TEMPORALLY AUTO-CORRELATED PREDATOR ATTACKS STRUCTURE ECOLOGICAL COMMUNITIES

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Abstract: For species regulated by a common predator, the P^* rule predicts that the prey species that supports the highest mean predator density (P^*) excludes the other prey species. This prediction is re-examined in the presence of temporal fluctuations in the vital rates of the interacting species including predator attack rates. When the fluctuations in predator attack rates are temporally uncorrelated, the P^* rule still holds even when the other vital rates are temporally auto-correlated. However, when temporal auto-correlations in attack rates are positive but not too strongly, the prey species can coexist due to the emergence of a positive covariance between predator density and prey vulnerability. This coexistence mechanism is similar to the storage effect for species regulated by a common resource. Strongly positive or negative auto-correlations in attack rates generate a negative covariance between predator density and prey vulnerability and a stochastic priority effect can emerge: with non-zero probability either prey species is excluded. These results highlight how temporally auto-correlated species' interaction rates impact the structure and dynamics of ecological communities.

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Introduction

Predation or resource limitation can regulate populations. When multiple species are regulated by the same limiting factor, long-term coexistence is not expected under equilibrium conditions. Regulation due to a common, limiting resource can result in the R^* rule: the species suppressing the resource to the lower equilibrium level excludes other competitors [Volterra, 1928, Tilman, 1990, Wilson et al., 2007]. Regulation due to a common predator can result in the P^* rule: the prey species supporting the higher equilibrium predator density excludes the other prey species [Holt and Lawton, 1993, Schreiber, 2004, Holt and Bonsall, 2017]. Yet, many coexisting species share a common resource or a common predator. Understanding mechanisms permitting this coexistence is central to community ecology. One of these coexistence mechanisms, the storage effect, relies on temporal fluctuations in environmental conditions [Chesson and Warner, 1981, Chesson, 1994, Ellner et al., 2016]. Whether an analogous, fluctuation-dependent mechanism exists for species sharing a common predator is studied here.

Similar to species competing for a common resource, species sharing a common predator can exhibit mutually antagonistic interactions Holt [1977]: increasing the density of one prey species leads to an increase in predator density and a resulting increase in predation pressure on the other prey species. Thus, to the uninformed observer, the prey appear to be competing. Empirical support for apparent competition is extensive [Morris et al., 2004, Chaneton and Bonsall, 2000, Holt and Bonsall, 2017] and has significant implications for conservation biology [Gibson, 2006]. When the shared predator is the primary regulating factor, Holt and Lawton [1993] demonstrated that one prey excludes the other via the P^* rule. Yet in nature, coexisting species often share common predators. Holt and Lawton [1993] found that spatial refuges, resource limitation, and donor-controlled predation could help mediate coexistence. However, environmentally driven fluctuations in demographic rates did not promote coexistence [Holt and Lawton, 1993, Schreiber, 2021b]. These studies, however, assumed environmental fluctuations are temporally uncorrelated.

In contrast, environmental fluctuations are known, both theoretically and empirically, to mediate coexistence for species competing for a common resource. Intuitively, Hutchinson [1961] argued that environmental fluctuations favoring different competitors at different times may promote coexistence.

In a series of influential papers [Chesson and Warner, 1981, Chesson, 1983, 1988, 1994], Chesson refined Hutchinson's idea and identified two fluctuation-dependent coexistence mechanisms: nonlinear averaging and the storage effect. Empirical support for these mechanisms exist in a diversity of systems [Cáceres, 1997, Adler et al., 2006, Angert et al., 2009, Usinowicz et al., 2012, Chu and Adler, 2015, Ellner et al., 2016, Letten et al., 2018]. A key ingredient for the storage effect is a positive covariance between favorable environmental conditions and species' densities. Temporal auto-correlations, which are commonly observed in environmental factors [Vasseur and Yodzis, 2004, Sun et al., 2018], can generate this positive covariance [Schreiber, 2021a].

Here, temporally auto-correlated fluctuations in predator attack rates are shown to generate non-zero covariances between predator densities and their prey-specific attack rates. These covariances are shown to alter ecological outcomes by mediating prey coexistence or generating stochastic priority effects. To derive these conclusions, stochastic models of predator-prey interactions are studied using a mixture of analytic and numerical methods.

Model and Methods

Following Holt and Lawton [1993], the model considers two prey species with densities N_1, N_2 that are regulated by a common predator with density P. In the absence of predation, the density of prey i increases by a factor, its intrinsic fitness $R_i(t)$, in generation t. The predator attack rate on prey i is $a_i(t)$ in generation t. Predator immigration equals $I(t)$ in generation t and ensures the prey populations are regulated [Holt and Lawton, 1993, Schreiber, 2021b]. The community dynamics are

$$\begin{aligned} N_i(t+1) =& N_i(t)R_i(t)\exp(-a_i(t)P(t)) \text{ with } i=1,2 \\ P(t+1) =& \sum_{i=1}^{2} c_i(t)N_i(t)(1-\exp(-a_i(t)P(t))) + I(t). \end{aligned} \tag{1}$$

