

Stability concerns in random matrices

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The below is a draft introductory paragraph or abstract. I believe that we could get [an article on the above](#) clearly in the space of 3500, or maybe even 1500 words. As far as I've been able to find, such an article would be novel and interesting (and, I hope, mathematically correct). These notes are divided into two parts at the moment.

1. [The effect of variation in generation time on community stability.](#)
2. [The effect of increasing numbers of evolutionary traits on eco-evolutionary stability.](#)

I suspect that part 2 will need to branch off soon, but I don't want to forget about it.

The effect of variation in generation time on community stability

Analyses of dynamic systems using random matrices find that stability generally decreases with increasing system size. But in ecological communities, the rate that species densities change as a consequence of species interactions will depend on relative species generation times. Densities of species with relatively short generation times will change more rapidly than densities of species with longer generation times. Interaction effects are therefore expected to be correlated within species, with some species densities changing more rapidly than others in a community. Here we show that by accounting for variation in generation time among species, community stability is substantially increased. Further, the influence of variation in generation time becomes exponentially more important as community size increases. We suggest that variation in species generation time might be a key contributor to stability of large ecological communities.

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 another. Yet I've not been able to find anything on this in the literature in a random matrix context (or any other context). I want to **determine if the effects of varying generation time among community members is stabilising or destabilising in an ecological system.** This work is partly inspired by the use of ε by Patel et al. (2018) to separate the time scale of ecological versus evolutionary dynamics, and partly inspired by Jirsa and Ding (2004) to separate generation time of different species in a community.

Here I will consider a Jacobian matrix of interacting species \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 effect that the density of any species j (N_j) has on the growth rate of a focal species i ($\partial N_i W_i / \partial N_j$) is consistently affected by a value γ_i (I am using γ_i instead of ε_i to avoid confusing generation time variance with ecological versus evolutionary rate difference). Higher values of γ_i correspond to shorter absolute generation times and lower values correspond to longer generation times. The matrix below \mathbf{A} describes the dynamics for two species i and j with effects of generation times γ_i and γ_j , respectively.

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

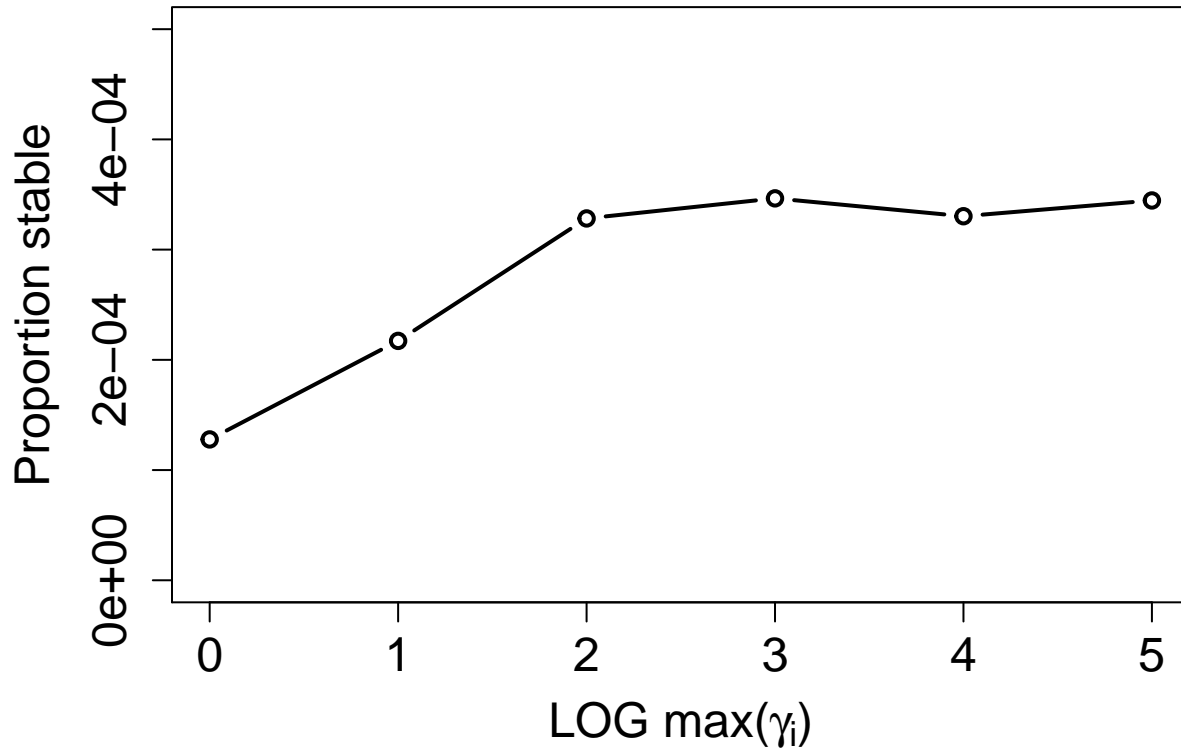
I will investigate **how the amount of variation in generation time (range of γ) in a community affects stability.** Below is some code to look at stability in random communities with eight species across

