

The relationship between species richness and ecosystem variability is shaped by the mechanism of coexistence

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Abstract

Theory relating species richness to ecosystem variability typically ignores the potential for environmental variability to promote species coexistence. Failure to account for fluctuation-dependent coexistence may explain deviations from the expected negative diversity–ecosystem variability relationship, and limits our ability to predict the consequences of increases in environmental variability. We use a consumer-resource model to explore how coexistence via the temporal storage effect and relative nonlinearity affects ecosystem variability. We show that a positive, rather than negative, diversity–ecosystem variability relationship is possible when ecosystem function is sampled across a natural gradient in environmental variability and diversity. We also show how fluctuation-dependent coexistence can buffer ecosystem functioning against increasing environmental variability by promoting species richness and portfolio effects. Our work provides a general explanation for variation in observed diversity–ecosystem variability relationships and highlights the importance of conserving regional species pools to help buffer ecosystems against predicted increases in environmental variability.

INTRODUCTION

MacArthur (1955), Elton (1958), and even Darwin (Turnbull et al. 2013) recognized the potential for compensatory dynamics among species to stabilize ecosystem functioning in fluctuating environments. This idea underlies the “insurance hypothesis” (Yachi & Loreau 1999), which states that ecosystem variability, defined as the coefficient of variation of ecosystem biomass over time, should decrease with diversity because species respond dissimilarly to environmental variation, broadening the range of conditions under which the community maintains function (Loreau 2010). A variety of theoretical models all predict a negative relationship between species richness and ecosystem variability (Lehman & Tilman 2000; Ives & Hughes 2002; Loreau & de Mazancourt 2013), and experimental tests tend to support such a prediction (Tilman et al. 2006; Hector et al. 2010).

However, the ability of biodiversity–ecosystem functioning (BEF) experiments to accurately

55 represent real-world dynamics is debated (Eisenhauer et al. 2016; Wardle 2016). Much of the
56 debate centers on the fact that BEF experimental protocols do not allow species additions from
57 the regional pool to offset species losses in local communities. Theoretical work on diversity–
58 ecosystem variability relationships typically suffers from the same limitation: it recognizes the role
59 of environmental variability in driving population fluctuations which destabilize ecosystems, but
60 ignores the potential for environmental variability to promote species richness and thereby help
61 stabilize ecosystems (Loreau 2010, but see Chesson et al. 2001).

62 Fluctuating environmental conditions are an important ingredient for stable species coexis-
63 tence, both in theoretical models (Chesson 2000a; Chesson et al. 2004) and in natural communities
64 (Cáceres 1997; Descamps-Julien & Gonzalez 2005; Adler et al. 2006; Angert et al. 2009). Such
65 “fluctuation-dependent” coexistence emerges most easily when species have unique environmental
66 responses and environmental conditions vary so that each species experiences both favorable and un-
67 favorable conditions, preventing competitive exclusion (Chesson 2000a). Chesson (2000) described
68 the two temporal fluctuation-dependent mechanisms, the storage effect and relative nonlinearity.
69 Both mechanisms operate when environmental variation favors different species at different times.
70 Under the storage effect, this happens because species are competing for resources at different
71 times (and escaping competition in unfavorable periods). Under relative nonlinearity, all species
72 are competing for resources at the same time, but each species alters resource availability in a way
73 that favors its competitors. We describe these mechanisms in more detail below (see *Materials and*
74 *Methods: Consumer-resource model*).

75 When coexistence is maintained by a fluctuation-dependent mechanism, an increase in envi-
76 ronmental variability might lead to an increase in species richness and, consequently, a decrease in
77 ecosystem variability. However, increasing environmental variability may also increase ecosystem
78 variability by increasing the fluctuations of individual species, regardless of species richness. These
79 countervailing effects of environmental variability present an interesting paradox: while we should
80 expect an increase in environmental fluctuations to increase ecosystem variability, this increase

81 might be buffered if fluctuation-dependent coexistence adds new species to the community. Such a
82 paradox complicates predictions about how ecosystems will respond to predicted departures from
83 historical ranges of environmental variability.

84 The opposing effects of environmental variability on ecosystem variability might explain
85 the mixed results from observational studies on the diversity–ecosystem variability relationship.
86 Observational tests of the diversity–ecosystem variability relationship, which require sampling
87 across natural diversity gradients, have yielded negative (Hautier et al. 2014), neutral (Valone
88 & Hoffman 2003; Cusson et al. 2015), and positive (Sasaki & Lauenroth 2011) relationships.
89 In a meta-analysis of diversity–ecosystem variability relationships, Jiang & Pu (2009) found no
90 significant evidence for an effect of species richness on ecosystem variability when restricting
91 data to observational studies in terrestrial ecosystems, perhaps because environmental variability
92 varies across natural diversity gradients, affecting both richness and ecosystem variability. The
93 idiosyncratic results of these observational studies contrast with the consistent conclusions from
94 experimental and theoretical work that ignore, or control, the feedbacks between variability and
95 richness.

96 The gap between theoretical expectations and empirical results of diversity–ecosystem vari-
97 ability relationships might reflect the divergence of theory developed to explain species coexistence
98 and theory developed to explain diversity and ecosystem variability. In his thorough review of the
99 topic, Loreau (2010) cautions that “one of the pieces of the stability jigsaw [puzzle] that is still
100 missing here is the interconnection between community stability and the maintenance of species
101 diversity due to temporal environmental variability.” One reason these two disciplines have diverged
102 is because they have focused on different questions. Diversity–ecosystem variability studies typi-
103 cally ask how ecosystem variability responds to different levels of species richness at a given level
104 of environmental variability (reviewed in Kinzig et al. 2001; Loreau 2010), whereas coexistence
105 studies ask how species richness responds to different levels of environmental variability (Chesson
106 & Warner 1981).

107 To reconcile these two perspectives, we extend theory on the relationship between species
108 richness and ecosystem variability to cases in which species coexistence explicitly depends on
109 environmental fluctuations and species-specific responses to environmental conditions. We focus
110 on communities where coexistence is maintained by either the temporal storage effect or relative
111 nonlinearity using a general consumer-resource model. We use the model to investigate two
112 questions:

- 113 1. Does the diversity–ecosystem variability relationship remain negative when species coexis-
114 tence is maintained by the temporal storage effect or relative nonlinearity?
- 115 2. How does increasing environmental variability impact ecosystem variability when coexistence
116 depends on the storage effect or relative nonlinearity?

117 **MATERIALS AND METHODS**

118 **Consumer-resource model**

119 We developed a semi-discrete consumer-resource model that allows multiple species to coexist on
120 one resource by either the storage effect or relative nonlinearity. In our model, the consumer can
121 be in one of two-states: a dormant state D and a live state N . The dormant state could represent
122 the seed bank of an annual plant or root biomass of a perennial plant. Transitions between N and
123 D occur at discrete intervals between growing seasons, with continuous-time consumer-resource
124 dynamics between the discrete transitions. Thus, our model is formulated as “pulsed differential
125 equations” (Pachepsky et al. 2008; Mailleret & Lemesle 2009; Mordecai et al. 2016). We refer to
126 τ as growing seasons and each growing season is composed of T daily time steps, indexed by t
127 ($t = 1, 2, 3, \dots, T$). The notation $\tau(t)$ reads as: “day t within growing season τ .”

128 At the beginning of growing season τ a season-specific fraction ($\gamma_{i,\tau}$) of dormant biomass is
129 activated as living biomass such that

$$N_{i,\tau(0)} = \gamma_{i,\tau} D_{i,\tau(0)}, \quad (1)$$

131 where i indexes each species and $\tau(0)$ denotes the beginning of growing season τ . Live biomass at
 130 the start of the growing season ($N_{i,\tau(0)}$) then serves as the initial conditions for continuous-time
 132 consumer-resource dynamics that are modeled as two differential equations:
 133

$$\frac{dN_i}{dt} = \varepsilon_i f_i(R) N_i, \quad (2)$$

$$\frac{dR}{dt} = - \sum_i f_i(R) N_i, \quad (3)$$

135 where the subscript i denotes species, N_i is living biomass, and ε_i is species-specific resource-to-
 134 biomass conversion efficiency. The growth rate of living biomass is a resource-dependent Hill
 136 function, $f_i(R) = r_i R^{a_i} / (b_i^{a_i} + R^{a_i})$, where r is a species' intrinsic growth rate and a and b define
 137 the curvature and scale of the function, respectively. Resource depletion is equal to the sum of
 138 consumption by all species.
 139