Consistent with meteorological models [Wilks and Wilby, 1999, Semenov, 2008], fluctuations in the demographic rates, $R_i(t), a_i(t), I(t)$, are modeled by first-order auto-regressive processes. For example, fluctuations in the predator's attack rate are modeled as $a_i(t+1) = \overline{a_i} + \rho(a_i(t) - \overline{a_i}) + \sqrt{1-\rho^2}Z_i(t)$ where $\overline{a_i}$ is the mean attack rate, $\rho = \mathrm{Cor}[\mathrm{a_i(t)}, \mathrm{a_i(t+1)}]$ is the auto-correlation in the attack rate, and

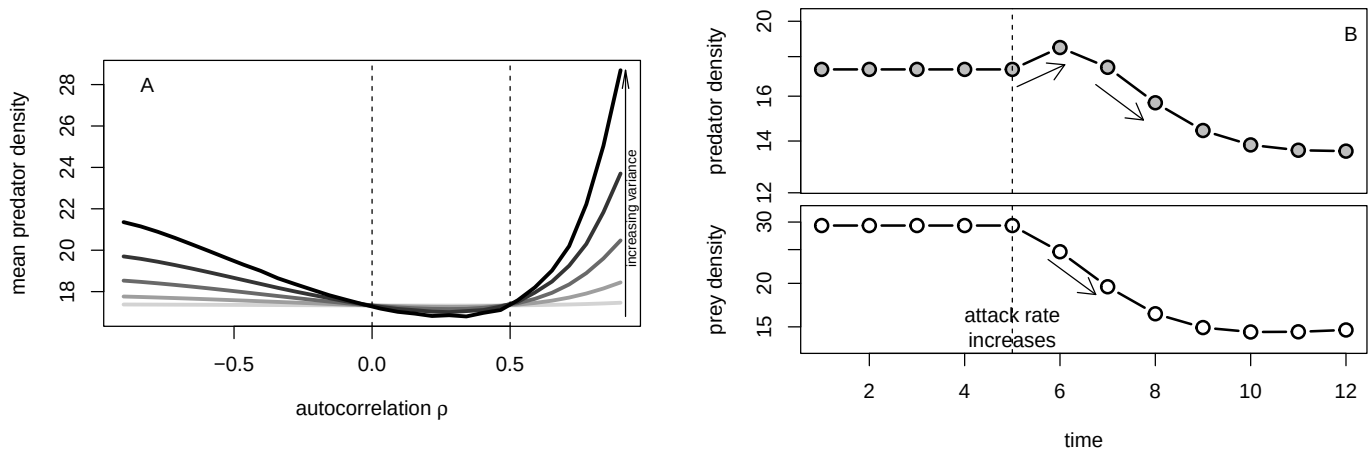

FIGURE 1. Auto-correlated attack rates have a nonlinear effect on mean predator densities. In (A), the mean predator density in the single prey and predator system is plotted a function of the auto-correlation $\rho = \mathrm{Cor}[\mathrm{a_j(t)}, \mathrm{a_j(t+1)}]$ in the predator attack rate. Shading of lines corresponds to the temporal variation in the attack rates. Dashed lines corresponds to where the small variance approximation (4) equals zero. In (B), the short-term versus long-term effects of an increase in the predator attack rate on the predator (top panel) and prey (bottom panel) densities.

$Z_i(t)$ are independent and identically distributed random variables with mean zero and variance σ_i^2. The stationary distribution of this auto-regressive process has mean $\overline{a_i}$ and variance $\mathrm{Var}[\mathrm{a_i}] = \sigma_\mathrm{i}^2$.

The dynamics of (1) are explored using analytical and numerical methods. The analytical methods are based invasion growth rates when rare of the prey species [Chesson, 1994, Schreiber, 2000, Schreiber et al., 2011, Grainger et al., 2019]. These invasion growth rates in conjunction with results from Benaïm and Schreiber [2019] allow one to determine whether each prey, in isolation, coexists with the predator, whether the two prey species can coexist, whether one prey excludes the other prey via apparent competition, or whether the system exhibits a stochastic priority effect i.e. with non-zero probability either prey species is excluded. Analytical approximations for these invasion growth rates are derived when the environmental fluctuations are small. To verify the analytical approximations provide the qualitatively correct predictions, the invasion growth estimated numerically. The details of the mathematical analysis are presented in the Appendix.

Results

Prey persistence. In the absence of the other prey species, prey species j coexists with the predator if its mean log fitness $\overline{\log R_j}$ exceeds the mean of the net attack rate $\overline{a_j I}$ of the immigrating predators. Equivalently,

$$\overline{\log R_j} > \overline{a_j} \times \overline{I} + \mathrm{Cov}[\mathrm{a_j}, \mathrm{I}] \tag{2}$$

Hence, negative covariances between prey vulnerability and predator immigration facilitate prey establishment, while positive covariances inhibit prey establishment. When this condition (2) is reversed, the prey is driven extinct by the immigrating predators.

When the predator and prey j coexist, the mean log fitness $\overline{\log R_j}$ of the prey is balanced by the mean of the net attack rate $\overline{a_j P_j}$ of the predator, where P_j denotes the predator's densities at the stationary coexistence state. When the attack rates are uncorrelated in time, one has $\overline{a_j P_j} = \overline{a_j}\,\overline{P_j}$ and the mean predator density, $\overline{P_j} = \overline{\log R_j}/\overline{a_j}$, decreases with the mean attack rate. Intuitively, with higher mean attack rates, the long-term balance between the log fitness of the prey and net predation is only maintained by lower mean predator densities.