41 different magnitudes of variance in generation time. Random values of γ_i are chosen for each species i from a
 42 uniform distribution $\mathcal{U}(1, \max(\gamma_i))$.

```
res <- NULL;
mags <- 10^(0:5);
for(i in mags){
  nn <- 8;
  A1_stt <- 0;
  A2_stt <- 0;
  iter <- 10000000;
  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);
    gamval <- runif(n = nn, min = 1, max = i);
    gam_dat <- rep(x = gamval, times = nn);
    gam_mat <- matrix(data = gam_dat, nrow = nn, ncol = nn, byrow = FALSE);
    A2 <- A2 * gam_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;
  }
  res <- rbind(res, c(A1_stt, A2_stt));
  print(i);
}
```

43 The code above produces the following results showing the proportion of random communities that are stable
 44 as $\max(\gamma_i)$ increases in orders of magnitude (note that I'm using eight species, so the y-axis shows a very low
 45 proportion range).

```
mag_var <- read.table(file = "var_gen_mag.csv", header = TRUE, sep = ",");
stabi_3 <- mag_var[,3] / 10000000;
par(mar = c(5, 5, 2, 1));
plot(x = log10(mag_var[,1]), y = stabi_3, type = "b", lwd = 2, ylim = c(0, 0.0005),
     xlab = expression(paste("LOG max(", gamma[i], ")")), ylab = "Proportion stable",
     cex.axis = 1.5, cex.lab = 1.5, lty = "solid");
```



46

47 **Once the generation time varies by an order of magnitude of around 1000, there is little return**
 48 **in terms of stability.** To continue, we can simulate different sizes of communities with species numbers
 49 between 2 and 8 for identical generation times versus magnitudes of generation time variation of 1000.

```
res <- NULL;
for(i in 2:8){
  nn      <- i;
  A1_stt <- 0;
  A2_stt <- 0;
  iter    <- 1000000;
  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 = 1000);
    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;
  }
  res <- rbind(res, c(A1_stt, A2_stt));
}
```

```

    print(i);
}

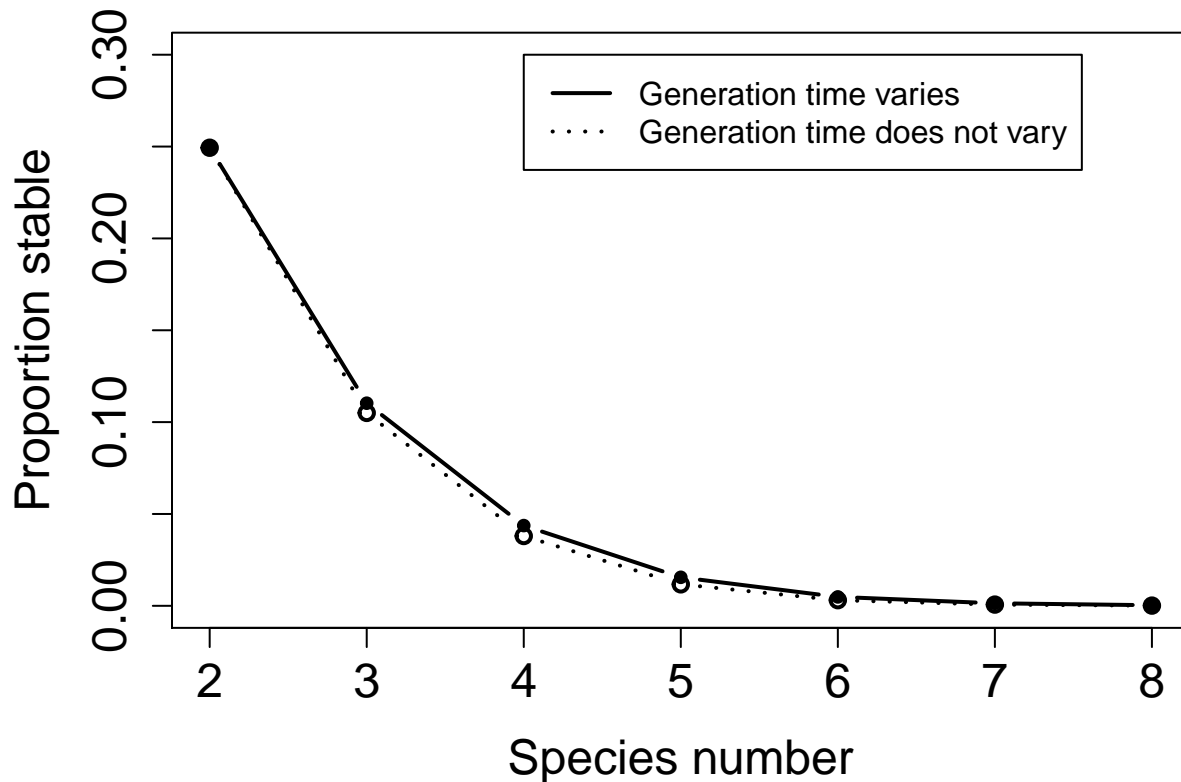
```