140 At the end of the growing season ($t = T$), a fraction (α_i) of live biomass is stored as dormant
 141 biomass and a fraction of dormant biomass survives ($1 - \eta_i$) to the next growing season, giving the
 142 following equation:

$$D_{i,\tau(0)+1} = [\alpha_i N_{i,\tau(T)} + D_{i,\tau(T)}] (1 - \eta_i) \quad (4)$$

144 where $\tau(T)$ denotes the end of growing season τ . We assume remaining live biomass
 143 ($N_{i,\tau(T)}(1 - \alpha_i)$) dies (i.e., this is not a closed system where all biomass must be in either N or D
 145 states). We do not include extinction thresholds, or any other form of demographic stochasticity,
 146 under the assumption that we are working with abundant species with generous seed dispersal.
 147

148 We assume the resource pool is not replenished within a growing season. Resource replenish-

149 ment occurs between growing seasons, and the resource pool (R) at the start of the growing season
 150 is $R_{\tau(0)} = R^+$, where R^+ is a random resource pulse drawn from a lognormal distribution with mean
 151 $\mu(R^+)$ and standard deviation $\sigma(R^+)$. Taken all together, we can combine equations 1 and 4 to
 152 define the discrete transitions between live and dormant biomass at the end of a growing season.
 153 Thus, the initial conditions for each state (D, N, R) at the beginning of growing season $\tau + 1$ are:

$$D_{i,\tau(0)+1} = (1 - \gamma_{i,\tau}) [\alpha_i N_{i,\tau(T)} + D_{i,\tau(T)}] (1 - \eta_i) \quad (5)$$

$$N_{i,\tau(0)+1} = \gamma_{i,\tau} [\alpha_i N_{i,\tau(T)} + D_{i,\tau(T)}] (1 - \eta_i) \quad (6)$$

$$R_{\tau(0)+1} = \text{lognormal}(\mu(R^+), \sigma(R^+))_0^{200}, \quad (7)$$

155 where, as above, $\tau(T)$ denotes the end of growing season τ and $\tau(0) + 1$ denotes the beginning of
 154 growing season $\tau + 1$. The subscript (0) and superscript (200) indicates a lognormal distribution
 156 truncated at those values to avoid extreme resource pulses that cause computational problems. We
 157 used the function `urlnorm` from the `Runuran` package (Leydold & Hörmann 2015) to generate
 158 values from the truncated lognormal distribution. Model parameters and notation are described in
 159 Table 1.
 160 Table 1.

161 Our model does not include demographic stochasticity, which can lead to stochastic extinction
 162 for small populations as environmental variability increases (Boyce 1992). Previous work has
 163 shown how demographic stochasticity and coexistence mechanisms can interact to create a weak
 164 “humped-shape” relationship between coexistence time and environmental variability (Adler &
 165 Drake 2008), because environmental variability increases coexistence strength and the probability
 166 of stochastic extinction simultaneously. We do not consider this potential effect here because our
 167 focus is on large populations that would most influence ecosystem functioning.

168 We limit our analysis to four-species communities because it is exceedingly difficult to get
 169 more than four species to coexist via relative nonlinearity without introducing another coexistence
 170 mechanism (Yuan & Chesson 2015). For consistency, we also constrain our focus to four species
 171 communities under the storage effect, but our conclusions apply to more species-rich communities

172 (see Supporting Information section SI.2).

173 **Implementing the Storage Effect** For the storage effect to operate, we need species-specific
174 responses to environmental variability, density-dependent covariance between environmental condi-
175 tions and competition (*EC* covariance), and subadditive population growth (Chesson 1994, 2000b).
176 If these conditions are present, all species can increase when rare and coexistence is stable. In the
177 storage effect, rare species increase by escaping the effects of *EC* covariance. Common species will
178 experience greater than average competition (*C*) in environment (*E*) years that are good for them
179 because common species cannot avoid intraspecific competition. However, a rare species can escape
180 intraspecific competition and has the potential to increase rapidly in a year when the environment
181 is good for them but bad for the common species. *EC* covariance emerges in our model because
182 dormant-to-live transition rates (γ) are species-specific and vary through time. In a high γ year for
183 a common species, resource uptake will be above average because combined population size will
184 be above average. In a year when γ is high for rare species and low for common species, resource
185 uptake will be below average because combined population size will be below average. Subadditive
186 population growth buffers populations against large population decreases in unfavorable years. It
187 is included in our model through a dormant stage with very low death rates, which limits large
188 population declines in bad *E* years.

189 We generated sequences of (un)correlated dormant-to-live state transition rates (γ) for each
190 species by drawing from multivariate normal distributions with mean 0 and a variance-covariance
191 matrix ($\Sigma(\gamma)$) of

$$\Sigma(\gamma) = \begin{bmatrix} 1 & \rho_{1,2} & \rho_{1,3} & \rho_{1,4} \\ \rho_{2,1} & 1 & \rho_{2,3} & \rho_{2,4} \\ \rho_{3,1} & \rho_{3,2} & 1 & \rho_{3,4} \\ \rho_{4,1} & \rho_{4,2} & \rho_{4,3} & 1 \end{bmatrix} \sigma_E^2, \quad (8)$$

192 where σ_E^2 is the variance of the environmental cue and $\rho_{i,j}$ is the correlation between species *i*'s
193

194 and species j 's transition rates. ρ must be less than 1 for stable coexistence, and in all simulations
195 we constrained all $\rho_{i,j}$'s to be equal. In a two-species community, the inferior competitor has
196 the greatest potential to persist when $\rho = -1$ (perfectly uncorrelated transition rates). However,
197 in a four-species community the minimum possible correlation among species is $-1/3$ given our
198 constraints that all ρ 's are equal and that $\Sigma(\gamma)$ must be positive-definite. We used the R function
199 `mvrnorm` to generate sequences of (un)correlated variates E that we converted to germination rates
200 in the 0-1 range: $\gamma = e^E / (1 + e^E)$.

201 **Implementing Relative Nonlinearity** In the absence of environmental fluctuations, the outcome
202 of competition between two species limited by the same resource is determined by the shape of
203 their resource uptake curves. That is, at constant resource supply, whichever species has the lowest
204 resource requirement at equilibrium (R^*) will exclude all other species (Tilman 1982). Resource
205 fluctuations create opportunities for species coexistence because the resource level will sometimes
206 exceed the R^* of the superior competitor. If the resource uptake curves of each species are relatively
207 nonlinear, then some species will be able to take advantage of resource levels that other species
208 cannot (Chesson 1994).

209 For example, in Fig. 1C we show uptake curves of two species with different degrees of
210 nonlinearity. Species B has the lowest R^* and would competitively exclude species A in the absence
211 of environmental fluctuations. But fluctuating resource supplies can benefit species A because it can
212 take advantage of relatively high resource levels due its higher saturation point. Stable coexistence
213 is only possible, however, if when each species is dominant it improves conditions for its competitor.
214 This occurs in our model because when a resource conservative species (e.g., species B in Fig. 1C)
215 is abundant, it will draw resources down slowly after a pulse, and its competitor can take advantage
216 of that period of high resource availability. Likewise, when a resource acquisitive species (e.g.,
217 species A in Fig. 1C) is abundant, after a pulse it quickly draws down resources to levels that favor
218 resource conservative species. Such reciprocity helps each species to increase when rare, stabilizing
219 coexistence (Armstrong & McGehee 1980; Chesson 2000a; Chesson et al. 2004).

220 Numerical simulations

221 To explore how fluctuation-dependent coexistence can affect the diversity–ecosystem variability
222 relationship, we simulated the model with four species under two scenarios for each coexistence
223 mechanism. First, we allowed the variance of the environment to determine how many species can
224 coexist, akin to a community assembly experiment with a species pool of four species. We simulated
225 communities with all species initially present across a gradient of annual resource variability for
226 relative nonlinearity (50 evenly-spaced values of σ_R in the range [0, 1.2]) or environmental cue
227 variability for the storage effect (100 evenly-spaced values of σ_E^2 in the range [0, 3]). Second, we
228 chose parameter values that allowed coexistence of all four species and then performed species
229 removals at a single level of environmental variability, akin to a biodiversity–ecosystem function
230 experiment. The two simulation experiments correspond to (i) sampling ecosystem function
231 across a natural gradient of species richness and (ii) sampling ecosystem function across diversity
232 treatments within a site. We refer to the former as a “regional” relationship, and the latter as a “local”
233 relationship. But we do not attribute any particular area size to “region”, it is simply any area over
234 which a gradient of environmental variability exists.