Auto-correlated predator attack rates generate a covariance $\mathrm{Cov}[\mathrm{a_j}, \mathrm{P_j}]$ between the attack rates and the predator densities. Call this covariance, the prey vulnerability-predator density covariance. When this covariance is positive, it increases the mean net predation, otherwise it decreases this mean i.e. $\overline{a_j P_j} = \overline{a_j}\,\overline{P_j} + \mathrm{Cov}[\mathrm{a_j}, \mathrm{P_j}]$. Hence, a positive covariance $\mathrm{Cov}[\mathrm{a_j}, \mathrm{P_j}]$ reduces the mean predator density, while a negative covariance increases the mean predator density. Specifically,

$$\overline{P_j} = \frac{1}{\overline{a_j}} \left(\overline{\log R_j} - \mathrm{Cov}[\mathrm{a_j}, \mathrm{P_j}] \right). \tag{3}$$

The prey vulnerability-predator density covariance depends on the auto-correlation ρ of the attack rate in a nonlinear fashion (Fig. 1A). The analytical approximation implies this covariance is proportional to the variance of the attack rate and a quadratic function of the auto-correlation ρ:

$$\mathrm{Cov}[\mathrm{a_j}, \mathrm{P_j}] \propto \mathrm{Var}[\mathrm{a_j}]\rho(1 - \rho\overline{\mathrm{R_j}}) \tag{4}$$

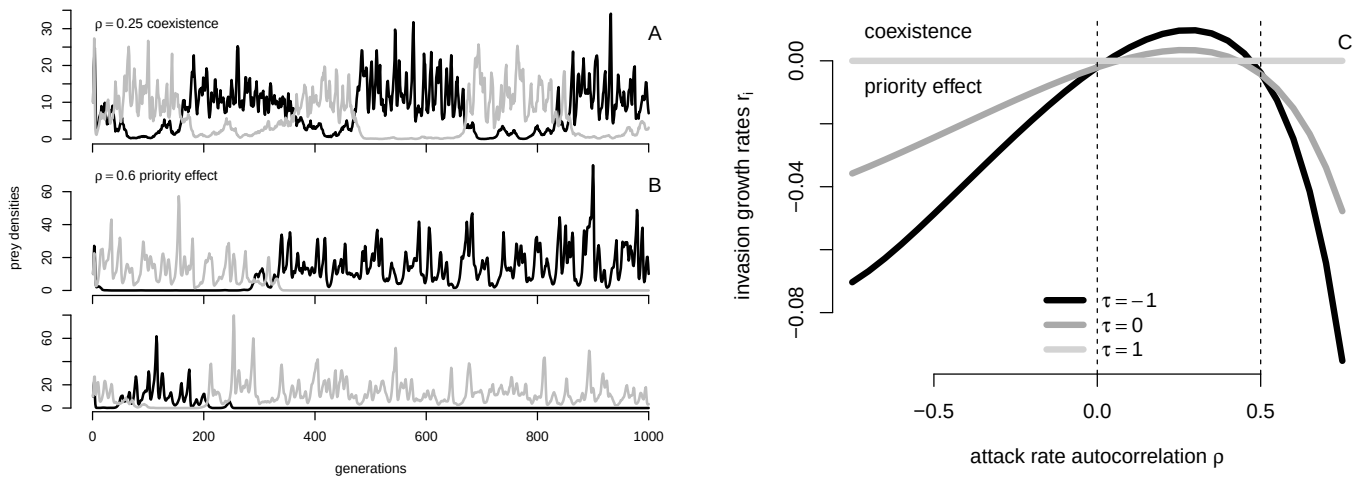

FIGURE 2. Auto-correlated attack rates alter ecological outcomes. In (A), the dynamics of coexisting prey species and (B) two realizations of the dynamics prey species exhibiting a stochastic priority effect. In (C), the invasion growth rates r_i for both prey species when rare as a function of the temporal auto-correlation ρ in attack rates. Different lines correspond to different cross-correlations $\tau = -1, 0, 1$ in the attack rates on the two prey species. Positive values correspond to the prey coexisting (A) and negative values correspond to a stochastic priority effect (B). Dashed lines correspond to where the prey vulnerability-predator density covariance is zero.

where $\overline{R_j}$ is the mean fitness of prey j . The prey vulnerability-predator density covariance is positive only if the auto-correlation is positive but not too positive, i.e. $0 < \rho < 1/\overline{R_j}$.

Figure 1B provide a graphical intuition for this non-linear relationship. When the predator's attack rate increases, there is a short-term increase in the predator's density, but in the long-term there is a decrease in the predator's density. The attack rates change on shorter time scales for weaker, positive auto-correlations and longer time scales for stronger auto-correlations. Weaker auto-correlations generate a positive prey vulnerability-predator density covariance. Stronger auto-correlations, which let the long-term dynamics play out, generate a negative covariance.

Uncorrelated attack rates and the $\overline{P_j}$-rule. When the attack rates are uncorrelated in time, extending arguments in [Schreiber, 2021a] demonstrates that the prey species that can support the higher mean predator density $\overline{P_j}$ excludes the other prey species.

