

# Supporting Information

A.T. Tredennick, P.B. Adler, & F.R. Adler, “The relationship between species richness and...”  
*Ecology Letters*

## Section SI.1 R Code for Consumer-Resource Model

Below is the R code for our model function, which is represented mathematically in the main text in Equations 1-4. The same code, along with all the code to reproduce our results, has been archived on Figshare (link) and is available on GitHub (<http://github.com/atredennick/Coexistence-Stability/releases>).

```
simulate_model <- function(seasons, days_to_track, Rmu,
                           Rsd_annual, sigE, rho,
                           alpha1, alpha2, alpha3, alpha4,
                           eta1, eta2, eta3, eta4,
                           r1, r2, r3, r4,
                           a1, a2, a3, a4,
                           b1, b2, b3, b4,
                           eps1, eps2, eps3, eps4,
                           D1, D2, D3, D4,
                           N1, N2, N3, N4, R) {

  require('deSolve') # for solving continuous differential equations
  require('mvtnorm') # for multivariate normal distribution functions

  ## Assign parameter values to appropriate lists
  DNR <- c(D=c(D1,D2,D3,D4), # initial dormant state abundance
           N=c(N1,N2,N3,N4), # initial live state abundance
           R=R)              # initial resource level

  parms <- list (
    r = c(r1,r2,r3,r4),      # max growth rate for each species
    a = c(a1,a2,a3,a4),      # rate parameter for Hill function
    b = c(b1,b2,b3,b4),      # shape parameter for Hill function
    eps = c(eps1,eps2,eps3,eps4) # resource-to-biomass efficiency
  )

  #####
  ##### Sub-Model functions -----
```

```

####
## Continuous model
updateNR <- function(t, NR, parms){
  with(as.list(c(NR, parms)), {
    dN1dt = N1*eps[1]*(uptake_R(r[1], R, a[1], b[1]))
    dN2dt = N2*eps[2]*(uptake_R(r[2], R, a[2], b[2]))
    dN3dt = N3*eps[3]*(uptake_R(r[3], R, a[3], b[3]))
    dN4dt = N4*eps[4]*(uptake_R(r[4], R, a[4], b[4]))
    dRdt = -1 * (dN1dt/eps[1] + dN2dt/eps[2] + dN3dt/eps[3] + dN4dt/eps[4])
    list(c(dN1dt, dN2dt, dN3dt, dN4dt, dRdt)) # output as list
  })
} # end continuous function

## Discrete model
update_DNR <- function(t, DNR, gammas,
                        alpha1, alpha2, alpha3, alpha4,
                        eta1, eta2, eta3, eta4) {
  with (as.list(DNR),{
    g1 <- gammas[1]
    g2 <- gammas[2]
    g3 <- gammas[3]
    g4 <- gammas[4]
    D1new <- (1-g1)*(alpha1*N1 + D1)*(1-eta1)
    D2new <- (1-g2)*(alpha2*N2 + D2)*(1-eta2)
    D3new <- (1-g3)*(alpha3*N3 + D3)*(1-eta3)
    D4new <- (1-g4)*(alpha4*N4 + D4)*(1-eta4)
    N1new <- g1*(alpha1*N1 + D1)*(1-eta1)
    N2new <- g2*(alpha2*N2 + D2)*(1-eta2)
    N3new <- g3*(alpha3*N3 + D3)*(1-eta3)
    N4new <- g4*(alpha4*N4 + D4)*(1-eta4)
    Rnew <- Rvector[t]
    return(c(D1new, D2new, D3new, D4new, N1new, N2new, N3new, N4new, Rnew))
  })
}

## Resource uptake function (Hill function)
uptake_R <- function(r, R, a, b) {
  return((r*R^a) / (b^a + R^a))
}