235 To understand how increasing environmental variability will impact ecosystem variability
236 when coexistence is fluctuation-dependent, we simulated the model over a range of species pool
237 sizes and environmental cue or resource variability. For each size of species pool (1, 2, 3, or 4
238 species), we simulated the model at 15 evenly-spaced levels of environmental cue (range = [0.1,
239 2]) for the storage effect and 25 evenly-spaced levels of resource variability (range = [0, 1.2]) for
240 relative nonlinearity. We also explored the influence of asymmetries in species’ competitive abilities
241 and correlations in species’ environmental responses within the storage effect model. We created
242 competitive hierarchies by making the live-to-dormant biomass fractions (α s) unequal among
243 species. Small differences among values of α were needed to create competitive hierarchies because
244 we chose a relatively constrained gradient of environmental cue variance. Larger differences among
245 values of α expand the region of coexistence farther along a gradient environmental cue variance.

246 Under relative nonlinearity, species' resource response curves (Fig. SI-5) reflect traits that
247 determine the temporal variability of each species' population growth. "Stable" species achieve
248 maximum resource uptake at low resource levels, but their maximum uptake rates are modest.
249 For these species, population responses to resource fluctuations are buffered. "Unstable" species
250 have very high maximum uptake rates, which they only achieve when resource availability is high,
251 leading to large population fluctuations. The difference in the intrinsic stability of these two kinds
252 of species makes our simulations sensitive to initial conditions. Therefore, we ran two sets of
253 simulations for relative nonlinearity: beginning with either stable or unstable species as a reference
254 point. For example, if species A is the most stable species and species D is the least stable, we ran
255 simulations where A then B then C then D were added to the initial pool of species. We then ran
256 simulations with that order reversed.

257 All simulations were run for 5,000 growing seasons of 100 days each. We averaged biomass
258 over the growing season, and yearly values of live-state biomass were used to calculate total
259 community biomass in each year. After discarding an initial 500 seasons to reduce transient effects
260 on our results, we calculated the coefficient of variation (*CV*) of summed species biomass through
261 time, which represents ecosystem variability, the inverse of ecosystem stability. We calculated
262 realized species richness as the number of species whose average biomass was greater than 1 over
263 the course of the simulation. In some cases, realized species richness is less than number of species
264 initialized for a simulation because of competitive exclusion.

265 For parameters that we did not vary, we chose values that would allow coexistence of all
266 four species at some point along the environmental variability gradients we simulated. Our focus
267 is specifically on communities where fluctuation-dependent coexistence is operating, and making
268 parameters increasingly asymmetric among species typically reduced coexistence strength or made
269 coexistence impossible (Supporting Information section SI.3). Changes in the absolute values of
270 parameters also altered the strength of coexistence, but in no case did altering parameter values
271 change our qualitative results and conclusions (Supporting Information section SI.3). Parameter

272 values for specific results are given in figure captions.

273 Within-season dynamics were solved given initial conditions using the package
274 `deSolve` (Soetaert et al. 2010) in R (R Core Team 2013). R code for our model
275 function is in the Supporting Information section SI.1. All model code has been de-
276 posited on Figshare (10.6084/m9.figshare.4985567) and is available on GitHub at <https://github.com/atredennick/Coexistence-Stability/releases>.
277

278 **RESULTS**

279 When we allowed the variance of the environment to determine which of four initial species co-
280 existed, similar to a study across a natural diversity gradient, we found a positive relationship
281 between richness and ecosystem variability, defined as the temporal *CV* of total community biomass
282 (Fig. 2A,C). This was true for the storage effect, where coexistence is maintained by fluctuating
283 dormant-to-live transition rates (γ), and for relative nonlinearity, where coexistence is maintained
284 by annual resource pulses. The relationship is driven by the fact that increasing environmental
285 variability increases the strength of both coexistence mechanisms (Fig. SI-6). More variable condi-
286 tions promoted species richness, creating a positive relationship between diversity and ecosystem
287 variability.

288 When we performed species removals but held environmental variability at a level that allows
289 coexistence of all four species, similar to a biodiversity–ecosystem functioning experiment, we found
290 a negative diversity–ecosystem variability relationship (Fig. 2B,D). Scatter around the relationship
291 was small for the storage effect because all species have similar temporal variances. Regardless
292 of species identity, the presence of more species always stabilized ecosystem functioning through
293 portfolio effects. In contrast, scatter around the relationship was larger for relative nonlinearity
294 (Fig. 2D) because species with different resource uptake curves had different population variances.
295 Depending on which species were present, two-species communities were sometimes less variable
296 than three-species communities. Furthermore, the slope of the relative nonlinearity diversity–

297 ecosystem variability relationship in Fig. 2D is sensitive to species' traits: the difference among
298 species' resource uptake determines the spread of single-species communities along the y-axis. This
299 means that the relationship can become flat as species become more similar.

300 For the storage effect, total community *CV* decreased with species richness at a given level
301 of environmental variability because additional species reduced the temporal standard deviation
302 due to portfolio effects (Fig. SI-7). Mean biomass remained the same because all species had
303 the same resource uptake functions, which was necessary to eliminate any potential effects of
304 relative nonlinearity. Portfolio effects under the storage effect remained strong in an eight-species
305 community, where total community *CV* saturated after addition of the fifth species (Fig. SI-1).
306 For relative nonlinearity, total community *CV* decreased with species richness at a given level
307 of environmental variability because additional species increased mean biomass (over-yielding)
308 and, at higher richness (three to four species), reduced the temporal standard deviation (Fig. SI-7).
309 Mean biomass increased because some species had higher growth rates (Fig. SI-5), increasing total
310 biomass.

311 To understand how much species additions might stabilize ecosystem functioning as envi-
312 ronmental variability increases, we simulated our model over a range of environmental variance
313 and species pool sizes. For both coexistence mechanisms, realized species richness increased with
314 environmental variability and, in some cases, increases in richness completely offset the effect of
315 moderate increases in environmental variability on ecosystem variability (Fig. 3 and 4). More
316 species rich communities were less variable on average and, under the storage effect, they increased
317 in ecosystem *CV* at a slower rate than communities with fewer species (e.g., lower slopes in log-log
318 space; Fig. SI-8). The buffering effect of species richness under the storage effect is also evident in
319 Fig. 2A because the relationship between species richness and ecosystem *CV* begins to saturate. In
320 fact, ecosystem *CV* remains relatively constant past four species when species have independent
321 responses to the environment ($\rho = 0$; Fig. SI-1).

322 The dampening effect of fluctuation-dependent coexistence on increasing environmental

323 variability depends on the specific traits (parameter values) of the species in the regional pool.
324 Under the storage effect, moderately asymmetric competition makes it more difficult for new
325 species to enter the local community, but once they do enter, ecosystem *CV* is similar between
326 communities with low and moderate competitive asymmetries (Fig. 3; compare top and bottom
327 panels). Moderately asymmetric competition does decrease the rate at which ecosystem *CV*
328 increases with environmental variance (Fig. SI-8) because the abundance of inferior competitors
329 is reduced and they do not influence ecosystem *CV* as much as when competitive asymmetry is
330 low. The correlation of species' environmental responses (ρ) also mediates the relationship between
331 environmental variance, species richness, and ecosystem *CV*: lower correlations make it easier for
332 new species to enter the community and contribute to portfolio effects (Fig. 3). When the correlation
333 of species' environmental responses were as negative as possible ($\rho = -1/3$), ecosystem *CV* of
334 the four-species community was immune to increases in the environmental cue variance (Fig. 3A).
335 However, more extreme increases in the variance of the environmental cue, which increase the
336 number of extremely low or high germination events (i.e., $\gamma \approx 0$ or 1; Fig. SI-9), eventually caused
337 ecosystem *CV* to increase in the four species community (Fig. SI-10).

338 In communities where species coexist via relative nonlinearity, the extent to which species
339 additions buffer ecosystem stability against increases in environmental variability depends on the
340 species traits of immigrating species and the order in which they enter the community. When
341 additional species, which immigrate from the regional pool, are less intrinsically stable than the
342 resident species, ecosystem variability increases at a relatively constant rate even as species are
343 added (Fig. 4A; Fig. SI-11). If more stable species colonize, species additions buffer the ecosystem
344 from increasing environmental variability (Fig. 4B).

345 We tested the generality of our results under different parameters by conducting a targeted
346 sensitivity analysis focused on parameter values and asymmetries that most affect species coexis-
347 tence (Supporting Information section SI.3). In general, altering any parameter in isolation will
348 make coexistence easier or harder at any given level of environmental variability. Our results are

349 only sensitive to whether or not fluctuation-dependent coexistence is operating.

