

Sustainable strategies for harvesting predators and prey in a fluctuating environment

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Abstract

The effects of harvest and fluctuating environment on inter-dependent predators and prey are complex and not well-known. We define a stochastic model where the predators and prey dynamically interact. The novelty of the model holds on the fact that predators and prey dynamics are simultaneously affected by correlated environmental noises. Interacting predators and prey are harvested using a proportional threshold harvesting strategy that accounts for stochastic population dynamics. Optimal yield of prey can be obtained with identical harvesting strategies when the predators and prey responded to the environment similarly (i.e., synchrony between species) and differently (i.e., asynchrony between species). Remarkably, our study demonstrates that two different harvesting strategies, the proportional harvesting strategy for the prey and the proportional threshold harvesting strategy for the predators, are needed to optimize the annual yield of predators and prey when both species are harvested simultaneously. Our study finds optimal harvest strategies of interacting species affected by environmental variations (i.e., correlated noises) with parameters representing the joint dynamics of predators and prey at a stable state.

Keywords: correlated environmental noises, optimal yield, population dynamics, population synchrony, proportional threshold harvesting, species interactions.

1. Introduction

Species interactions are the basis of highly complex dynamical systems that form food webs where the predator-prey relationships are essential in maintaining the equilibrium between different species (May, 1972; Pimm, 1984). Predation can reduce competition among prey species, and certain prey species might produce more offsprings. Although, in the absence of predation, some prey species can lead to the extinction of other species as an outcome of the competition (Abrams, 2000; Cramer and May, 1971; Gurevitch et al., 2000; Holt, 1977). Predators may occasionally bring the prey density to low values and possibly to extinction, which may also lead to the disappearance of the predators, and disrupt the functions of the food webs (Pace et al., 1999; Paine, 1966). Other studies show that predators and prey populations can have coupled oscillations in abundances (Kendall et al., 1999; Turchin and Hanski, 1997). Interactions among species and reciprocal interactions between ecological and evolutionary processes are essential for maintaining diversity in natural communities (Chesson, 2000; Loreau, 2010b; Paine, 1966; Yoshida et al., 2003).

Besides, populations are also influenced by random perturbations and stochasticity, which affect the persistence of population dynamics (May, 1973). Environmental effects on two populations of different species can be correlated. If the environmental noise terms are negatively correlated, then optimal conditions for one population are sub-optimal for the other (Abrams, 1984; Lehman and Tilman, 2000; Ripa and Ives, 2003). Hence, the dynamics of the predator-prey system is also driven by environmental stochasticity. The degree of correlation in environmental noises may affect the dynamics of interacting predators and prey (Caswell and Cohen, 1995; Ripa et al., 1998; Roughgarden, 1975).

In a predator-prey system, if one species is protected, only the species that does not need protection can be harvested. Otherwise, both species could be harvested simultaneously. Exploiting only the predators could increase the competition among prey species resulting in

increased risks of extinction of others species (Leibold, 1989; Scheffer and Carpenter, 2003; Schmitz, 2004). Predators reduce the density of prey and then moderate the competition among prey, increasing the resource level for the prey and thus their fecundity, growth and maturation rates (De Roos et al., 2003; McCauley and Murdoch, 1990). A decrease in predator density can also cause prey to grow and reproduce more slowly (Abrams, 2000; Chase et al., 2002). Consequently, lower abundances of prey are produced, which can restrict the recovery of predators making the collapse irreversible (Persson et al., 2007; Schmitz et al., 2004). When harvesting the prey, the predators are indirectly affected by the harvest and can go extinct if its resources are overexploited (Abrams and Matsuda, 1996; Chase, 1999; Smith and Slatkin, 1973). When both trophic levels are harvested, both species can go extinct if they are overexploited. Therefore, differential strategies are needed for sustainable exploitation of predator-prey systems that keep an equilibrium between predators and prey at reasonable abundances (De Roos and Persson, 2002).

By analyzing the effects of harvest in a multispecies system, May et al. (1979) demonstrated that consideration of maximum sustainable yield, species by species, is inadequate for setting management principles for interacting species. Beddington and May (1977) showed that harvested populations for sustained yield have reduced growth and stability, which slow down their abilities to recover from environmental disturbances. Moreover, May et al. (1978) suggested that population abundances and yields display higher fluctuations as harvesting effort increases for any level of environmental stochasticity.

The exploitation of food webs most often ignored ecological processes (i.e., such as predation, competition, effects of environmental variations on inter- and intra-specific population processes), which leads to the overexploitation of natural populations and the degradation of the ecosystems that sustain them (Pikitch et al., 2004). Enhancing conservation and economic outcomes of natural resources requires coordinated management in line with the

ecosystem's ecological properties (White et al., 2012). Overexploitation of single species can have critical consequences for the whole ecosystem by causing trophic cascades that disturb the ecosystems' overall functioning (Carpenter et al., 2001; Frank et al., 2005; Schmitz et al., 2000). Furthermore, harvesting strategies based on deterministic models, such as maximum sustained yield, are still commonly used but do not account for stochastic population dynamics, leading to resource collapse or extinction (Hilborn, 2010; Larkin, 1977).

Lande et al. (1997) found harvest strategies that minimize the risks of extinction while at the same time optimize yields that for a large class of population dynamics and different kinds of organisms. When the population size is uncertain, the adequate harvesting strategy is the proportional threshold strategy, which involves the harvest of only a fraction of the excess in the estimated population above the threshold. These generalized threshold harvest strategies have the advantages of accounting for stochastic population dynamics, fluctuations in population size estimates reducing the variance of the yields, which allows considering resources conservation and sustainability of renewable resources (Lande et al., 2003).