50 The plot below shows the result for the proportion of stable random communities when generation time varies
 51 (solid line, closed points) versus when generation time varies over two orders of magnitude (dotted line, open
 52 points).

```

gen_var <- read.table(file = "dif_sp_gen_var.csv", header = TRUE, sep = ",");
stabi_1 <- gen_var[,2] / 1000000;
stabi_2 <- gen_var[,3] / 1000000;
par(mar = c(5, 5, 2, 1));
plot(x = gen_var[,1], y = stabi_1, type = "b", lwd = 2, ylim = c(0, 0.3),
     xlab = "Species number", ylab = "Proportion stable",
     cex.axis = 1.5, cex.lab = 1.5, lty = "dotted");
points(x = gen_var[,1], y = stabi_2, type = "b", lwd = 2, ylim = c(0, 0.3),
       lty = "solid", pch = 20);
legend(x = 4, y = 0.3, lwd = 2,
       legend = c("Generation time varies", "Generation time does not vary"),
       lty = c("solid", "dotted"));

```



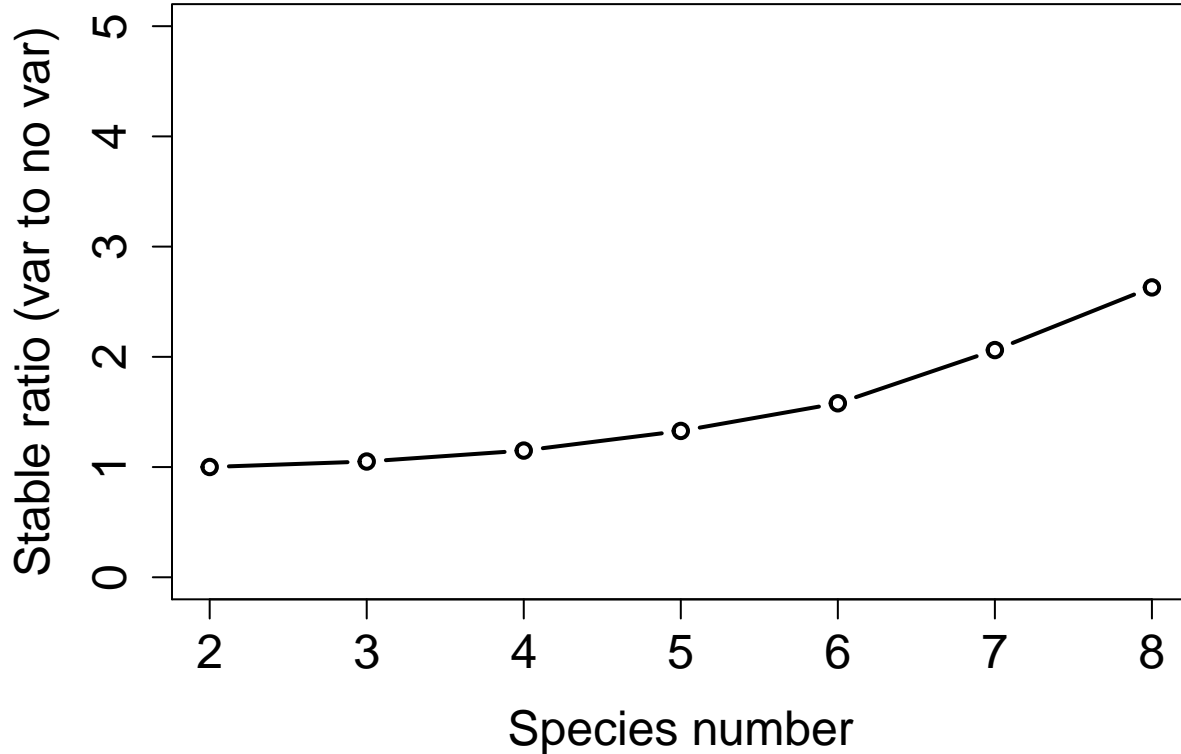
53

54 It is difficult to see the difference between these two numbers, so the figure below shows the ratio
 55 of the proportion of stable communities given generation variation relative to no generation variation
 56 (No_gen_var:Gen_var).

```

par(mar = c(5, 5, 2, 1));
plot(x = gen_var[,1], y = stabi_2 / stabi_1, type = "b", lwd = 2, ylim = c(0, 5),
     xlab = "Species number", ylab = "Stable ratio (var to no var)",
     cex.axis = 1.5, cex.lab = 1.5, lty = "solid");

```



As species number increases, variation in generation time appears to have a stronger influence in stabilising random communities. In other words, all else being equal, variation in generation time becomes more important for stabilising system dynamics as the size of the system increases.

The effect of increasing numbers of evolutionary traits on eco-evolutionary stability

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.

Hence, the goal here is to demonstrate the inherent destabilising effect of rapid evolution, which can also be interpreted as plasticity (Patel et al. 2018), on ecological communities.

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 ε defines the rate of evolutionary change relative to ecological change; here I will just assume a high value of ε , 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 ε 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 100000 replicates of species numbers from $n = 2$ to $n = 8$.