350 **DISCUSSION**

351 Theory developed for biodiversity–ecosystem function experiments emphasizes that increases in
352 species richness should reduce ecosystem variability. Consistent with theoretical expectations from
353 models in which species coexistence is maintained by fluctuation-independent mechanisms and with
354 results from biodiversity–ecosystem functioning experiments, our model of fluctuation-dependent
355 species coexistence (also see Chesson et al. 2001) produced a negative diversity–ecosystem
356 variability relationship (Fig. 2B,D). This agreement is encouraging because empirical evidence for
357 fluctuation-dependent coexistence is accumulating (Pake & Venable 1995; Cáceres 1997; Descamps-
358 Julien & Gonzalez 2005; Adler et al. 2006; Angert et al. 2009; Usinowicz et al. 2012) and
359 species almost certainly coexist by some combination of fluctuation-independent (e.g., resource
360 partitioning) and fluctuation-dependent mechanisms (Ellner et al. 2016). By extending theory
361 to communities where species richness is explicitly maintained by temporal variability, we have
362 gained confidence that experimental findings are generalizable to many communities. In local
363 settings where environmental variability is relatively homogeneous, reductions in the number of
364 species should increase the variability of ecosystem functioning, regardless of how coexistence is
365 maintained.

366 When we allowed communities to assemble at sites across a gradient of environmental
367 variability, we discovered a positive relationship between species richness and ecosystem variability
368 (Fig. 2A,C). While surprising when viewed through the lens of biodiversity–ecosystem functioning
369 theory and experimental findings, such a relationship is predicted by theory on coexistence in
370 fluctuating environments. Environmental variability is a prerequisite for the storage effect and
371 relative nonlinearity to stabilize coexistence (Chesson 2000a). These mechanisms can translate
372 increased variability into higher species richness (Fig. SI-6), but the increase in environmental
373 variability also increases ecosystem variability. However, the apparent saturation of the relationship

374 in Fig. 3A suggests that the portfolio effects that buffer ecosystems against environmental variability,
375 and inherently emerge under the storage effect, get stronger as more species are able to coexist.
376 Indeed, the relationship between species richness and ecosystem *CV* completely saturates under
377 the storage effect in more species rich communities (Fig. SI-1). This suggests neutral diversity–
378 ecosystem variability relationships are possible due to the storage effect.

379 Our results may explain why deviations from the negative diversity–ecosystem variability
380 relationship often come from observational studies (Jiang & Pu 2009). Observational studies must
381 rely on natural diversity gradients, which do not control for differences in environmental variability
382 among sites. If species richness depends on environmental variability, it is entirely possible to
383 observe positive diversity–ecosystem variability relationships. For example, DeClerck et al. (2006)
384 found a positive diversity–ecosystem variability when sampling conifer richness and the variability
385 of productivity across a large spatial gradient in the Sierra Nevada, across which environmental
386 variability may have promoted coexistence. Sasaki and Lauenroth (2011) also found a positive
387 relationship between species richness and the temporal variability of plant abundance in a semi-arid
388 grassland. Their data came from a six sites that were 6 km apart. While Sasaki and Lauenroth
389 explained their results in terms of dominant species’ effects (e.g., Thibaut & Connolly 2013), our
390 findings suggest an alternative explanation: each site may have experienced sufficiently different
391 levels of environmental variability to influence species coexistence.

392 While our modeling results show that fluctuation-dependent coexistence can create positive
393 diversity–ecosystem variability relationships, whether such trends are detected will depend on the
394 particular traits of the species in the community and the relative influence of fluctuation-dependent
395 and fluctuation-independent coexistence mechanisms. Thus, our results may also help explain
396 observational studies where no relationship between diversity and variability is detected. For
397 example, Cusson et al. (2015) found no relationship between species richness and variability of
398 abundances in several marine macro-benthic ecosystems. Many of their focal ecosystems were
399 from highly variable intertidal environments. If coexistence was at least in part determined by

400 environmental fluctuations, then the confounding effect of environmental variability and species
401 richness could offset or overwhelm any effect of species richness on ecosystem variability. This may
402 be particularly common in natural communities, where environmental fluctuations can help promote
403 species coexistence even in cases where fluctuation-independent coexistence mechanisms are most
404 important (Ellner et al. 2016). Previous theoretical work showed how environmental variation can
405 mask the effect of species diversity on ecosystem productivity when sampling across sites (Loreau
406 1998). Our mechanistic model extends that conclusion to ecosystem variability.

407 Whether coexistence is fluctuation-independent or fluctuation-dependent becomes especially
408 important when we consider how ecosystem variability responds to increasing environmental
409 variability. In the fluctuation-independent case, species richness is essentially fixed because the
410 niche and fitness differences that determine coexistence are not linked to environmental variability.
411 Therefore, increasing environmental variability will always increase ecosystem variability by
412 increasing the fluctuations of individual species' abundances. When coexistence is fluctuation-
413 dependent, however, the outcome is less certain. By simulating communities with different species
414 pool sizes across a gradient of environmental variability, we showed that species gains due to
415 increasing environmental variability can buffer the direct effect of environmental variability on
416 ecosystem variability (Figs. 3 and 4).

417 We relied on numerical simulations of a mechanistic model to reach our conclusions, meaning
418 our results could be sensitive to the specific parameter values we chose. In a targeted sensitivity
419 analysis (Supporting Information section SI.3), we found that our qualitative results are robust so
420 long as specific parameter combinations allow fluctuation-dependent species coexistence (by either
421 the storage effect or relative nonlinearity). Investigating the case in which both the storage effect
422 and relative nonlinearity operate remains a future challenge.

423 Another future challenge is to consider how extinction risk due to demographic stochasticity
424 might dampen the richness promoting effect of increased environmental variability. Environmental
425 variability increases small population's risk of stochastic extinction (Boyce 1992), and increasing

426 species richness can reduce the average density of each species through density compensation
427 (Gonzalez & Loreau 2009). Because environmental variability promotes coexistence and stochastic
428 extinction simultaneously (Ebenman et al. 2004; Adler & Drake 2008; Kaneryd et al. 2012), the
429 positive effects of increased richness and stability generated by our models might ultimately be
430 offset by an increase in extinctions of very small populations.

431 Overall, our results lead to two conclusions. First, when predicting the impacts of increas-
432 ing environmental variability on ecosystem variability, the mechanism of coexistence matters.
433 Fluctuation-dependent coexistence can buffer ecosystems from increasing environmental variability
434 by promoting increased species richness. Whether our theoretical predictions hold in real communi-
435 ties is unknown and requires empirical tests. Doing so would require manipulating environmental
436 variability in communities where coexistence is known to be fluctuation-dependent, at least in part.
437 Such data do exist (Angert et al. 2009), and a coupled modeling-experimental approach could
438 determine if our predictions hold true in natural communities.

439 Second, whether local fluctuation-dependent communities can receive the benefit of additional
440 species depends on a diverse regional species pool. If the regional pool is not greater in size than
441 the local species pool, then ecosystem variability will increase with environmental variability in a
442 similar manner as in fluctuation-independent communities because species richness will be fixed
443 (Fig. 5A,B). Metacommunity theory has made clear the importance of rescue effects to avoid
444 species extinctions (Brown & Kodric-Brown 1997; Leibold et al. 2004). Here, instead of local
445 immigration by a resident species working to rescue a species from extinction, immigration to the
446 local community by a new species rescues ecosystem processes from becoming more variable (Fig.
447 5C,D). Thus, our results reinforce the importance of both local and regional biodiversity conservation.
448 Just as declines in local species richness can destabilize ecosystem functioning (Tilman et al. 2006;
449 Hector et al. 2010; Hautier et al. 2014), species losses at larger spatial scales can also increase
450 ecosystem variability. Wang & Loreau (2014) show that regional ecosystem variability depends on
451 regional biodiversity through its effects on beta diversity and, in turn, the asynchrony of functioning

452 in local communities. Our results show that, when coexistence is fluctuation-dependent, regional
453 biodiversity declines could also affect local ecosystem functioning by limiting local colonization
454 events that could be possible under scenarios of increasing environmental variability (Fig. 5).