Here, we define a stochastic model where the predators and prey interact through a functional response (Holling, 1959, 1965). They are both affected by environmental fluctuations to take into account that the predators and prey can respond differently to environmental stochasticity. The novelty of the model stands how we introduce correlated environmental noises that affect both species simultaneously. To go beyond the maximum sustainable yield, we use a proportional threshold harvesting strategy to harvest the predators and prey either separately or simultaneously. The maximum sustainable yield is based on how population growth varies with population densities. The population growth rates rise to a maximum value that provides the maximum number that can be harvested, called the maximum sustainable yield (Jennings et al., 2009). Maximum sustainable yield ignores the fact that populations undergo natural fluctuations in abundances and treats the environment as unvarying

(Jennings et al., 2009; Larkin, 1977). Therefore, our approach aims to take steps beyond maximum sustainable yield because it considers of stochastic population dynamics, fluctuations in population size estimates, and the effects of environmental stochasticity on predators and prey. This approach favors resource conservation and sustainability in the long-term rather than continued harvest in the short term as dedicated by maximum sustainable yield strategy. Our goal is to investigate how the long-term yield can be optimized with parameters representing the harvesting strategy and the joint dynamics of predators and prey at a stable state. Based on results on the harvest of single populations from the studies of Engen et al. (1997) and Lande et al. (1995), we predict that a low harvest proportion with a zero threshold should provide low variance in the annual yield of prey and predators. Differently, higher harvest proportion with non-zero thresholds should produce higher expected harvests of prey and predators, but with higher variance in annual yield than expected under deterministic theory (e.g., proportional harvest). This study will enable us to provide theoretical scenarios of harvest for sustainable use of natural resources.

2. Methods

2.1 Predator-prey model

We based the development of our predator-prey model on classical population growth models that have a long-standing use in ecology. The dynamics of the prey follows a discrete form of the standard logistic equation which prevents the amount of prey to increase beyond the carrying capacity K . The number of individuals of prey N varies through time t under predation as,

$$N_t = N_{t-1} + rN_{t-1} \left(1 - \frac{N_{t-1}}{K}\right) - \frac{\alpha N_{t-1}}{1 + \beta N_{t-1}} P_{t-1} + N_{t-1} \varepsilon_{t-1} + \zeta_{1,t} \quad (1)$$

where r is the average prey-population growth rate in the absence of predators. N_{t-1} refers to the number of individuals in the previous generation, so the dynamics behavior of the prey

population is jointly determined by r and K , the per capita rate of increase and the population's carrying capacity. $\alpha N_{t-1} / (1 + \beta N_{t-1})$ is the number of prey eaten per predator P per unit time, α is the predator attack rate, and β is a measure of the time taken to handle each prey item. Simultaneous environmental effects specific to the prey (ε) and predators (δ) at time t are expressed by a bivariate normal distribution with mean $(\mu_\varepsilon, \mu_\delta)$ and variance $(\sigma_\varepsilon^2, \sigma_\delta^2)$ and correlation coefficient ρ . These correlated environmental noises represent a fluctuating environment defined by $\Gamma \sim N(\mu, \Sigma)$ (Genz, 1992) such as,

$$\begin{pmatrix} \varepsilon_t \\ \delta_t \end{pmatrix} \sim N \left[\begin{pmatrix} \mu_\varepsilon \\ \mu_\delta \end{pmatrix}, \begin{pmatrix} \sigma_\varepsilon^2 & \sigma_\varepsilon \sigma_\delta \rho \\ \sigma_\varepsilon \sigma_\delta \rho & \sigma_\delta^2 \end{pmatrix} \right] \quad (2)$$

where ρ is the correlation between ε and δ , and where $\sigma_\varepsilon > 0$ and $\sigma_\delta > 0$. The variance-covariance matrix Σ is a positive-definite symmetric matrix. In our model, when the correlation of the environmental noises is positive ($\rho = 1$), the environmental fluctuations affect the prey and predator's population growth in the same way (i.e., the environmental conditions are optimal for both species). At the opposite, when the correlation of the environmental noises is negative ($\rho = -1$), the environmental noise will increase the population growth of one species and decrease the population of growth of the other species (i.e., the conditions are optimal for one species and suboptimal for the other). When there is no correlation in the noise ($\rho = 0$), both species have independent population growth. The environmental noises affecting the prey (ε , see Eq.1) and the predators (δ , see Eq. 3) are generated from the eigenvalue decomposition of the covariance matrix Σ (Genz, 1992; Ripley, 2009). Hence, the environmental noise of the prey ε_t are temporarily independent noise terms which are normally distributed with zero mean and variance σ_ε^2 . The environmental noise of the prey is linearly multiplied by the number of individuals as it allows to link the influence of climate to population dynamics (Royama, 1992). Many harvested populations have metapopulation structures (Abrams et al., 2012; Lundberg and Jonzén; Tuck and Possingham, 1994). Indeed, dispersal is a natural process in many natural

populations (Hanski, 1999; Hanski, 1998; Levins, 1970) and very few predator-prey system are isolated (Holyoak and Lawler, 1996). Therefore, populations are not closed and likely to be subject to emigration and immigration (i.e., open population) (Hanski, 1999). Immigrants coming from extant populations may recolonize the local population which can avoid that a local population goes to extinction (Hanski, 1999; Mac Arthur and Wilson, 1967). Moreover, immigrants from surrounding populations can contribute to the dynamics of existing populations through continuous immigration processes that can lead to reduced extinction rates (i.e., rescue effect) (Brown and Kodric-Brown, 1977). Density-dependent migration strongly influences both the establishment and rescue effects in the local dynamics of metapopulation (Sæther et al., 1999). Such effects can have a substantial influence on food-web at different localities (Holyoak et al., 2005; Leibold et al., 2004). Therefore, we included a random number of prey migrants ζ_1 which enters in the prey population at time t and is Poisson distributed with mean λ_1 .