Auto-correlated attack rates alter ecological outcomes. Auto-correlated fluctuations in attack rates can alter the outcome of exclusion. Consider the informative case where prey only differ in their vulnerability. In this case, the invasion growth rate of prey i equals the difference in the prey

vulnerability-predator density covariances:

$$r_i = \mathrm{Cov}[\mathrm{a_j}, \mathrm{P_j}] - \mathrm{Cov}[\mathrm{a_i}, \mathrm{P_j}] \tag{5}$$

where prey $j \neq i$ is common and prey i is rare. If the common prey's vulnerability covaries more strongly with the predator's density than the rare prey's vulnerability, then the rare species increases from low densities and the prey species coexist (Fig. 2A). Alternatively, if rare species' vulnerability covaries more strongly with the predator's density, then the rare species tends to decrease leading to a stochastic priority effect: either prey species is lost with non-zero probability (Fig.2B).

A small variance approximation demonstrates that the difference in these covariances is proportional the variance between the attack rates and a quadratic function in ρ (Fig.2C):

$$\mathrm{Var}[\mathrm{a_i} - \mathrm{a_j}]\rho(1 - \rho\overline{\mathrm{R}}) \tag{6}$$

where $\overline{R}$ is intrinsic fitness of both prey species. Provided there is differential vulnerability to the predator (i.e. $\mathrm{Var}[\mathrm{a_i} - \mathrm{a_j}]$), auto-correlations in these attack rates alter the ecological outcomes. When this auto-correlation is positive but not too strong (i.e. less than $1/\overline{R}$ – see dashed line in Fig.2C), the common prey's vulnerability has a greater covariance with the predator's densities, than the rare prey. This results in a lower mean predator density and allows the rare prey to increase. When the auto-correlation is too strong (i.e. greater than $1/\overline{R}$), the negative covariance between the common prey's vulnerability and predator density leads to a higher predator density and, thereby, causes a stochastic priority effect.

More generally, when the prey species differ in their intrinsic fitness R_i and differ in their mean vulnerability, the invasion growth rate of the prey i depends on these differences:

$$r_i = \overline{\log R_i} - \overline{\log R_j} + (\overline{a_j} - \overline{a_i})\overline{P_j} + \mathrm{Cov}[\mathrm{a_j} - \mathrm{a_i}, \mathrm{P_j}]. \tag{7}$$

The first term $\overline{\log R_i} - \overline{\log R_j}$ corresponds the difference in the mean log fitness of the two prey species. When prey species i has a larger mean log fitness, this term is positive, otherwise it is negative. The second term, $(\overline{a_j} - \overline{a_i})\overline{P_j}$, is proportional to the difference in the mean attack rates. When the common prey species is less vulnerable on average (i.e. $\overline{a_i} < \overline{a_j}$), this term is positive, otherwise it is negative.

The final term, $\mathrm{Cov}[a_j - a_i, P_j]$, is equivalent to (5). However, differences in the variances leads to a more complicated analytical approximation of this covariance term. Specifically, the term $\mathrm{Var}[a_i - a_j]$ in (6) is replaced by $\mathrm{Var}[a_1 - a_2] + \mathrm{Var}[a_j] - \mathrm{Var}[a_i]$. For weak, positive auto-correlations, greater variation in the common prey's vulnerability increases its invasion growth rate. Intuitively, greater variation increases the covariance $\mathrm{Cov}[a_j, P_j]$ that reduces the mean predator density (see (3)) and, thereby, increases the invasion growth rate of the rare species.

Discussion

For species regulated by a common predator, coexistence isn't expected under equilibrium conditions: the prey supporting the higher predator density excludes the other via apparent competition [Holt and Lawton, 1993, Schreiber, 2021b]. Similar to the storage effect for competing species [Chesson, 1994, 2018], we found that environmental fluctuations impacting prey specific attack rates can modify this ecological outcome. Two conditions are necessary for alternative outcomes. First, fluctuating environmental conditions must differentially impact the vulnerability of each prey species to the predator. This condition is equivalent to "species-specific responses to environmental conditions" required for the storage effect [Chesson, 1994]. The second condition requires a non-zero, within-generation covariance between prey vulnerability and predator density. When positive, the prey vulnerability-predator density covariance results in a reduction of the density of the predator and facilitates the recovery of the rarer prey species. Hence, coexistence is more likely. When the prey vulnerability-predator density covariance is negative, each prey species tends toward extinction whenever they become rare. This results in a stochastic priority effect. This second condition is analogous to the "environment-competition covariance" condition of the storage effect [Chesson, 1994].

The sign and magnitude of the temporal auto-correlations in predator attack rates determine the sign of the prey vulnerability-predator density covariance. For positive auto-correlations, the sign of this covariance depends on the time-scale at which the fluctuations occur. When temporal auto-correlation is weak, fluctuations occur on shorter time scales, generate a positive prey vulnerability-predator density covariance, and promote coexistence. In contrast, when temporal auto-correlations are strong, fluctuations occur over longer-time scales, generate a negative prey vulnerability-predator density covariance,

and promote stochastic priority effects. Similarly, for continuous-time models of species competing for a common resource, Li and Chesson [2016] found that fast resource depletion generates a positive environment-competition covariance and, thereby, can promote coexistence. Although not stated by Li and Chesson [2016], this positive environment-competition covariance arises from consumer attack rates being positively auto-correlated at the time scale of the resource depletion.

