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

5 Below is the R code for our model function, which is represented mathematically in the main text in Equations
6 1-4. The same code, along with all the code to reproduce our results, has been archived on Figshare (link)
7 and is available on GitHub (http://github.com/atredennick/Coexistence-Stability/releases).

```r
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
  require('Runuran') # for truncated log normal random number generator


  ##  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
  DNR_inits <- DNR


  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) {
```

```r
    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 roundi
  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)

if(Rsd_annual == 0) { # urlnorm can't handle zero variance
  Rvector      <- rlnorm(seasons, Rmu, Rsd_annual)
}
if(Rsd_annual > 0) { # when variance greater than zero
  Rvector      <- urlnorm(seasons, Rmu, Rsd_annual, lb = 0, ub = 200)
}

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
```

```r
    output    <- ode(y = NR, times = days, func = updateNR, parms = parms, atol = 1e-100)
    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   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.*
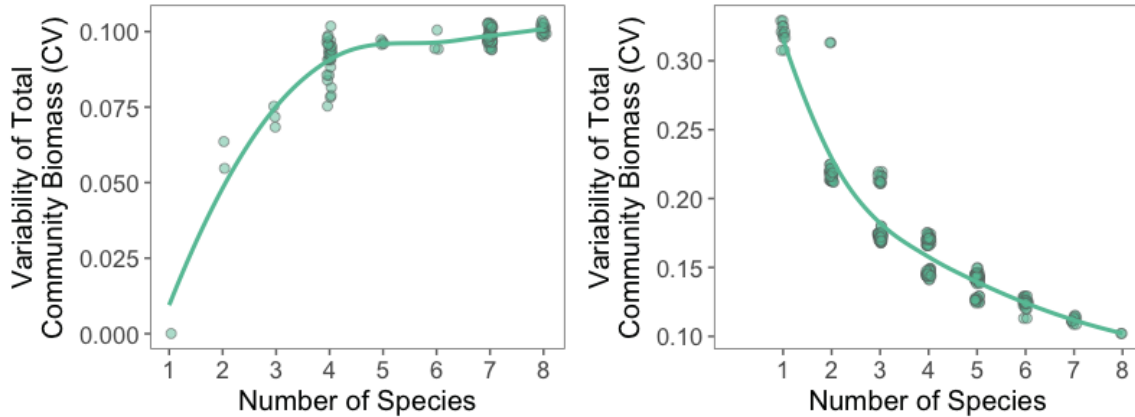


**Figure SI-1**   Variability of total community biomass as a function of species richness when coexistence is maintained by the storage effect. The left panel shows results from simulations where environmental cue variance determines the number of species that coexist in a community. The right panel shows results from simulations where environmental cue variance is fixed at a level ($\sigma_E^2 = 10$, which is where the far right cluster of points are in the left panel) that allows coexistence of all eight species, but species are removed to manipulate diversity. The left-hand panel represents a "regional" diversity–ecosystem variability relationship across a natural diversity gradient, whereas the right-hand panel represents a "local" diversity–ecosystem variability relationship. Points are jittered within discrete richness values for visual clarity. Lines show the mean trend (loess fits).

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 population fluctuations to increase (Figure SI-4). 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 SI-4). Thus, our results provide novel theoretical explanations for positive and flat diversity–ecosystem variability relationships.

# Section SI.3  Sensitivity of Results to Parameters

We relied on numerical simulations to reach the conclusions presented in the main text, which means our results could be sensitive to the particular parameter values chosen. Here we assess the sensitivity of the results by taking a targeted approach to exploring parameter space. Specifically, we examine the sensitivity of our results to parameters that control the strength of each coexistence mechanism.

In the main text we did explore some parameter space by conducting simulations across gradients of environmental variance (whether the cue or the resource), correlations of species' responses to environmental conditions, and competitive asymmetries. 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 asymmetric among species we achieve similar results as shown in Figure 3 (Fig. SI-1).