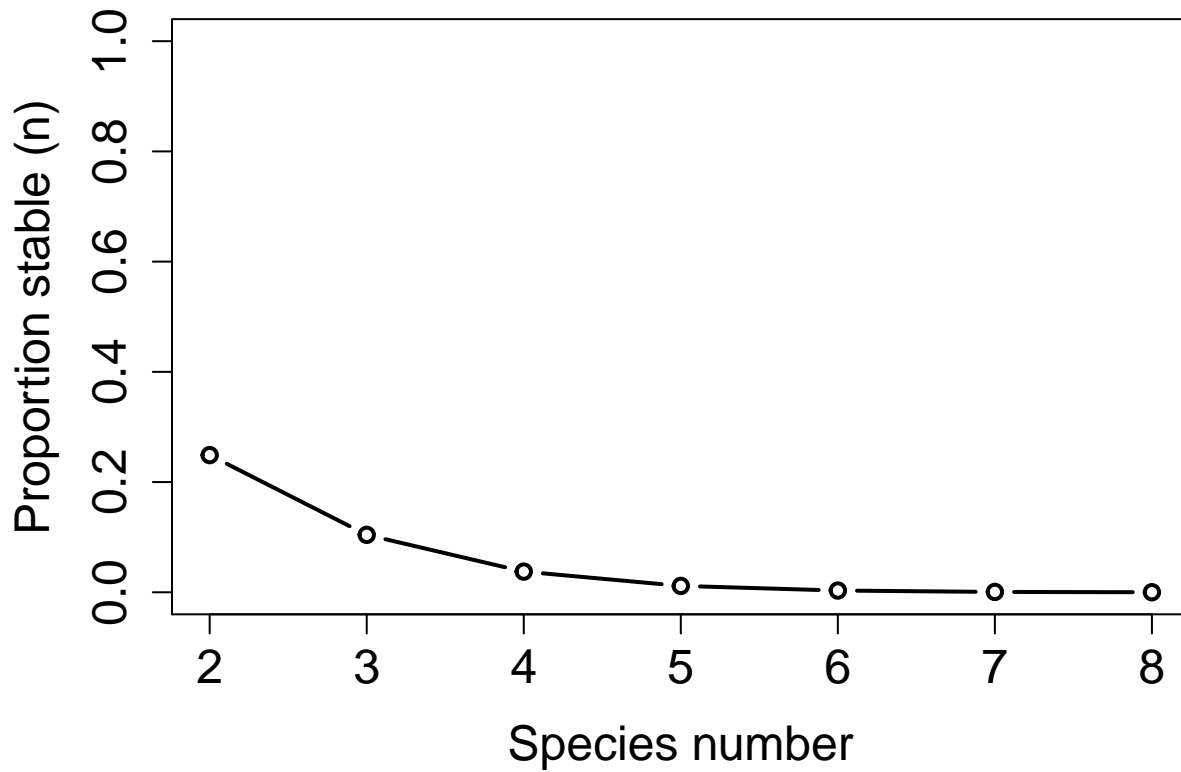
```
random_comm <- function(dm = 2, iter = 10000){
  stabilised_fastevo <- NULL;
  unstabled_fastevo <- NULL;
  nn <- dm * dm;
  tot_stabled <- 0;
  tot_unstabled <- 0;
  tot_eco_stab <- 0;
  stabilised_fastevo <- NULL;
  unstabled_fastevo <- NULL;
  while(iter > 0){
    stabilised <- 0;
    unstabilised <- 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$D[[list_ele]] <- D;