Taken together, the work presented here and earlier work [Li and Chesson, 2016, Schreiber, 2021a] highlight that covariances between species densities and per-capita species interaction rates can fundamentally alter the composition and dynamics of ecological communities. These covariances can be driven by the sign and magnitude of auto-correlated fluctuations in environmental conditions. Importantly, the magnitude of these auto-correlations can lead to different ecological outcomes due to differences in transient versus long-term responses of species to changing per-capita interaction rates [Bender et al., 1984, Hastings et al., 2018]. Understanding how these effects combine across multiple species to influence the composition and dynamics of ecological communities provides significant challenges for future work.

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APPENDIX FOR "TEMPORALLY AUTO-CORRELATED PREDATOR ATTACKS STRUCTURE ECOLOGICAL COMMUNITIES"

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This appendix provides the mathematical details for the analysis reported in the main text. With the demographics rates modeled as a first-order auto-regressive processes, the full model is

$$
\begin{aligned}
N_i(t+1) =& N_i(t)R_i(t)\exp(-a_i(t)P(t)) \text{ with } i=1,2\\
P(t+1) =& \sum_{i=1}^{2} N_i(t)(1-\exp(-a_i(t)P(t)))+I(t)\\
a_i(t+1) =& \overline{a}_i+\rho(a_i(t)-\overline{a}_i)+\sqrt{1-\rho^2}X_i(t)\\
R_i(t+1) =& \overline{R}_i+\rho_R(R_i(t)-\overline{R}_i)+\sqrt{1-\rho_R^2}Y_i(t)\\
I(t+1) =& \overline{I}_i+\rho_I(I(t)-\overline{I})+\sqrt{1-\rho_I^2}Z(t)
\end{aligned}
\tag{A1}
$$

where $X_i(1), X_i(2), \ldots$ are a sequence of i.i.d. random variables with mean 0, variance σ_i^2 and cross-correlation τ, $Y_i(1), Y_i(2), \ldots$ are a sequence of i.i.d. random variables with mean 0 and variance $\sigma_{R,i}^2$, and $Z(1), Z(2), \ldots$ are a sequence of i.i.d. random variables with mean 0 and variance σ_I^2. These sequences of i.i.d. random variables are assumed to take values in a compact set. Provided the auto-correlation coefficients are strictly less than one, the processes $a_i(t), R_i(t), I(t)$ converge to a compactly supported stationary distribution with means $\overline{a}_i, \overline{R}_i, \overline{I}$ and variances $\sigma_i^2, \sigma_{R,i}^2, \sigma_I^2$.

The dynamics of (A1) are analyzed in four steps. First, using results from Benaïm and Schreiber [2019], I determine under what conditions a single prey species can coexist with the predator. When this condition doesn't hold, the prey asymptotically goes extinct with probability one. For the remainder of the stochastic analysis, I assume that the condition for each prey species coexisting with the predator

holds. Second, I consider the dynamics of the three species model when the predator attack rates are uncorrelated in time; the other demographic rates are allowed to be auto-correlated. Extending the results of Schreiber [2021], I show that the prey species supporting the higher mean predator density excludes the other prey species. Third, I use results from Benaïm and Schreiber [2019] to characterize the general ecological outcomes using the invasion growth rates when rare. Finally, I use a diffusion approximation [Karlin and Taylor, 1981] to derive the approximations for the invasion growth rates r_i presented in the main text.

Persistence of a single prey species. The proof of the persistence of the single prey species, say species j, in the absence of the other prey species closely follows the proof of Theorem 3.1 in [Schreiber, 2021]. The main difference is that [Schreiber, 2021] assumed that the demographic parameters are independent in time i.e. $\rho = \rho_I = \rho_R = 0$. Relaxing this assumption changes the stochastic persistence condition and the expression of the mean predator density. Assume $\widehat{a}_j$, $\widehat{I}$, and $\widehat{R}_j$ are random variables whose distributions correspond to the stationary distributions of the $a_j(t)$, $R_j(t)$, and $I(t)$ auto-regressive processes. The invasion growth rate of prey j is given by

$$\mathbb{E}[\ln \widehat{\mathbb{R}}_j] - \mathbb{E}[\widehat{a}_j \widehat{I}]$$

where $\mathbb{E}[\cdot]$ denotes the expectation of a random variable.

Assume that $\mathbb{E}[\ln \widehat{\mathbb{R}}_j] - \mathbb{E}[\widehat{a}_j \widehat{I}] < 0$. As $P(t) \geq I(t-1)$ for all $t \geq 1$, it follows that for all $t \geq 1$

$$\begin{aligned} N_j(t+1) \leq & R_j(t) N_j(t) \exp(-a_j(t) I(t-1)) \\ \leq & N_j(0) \prod_{s=0}^{t} R_j(s) \exp(-a_j(s) I(s-1)). \end{aligned}$$

The ergodic theorem for auto-regressive processes implies that with probability one

$$\limsup_{t\to\infty} \frac{\ln N_j(t+1)}{t+1} \leq \lim_{t\to\infty} \frac{1}{t+1} \left(\ln x_1(0) + \sum_{s=0}^{t} (\ln R_1(s) - a_j(s) I(s-1)) \right) = \mathbb{E}[\ln \widehat{\mathbb{R}}_j] - \mathbb{E}[\widehat{a}_j \widehat{I}] < 0.$$

Now assume $\mathbb{E}[\ln \widehat{\mathbb{R}}_j] - \mathbb{E}[\widehat{a}_j \widehat{I}] > 0$. [Benaïm and Schreiber, 2019, Theorem 1] with N_j as the only species density and the remaining variables P, a_j, I, R_j as auxiliary variables implies that prey j coexists with the predator in the sense of stochastic persistence.