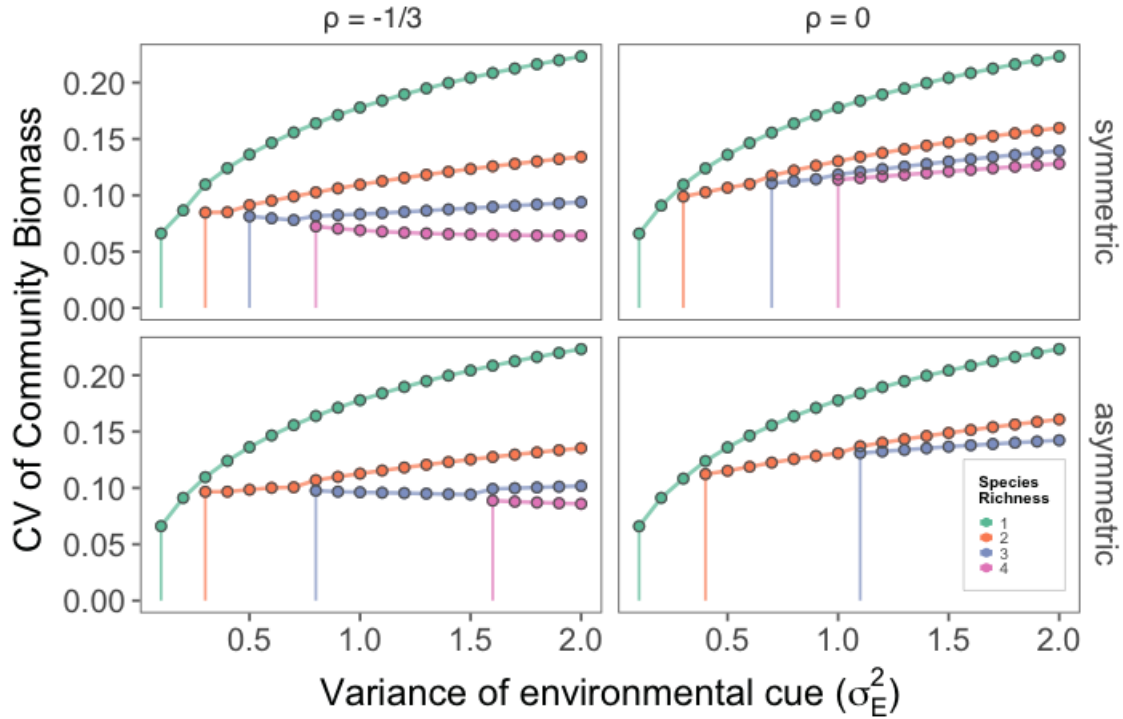


**Figure SI-2**  The effect of increasing environmental variability on ecosystem variability when species coexist via the storage effect. Top panels show simulation results where species have relatively symmetric dormant mortality rates ($\eta_1 = 0.1, \eta_2 = 0.115, \eta_3 = 0.12, \eta_4 = 0.125$), 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: $\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = 0.5$.

This result (Fig. SI-1 and Figure 3 in the main text) reinforces the notion that our conclusion about a positive diversity–ecosystem variability relationship is contingent upon the regional community consisting of species that *can* coexist at some level of environmental variance. If there is no species that can take advantage of more variable conditions, then fluctuation-dependent coexistence is not possible and neither are the results we present in the main text.

While the results of competitive asymmetries among species tend to limit coexistence, within the range of parameters allowing fluctuation-dependent coexistence we can explore sensitivity of our results to changes in the absolute values of parameters. Below we describe simulations designed to test whether our results change qualitatively or quantitatively due to changes in the absolute values of select parameters. We chose parameters to investigate based on their influence on species coexistence for each mechanism, assuming our results would be most sensitive to those parameters.

## Section SI.3.1  Parameter sensitivity: storage effect

For the storage effect, coexistence strength declines as:

1. Environment-competition covariance (*EC* covariance) becomes less positive
2. Environmental variation decreases
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 (richness increases along x-axes within panels); (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. SI-2). Although the qualitative patterns are similar, increasing the dormant mortality rate has three consistent effects: (1) it makes coexistence more difficult, (2) it reduces the absolute value of ecosystem *CV* by slightly reducing mean population size and significantly reducing temporal standard deviation, and (3) it weakens the buffering effect of additional species (compare the spread of the lines between top and bottom panels of Fig. SI-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 as much with the addition of another species.