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461 **REFERENCES**

- 462 Adler, P.B. & Drake, J.M. (2008). Environmental variation, stochastic extinction, and competitive
463 coexistence. *The American Naturalist*, 172, 186–195.
- 464 Adler, P.B., HilleRisLambers, J., Kyriakidis, P.C., Guan, Q. & Levine, J.M. (2006). Climate
465 variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National
466 Academy of Sciences*, 103, 12793–12798.
- 467 Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine
468 species coexistence via the storage effect. *Proceedings of the National Academy of Sciences of the
469 United States of America*, 106, 11641–11645.
- 470 Armstrong, R.A. & McGehee, R. (1980). Competitive Exclusion. *The American Naturalist*, 115,
471 151–170.
- 472 Boyce, M.S. (1992). Population viability analysis. *Annual Review of Ecology and Systematics*, 23,
473 481–506.
- 474 Brown, J.H. & Kodric-Brown, A. (1997). Turnover Rates in Insular Biogeography : Effect of
475 Immigration on Extinction. *Ecology*, 58, 445–449.
- 476 Cáceres, C.E. (1997). Temporal variation, dormancy, and coexistence: a field test of the storage
477 effect. *Proceedings of the National Academy of Sciences*, 94, 9171–9175.
- 478 Chesson, P. (2000a). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology
479 and Systematics*, 31, 343–366.
- 480 Chesson, P. (2000b). General theory of competitive coexistence in spatially-varying environments.

- 481 *Theoretical population biology*, 58, 211–37.
- 482 Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., et al.
483 (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid
484 environments. *Oecologia*, 141, 236–253.
- 485 Chesson, P., Pacala, S.W. & Neuhauser, C. (2001). Environmental Niches and Ecosystem Function-
486 ing. In: *The functional consequences of biodiversity: Empirical progress and theoretical extensions*
487 (eds. Kinzig, A.P., Pacala, S.W. & Tilman, D.). Princeton University Press, Princeton, pp. 213–245.
- 488 Chesson, P.L. (1994). Multispecies Competition in Variable Environments. *Theoretical Population*
489 *Biology*, 45, 227.
- 490 Chesson, P.L. & Warner, R.R. (1981). Environmental Variability Promotes Coexistence in Lottery
491 Competitive Systems. *The American Naturalist*, 117, 923–943.
- 492 Cusson, M., Crowe, T.P., Araújo, R., Arenas, F., Aspden, R., Bulleri, F., et al. (2015). Relationships
493 between biodiversity and the stability of marine ecosystems: Comparisons at a European scale using
494 meta-analysis. *Journal of Sea Research*, 98, 5–14.
- 495 DeClerck, F.A.J., Barbour, M.G. & Sawyer, J.O. (2006). SPECIES RICHNESS AND STAND
496 STABILITY IN CONIFER FORESTS OF THE SIERRA NEVADA. *Ecology*, 87, 2787–2799.
- 497 Descamps-Julien, B. & Gonzalez, A. (2005). Stable coexistence in a fluctuating environment: An
498 experimental demonstration. *Ecology*, 86, 2815–2824.
- 499 Ebenman, B., Law, R. & Borrvall, C. (2004). Community viability analysis: The response of
500 ecological communities to species loss. *Ecology*, 85, 2591–2600.
- 501 Eisenhauer, N., Barnes, A.D., Cesarz, S., Craven, D., Ferlian, O., Gottschall, F., et al. (2016).
502 Biodiversity-ecosystem function experiments reveal the mechanisms underlying the consequences
503 of biodiversity change in real world ecosystems. *Journal of Vegetation Science*, 27, 1061–1070.
- 504 Ellner, S.P., Snyder, R.E. & Adler, P.B. (2016). How to quantify the temporal storage effect using
505 simulations instead of math. *Ecology Letters*, 19, 1333–1342.
- 506 Elton, C. (1958). *The Ecology of Invasions by Animals and Plants*. University of Chicago Press,
507 Chicago.
- 508 Gonzalez, A. & Loreau, M. (2009). The Causes and Consequences of Compensatory Dynamics in
509 Ecological Communities. *Annual Review of Ecology, Evolution, and Systematics*, 40, 393–414.
- 510 Hautier, Y., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hillebrand, H., et al. (2014).
511 Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*, 508, 521–5.
- 512 Hector, A., Hautier, Y., Saner, P., L.Wacker, Bagchi, R., Joshi, J., et al. (2010). General stabilizing
513 effects of plant diversity on grassland productivity through population asynchrony and overyielding.
514 *Ecology*, 91, 2213–2220.
- 515 Ives, A.R. & Hughes, J.B. (2002). General relationships between species diversity and stability in
516 competitive systems. *The American naturalist*, 159, 388–395.
- 517 Jiang, L. & Pu, Z. (2009). Different effects of species diversity on temporal stability in single-trophic

- 518 and multitrophic communities. *The American Naturalist*, 174, 651–659.
- 519 Kaneryd, L., Borrvall, C., Berg, S., Curtsdotter, A., Eklöf, A., Hauzy, C., et al. (2012). Species-rich
520 ecosystems are vulnerable to cascading extinctions in an increasingly variable world. *Ecology and*
521 *Evolution*, 2, 858–874.
- 522 Kinzig, A.P., Pacala, S.W. & Tilman, D. (Eds.). (2001). *The functional consequences of biodiversity:*
523 *Empirical progress and theoretical extensions*. Princeton University Press, Princeton.
- 524 Lehman, C.L. & Tilman, D. (2000). Biodiversity, Stability, and Productivity in Competitive
525 Communities. *The American Naturalist*, 156, 534–552.
- 526 Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., et al.
527 (2004). The metacommunity concept: A framework for multi-scale community ecology.
- 528 Leydold, J. & Hörmann, W. (2015). Runuran: R Interface to the UNU.RAN Random Variate
529 Generators.
- 530 Loreau, M. (1998). Biodiversity and ecosystem functioning: a mechanistic model. *Proceedings of*
531 *the National Academy of Sciences of the United States of America*, 95, 5632–5636.
- 532 Loreau, M. (2010). *From Polutations to Ecosystems: Theoretical Fondations for a New Ecological*
533 *Synthesis*.
- 534 Loreau, M. & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of
535 underlying mechanisms. *Ecology Letters*, 16, 106–115.
- 536 MacArthur, R. (1955). Fluctuations of Animal Populations and a Measure of Community Stability.
537 *Ecology*, 36, 533–536.
- 538 Mailleret, L. & Lemesle, V. (2009). A note on semi-discrete modelling in the life sciences.
539 *Philosophical transactions. Series A, Mathematical, physical, and engineering sciences*, 367,
540 4779–4799.
- 541 Mordecai, E.A., Gross, K. & Mitchell, C.E. (2016). Within-Host Niche Differences and Fitness
542 Trade-offs Promote Coexistence of Plant Viruses. *The American Naturalist*, 187, E13–E26.
- 543 Pачepsky, E., Nisbet, R.M. & Murdoch, W.W. (2008). Between discrete and continuous: Consumer-
544 resource dynamics with synchronized reproduction. *Ecology*, 89, 280–288.
- 545 Pake, C.E. & Venable, D.L. (1995). Is coexistence of Sonoran Desert annuals mediated by temporal
546 variability in reproductive success? *Ecology*, 76, 246–261.
- 547 Sasaki, T. & Lauenroth, W.K. (2011). Dominant species, rather than diversity, regulates temporal
548 stability of plant communities. *Oecologia*, 166, 761–768.
- 549 Soetaert, K., Petzoldt, T. & Setzer, R.W. (2010). Package deSolve : Solving Initial Value Differential
550 Equations in R. *Journal Of Statistical Software*, 33, 1–25.
- 551 R Core Team. (2013). *R: A Language and Environment for Statistical Computing*, Vienna, Austria.
552 <https://www.r-project.org/>.
- 553 Thibaut, L.M. & Connolly, S.R. (2013). Understanding diversity-stability relationships: Towards a

- 554 unified model of portfolio effects. *Ecology Letters*, 16, 140–150.
- 555 Tilman, D. (1982). *Resource competition and community structure*.
- 556 Tilman, D., Reich, P.B. & Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a decade-
557 long grassland experiment. *Nature*, 441, 629–632.
- 558 Turnbull, L.A., Levine, J.M., Loreau, M. & Hector, A. (2013). Coexistence, niches and biodiversity
559 effects on ecosystem functioning. *Ecology Letters*, 16, 116–127.
- 560 Usinowicz, J., Wright, S.J., Ives, A.R. & Doak, D.F. (2012). Coexistence in tropical forests through
561 asynchronous variation in annual seed production. *Ecology*, 93, 2073–2084.
- 562 Valone, T.J. & Hoffman, C.D. (2003). A mechanistic examination of diversity-stability relationships
563 in annual plant communities. *Oikos*, 103, 519–527.
- 564 Wang, S. & Loreau, M. (2014). Ecosystem stability in space: α , β and γ variability. *Ecology*
565 *Letters*, 17, 891–901.
- 566 Wardle, D.A. (2016). Do experiments exploring plant diversity-ecosystem functioning relationships
567 inform how biodiversity loss impacts natural ecosystems? *Journal of Vegetation Science*, 27,
568 646–653.
- 569 Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment:
570 the insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of*
571 *America*, 96, 1463–1468.
- 572 Yuan, C. & Chesson, P. (2015). The relative importance of relative nonlinearity and the storage
573 effect in the lottery model. *Theoretical Population Biology*, 105, 39–52.