The dynamics of the predator P is modelled from a Ricker function (Ricker, 1954) which represents population with intra-specific competition and assume that the individuals do not monopolize the resource (Brännström and Sumpter, 2005). The predator population growth is influenced by the prey density through a type II functional response (Bonsall and Hassel, 2007; Holling, 1959, 1965; Solomon, 1949), which assumes that there is a high prey density at which the predation rate is saturated and that the per prey capture rate decreases with prey density, such as $c' = c \frac{\alpha N_{t-1}}{1 + \beta N_{t-1}}$, where c is the positive impact of prey on predators. The Ricker model allows an exponential growth of the population with density-dependent feedback mechanisms that hinders the population from growing unreasonably and so accounts for density-regulation,

$$P_t = c' P_{t-1} e^{-\beta_1 P_{t-1}} \Lambda_{t-1} + \zeta_{2,t} . \quad (3)$$

We assume that the size of the predator population is regulated by some kind of social limitation (e.g., access to space) described by $e^{-\beta_1 P_{t-1}}$ (Bonsall and Hassel, 2007; Hassell and Comins, 1976) as well as being influenced by environmental stochasticity modelled as $\Lambda_{t-1} = e^{\delta_{t-1} - \frac{1}{2}\sigma_\delta^2}$. Here δ_{t-1} is a noise term that is normally distributed with zero mean and unit variance so that $E(\Lambda_{t-1}) = 1$. In such a way, the population growth of predators can vary as function of environmental fluctuations and the correlation coefficient ρ joins the prey-environmental noise ε and predator-environmental noise δ . We used two different population dynamics model for the prey and predators (i.e., logistic model for the prey and Ricker model for the predators) because we assume that species population dynamics characteristics are distributed along a slow-fast continuum of life-history variations (Sæther and Bakke, 2000). Therefore, we introduced the environmental noise differently in the dynamics of the both species. For the prey (Eq. 1), which are more strongly affected by density (i.e., density dependence) as well as environment fluctuations, both are formulated by multiplicative terms (Eq. 1). In the predator dynamics (Eq. 3), the noise term enters in an exponential function because the predator dynamics is based on a Ricker model. Moreover, in the predator dynamics the density regulation is formulated by an additive term, then it is natural that the environmental noise term is also additive. Prey are more likely to have *r*-selected species characteristics such as short generation time, early age at maturity, a large number of offspring and small body size, high growth rate, strong density-dependence at low population size, and can be strongly influenced by environmental stochasticity. In contrast, predators are more likely to be *K*-selected species that present the opposite characteristics. Hence, predators might be less likely to be strongly influenced by environmental stochasticity. Species dynamics characteristics might be influenced differently as a function of their life history characteristics and respond in a different way to climate change (Ellner et al., 2011; Tuljapurkar, 1990). Then, in the same way than for the prey, a random number of predator migrants ζ_2 enters in the predator's

population at time t and is Poisson distributed with mean Y_2 to take account of dispersal of predators among communities (Hanski, 1999; Holyoak et al., 2005; Mac Arthur and Wilson, 1967).

2.2 Proportional threshold harvesting

The proportional threshold harvesting strategy (Engen et al., 1997) accounts for fluctuations in the population estimates \hat{N} by more conservatively harvesting only a fraction q of the excess of the estimated population size above a threshold ω . Indeed, in practice, the population size is usually not known exactly and population estimates of many harvested species are often extremely uncertain. Proportional threshold harvesting is defined by the yield,

$$y(\hat{N}) = \begin{cases} 0, & \text{for } \hat{N} < \omega \\ q(\hat{N} - \omega), & \text{for } \hat{N} \geq \omega, \end{cases} \quad (4)$$

where $0 < q < 1$. If $q = 1$ this is pure threshold harvesting, whereas $\omega = 0$ corresponds to proportional harvesting. If the variance of \hat{N} is large, one can intuitively see that threshold harvesting ($q = 1$) can perform very badly. Suppose that the estimate one year is much larger than the real population size. Then $\hat{N} - \omega$ is much larger than $N - \omega$ so if we harvest the amount $\hat{N} - \omega$ the population will after harvesting end up far below ω , which may under a worst-case scenario lead to extinction. The full predator-prey model including harvest for both predators and prey is,

$$N_t = N_{t-1} + rN_{t-1} \left(1 - \frac{N_{t-1}}{K}\right) - \frac{\alpha N_{t-1}}{1 + \beta N_{t-1}} P_{t-1} + N_{t-1} \varepsilon_{t-1} + \zeta_{t,1} - y(\hat{N}) \quad (5)$$

$$P_t = c' P_{t-1} e^{-\beta_1 P_{t-1}} \Lambda_{t-1} + \zeta_{2,t} - y(\hat{P}). \quad (6)$$

Where the function $y = (\hat{N})$ represents annual losses or yields from proportional threshold harvesting (Eq. 4) for an estimated prey population size \hat{N} and the function $y = (\hat{P})$ represents annual losses or yields from proportional threshold harvesting as function of the actual P and

estimated population size of the predators. In this study, we define a harvest threshold for the prey that we call ω_N and a harvest threshold for the predators that we call ω_P . We specify a harvest fraction for the prey q_N and a harvest fraction q_P for the predators. The diagram of the model is provided in Fig. A.1 in Appendix A.

2.3 Simulation study

We performed a simulation study of harvesting in a coupled predator-prey system with correlated dynamics to investigate sustainable and optimal harvesting strategies in a fluctuating environment. The coexistence equilibrium values (Eqs. (A.5) and (A.6) and Table A.1 in Appendix A) were used to initiate the simulation to make sure that the dynamics of the prey and predators fluctuates around their equilibrium densities (Fig. A.2 in Appendix A). We tuned the migration rates of prey and predators low (i.e., minimal regarding the population size of predators and prey) so that the prey and predators' dynamics do not change and the equilibrium stays unique.