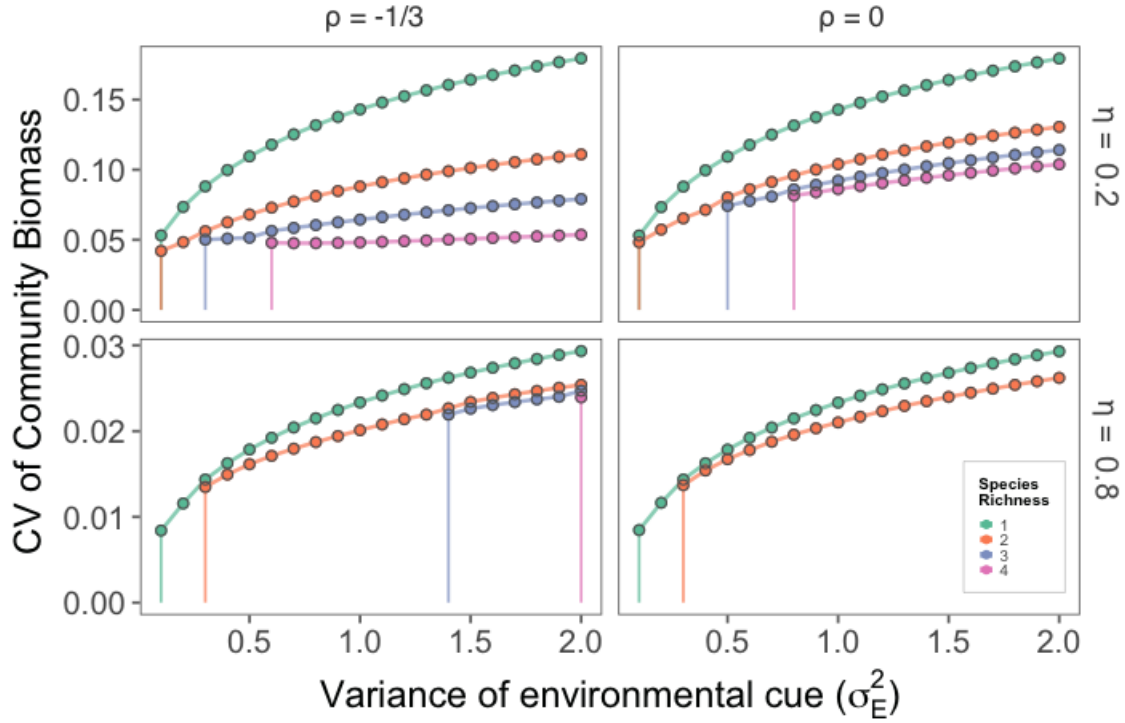
8

**Figure SI-3** The effect of increasing environmental variability on ecosystem variabilty 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: $\alpha_1 = 0.5, \alpha_2 = 0.495, \alpha_3 = 0.49, \alpha_4 = 0.485$.

## Section SI.3.2   Parameter sensitivity: relative nonlinearity

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 in the main text). 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 could create situations where species may not coexist, but it could also weaken the diversity–ecosystem variabilty 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: $\mu_R = 1, 2, 3, 4$).

9

As expected, lower mean levels of resource make coexistence more difficult because resource acquisitive species are never favored (Fig. SI-3). 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 the extent of the resource variability gradient and the traits of individual species (e.g., resource uptake curves). In other words, the patterns we report in the main text require that fluctuation-dependent species coexistence be possible given the environmental conditions and species' traits.