  stabilised    <- 1;
}
if(eco_stable == TRUE & stable_fast_evo == FALSE){
  list_ele <- length(unstabilised_fastevo$A) + 1;
  unstabilised_fastevo$A[[list_ele]] <- A;
  unstabilised_fastevo$B[[list_ele]] <- B;
  unstabilised_fastevo$C[[list_ele]] <- C;
  unstabilised_fastevo$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 = unstabilised_fastevo);
return(results);
}

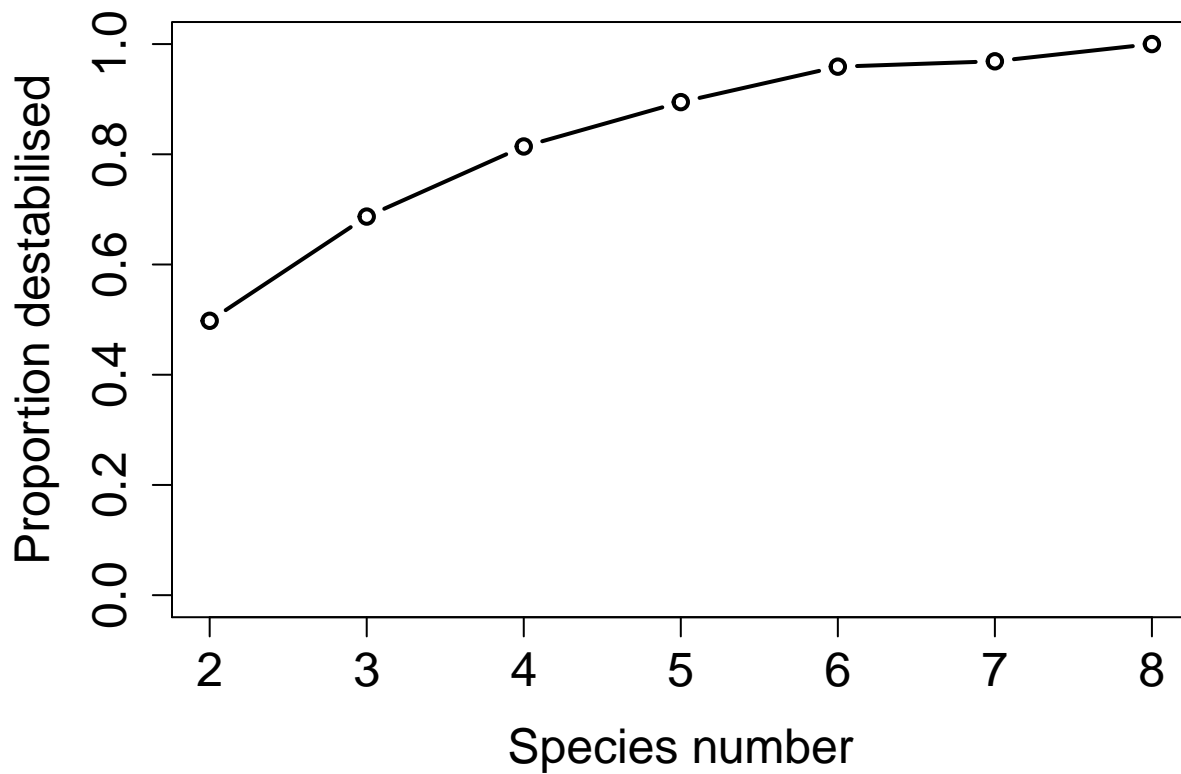
```