We defined eight different fluctuating environments by making varying the variance of the environmental noise specific to the prey (σ_ε^2), the variance of the environmental noise specific to the predator (σ_δ^2) and the environmental noises correlation (ρ) which concerns each species (Table B.2 and Table B.3 in Appendix B). We defined a low fluctuating state of the populations where the coefficient of variation (CV) was set at 0.2 and a high fluctuating state where the CV was set at 0.5. The CV quantifies the uncertainty on the true population size. The estimated population size of prey was defined such as $\hat{N} \sim Normal(N, NCV^2)$ and the estimated population size of predators was as $\hat{P} \sim Normal(P, PCV^2)$. We analyzed the harvest of the predators and prey without fluctuating environment (see Table B.1 in Appendix B). Then, under each fluctuating environment (Table B.2 in Appendix B), firstly, we harvested with the proportional threshold strategy only the prey with five different harvest fraction q_N ranging from

0.2 to 1 as a function of increasing fraction of population size of prey at equilibrium. This fraction corresponds to the harvest threshold of prey (see section *Harvest threshold of predators and prey* in the Appendix B) divided by the population size of prey (or predators) at equilibrium (i.e., ω_P/P_0) for each time unit (i.e., a year) over a time duration of 1×10^6 years. Secondly, we harvested only the predators with five different harvest fraction q_P ranging from 0.2 to 1 as a function of increasing fraction of population size of predators at equilibrium (i.e., ω_P/P_0). Thirdly, we harvested both the prey and predators simultaneously. By making varying the harvest threshold ω_N for the prey or ω_P for the predators and the harvest fraction q_N for the prey or q_P for the predators, we expect to obtain the *optimal yield* which is the highest expected mean annual yield (Eq. (B.1) in Appendix B). The variability of the yield was obtained by estimating the standard deviation of the yield over the time of simulation (Eq. (B.2) Appendix B) for given values of the harvest threshold ω_N for the prey or ω_P for the predators and harvest fraction q_N for the prey or q_P for the predators. The optimal harvest strategy is obtained when the optimal yield is reached and is characterized by a given value of q_N and $\widehat{\omega}_N$ for the prey or q_P and $\widehat{\omega}_P$ for the predators. In all, we investigated 120 scenarios of harvest within eight different fluctuating environments (Tables B.2 and B.3 in Appendix B).

3. Results

We analyzed the predator-prey dynamics from the characteristic's parameters of the deterministic equilibrium (Table A.1 in Appendix A). Without a fluctuating environment, the prey and predator's populations showed a cycling dynamic which suggest that the predator-prey system fluctuates toward the equilibrium and is in a stable state (see Figs. A.2 and A.3). Without migration, the predators and prey presented a stable cycling dynamic (Figs. A.4 and A.5). Our predator-prey system without migration has similar dynamics and oscillate around the equilibrium in the same way as with migration. We analyzed the effect of the correlation

between environmental noises acting simultaneously on prey and predators (Fig. 1). When the correlation in environmental noises acting on both species was positive ($\rho=1$), the dynamics of the prey and predators fluctuated in synchrony (Fig. 1). When there was no correlation in the environmental noises ($\rho=0$), the dynamics of prey and predators did not show any particularity (Fig. 1). When the correlation in environmental noises was negative ($\rho=-1$), the dynamics of prey and predators fluctuated in asynchrony (Fig. 1).

Under weak environmental stochasticity (i.e., $\sigma_\varepsilon=\sigma_\delta=0.1$) and when the correlation in the environmental noises was positive ($\rho=1$), the populations of prey and predators fluctuated in synchrony (Fig. 1), the populations moved with time from low densities of prey and predators to high densities of prey and predators (Fig. 2a). At the opposite, when the correlation in the environmental noises was negative ($\rho=-1$), the prey and predators fluctuated in asynchrony (Fig. 2b), and the joint dynamics of predators and prey oscillated through time between low and high densities of predators (Fig. 2b). The environment with strong environmental stochasticity (i.e., $\sigma_\varepsilon=\sigma_\delta=0.2$) amplified these differences, and both joint population dynamics fluctuated oppositely either when the correlation in environmental noises was either positive ($\rho=1$) or negative ($\rho=-1$) (Figs. 2c-d).

3.1 Harvest of the prey

When there were no fluctuating environment and the population fluctuations were low, the optimal yield of prey was obtained for a fraction of harvest $q_N=0.6$ and a fraction equal to 0.35 of the population size of prey at equilibrium (i.e., ω_N/N_0) (Fig. C.1 and Table C.1 in Appendix C). High population fluctuations decreased the optimal yield of prey (Fig. C1 and Table C.1 in Appendix C). The optimal yield of prey was also obtained for a fraction of harvest $q_N = 0.6$ and a fraction equal to 0.35 of the population size of prey at equilibrium (i.e., ω_N/N_0) (Fig. 3a-b, and Table C.5 in Appendix C) under weak environmental stochasticity (i.e., $\sigma_\varepsilon = \sigma_\delta$

= 0.1). The sign of the correlation in environmental noises ($\rho = 1$ or $\rho = -1$) does not affect the harvest fraction q_N and harvest threshold ω_N associated with the optimal yield of prey. High population fluctuations (i.e., $CV = 0.5$) decreased the optimal yields of prey, which were attained with a less intense harvest (i.e., $q_N = 0.4$ and a fraction equal to 0.3 of N_0) for both opposite correlations in environmental noises (Fig. 3c-d, and Table C.5 in Appendix C).

Strong environmental stochasticity and positive environmental correlation increased harvest fraction ($q_N = 0.8$) and the harvest threshold (fraction equal to 0.45 of N_0) (Table C.5 in Appendix C) needed to obtain the optimal yield of prey. When the correlation in environmental noise was negative, the optimal yield of prey was lower and obtained from less intense harvest ($q_N = 0.4$) and lower harvest threshold (i.e., fraction equal to 0.35 of N_0) (Fig. C5a-b and Table C.5 in Appendix C). A positive environmental correlation increased the variance of the optimal yields of prey (Fig. 3e-h). When the population fluctuations were high (i.e., $CV = 0.5$), the optimal yields of prey were obtained for similar values of harvest fraction $q = 0.4$ and a fraction equal to 0.3 of N_0 for both environmental correlations (Table C.5 in Appendix C).