```

```

## Generate germination fractions
getG <- function(sigE, rho, nTime, num_spp) {
  varcov      <- matrix(rep(rho*sigE,num_spp*2), num_spp, num_spp)
  diag(varcov) <- sigE
  if(sigE > 0) { varcov <- Matrix::nearPD(varcov)$mat } # crank through nearPD to fix rounding
  varcov <- as.matrix(varcov)
  e      <- rmvnorm(n = nTime, mean = rep(0,num_spp), sigma = varcov)
  g      <- exp(e) / (1+exp(e))
  return(g)
}

####
#### Simulate model -----
####
days      <- c(1:days_to_track)
num_spp    <- length(parms$r)
nmsDNR     <- names(DNR)
dormants   <- grep("D", names(DNR))
NR         <- DNR[-dormants]
nmsNR      <- names(NR)
gVec       <- getG(sigE = sigE, rho = rho, nTime = seasons, num_spp = num_spp)
Rvector    <- rlnorm(seasons, Rmu, Rsd_annual)
saved_outs <- matrix(ncol=length(DNR), nrow=seasons+1)
saved_outs[1,] <- DNR

## Loop over seasons
for(season_now in 1:seasons) {
  # Simulate continuous growing season
  output <- ode(y = NR, times=days, func = updateNR, parms = parms)
  NR     <- output[nrow(output),nmsNR]
  dormants <- grep("D", names(DNR))
  DNR     <- c(DNR[dormants], NR)

  # Save end of season biomasses, before discrete transitions
  saved_outs[season_now+1,] <- DNR

  names(DNR) <- nmsDNR

```

```

DNR      <- update_DNR(season_now, DNR, gVec[season_now,],
                      alpha1 = alpha1, alpha2 = alpha2,
                      alpha3 = alpha3, alpha4 = alpha4,
                      eta1 = eta1, eta2 = eta2, eta3 = eta3, eta4 = eta4)

names(DNR) <- nmsDNR
NR        <- DNR[-dormants]
names(NR)  <- nmsNR
} # next season

return(saved_outs)

} #end simulation function

```

## Section SI.2 Exploring Parameter Space

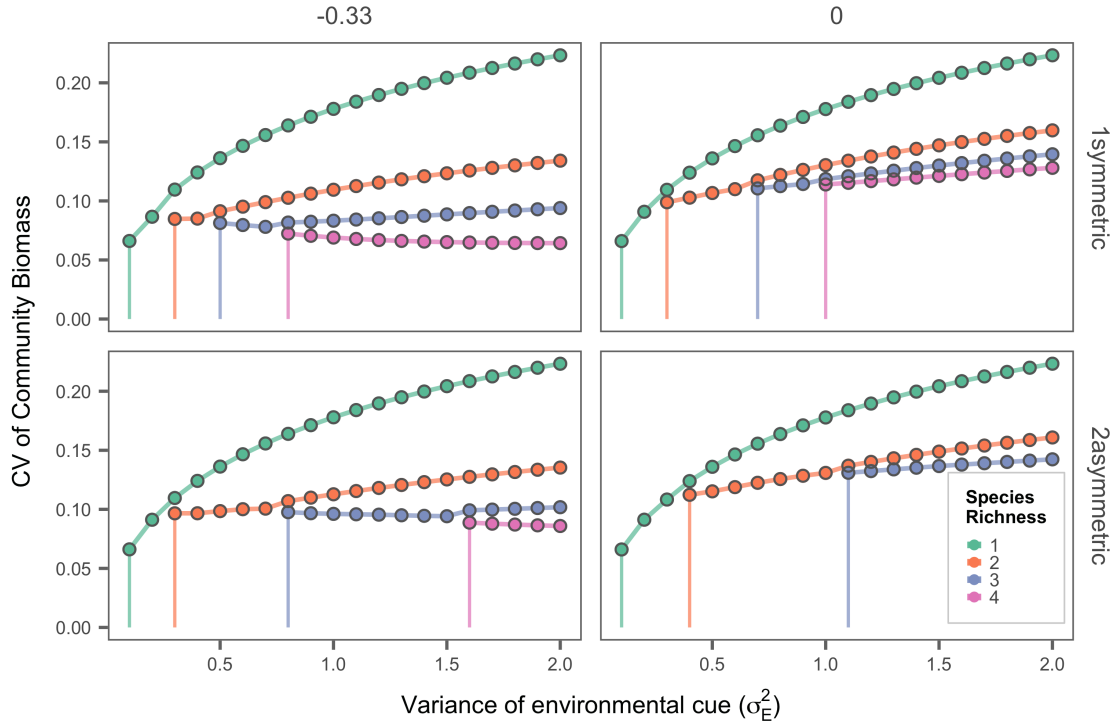
In the main text we presented results that most clearly demonstrated our main point, sacrificing some quantitative rigor in terms of exploring the parameter space of the model. In many cases, altering model parameters, or making them asymmetric among species, makes coexistence more difficult. For example, as we show in Figure 3 in the main text, imposing competitive hierarchies makes it more difficult for species to coexist, but it does not impact our conclusion that a positive diversity–ecosystem variability relationship is possible. We imposed competitive hierarchies by making the live-to-dormant biomass fractions unique for each species, but any parameter that controls population growth would do the same. For example, if we make dormant mortality rates assymetric among species we achieve similar results as shown in Figure 3 (Fig. S1-1).