Still assuming that $\mathbb{E}[\ln \widehat{\mathbb{R}}_j] - \mathbb{E}[\widehat{a}_j \widehat{I}] > 0$, let $(\widehat{N}_j, \widehat{P}_j, \widehat{a}_j, \widehat{I}, \widehat{R}_j)$ be a random vector that corresponds to a stationary distribution of the model with $\widehat{N}_j > 0$ with probability one. Then, [Benaïm and Schreiber, 2019, Proposition 1] implies that the average per-capita growth rate of prey j is zero at this stationary distribution i.e.

$$0 = \mathbb{E}[\ln \widehat{R}_j] - \mathbb{E}[\widehat{a}_j \widehat{P}_j]. \tag{A2}$$

The expressions for the mean predator density, $\overline{P}_j = \mathbb{E}[\widehat{P}_j]$, presented in the main text follow from (A2).

P^* rule when attack rates are serially uncorrelated. Assume that the attack rates are temporally uncorrelated and both prey species can coexist with the predator i.e. $\mathbb{E}[\ln \widehat{\mathbb{R}}_j] > \mathbb{E}[\widehat{a}_j \widehat{I}]$ for $j = 1, 2$. Without loss of generality, assume that prey 1 can maintain the higher mean predator density i.e. $\mathbb{E}[\widehat{P}_1] = \mathbb{E}[\ln \widehat{R}_1]/\mathbb{E}[\widehat{a}_1] > \mathbb{E}[\ln \widehat{R}_2]/\mathbb{E}[\widehat{a}_2] = \mathbb{E}[\widehat{P}_2]$. The proof of the exclusion of prey 2 is similar to the proof of Theorem 3.2 in [Schreiber, 2021]. However, [Schreiber, 2021] assumed all the demographic parameters, not only the attack rates, are serially uncorrelated.

First, I show that prey species 1 is stochastically persists despite the presence of prey species 2. Consider any random vector $(P_1 = 0, N_2 = \widehat{U}, P = \widehat{V}, \widehat{a}_1, \widehat{a}_2, \widehat{R}_1, \widehat{R}_2, \widehat{I})$ that corresponds to an ergodic, stationary distribution of the model with prey 1 absent. By ergodicity, there are two cases to consider: either $\widehat{U} = 0$ with probability one or $\widehat{U} > 0$ with probability one. In the first case, $\widehat{V} = \widehat{I}$ and the invasion growth rate of prey 1 is given by

$$\mathbb{E}[\ln \widehat{R}_1] - \mathbb{E}[\widehat{a}_1 \widehat{I}] > 0.$$

In the second case, stationarity and $\widehat{U} > 0$ implies the average per-capita growth rate of prey species 2 equals zero i.e.

$$0 = \mathbb{E}[\ln \widehat{R}_2] - \mathbb{E}[\widehat{a}_2 \widehat{V}] = \mathbb{E}[\ln \widehat{R}_2] - \mathbb{E}[\widehat{a}_2]\mathbb{E}[\widehat{V}]$$

where the second equality follows from $a_2(t)$ being i.i.d. in time. Hence,

$$\mathbb{E}[\widehat{V}] = \mathbb{E}[\ln \widehat{R}_2]/\mathbb{E}[\widehat{a}_2].$$

On the other hand, the invasion growth rate of species 1 at this distribution equals

$$\begin{aligned}\mathbb{E}[\ln \widehat{R}_1] - \mathbb{E}[\widehat{a}_1 \widehat{V}] =& \mathbb{E}[\ln \widehat{R}_1] - \mathbb{E}[\widehat{a}_1]\mathbb{E}[\ln \widehat{R}_2]/\mathbb{E}[\widehat{a}_2] \\ =& \mathbb{E}[\widehat{a}_1]\left(\mathbb{E}[\ln \widehat{R}_1]/\mathbb{E}[\widehat{a}_1] - \mathbb{E}[\ln \widehat{R}_2]/\mathbb{E}[\widehat{a}_2]\right) > 0\end{aligned}$$

where the last equality follows from the assumption that prey 1 can support the higher mean predator density. [Benaïm and Schreiber, 2019, Theorem 1] treating all but N_1 as auxiliary variables implies that prey 1 persists whether or not prey 2 is in the system.

