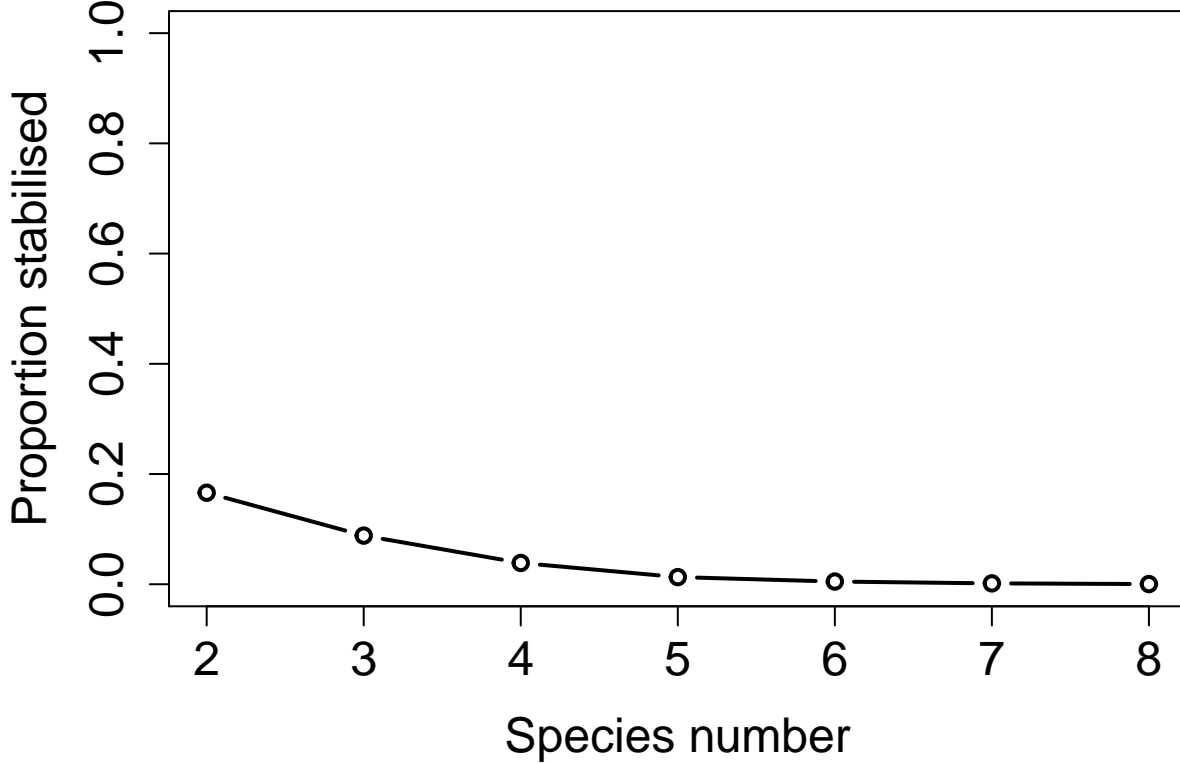
58

59 More interesting, the plot below shows eco-evolutionary results for ecological communities that **are** stable.  
 60 The x-axis shows the number of species in the community (recall that each species has the same evolving trait  
 61 potentially affecting ecology and evolution), and the y-axis shows the proportion of of these communities that  
 62 are *destabilised* by eco-evolutionary dynamics.



63

Note that the proportion of communities that are destabilised by eco-evolutionary effects increases with increasing species number. The plot below shows the eco-evolutionary results for ecological communities that are unstable. The y-axis here shows the proportion of communities that are *stabilised* by eco-evolutionary dynamics. This decreases with increasing species number.



Hence, overall, as species number and therefore evolving species traits increases, the probability that stable ecological communities become destabilised increases rapidly and the probability that unstable ecological communities are stabilised becomes vanishingly small. I am not sure if I can prove this mathematically, but I don't think I need to for the point to be made effectively. What I want to figure out is whether or not this point can or should be published in the peer-reviewed literature – else it's a blog post.