While the results of competitive assymetries among species are rather intuitive, the sensitivity of our results to changes in the absolute values of parameters is less intuitive and requires exploration. We took a targeted approach to exploring parameter space by focusing on particular processes. First, we examined the sensitivity of our results to parameters that control the strength of each coexistence mechanism. Second, we examined the sensitivity of our results to parameters that previous theory have identified as important for the diversity–ecosystem variability relationship. We describe each in turn.

### Section SI.2.1 Parameter sensitivity: coexistence strength

For the storage effect, coexistence strength declines as:

1. Environment-competition covariance (*EC* covariance) becomes less positive
2. Environemntal variation decreases



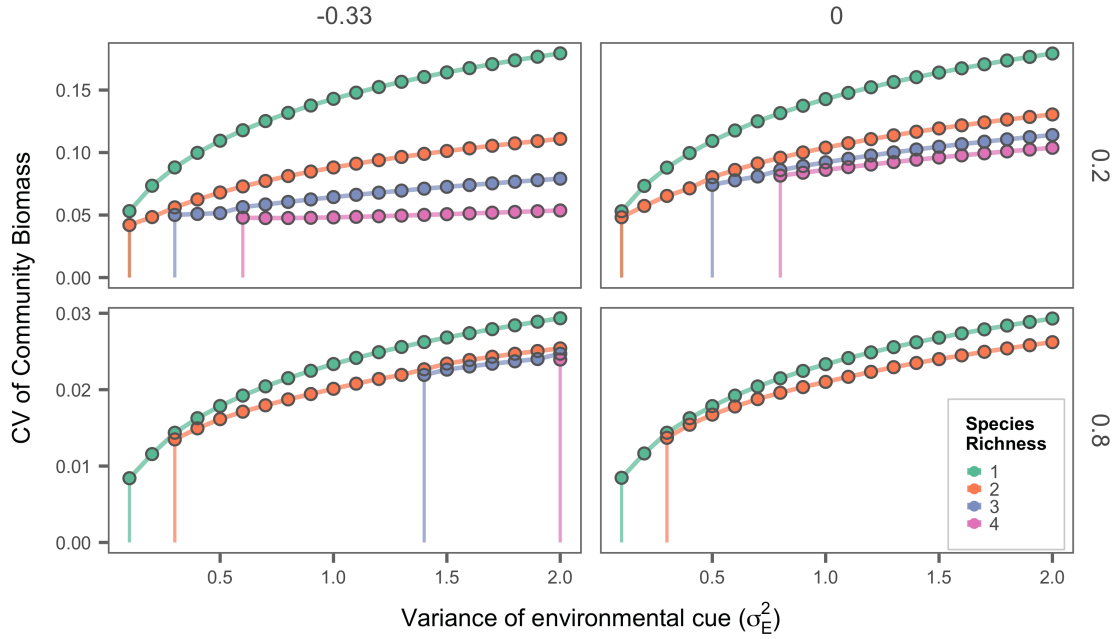
**Figure S1-1** The effect of increasing environmental variability on ecosystem variability when species coexist via the storage effect. Top panels show simulation results where species have relatively symmetric dormant mortality rates ( $\eta_1 = 0.1, \eta_2 = 0.115, \eta_3 = 0.12, \eta_4 = 0.125$ ), whereas bottom panels show results with slightly more asymmetric dormant mortality rates ( $\eta_1 = 0.1, \eta_2 = 0.12, \eta_3 = 0.13, \eta_4 = 0.14$ ). Columns show results for different levels of correlations of species' environmental responses,  $\rho = -1/3$  and  $\rho = 0$ . Colored vertical lines show the magnitude of environmental variability at which each level of species richness first occurs. Parameter values are as in Figure 2A except for  $\alpha$ s:  $\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = 0.5$ .