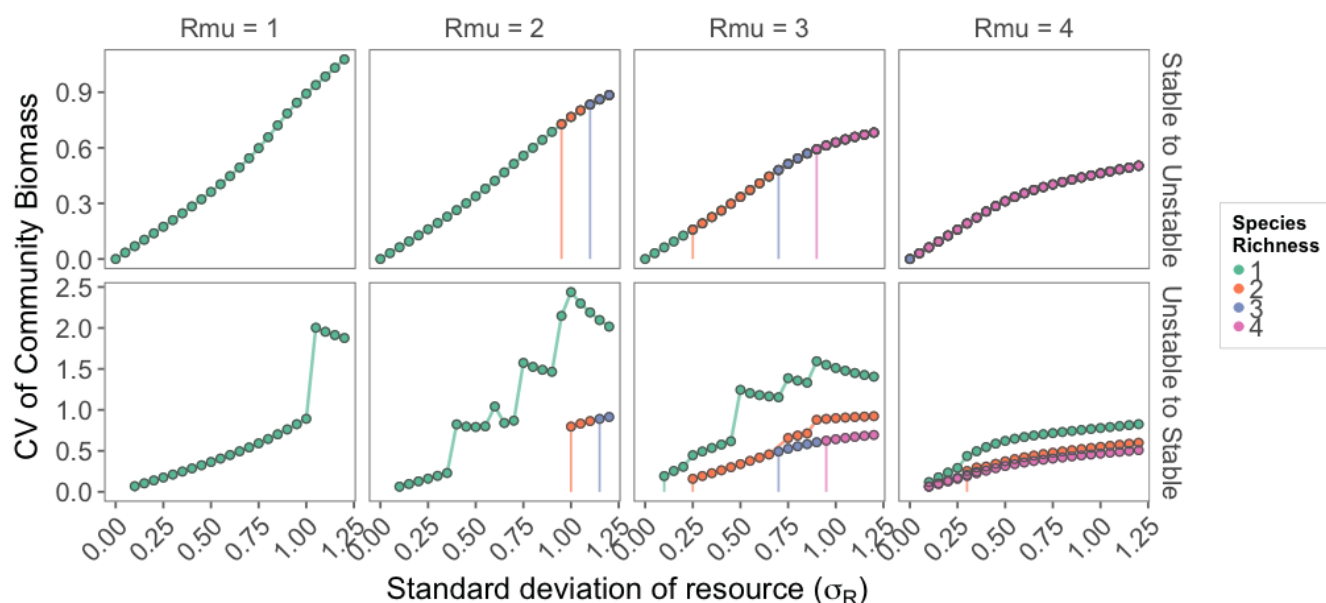


**Figure SI-4** The effect of environmental variability on ecosystem variability when species coexist via relative nonlinearity. The species pool increases from one to four species, with the fourth species being most unstable (e.g., resource conservative to resource acquisitive). Increasing environmental 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.
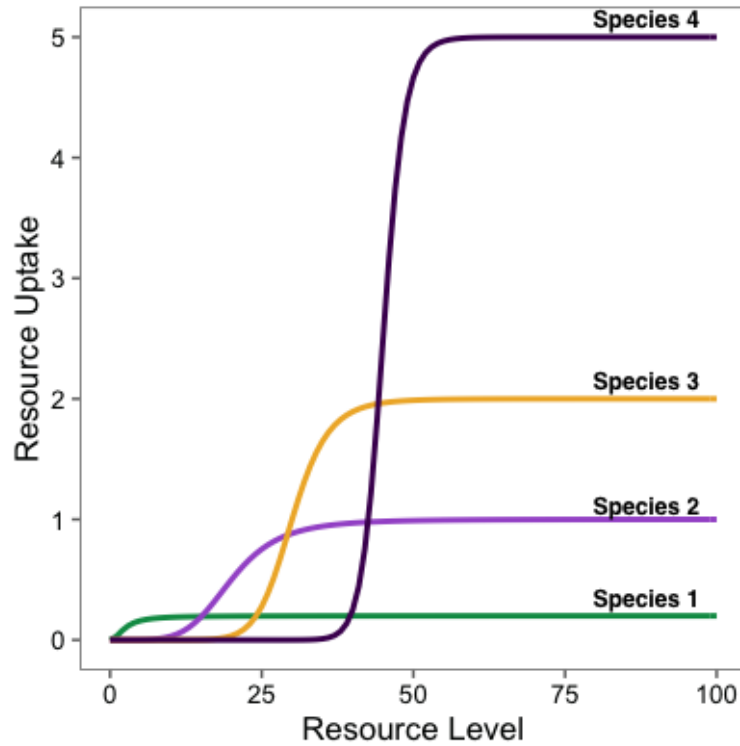
# Section SI.4    Additional Figures