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



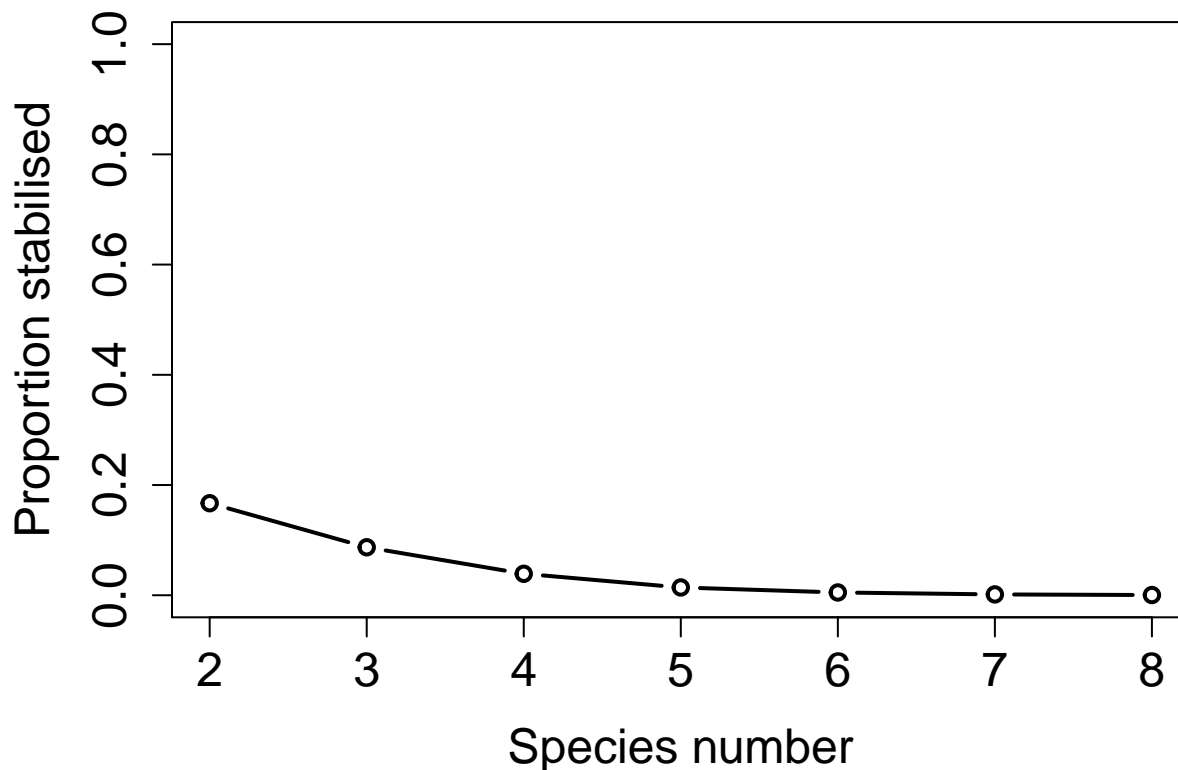
107

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



112

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.

References

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¹³⁷ community stability. *American Naturalist* 191:1–29.