### 3. Buffering of population growth rate declines

Conditions 1 & 2 are already included in our main analysis because we present results across a spectrum of correlations among species' environmental responses (condition 1) and across gradients of environmental variation (condition 2). Here, we show how the patterns described in the main text change as the buffering of population growth declines (condition 3). We do this by conducting the same simulations as in Figure 3 of the main text, but for one set of live-to-dormant transition rates ( $\alpha$ s) and with two levels (high and low) of dormant mortality rates ( $\eta$ s).

Our results are qualitatively similar: (1) increasing environmental variation allows more species to coexist, creating a positive relationship between species richness and ecosystem variability; (2) and at any given level of environmental variability, it is always better to have more species, creating a within-site negative relationship between species richness and ecosystem variability (Fig. S1-2). Although the qualitative patterns are similar, increasing the dormant mortality rate has two interesting effects: (1) it makes coexistence more difficult, (2) it reduces the absolute value of ecosystem CV by reducing mean population size a little bit

and by reducing the temporal standard deviation a lot, and (3) it weakens the buffering effect of additional species (compare the spread of the lines between top and bottom panels of Fig. S1-2). The second result occurs because population fluctuations are reduced when very little biomass can be activated to the live stage at the beginning of each season. That is, in terms of an annual plant, germination of live biomass is always a fraction of a very small number. The third result is a consequence of the second: populations are not fluctuating that much, so total CV can only be reduced by so much with the addition of another species.



**Figure S1-2** The effect of increasing environmental variability on ecosystem variability when species coexist via the storage effect. Top panels show simulation results where species have low dormant mortality rates ( $\eta = 0.2$ ), whereas bottom panels show results with high dormant mortality rates ( $\eta = 0.8$ ). Columns show results for different levels of correlations of species' environmental responses,  $\rho = -1/3$  and  $\rho = 0$ . Colored vertical lines show the magnitude of environmental variability at which each level of species richness first occurs. Parameter values are as in Figure 2A except for  $\alpha$ s:  $\alpha_1 = 0.5$ ,  $\alpha_2 = 0.495$ ,  $\alpha_3 = 0.49$ ,  $\alpha_4 = 0.485$ .

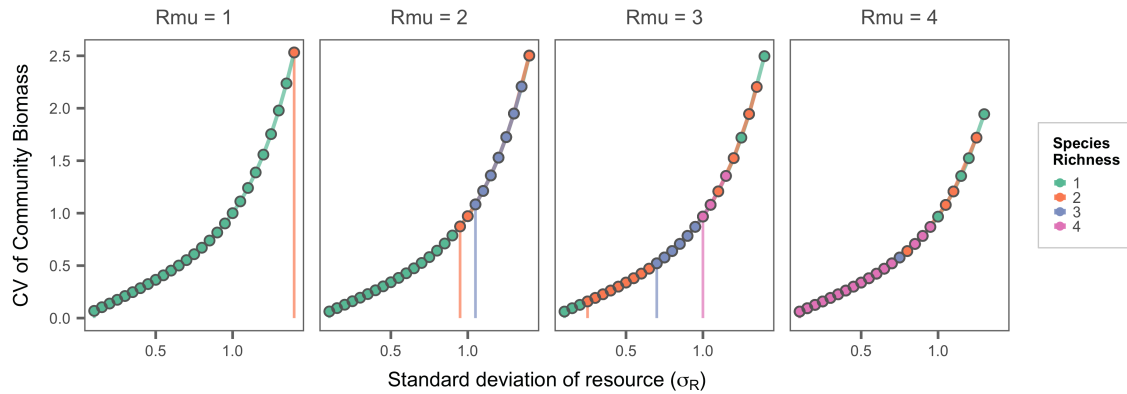
For relative nonlinearity, coexistence strength declines as:

1. Variability in population densities, here driven by resource variability, declines
2. Species' resource uptake curves become more similar
3. Mean resource level declines

Condition 1 is already included in our main analysis (Figures 2 and 4). Condition 2 simply creates conditions where some species cannot coexist, which would not change the relationship between species richness and ecosystem variability, but rather disallow it. Condition 3 is more interesting, because it could create situations where species may not coexist, but it could also weaken the diversity–ecosystem variability relationship by reducing mean biomass and the effect of species with very nonlinear growth rates. To explore the effect of condition 3, we ran simulations across a gradient of resource variability (11 levels) crossed with a gradient of

mean resource levels (4 levels:  $\mu_R = 1, 2, 3, 4$ ).

As expected, lower mean levels of resource make coexistence more difficult because resource acquisitive species are never favored (Fig. S1-x). Our general conclusion remains, however, that positive diversity–ecosystem variability relationships are possible. However, the occurrence of a positive diversity–ecosystem variability relationship depends on amount of resource variability being sampled over and the traits of individual species (e.g., resource uptake curves). In other words, the patterns we report in the main text require that species coexistence be possible given the environmental conditions.



**Figure S1-3** The effect of environmental variability on ecosystem variability when species coexist via relative nonlinearity. The species pool increases from one to four species, with the fourth species being most unstable (e.g., resource conservative to resource acquisitive). Increasing environmental variability (the SD of annual resource availability) allows for greater species richness, but species additions do not modulate the effect of environmental variability on ecosystem variability. Higher values of mean resource availability (left to right across panels) makes coexistence easier. Parameter values are as in Figure 2C in the main text.

## Section SI.2.2 Parameter sensitivity: diversity–ecosystem variability parameters

**THIS SECTION IN PROGRESS...** Previous theory (Loreau & de Mazancourt 2013) identifies three main mechanisms by which diversity can reduce ecosystem variability:

1. Aysnchrony of species' responses to environmental conditions
2. Reduced mean competition at the community-level
3. Differences in population growth rates, which differentiates the speed at which species respond to perturbations.

CV scaled by the mean, and we don't have demographic stochasticity because we are assuming large populations, so reducing overall competition to get over-yielding doesn't matter here. . .

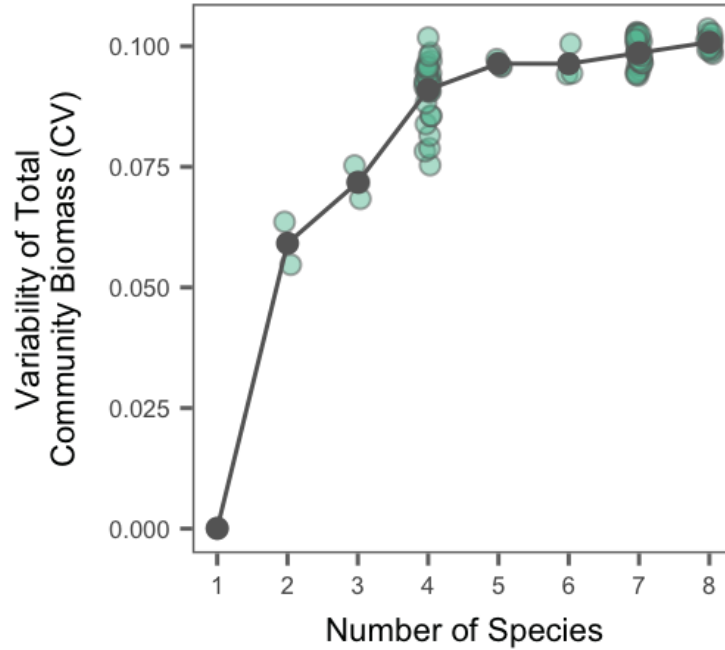
### Section SI.3 Eight-Species Storage Effect Model