3.2 Harvest of the predators

When there were no fluctuating environment and the population fluctuations were low, the optimal yield of predators was obtained for a fraction of harvest $q_P=0.4$ and a fraction equal to 0.08 of the population size of predators at equilibrium (i.e., ω_P/P_0) (Fig. C.2 and Table C.2 in Appendix C). High population fluctuations decreased the optimal yield of predators (Fig. C.2 and Table C.2 in Appendix C). The optimal yield of predators was obtained for a harvest fraction $q_P = 0.6$ and a fraction 0.32 of the equilibrium value of the predator's population P_0 (Fig. 4a-d and Fig. C.6 in Appendix C) under weak environmental stochasticity (i.e., $\sigma_\varepsilon = \sigma_\delta = 0.1$) and when the environmental correlation was positive ($\rho = 1$). The negatively correlated

environment ($\rho = -1$) provided the optimal yield of predators for lower harvest fraction ($q_P = 0.4$) and a lower fraction of predator's population at equilibrium (i.e., 0.08 of P_0). The associated variance was higher in the positively correlated environment than in the negatively correlated environment (Table C.6 in Appendix C). When the population fluctuations were high ($CV = 0.5$), the optimal yield of predators was obtained from an identical harvest fraction $q_P = 0.4$ for both inverse environmental noises correlation (Fig. 4c, and Table C.6 in Appendix C). However, the optimal yield of predators was associated with a lower threshold when the correlation was positive (i.e., a fraction of 0.12 of P_0) than when the correlation was negative (i.e., a fraction of 0.14 of P_0) (Table C.6 in Appendix C). Under strong environmental stochasticity, the harvest of the predators when the correlation in environmental noises was positive provided the optimal yield for a harvest fraction $q_P = 0.6$ and a threshold which corresponded to a fraction of 0.3 of P_0 (i.e., ω_P/P_0) (Fig C.6e-h and Table C.6 in Appendix C). When the correlation was negative, the optimal yield of predators was obtained for a higher harvest fraction $q_P = 0.8$ and a higher fraction of P_0 (i.e., a fraction of 0.4 of P_0) (Fig C.6a and Table C.6 in Appendix C). High population fluctuations (i.e., $CV = 0.5$) decreased the optimal predator's yield as well as harvest rates (Fig. C.6c-d in Appendix C). The optimal yield was attained from a lower harvest fraction ($q_P = 0.4$) and a lower fraction of P_0 (i.e., a fraction of 0.14 of P_0) either the environmental noises correlation was positive or negative (Fig. C.6c-d in Appendix C).

3.3 Harvest of the prey and predators simultaneously

Simultaneously harvesting the prey and predators produced the optimal yield of prey from a harvest fraction $q_N = 0.2$ with a threshold $\omega_N = 0$ or $\omega_P = 0$ (i.e., no threshold which corresponds to proportional harvesting), no matter the level of population fluctuations and correlation in the environmental noises (Figs. 5a-d, and Table C.7 in Appendix C). Remarkably,

harvesting the predators also provided the optimal yield for a harvest fraction (q_P) of 0.2, but a harvest threshold was necessary (i.e., proportional threshold harvesting) (Fig. 5e-g, and Table C.8 in Appendix C). In all, higher optimal yields of prey were obtained than when the prey were harvested alone. Oppositely, much lower optimal yields of predators were obtained when harvesting simultaneously the prey and the predators than when harvesting the predators exclusively. The variances in annual yield of prey, when harvesting the prey and the predators simultaneously, were overall lower than when harvesting only the prey (Fig. 6a-d, and Table C.7 in Appendix C). High population fluctuations decreased the optimal yield of predators (Fig. 5e-h, and Table C.8 in Appendix C). Higher optimal yields of predators were obtained when the correlation in environmental noises was positive than when the correlation was negative (Figs. C.7e-g, and Table C.8 in Appendix C). An increase in population fluctuations (i.e., $CV = 0.5$) increased the harvest intensity needed to obtain the optimal yield of predators (Table C.8 in Appendix C).

Overall, slightly higher prey and predator's optimal yields were obtained when the fluctuating environment was not included in the model than when the fluctuating environment was included in the model (Table C.1 to C.4 in Appendix D). Without a fluctuating environment, the optimal yield of predators and prey was associated with lower variability of the optimal yields (Table C.1 to C.4 in Appendix D).

4. Discussion

In this study, we have determined parameter values from the deterministic equilibrium that qualitatively give typical stable dynamics (i.e., stationary oscillations) of predator-prey systems (Eqs. (A.5) and (A.6) in Appendix A) as the dynamics is most often characterized by oscillations in the population sizes of both prey and predators (Kendall et al., 1999; Turchin and Hanski,

1997). We studied the model at a stable state with harvest because the stable state (i.e., the system at equilibrium) is the most natural state of wild populations. The information obtained from our study could be useful to inform relevant conservation measures. Our predator-prey model and simulation study enabled us to take steps over previous theoretical studies on the effects of harvest on predator-prey systems (Basson and Forgy, 1997; Hening et al., 2019; Hilker and Liz, 2019; Holden and Conrad, 2015). These earlier predator-prey models did not include correlated environmental noises acting simultaneously on both species, as in our model. Furthermore, these studies did not analyze the effects of proportional threshold harvesting for both predators and prey (i.e., separately and simultaneously) for a wide range of harvest parameters. The correlated environmental noises affected the amplitude of the population dynamics of both predators and prey. The negative correlation in environmental noises increased the amplitude of the joint dynamic of predators and prey; differently, the amplitude was lower when the correlation in environmental noises was positive (Fig. A.7 in Appendix A). This result is consistent with Ripa and Ives (2003) study that showed that positive correlation weakens the joint dynamics of predators and prey, which may have different consequences on the functioning of the food webs (Ripa et al., 1998). The functional response that we used follow Bonsall and Hassel (2007) and is slightly different from the usual type II functional response as β the measure of the time taken to handle each prey item replace the product of the attack rate and handling time (Britton, 2003; Turchin, 2003). The functional response is coming from the time-continuous model, so using it in a difference equation can introduce discretization lags as for the prey's logistic growth model. In our model, the predators' yearly survival depends on some kind of social limitation (e.g., access to space), which corresponds to $e^{-\beta_1 P_{t-1}}$ and of the level of environmental variation Λ_{t-1} . So, the predators in year t are not exclusively new predator individuals that come from population growth due to consuming prey; there are also some predators surviving from the previous year.