574 **TABLE**

Table 1 Default values of model parameters and their descriptions. Parameters that vary depending on the mode and strength of species coexistence or depending on species competitive hierarchies are labeled as “variable” in parentheses. The dormant-to-live biomass transition fraction (γ) is a function of other parameters, so has no default value.

Parameter	Description	Value
r	maximum per capita growth rate	0.2 (variable)
a	Hill function curvature parameter	2.0 (variable)
b	Hill function scale parameter	2.5 (variable)
ε	resource-to-biomass conversion efficiency	0.5
α	allocation fraction of live biomass to dormant biomass	0.5 (variable)
γ	dormant-to-live biomass transition fraction	—
ρ	correlation of species’ response to the environment	0.0 (variable)
σ_E	variance of the environmental cue	2.0 (variable)
η	dormant biomass mortality rate	0.1
$\mu(R^+)$	mean annual resource pulse	20
$\sigma(R^+)$	standard deviation of annual resource pulse	0.0 (variable)

FIGURE CAPTIONS

575
576 FIGURE 1: Resource uptake functions and example time series of (un)correlated germination
577 fractions for the storage effect (A,B) and relative nonlinearity (C,D) formulations of the consumer-
578 resource model. The resource uptake functions for both species are equivalent for the storage
579 effect, but their dormant-to-live transition fractions (γ) are uncorrelated in time. The opposite is
580 true for relative nonlinearity: the two species have unique resource uptake functions, but their
581 dormant-to-live transition fractions (γ) are perfectly correlated in time.

582 FIGURE 2: Variability of total community biomass as a function of species richness when co-
583 existence is maintained by the storage effect (A,B) or relative nonlinearity (C,D). Left panels
584 show results from simulations where environmental or resource variance determine the number
585 species that coexist in a community. Right panels show results from simulations where envi-
586 ronmental or resource variance is fixed at a level that allows coexistence of all four species, but
587 species are removed to manipulate diversity. The left-hand panels represent “regional” diversity-
588 ecosystem variability relationships across natural diversity gradients, whereas the right-hand panels
589 represent “local” diversity-ecosystem variability relationships. Note that we do not attribute any
590 particular area size to "region", it is simply any area over which a gradient of environmental
591 variability can emerge. Points are jittered within discrete richness values for visual clarity. Pa-
592 rameter values, where species are denoted by numeric subscripts: (A) $r_1 = r_2 = r_3 = r_4 = 0.2$,
593 $a_1 = a_2 = a_3 = a_4 = 2$, $b_1 = b_2 = b_3 = b_4 = 2.5$, $\alpha_1 = 0.5, \alpha_2 = 0.49, \alpha_3 = 0.48, \alpha_4 = 0.47$,
594 $\rho_1 = \rho_2 = \rho_3 = \rho_4 = 0$, $\sigma_E = \text{variable}$; (B) $r_1 = r_2 = r_3 = r_4 = 0.2$, $a_1 = a_2 = a_3 = a_4 = 2$,
595 $b_1 = b_2 = b_3 = b_4 = 2.5$, $\alpha_1 = 0.5, \alpha_2 = 0.49, \alpha_3 = 0.48, \alpha_4 = 0.47$, $\rho_1 = \rho_2 = \rho_3 = \rho_4 = -1/3$,
596 $\sigma_E = 4$; (C) $r_1 = 0.2, r_2 = 1, r_3 = 2, r_4 = 5$, $a_1 = 2, a_2 = 5, a_3 = 10, a_4 = 25$, $b_1 = 2.5, b_2 =$
597 $20, b_3 = 30, b_4 = 45$, $\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = 0.5$, $\rho_1 = \rho_2 = \rho_3 = \rho_4 = 1$, $\sigma(R^+) = \text{variable}$; (D)
598 $r_1 = 0.2, r_2 = 1, r_3 = 2, r_4 = 5$, $a_1 = 2, a_2 = 5, a_3 = 10, a_4 = 25$, $b_1 = 2.5, b_2 = 20, b_3 = 30, b_4 = 45$,
599 $\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = 0.5$, $\rho_1 = \rho_2 = \rho_3 = \rho_4 = 1$, $\sigma(R^+) = 1.1$.

600 FIGURE 3: The effect of increasing environmental variability on ecosystem variability when species
601 coexist via the storage effect. Panels (A-C) show simulation results where species have slightly
602 asymmetrical competitive effects, whereas panels (D-F) show results when competition is more
603 asymmetric. Columns show results for different levels of correlations of species’ environmental
604 responses, ρ . Colored vertical lines show the magnitude of environmental variability at which each
605 level of species richness first occurs. Parameter values are as in Figure 2A except for α s: (A-C)
606 $\alpha_1 = 0.5, \alpha_2 = 0.495, \alpha_3 = 0.49, \alpha_4 = 0.485$; (D-F) $\alpha_1 = 0.5, \alpha_2 = 0.49, \alpha_3 = 0.48, \alpha_4 = 0.47$.

607 FIGURE 4: The effect of environmental variability on ecosystem variability when species coexist via
608 relative nonlinearity. (A) The species pool increases from one to four species, with the fourth species
609 being most unstable (e.g., resource conservative to resource acquisitive). Increasing environmental
610 variability (the SD of annual resource availability) allows for greater species richness, but species
611 additions do not modulate the effect of environmental variability on ecosystem variability. (B) The
612 species pool increases from one to four species, with the fourth species being most stable (e.g.,
613 resource acquisitive to resource conservative). In this case, increasing environmental variability
614 allows for greater realized species richness and can temper the effect of environmental variability.
615 Parameter values are as in Figure 2C.

616 FIGURE 5: Example of how species additions under increasing environmental variability can buffer
617 ecosystem stability when species coexist via the storage effect. Environmental variability (σ_E^2)
618 increases linearly with time on the x -axis. (A) Time series of species' biomass (colored lines) in a
619 closed community where colonization of new species is prevented and (B) its associated coefficient
620 of variation (Rolling CV; calculated over 100-yr moving window) through time. (C) Time series
621 of species' biomass in an open community where colonization by new species from the regional
622 pool of four species becomes possible as environmental variation increases. The trajectory of
623 total biomass CV in the open community (D) asymptotes at lower variability than in the closed
624 community (B) due to the buffering effect of species richness. Parameter values are as in Figure 2A
625 except for α s: $\alpha_1 = 0.5$, $\alpha_2 = 0.494$, $\alpha_3 = 0.49$, $\alpha_4 = 0.483$.