**Figure SI-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: $r = 5$, $a = 25$, $b = 45$.
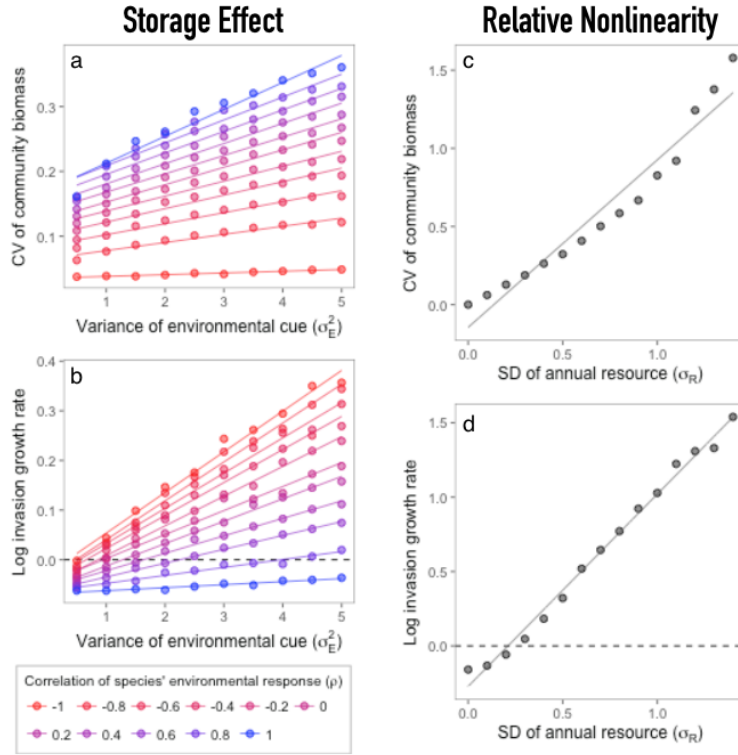
**Figure SI-6** Variability of community biomass and invasion growth rates of the inferior competitor in a two-species community under different parameter combinations. Points are mean values from 5,000 growing seasons and lines are linear fits to show trends. In **Storage Effect** plots (a,b), resource 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.
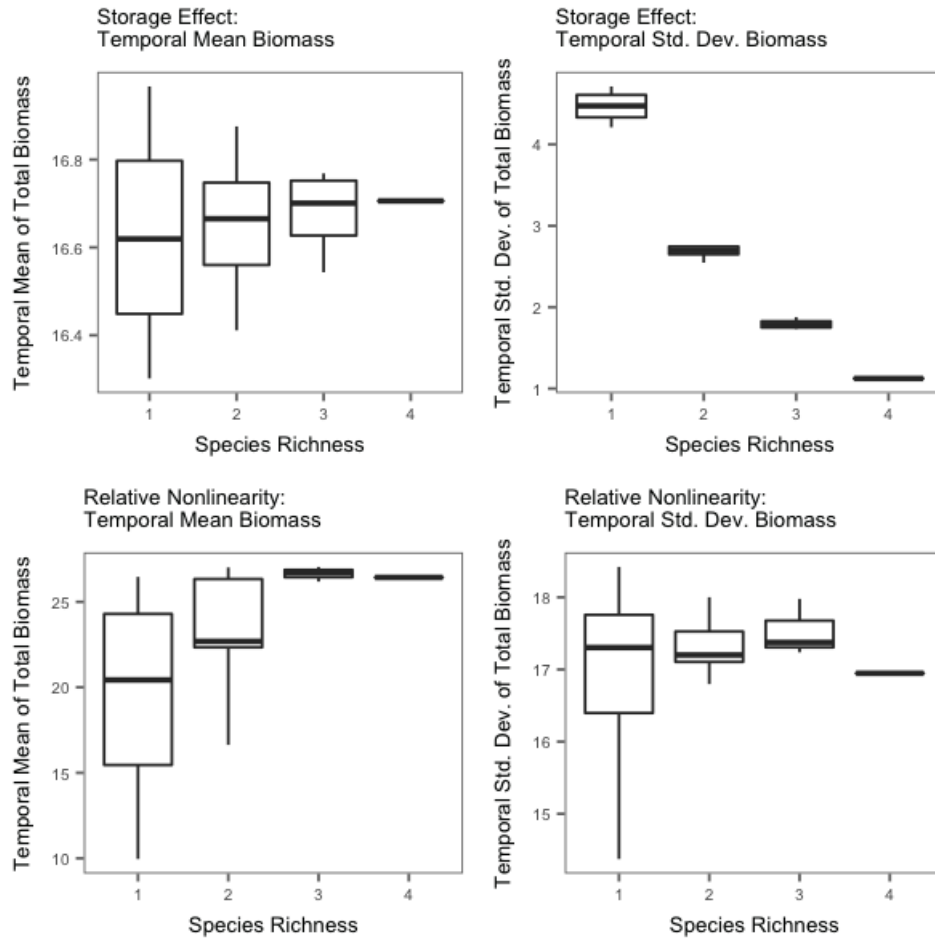
**Figure SI-7** Temporal means and standarad deviations of total community biomass at each level of species richness. Values come from the simulations represented in the main text Figure 2B (storage effect) and Figure 2D (relative nonlinearity). These plots show how the components of the coefficient of variability change with species richness at a given level of environmental variability (e.g., a "local" diversity–ecosystem variability relationship).