The predator-prey systems are often analyzed with the continuous-time Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963), which assumes, as in our model, that the predators' appetite is bounded. Our discrete predator-prey model includes a functional response of type II to describe the predation in a way close to that of the Rosenzweig-MacArthur model. However, in the Rosenzweig-MacArthur model, the environment does not change in favor of one species, as in our discrete-time predator-prey model. Some ecological dynamics systems are better represented by discrete-time models because the order of which the ecological processes take place can be different as function of the predator-prey system considered, which might better contribute to understand different natural ecological systems (Weide et al., 2019). Besides, natural predators and prey systems are regulated through migration mechanisms that are not described in the Rosenzweig-MacArthur predator-prey model (Gause, 1934; Huffaker, 1958). Thus, our model has additional characteristics as it includes a formulation of prey and predators' migration. In our model, the dynamics of predators was modelled by a Ricker model representing population having reproductive success reduced by competition with neighbors (i.e., scramble competition). The dynamics of predators could be easily extended to a Beverton-Holt model (Beverton and Holt, 1957), which assumes intra-specific contest competition and that the given species can monopolize resources (Brännström and Sumpter, 2005; Geritz and Kisdi, 2004). In this study, we tuned the migration rates of prey and predators small (i.e., minimal) so that the prey and predators' dynamics do not change, and the equilibrium stays unique. Although emigration is not included in our model, it can be easily taken into account. In our model, what is essential is the number of new individuals in the system (i.e., migration rate), which is very small regarding the population size of prey and predators. If the emigration is lower than immigration, then we are still in the case where a small number of migrating individuals remain in the system as only immigration. If the emigration is higher than immigration, the population will go faster to extinction, depending on

the number of emigrants. The goal of the study was to analyze the harvest of a predator-prey system with the proportional threshold harvest strategy; if the system in the presence of harvest goes too fast to the extinction, the cases where harvesting is possible would have been very narrow.

Proportional harvesting of prey (i.e., with $\omega_N = 0$) did not produce any prey yield, suggesting that the population went immediately almost to extinction. Increasing the threshold enabled to obtain an optimal yield, showing that establishing a harvest threshold is efficient to keep the population going extinct (Lande et al., 2003; Lande et al., 1997). All the threshold values needed to obtain the optimal prey yields, whatever the environmental conditions and population fluctuations, were lower than the population size at the equilibrium N_0 . Moreover, in a different kind of model (i.e., single-species model with continuous time, demographic rather environmental stochasticity, and no over-compensatory population dynamics), the harvest threshold is relatively independent of the form of the density-dependence (Sæther et al., 1996). Our results show that the proportional harvesting of prey can be exceeded by more intensive harvesting by setting thresholds to the detriment of the yields' predictability. However, the year without harvesting (i.e., when the size of the population is below the harvest threshold) allowed the population to recover at its maximum natural rate, which provides a more conservative approach for sustainable harvesting. Proportional harvesting allows focusing on short-term goals for maximizing harvest. Still, it can lead to a high risk of extinction of species because harvesting at a small population size strongly influences the meantime to extinction (Lande et al., 1995). Our results show that strong environmental fluctuations do not change the optimal yield of prey, as well as the intensity of harvest, most likely because prey dynamics arise from different ecological processes such as the kill rates by the predators (Holling, 1959; Sinclair and Pech, 1996), the intra-specific competition, as well as the level of synchrony with the dynamics of the predators. However, strong environmental stochasticity increased the

variance in the yield of prey, making the harvest of prey less predictable. Besides, a higher threshold was needed to obtain the optimal yields of prey, when the correlation in environmental noises was negative (i.e., predators and prey fluctuate in asynchrony) than when the correlation was positive (i.e., predators and prey fluctuate in synchrony). Climate change can hamper species interactions by disrupting the synchrony of species' phenology unequally across trophic levels (Both et al., 2009; Winder and Schindler, 2004). Our results emphasize that considering the synchrony of populations is essential when analyzing the harvest of a predator-prey system.

Likewise, to the harvest of the prey, predators were almost extinct for harvest fraction higher or equal to 0.4 when there was no threshold, meaning that the threshold is also essential for keeping the predator's population to go extinct. As for the prey, threshold harvesting of predators (i.e., $\omega_P=0$) provided a higher yield of predators than proportional harvesting (i.e., $q_P=1$) but was associated with a high annual yield variance. High variance in annual yield leads to years of no harvest when predators' population is below the harvest threshold. Nonetheless, predators have the most often slow-life history and particularly needs time to recover from harvesting. Therefore, the proportional threshold harvesting of predators offers a more conservative approach with the possibility of long-term use of the resource that might reduce the risk of resource collapse. Keeping viable predator populations is essential as predators can dampening prey populations fluctuations if the temporal correlation in climatic conditions increases in the future (Wilmers et al., 2007). Unlike the harvest of the prey, the yield of predators was higher when the joined dynamics of predators and prey fluctuated in temporal synchrony. In our model, the prey population is regulated by different processes, such as density-dependence, the correlation in environmental noise and by predation. The predators eat more prey when their density increases, but the appetite of the predators tends to an asymptote due to handling time and satiation (Holling, 1959, 1965). The predators decrease their capacity to assimilate more prey as its functional response reaches its saturation level (Abrams, 2002).

Therefore, at some point, the predators' population will decline rapidly and might respond more strongly to environmental stochasticity. Accordingly, lower optimal yields of predators under strong environmental stochasticity suggest that the level of environmental stochasticity is essential to consider when setting harvesting strategies for predators.