Figure 1

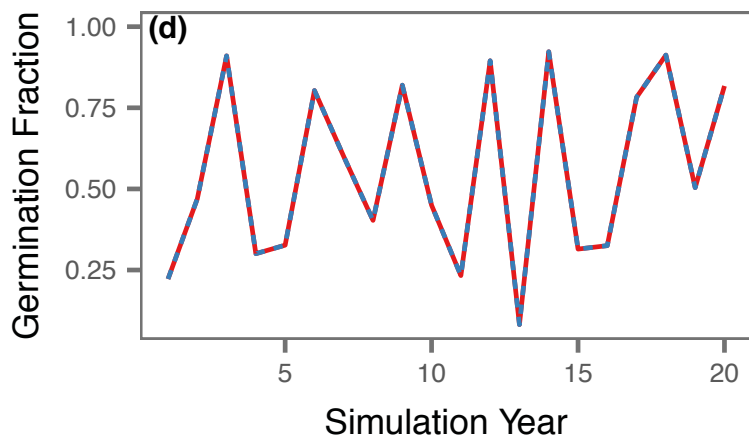
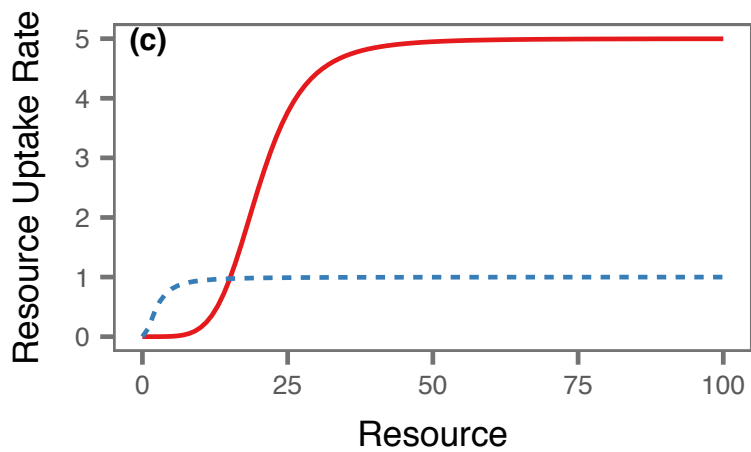
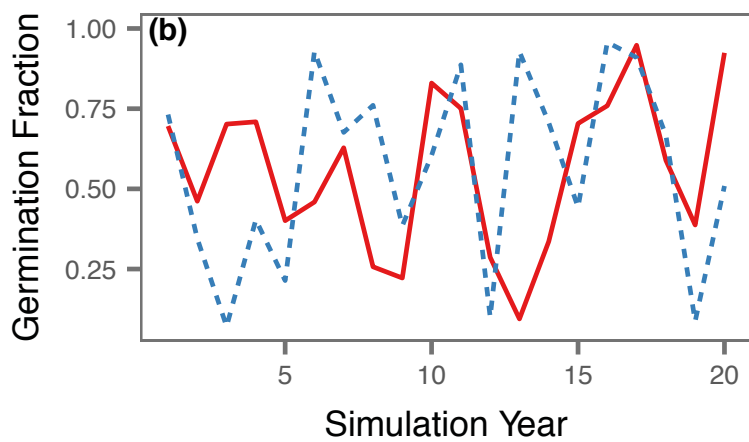
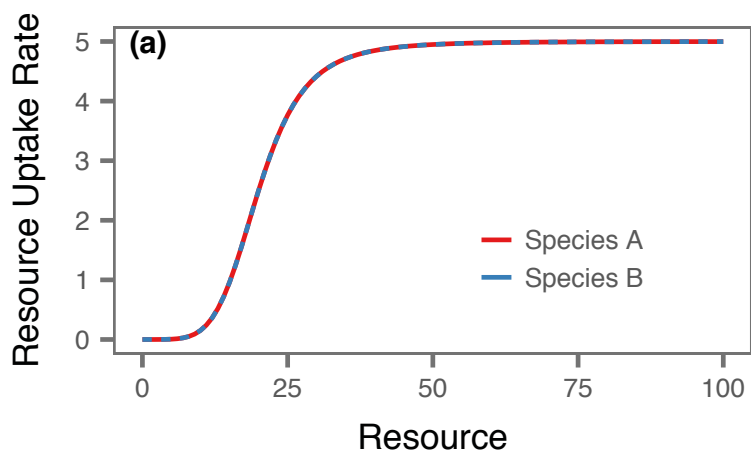


Figure 2

“Regional” Relationship

“Local” Relationship

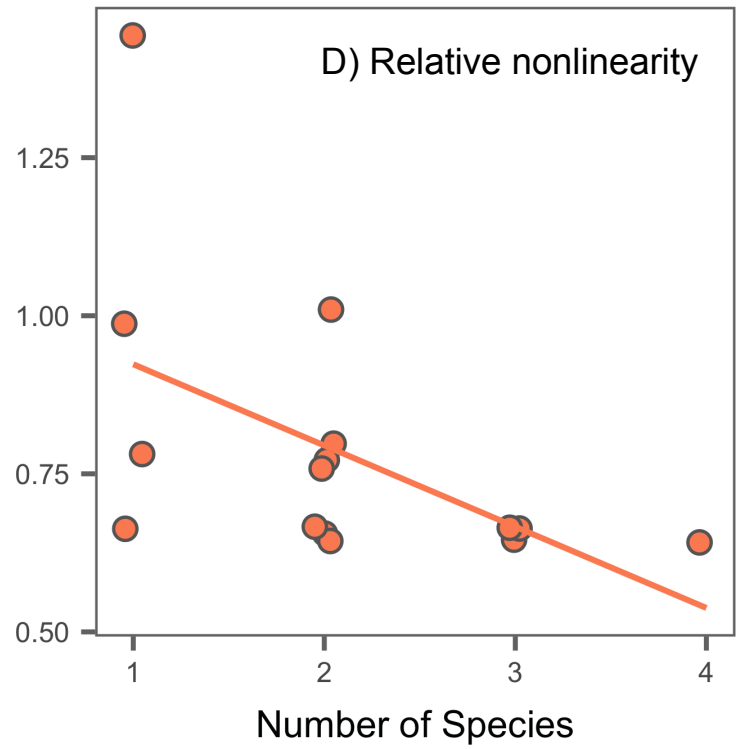
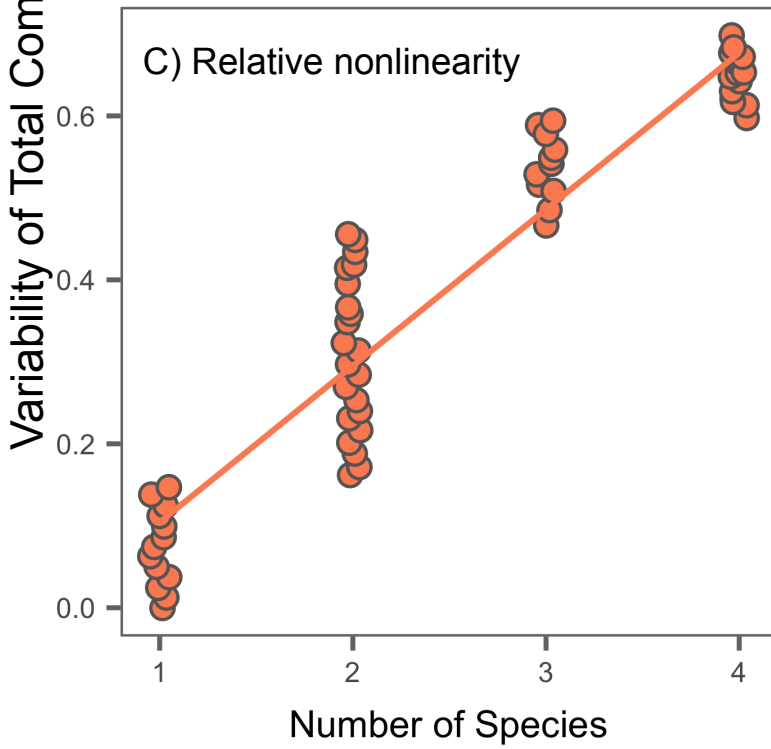
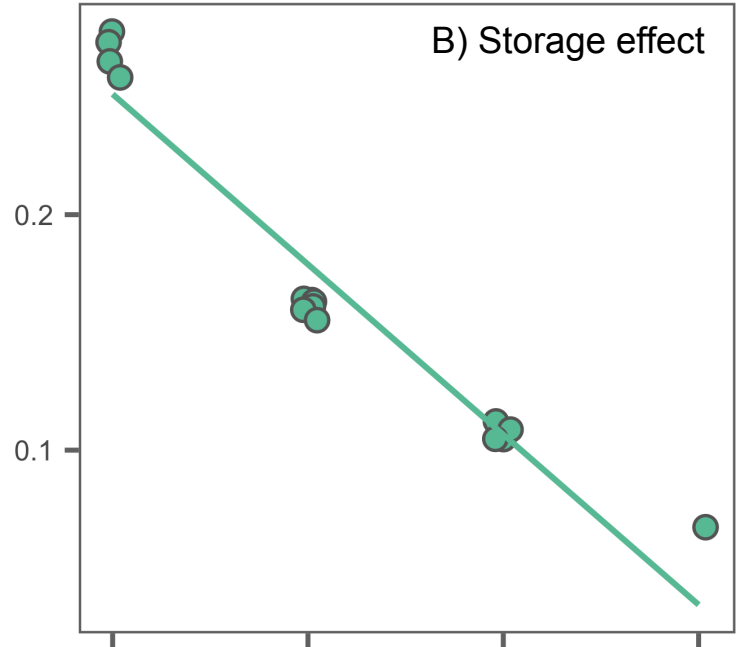
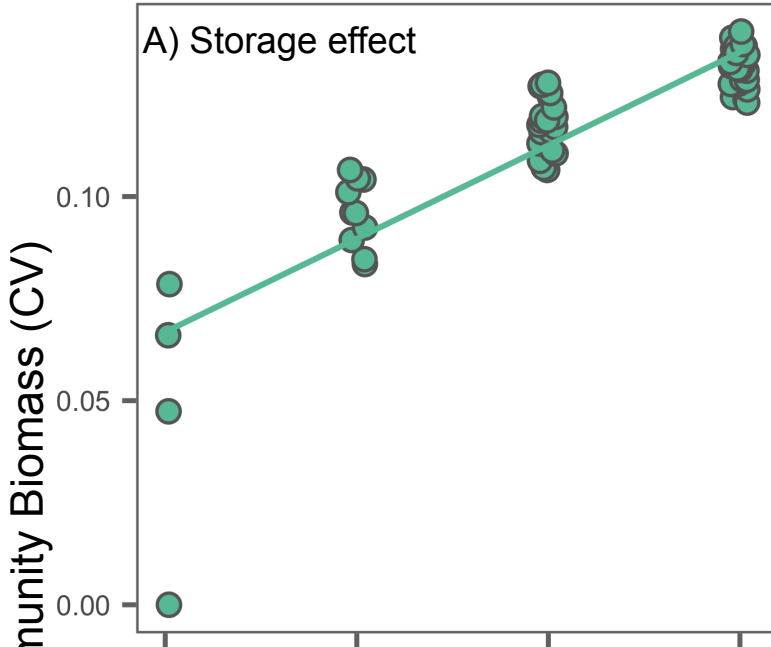