In the main text we constrained our focus to four-species communities because getting more than four species to coexist by relative nonlinearity is tricky, and usually requires adding another coexistence mechanism on top of relative nonlinearity (Yuan & Chesson 2015). The storage effect does not suffer from this limitation, but we wanted our results in the main text to be easily comparable between coexistence mechanisms. Here, we show that our results are qualitatively similar if we simulate an eight-species community with species coexistence maintained by the storage effect. We conducted the same numerical simulations described in the main text for Figure 2. Quoting from the main text:

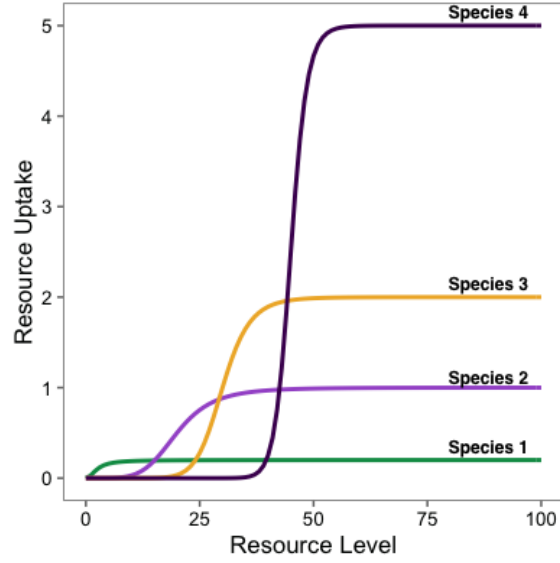
*First, we allowed the variance of the environment to determine how many species can coexist, akin to a community assembly experiment with a species pool of four species. To do this, we simulated communities with all species initially present across a gradient of annual resource variability (for relative nonlinearity) or environmental cue variability (for the storage effect). Second, we chose parameter values that allowed coexistence of all four species and then performed species removals, akin to a biodiversity–ecosystem function experiment. The two simulation experiments correspond to (i) sampling ecosystem function across a natural gradient of species richness and (ii) sampling ecosystem function across diversity treatments within a site.*

From one to four species, the relationship is as presented in the main text: total community CV increases approximately linearly with environmental variability because (1) environmental variability promotes species coexistence and (2) environmental variability causes populations fluctuations to increase (Figure S1-x). However, after four species, the relationship saturates — species additions due to coexistence by the storage effect completely buffer ecosystem variability from further increases in environmental variability (Figure S1-x). Thus, our results provide novel theoretical explanations for positive and flat diversity–ecosystem variability relationships.





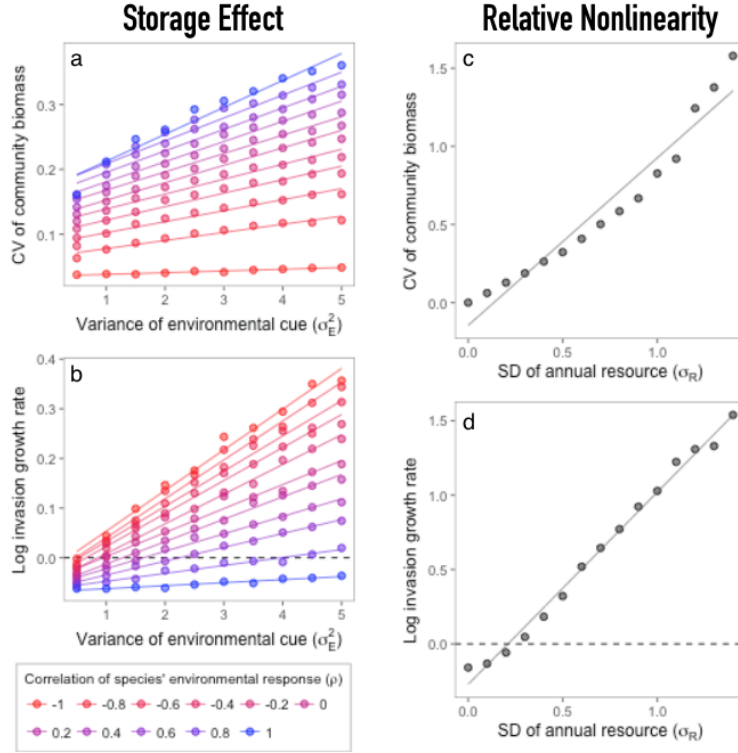
**Figure S1-4** Variability of total community biomass as a function of species richness when coexistence is maintained by the storage effect. Results are from simulations where environmental variance determines the number species that coexist in a community (e.g., a “regional” relationship). Colored points show results from individual simulations and the gray points with connecting line show the mean at each level of environmental variance.