Remarkably, our analysis demonstrates that two different harvesting strategies, such as the proportional harvesting strategy for the prey and the proportional threshold harvesting strategy for the predators, are needed to optimize the annual yield of predators and prey when harvesting both species at the same time. Thus, harvesting the predators with a conservative approach allowed us to continuously harvest the prey with a low variance in the prey's annual yield. Differently, Hening (2019) showed that by using a two-dimensional Lotka-Volterra predator-prey model and a proportional harvest strategy, the optimal harvest of both the predators and prey cannot be obtained by harvesting the predators and the prey simultaneously. Specifically, our results show that life-history traits should be considered when setting a harvest strategy of predators as most predators have the slowest life-history (May et al., 1979; Winemiller, 2005). Interestingly, the predators' population increased (i.e., suggested by the higher optimal yield of predators) when the harvest of the prey population was less intense. This result is consistent with the study of Persson et al. (2007), showing that prey harvesting allows the predator population to recover because it increases prey growth and reproduction. The depletion of a predator population can increase the intra-specific competition of prey (De Roos and Persson, 2002; Loreau, 2010a; Matsuda and Abrams, 2006), which could have negative effects on prey yields. Thus, establishing optimal harvest strategies for predators is essential.

Our results indicate that the predator's harvest rates associated with the optimal yield should be used to set the prey's appropriate harvest strategy to avoid the predator's population's collapse. In our study, when predators and prey responded differently to the environment, the joint dynamics had a larger amplitude. The optimal yield variability was the highest, suggesting

that predators and prey populations might return to the equilibrium slowly. Reductions in the abundance of predation through harvest can propagate through the food chain resulting in increasing consumer abundances, which can destabilize the food web (Bascompte et al., 2005).

Our simulation study demonstrates that harvest strategies can be implemented in our predator-prey system in a stable state. Our results could apply well to populations that do not show long-term trends in abundances and uncertainty in their population size. For instance, in cases where one can assume that individuals can migrate from areas where the population density is higher (e.g., protected areas, high-quality habitat). We showed that our model would be a frame to analyze how variation in the predators' strength and prey's interactions influences optimal yields of different multispecies systems in marine, aquatic and terrestrial ecosystems by parametrizing our model as a function of the species characteristics of the predator-prey system considered. Furthermore, our model could be useful to analyze how harvesting and environmental fluctuations might alter the stability of different natural multispecies systems. Our study finds optimal harvesting strategies for interacting predators and prey affected by environmental variations and opens a way of joining the harvest and conservation of interacting species.

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Figure Legends

Figure 1 Standardized densities of prey (Eq. A.9, plain line) and predators (Eq. A.10, dotted line) for interacting prey-predators dynamics with parameters values obtained from the deterministic equilibrium (from Eqs. (A.5) and (A.6) and Table A.1 in Appendix A), under weak environmental stochasticity ($\sigma_\varepsilon = \sigma_\delta = 0.1$) as a function of time (t) for different correlation in environmental noises. (a), when the predators and prey responded similarly to the environment ($\rho = 1$); (b), when there were no correlation in the environmental noises ($\rho = 0$); (c), when the predators and prey responded differently to the environment ($\rho = -1$).

Figure 2 Predators densities as a function of the prey densities (i.e., phase plane) for interacting prey-predators dynamics with parameters values obtained from the deterministic equilibrium (from Eqs. (A.5) and (A.6) and Table A.1 in Appendix A); (a), under weak environmental stochasticity ($\sigma_\varepsilon = \sigma_\delta = 0.1$) and positive environmental correlation ($\rho=1$); (b), under weak environmental stochasticity ($\sigma_\varepsilon = \sigma_\delta = 0.1$) and negative environmental correlation ($\rho=-1$); (c), under strong environmental stochasticity ($\sigma_\varepsilon = \sigma_\delta = 0.2$) and negative environmental correlation ($\rho=-1$); (d), under strong environmental stochasticity ($\sigma_\varepsilon = \sigma_\delta = 0.2$) and positive environmental correlation ($\rho=1$).

Figure 3 Mean yield of prey $y(\hat{N})$ over time, when only the population of prey was harvested, as a function of the fraction of population size of prey at equilibrium (i.e., harvest threshold of prey / population size of prey at equilibrium (ω_N/N_0)) with model parameters as in Table A.1 in Appendix A (i.e., predator-prey at equilibrium) for different harvest fractions (q_N); (a) – (d), under weak environmental stochasticity ($\sigma_\varepsilon = \sigma_\delta = 0.1$) with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$) and opposite environmental correlations ($\rho = 1$ and $\rho = -1$). The red curve represents the harvest fraction (q_N) which provided the optimal yield of prey. The vertical grey line represents the harvest threshold of prey (i.e., harvest threshold of prey relative to the population size of prey at equilibrium (ω_N/N_0)) for which the optimal yield of

prey was obtained; (e) – (h), standard deviation of prey's yields $y(\hat{N})$ (i.e., variability of prey's yields) over time under the same conditions than (a) – (d).

Figure 4 Mean yield of predators $y(\hat{P})$ over time, when only the population of predators was harvested, as a function of the fraction of population size of predators at equilibrium (i.e., harvest threshold of predators / population size of predators at equilibrium (ω_P/P_0)) with model parameters as in Table A.1 in Appendix A (i.e., predator-prey at equilibrium) for different harvest fractions (q_P); (a) – (d), under weak environmental stochasticity ($\sigma_\varepsilon = \sigma_\delta = 0.1$) with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$) and opposite environmental correlations ($\rho = 1$ and $\rho = -1$). (e) – (h), Standard deviation of predator's yields $y(\hat{P})$ (i.e., variability of the predator's yields) over time under the same conditions than (a) – (d). The red curve represents the harvest fraction (q_P) which provided the optimal yield of predators. The vertical grey line represents the harvest threshold of predators (i.e., harvest threshold of predators relative to the population size of predators at equilibrium (ω_P/P_0)) for which the optimal yield of predators was obtained.