Next I show that prey 2 is excluded whenever prey 1 is in the system. Assume $N_1(0) > 0$ and let $W(t) = (N_1(t), N_2(t), P(t), a_1(t), a_2(t), I(t), R_1(t), R_2(t))$. Let $\Pi_t(dw)$ be the occupational measure at time t i.e. the random measure defined by

$$\int h(w)\Pi_t(dw) = \frac{1}{t}\sum_{s=1}^{t} h(W(t))$$

for any continuous bounded function h. With probability one, the weak* limit points of Π_t as $t \to \infty$ are an invariant probability measure. Let $\widehat{W} = (\widehat{N}_1, \widehat{N}_2, \widehat{P}, \widehat{a}_1, \widehat{a}_2, \widehat{I}, \widehat{R}_1, \widehat{R}_2)$ be a random vector whose distribution is given by one of these invariant probability measures. By stochastic persistence of prey 1, $\widehat{N}_1 > 0$ with probability one. Furthermore, by stationarity, the average per-capita growth rate of prey 1 at this distribution equals zero:

$$0 = \mathbb{E}[\ln \widehat{R}_1] - \mathbb{E}[\ln \widehat{a}_1]\mathbb{E}[\ln \widehat{P}].$$

On the other hand, the average per-capita growth rate of prey 2 at this distribution equals

$$\begin{aligned}\mathbb{E}[\ln \widehat{R}_2] - \mathbb{E}[\widehat{a}_2 \widehat{P}] =& \mathbb{E}[\ln \widehat{R}_2] - \mathbb{E}[\widehat{a}_2]\mathbb{E}[\ln \widehat{R}_1]/\mathbb{E}[\widehat{a}_1] \\ =& \mathbb{E}[\widehat{a}_2]\left(\mathbb{E}[\ln \widehat{R}_2]/\mathbb{E}[\widehat{a}_2] - \mathbb{E}[\ln \widehat{R}_1]/\mathbb{E}[\widehat{a}_1]\right) =: \beta < 0\end{aligned}$$

As this holds for all weak* limit points of Π_t, it follows that

$$\begin{aligned}\lim_{t\to\infty} \frac{1}{t}\log\frac{N_2(t)}{N_2(1)} =& \lim_{t\to\infty}\frac{1}{t}\sum_{s=1}^{t}(\log R_2(s) - a_2(s)P(s)) \\ =& \beta < 0\end{aligned}$$

with probability one. Hence, prey species 2 goes extinct asymptotically an exponential rate.

General conditions for coexistence, bistability, and exclusion

When the attack rate is auto-correlated ecological outcomes are characterized the invasion growth rates of both prey species. As before, assume that each prey species can persist with the predator in isolation of the other prey species i.e. $\mathbb{E}[\ln \widehat{R}_j] > \mathbb{E}[\widehat{a}_j \widehat{I}]$ for $j = 1, 2$. Under this assumption, the predator-prey j subsystem supports at least one stationary distribution for which $N_j > 0$ and $N_i = 0$ with probability one. Let $(\widehat{N}_j, \widehat{P}_j, \widehat{a}_1, \widehat{a}_2, \widehat{R}_1, \widehat{R}_2, \widehat{I})$ be a random vector whose distribution corresponds to this stationary distribution. Assume this stationary distribution is unique – this happens for example, when the environmental fluctuations are sufficiently large or when the environmental fluctuations are sufficiently small and the predator-prey system without fluctuations has a globally stable equilibrium.

At this stationary distribution, the invasion growth rate of prey i is

$$r_i = \mathbb{E}[\ln \widehat{R}_i] - \mathbb{E}[\widehat{a}_i \widehat{P}_j]$$

Furthermore, at this stationary distribution, the resident prey j growth rate is zero

$$0 = \mathbb{E}[\ln \widehat{R}_j] - \mathbb{E}[\widehat{a}_j \widehat{P}_i]$$

Subtracting this expression from r_j and recalling that $\mathbb{E}[\widehat{a}_i \widehat{P}_i] = \mathbb{E}[\widehat{a}_i]\mathbb{E}[\widehat{P}_j] + \mathrm{Cov}[\widehat{\mathrm{a}}_\mathrm{i}, \widehat{\mathrm{P}}_\mathrm{j}]$ yields

$$r_i = \mathbb{E}[\ln \widehat{R}_i] - \mathbb{E}[\ln \widehat{R}_j] + (\mathbb{E}[\widehat{a}_j] - \mathbb{E}[\widehat{a}_i])\mathbb{E}[\widehat{P}_j] + \mathrm{Cov}[\widehat{\mathrm{a}}_\mathrm{j}, \widehat{\mathrm{P}}_\mathrm{j}] - \mathrm{Cov}[\widehat{\mathrm{a}}_\mathrm{i}, \widehat{\mathrm{P}}_\mathrm{j}]$$

as claimed in the main text.

Benaïm and Schreiber [2019, Theorem 1] implies that if $r_1 > 0, r_2 > 0$, then the prey coexist in the sense of stochastic persistence. When $r_i < 0$ and $r_j > 0$, Benaïm and Schreiber [2019, Corollary 3] implies that species i goes exponentially quickly toward extinction when prey j is initially present. Finally, when $r_1 < 0, r_2 < 0$, the same corollary implies that each species is excluded with positive probability whenever the other species is present.

Diffusion approximations for prey invasion growth rates

To approximate the invasion growth rates r_i from the previous section, consider the case of small fluctuations in the predator attack rates. Namely, $X_i(t) = \varepsilon\eta_i(t)$ in equation (A1) where $\varepsilon > 0$ is small, and $\eta_i(t)$ are i.i.d. with mean zero, variance v_i, and $\mathbb{E}[\eta_1(t)\eta_2(t)] = \tau$ and $\overline{a}_i = \overline{a} + \varepsilon^2\alpha_i$. These choices correspond to the classical diffusion scaling [see, e.g., Karlin and Taylor, 1981, Chapter 15]. Furthermore, for simplicity, assume that there are no fluctuations in the intrinsic prey fitness or predator immigration i.e. $Y_i(t) = Z(t) = 0$ for all time t in equation (A1). As in the previous two sections, assume each prey species can persist in the absence of the other i.e. $\ln \overline{R}_i > \overline{a}_i\overline{I}$ for $i = 1, 2$.