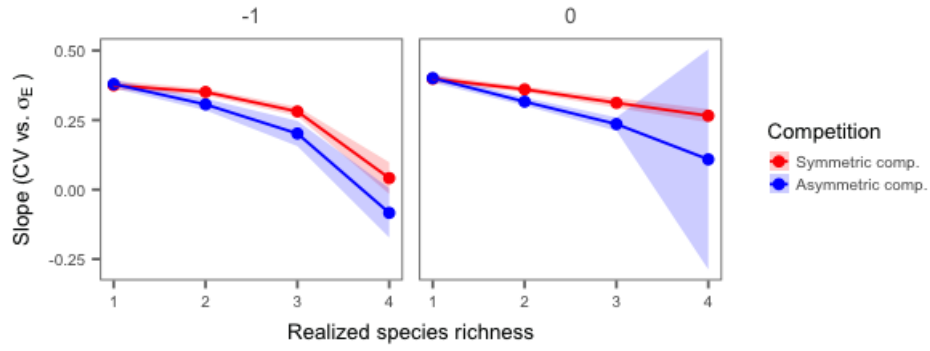
**Figure SI-8**  Slopes of linear fits for the relationship between log($CV$) and log($\sigma_E$) at different levels of realized species richness from storage effect simulations. The slopes come from linear models fit to log-transformed versions of Figure 3 in the main text. For these simulations, "symmetric 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).
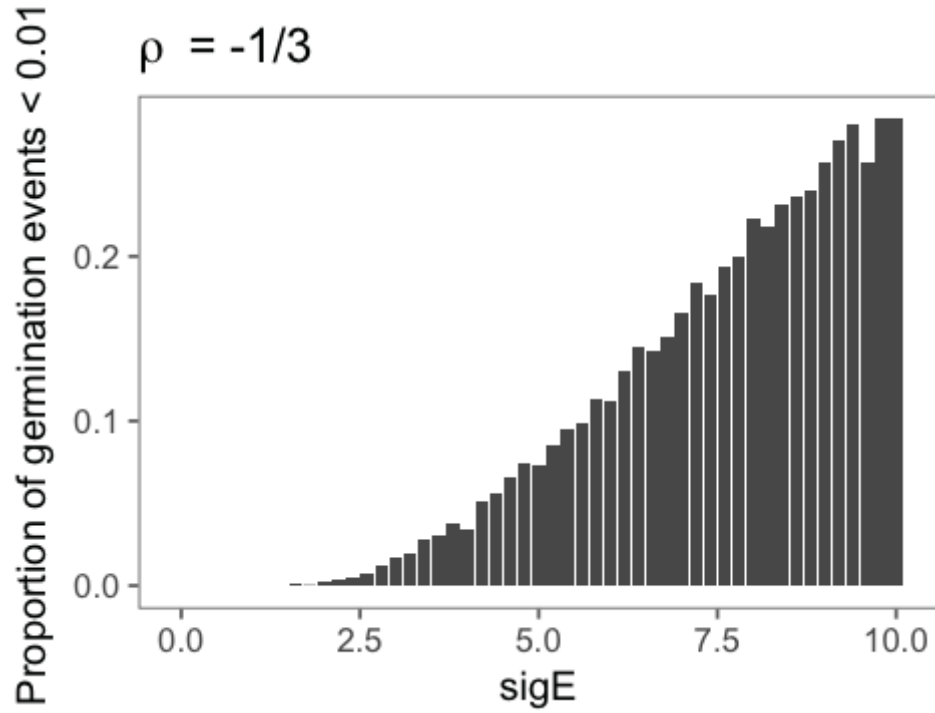
**Figure SI-9** The number of extreme germination events ($\gamma < 0.01$) at different levels of germination cue variance($\sigma_E^2$). Past $\sigma_E^2 = 2$ the number of extreme germination events increases rapidly. This is why, in a four-species community, ecosystem *CV* is flat up to $\sigma_E^2 = 2$ (as in Fig. 3A of the main text) but then begins to increase (Fig. SI-9). Because germination is bounded at 0 and 1, once germination begins to approah those values more frequently, the portfolio effects possible when species are perfectly anti-correlated can no longer perfectly compensate for increased population variability.