## The effect of variation in generation time on ecological stability

Here I will only consider  $\mathbf{A}$  and focus on the stability of ecological interactions given variation in generation time. I will use the same technique of Patel et al. (2018) for varying ecological and evolutionary time scales, but a bit differently. I assume that the response of a particular species' growth rate (rows in  $\mathbf{A}$ ) is consistently affected by a value  $\varepsilon_i$ ; higher values of  $\varepsilon_i$  correspond to shorter absolute generation times and lower values correspond to longer generation times. The matrix below  $\mathbf{A}$  for two species  $i$  and  $j$  with generation times  $\varepsilon_i$  and  $\varepsilon_j$ , respectively.

$$\mathbf{A} = \begin{bmatrix} \varepsilon_i \frac{\partial N_i W_i}{\partial N_i} & \varepsilon_i \frac{\partial N_i W_i}{\partial N_j} \\ \varepsilon_j \frac{\partial N_j W_j}{\partial N_i} & \varepsilon_j \frac{\partial N_j W_j}{\partial N_j} \end{bmatrix}.$$

I will allow random values of  $\varepsilon_i$  to vary from 1 to 100, modelling two orders of magnitude of generation times. I will compare the stability of two sets of random community matrices – one in which all  $\varepsilon = 1$  and another in which  $\varepsilon$  varies.

```

nn      <- 8;
A1_stt <- 0;
A2_stt <- 0;
iter    <- 100000;
while(iter > 0){
  A1_dat <- runif(n = nn * nn, min = -4, max = 4);
  A1      <- matrix(data = A1_dat, nrow = nn, ncol = nn);
  A2_dat <- runif(n = nn * nn, min = -4, max = 4);
  A2      <- matrix(data = A2_dat, nrow = nn, ncol = nn);
  epsil   <- runif(n = nn, min = 1, max = 100);
  eps_dat <- rep(x = epsil, times = nn);
  eps_mat <- matrix(data = epsil, nrow = nn, ncol = nn, byrow = FALSE);
  A2       <- A2 * eps_mat;
  A1_stb   <- max(Re(eigen(A1)$values)) < 0;
  A2_stb   <- max(Re(eigen(A2)$values)) < 0;
  if(A1_stb == TRUE){
    A1_stt <- A1_stt + 1;
  }
  if(A2_stb == TRUE){
    A2_stt <- A2_stt + 1;
  }
  iter     <- iter - 1;
}

```

The number of stable random matrices when  $\varepsilon$  does not vary was 13, and the number of stable random matrices when it does was 48 (several re-runs of the above code found this result to be roughly the same for  $n = 8$ , with smaller differences for lower  $n$ , and presumably larger differences for higher  $n$ ). The effect of varying  $\varepsilon$  appears to be more extreme with an increasing number of species. Hence, overall, **variation in generation time appears to be stabilising for random ecological communities**. Again, I am not sure if this is something that I can prove mathematically, and I cannot decide whether the result is interesting enough to try to publish by itself or in tandem with the above. If not, it might be another blog post.

## References

- Allesina, S., and J. M. Levine. 2011. A competitive network theory of species diversity. *Proceedings of the National Academy of Sciences of the United States of America* 108:5638–5642.
- Allesina, S., and S. Tang. 2012. Stability criteria for complex ecosystems. *Nature* 483:205–208. Nature Publishing Group.
- Allesina, S., and S. Tang. 2015. The stability–complexity relationship at age 40: a random matrix perspective. *Population Ecology* 63–75.
- Jirsa, V. K., and M. Ding. 2004. Will a large complex system with time delays be stable? *Physical Review Letters* 93:1–4.
- May, R. M. 1971. Stability in multispecies community models. *Mathematical Biosciences* 12:59–79.
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- Patel, S., M. H. Cortez, and S. J. Schreiber. 2018. Partitioning the effects of eco-evolutionary feedbacks on community stability. *American Naturalist* 191:1–29.