Figure 3

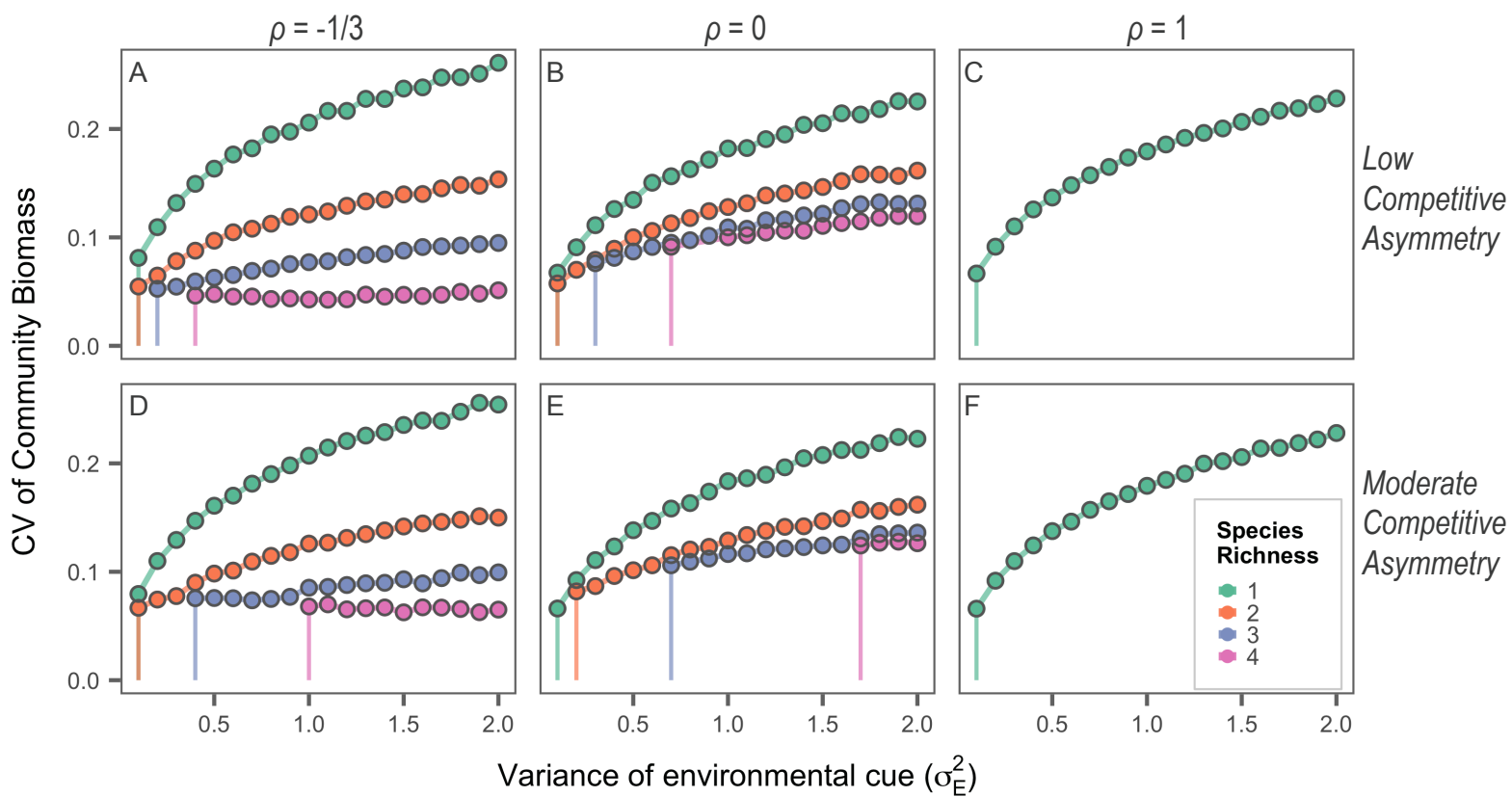
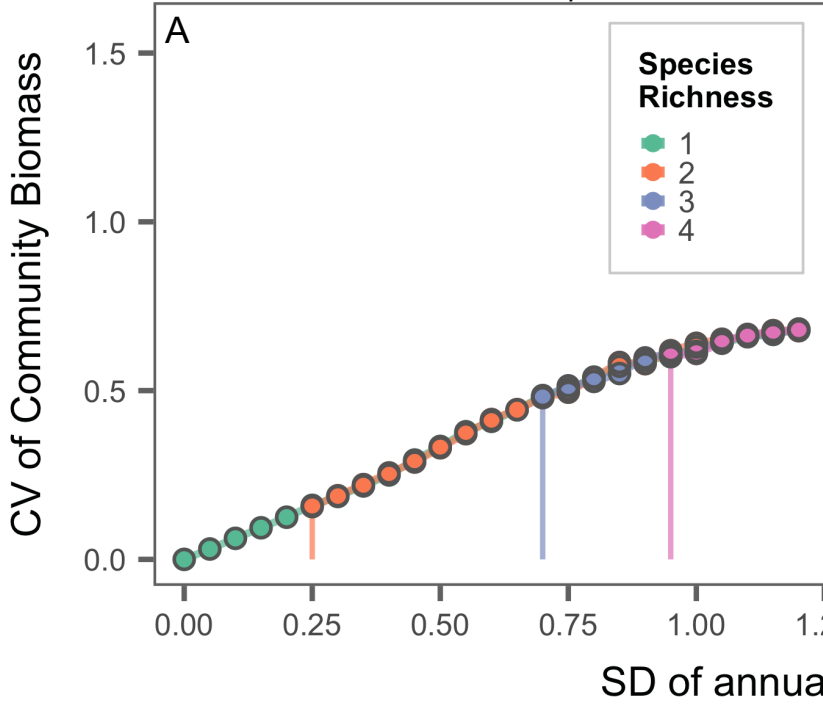


Figure 4

*Species Addition Order:
Conservative to Acquisitive*



*Species Addition Order:
Acquisitive to Conservative*

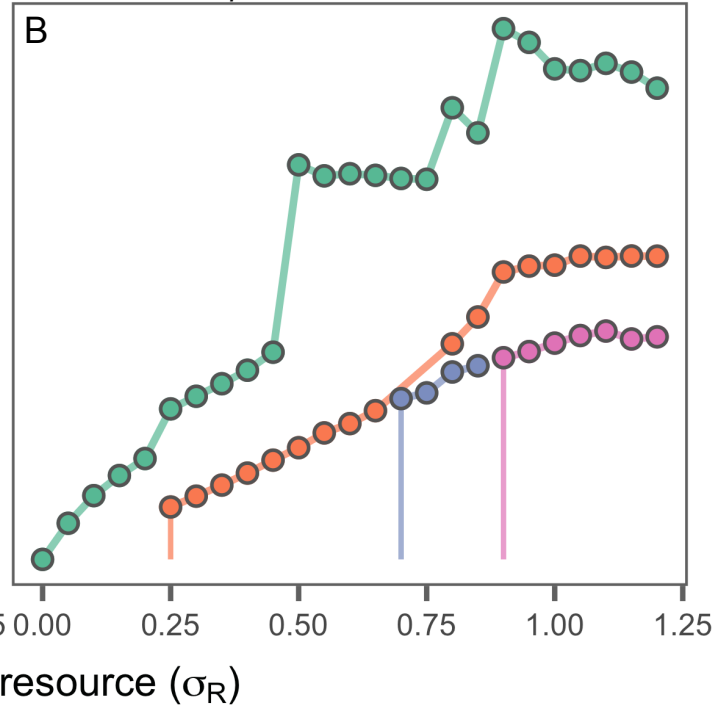


Figure 5