In the absence of the fluctuating attack rates, the dynamics of the predator with only prey j are given by the deterministic difference equations:

$$\begin{aligned} N_j(t+1) =& N_j(t)\overline{R}_j \exp(-\overline{a}_j P(t)) \\ P(t+1) =& N_j(t)(1 - \exp(-\overline{a}_j(t)P(t))) + \overline{I} \end{aligned} \tag{A3}$$

for which the two species coexist about the equilibrium (N_j^*, P_j^*) given by

$$P_j^* = \frac{\ln \overline{R}_j}{\overline{a}_j} \text{ and } N_j^* = (P_j^* - \overline{I})/(1 - 1/\overline{R}_j).$$

The Jacobian matrix of (A3) at this equilibrium equals

$$\begin{pmatrix} 1 & -\overline{a}_j N_j^* \\ 1 - 1/\overline{R}_j & \overline{a}_j N_j^*/\overline{R}_j \end{pmatrix}.$$

For small fluctuations (i.e. small $\varepsilon > 0$), one can approximate the fluctuations

$$\begin{pmatrix} u(t) \\ v(t) \\ w(t) \end{pmatrix} = \begin{pmatrix} N_j(t) - N_j^* \\ P(t) - P_j^* \\ a_j(t) - \overline{a}_j \end{pmatrix}$$

around the equilibrium values as a first-order auto-regressive process:

$$\begin{pmatrix} u(t+1) \\ v(t+1) \\ w(t+1) \end{pmatrix} = \underbrace{\begin{pmatrix} 1 & -\overline{a}_j N_j^* & -N_j^* P_j^* \\ 1 - 1/\overline{R}_j & \overline{a}_j N_j^*/\overline{R}_j & N_j^* P_j^*/\overline{R}_j \\ 0 & 0 & \rho \end{pmatrix}}_{=:A} \begin{pmatrix} u(t) \\ v(t) \\ w(t) \end{pmatrix} + \underbrace{\begin{pmatrix} 0 \\ 0 \\ \sqrt{1-\rho^2}\xi_j(t) \end{pmatrix}}_{=:b(t)}.$$

The covariance matrix C of $\begin{pmatrix} u(t) \\ v(t) \\ w(t) \end{pmatrix}$ at stationarity [see, e.g., Schreiber and Moore, 2018] satisfies

$$\mathrm{vec(C) = (Id - A \otimes A)^{-1} vec(Cov[b(t)])}$$

where vec($*$) is a column vector given by concatenating the columns of its argument $*$ and $\otimes$ denotes the Kroenker product. Carrying out this calculation yields the approximation

$$\mathrm{Cov[a_j(t), P_j(t)] \approx Cov[w(t), v(t)]} = \underbrace{\frac{\mathrm{N_j^* P_j^*}}{\overline{a}_j \rho N_j^*(\rho \overline{R}_j - 1) + (1-\rho)\overline{R}_j}}_{=:\Psi} \times \sigma^2 \rho \left(1 - \rho \mathrm{\overline{R}_j}\right).$$

Next I show that $\Psi > 0$ whenever $\overline{R}_j > 1$. The definition of N_j^* implies that

$$\Psi/\overline{R}_j = \rho \frac{\ln \overline{R}_j - \overline{a}_j \overline{I}}{\overline{R}_j - 1}(\rho \overline{R}_j - 1) + (1-\rho).$$

Note that $\ln \overline{R}_j - \overline{a}_j \overline{I} > 0$ by assumption. For $\rho \leq 0$, the first term of $\Psi/\overline{R}_j$ is non-negative and the second term is positive. Hence, $\Psi > 0$ for $\rho \leq 0$. Assume $0 < \rho < 1$ and define $f(x) = \ln x/(x-1)$. I claim that $f(x) < 1$ for $x > 1$ in which case

$$\Psi/\overline{R}_j > \rho(\rho - 1) + (1-\rho) = (1-\rho)^2 > 0.$$

To prove the claim about f, l'Hopital's rule implies that

$$\lim_{x \downarrow 1} f(x) = \lim_{x \downarrow 1} \frac{1/x}{1} = 1.$$

Furthermore,

$$f'(x) = \frac{\overbrace{1 - 1/x - \ln x}^{=:g(x)}}{(x-1)^2}.$$

For $x > 1$, the sign of $f'(x)$ is determined by the sign of $g(x)$. As $g(1) = 0$ and $g'(x) = (1/x)(1/x-1) < 0$ for $x > 1$, $f'(x) < 0$ for $x > 1$. Hence, as claimed, $f(x) < 1$ for $x > 1$. Thus, as claimed in the main text, $\mathrm{Cov}[\mathrm{a_j(t)}, \mathrm{P_j(t)}]$ is proportional to $\sigma^2\rho(1 - \rho\overline{R}_j)$.

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