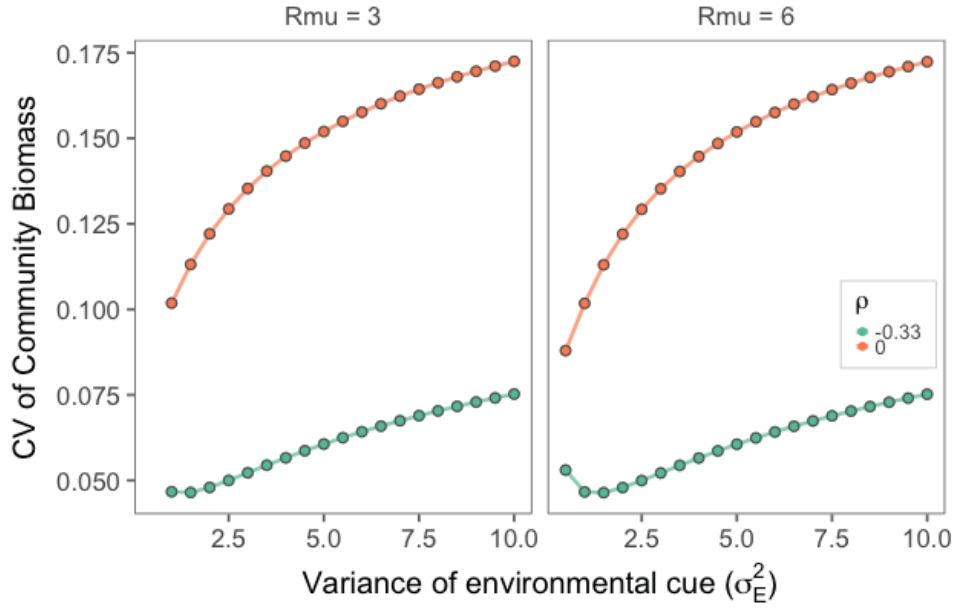
**Figure SI-10**   Ecosystem *CV* of a four-species community coexisting via the storage effect as a function of environmental cue variance at two levels of mean resource availability (Rmu across tops of panels) and two levels of correlation of species' responses to environmental conditions ($\rho$). 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.
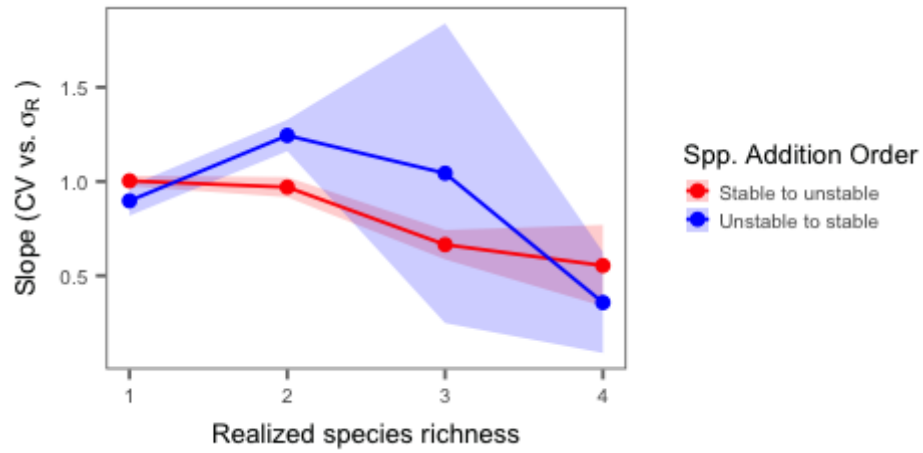
**Figure SI-11** Slopes of linear fits for the relationship between $\log(CV)$ and $\log(\sigma_R)$ at different levels of realized species richness from relative nonlinearity simulations. The slopes come from linear models fit to log-transformed versions of Figure 4 in the main text.

# References

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.