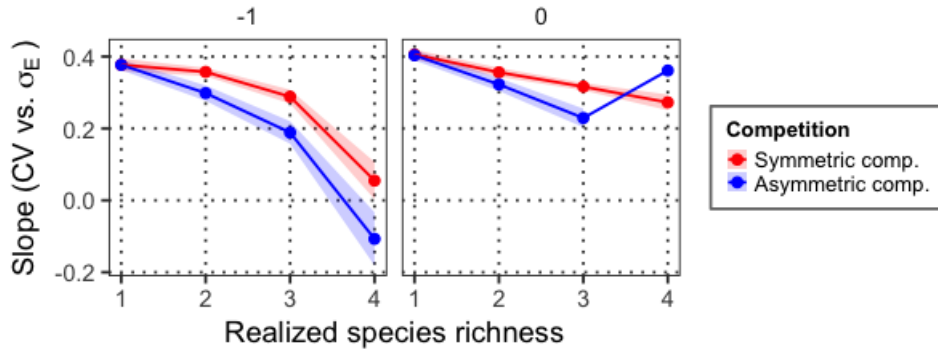
**Figure S1-5** Resource uptake curves for each species (represented by different colors) as used in relative nonlinearity simulations. The equation for resource uptake is:  $f_i(R) = r_i R^{a_i} / (b_i^{a_i} + R^{a_i})$ . Parameter values are as follows. Species 1:  $r = 0.2$ ,  $a = 2$ ,  $b = 2.5$ ; Species 2:  $r = 1$ ,  $a = 5$ ,  $b = 20$ ; Species 3:  $r = 2$ ,  $a = 10$ ,  $b = 30$ ; Species 4:  $r = 5$ ,  $a = 25$ ,  $b = 45$ .

## References

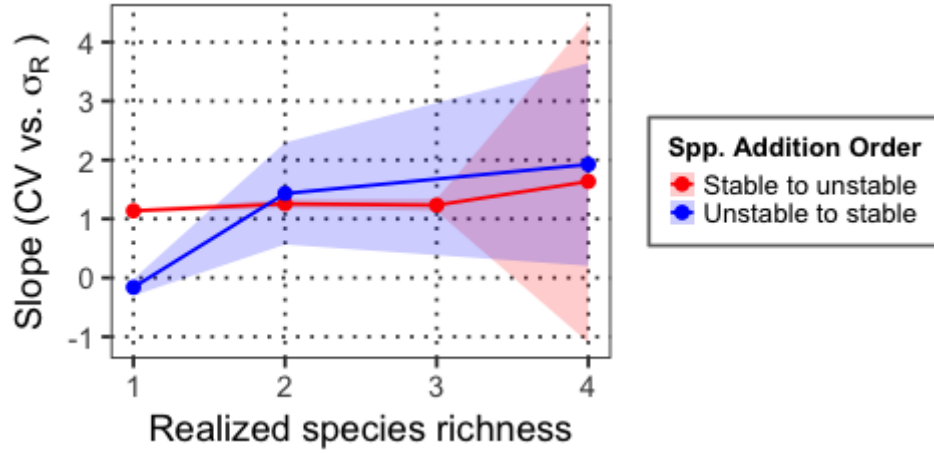
- Loreau, M. & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, 16, 106–115.
- Yuan, C. & Chesson, P. (2015). The relative importance of relative nonlinearity and the storage effect in the lottery model. *Theoretical Population Biology*, 105, 39–52.



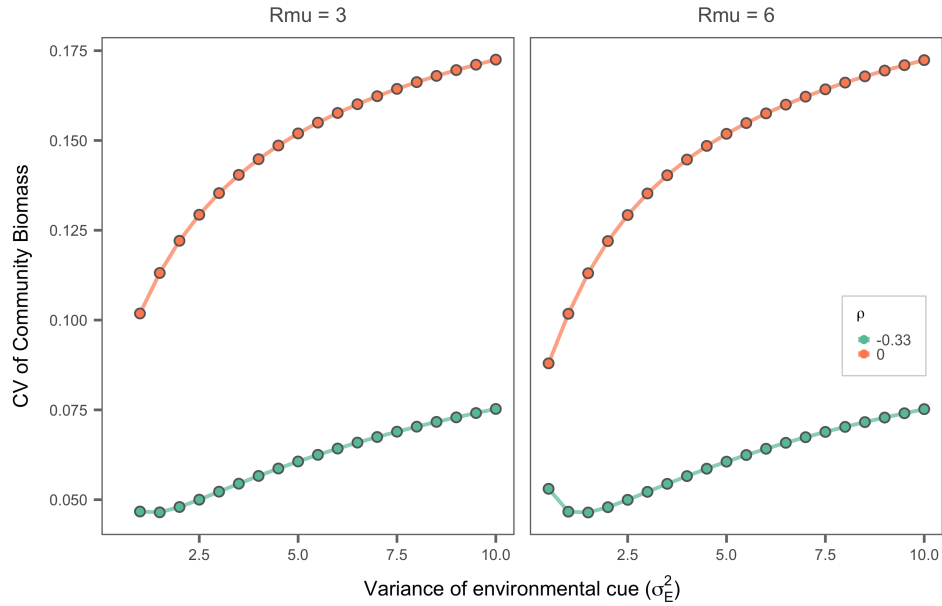
**Figure S1-6** Variability of community biomass and invasion growth rates of the inferior competitor in a two-species community under different parameter combinations. Points are mean values from 5,000 growing seasons and lines are linear fits to show trends. In **Storage Effect** plots (a,b), resource supply is held constant between growing seasons. Resource supply varies each year in **Relative Nonlinearity** simulations (c,d), while the environmental cue variance is set to 0.



**Figure S1-7** Slopes of linear fits for the relationship between  $\log(CV)$  and  $\log(\sigma_E)$  at different levels of realized species richness from storage effect simulations. The slopes come from linear models fit to log-transformed versions of Figure 3 in the main text. For these simulations, “symmetric competition” (●) refers to similar live-to-dormant biomass allocation fractions ( $\alpha = [0.5, 0.495, 0.49, 0.485]$  for the four species), and “asymmetric competition” (●) refers to more dissimilar live-to-dormant biomass allocation fractions ( $\alpha = [0.5, 0.49, 0.48, 0.47]$  for the four species).



**Figure S1-8** Slopes of linear fits for the relationship between  $\log(CV)$  and  $\log(\sigma_R)$  at different levels of realized species richness from relative nonlinearity simulations. The slopes come from linear models fit to log-transformed versions of Figure 4 in the main text.



**Figure S1-9** Ecosystem CV of a four-species community as a function of environmental cue variance at two levels of mean resource availability ( $R_{mu}$  across tops of panels) and two levels of correlation of species' responses to environmental conditions ( $\rho$ ). Here we simulated community dynamics across a greater range of environmental cue variance (up to 10) to show that the CV of four-species communities does not remain flat as environmental variance increases beyond levels shown in the main text. The mean resource level has no effect on the results.