Figure 5 Mean yield of prey $y(\hat{N})$ over time (a) – (d), when prey and predators were harvested simultaneously as a function of threshold population size of prey (i.e., the fraction of population size of prey at equilibrium (ω_N/N_0)) with model parameters as in Table A.1 in Appendix A (i.e., predator-prey at equilibrium) for different harvest fractions (q_N for the prey and q_P for the predator) under weak environmental stochasticity ($\sigma_\varepsilon = \sigma_\delta = 0.1$) with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$) and opposite environmental correlations ($\rho = 1$ and $\rho = -1$); symbols are as in Fig. 3. (e) – (h), mean yield of predators $y(\hat{P})$ over time as a function of threshold population size (i.e., the fraction of population size of predators at equilibrium (ω_P/P_0)) under the same conditions than (a) – (d); symbols are as in Fig. 4.

Figure 6 Standard deviation of prey's yields $y(\hat{N})$ (i.e., variability of prey's yields) (a) – (d), when prey and predators were harvested simultaneously, as a function of threshold population size (i.e., fraction of population size of prey at equilibrium (ω_N/N_0)) with model parameters as in Table A.1 in Appendix A (i.e., predator-prey at equilibrium) for different harvest fractions (q_N and q_P) under weak environmental stochasticity ($\sigma_\varepsilon = \sigma_\delta = 0.1$) with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$) and opposite environmental correlations ($\rho = 1$ and $\rho = -1$). (e) – (h), standard deviation of predator's yield $y(\hat{P})$ (i.e., variability of predator's yields) over time as a function of threshold population size (i.e., fraction of population size of predators at equilibrium (ω_P/P_0)) under the same conditions than (a) – (d). The red curve represents the variability of the yield of prey ((a) – (d)) and predators ((e) – (h)) associated with the harvest fractions q_N or q_P which provided the optimal yields shown in Fig. 5. The vertical grey line represents the threshold population size (i.e., ω_N/N_0 or ω_P/P_0) for which the optimal yields of prey ((a) – (d)) and predators ((e) – (h)) was obtained as shown in Fig. 5.

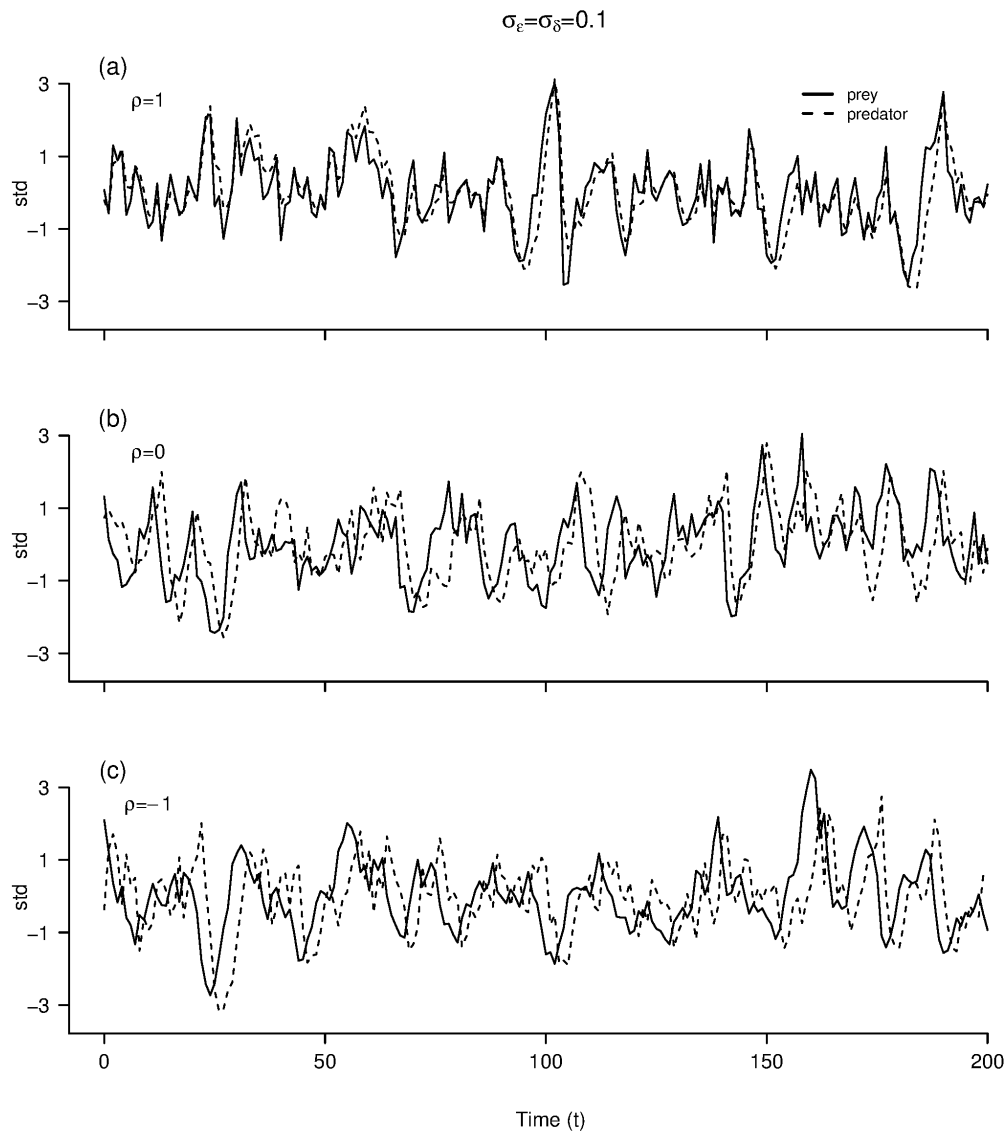


Figure 1

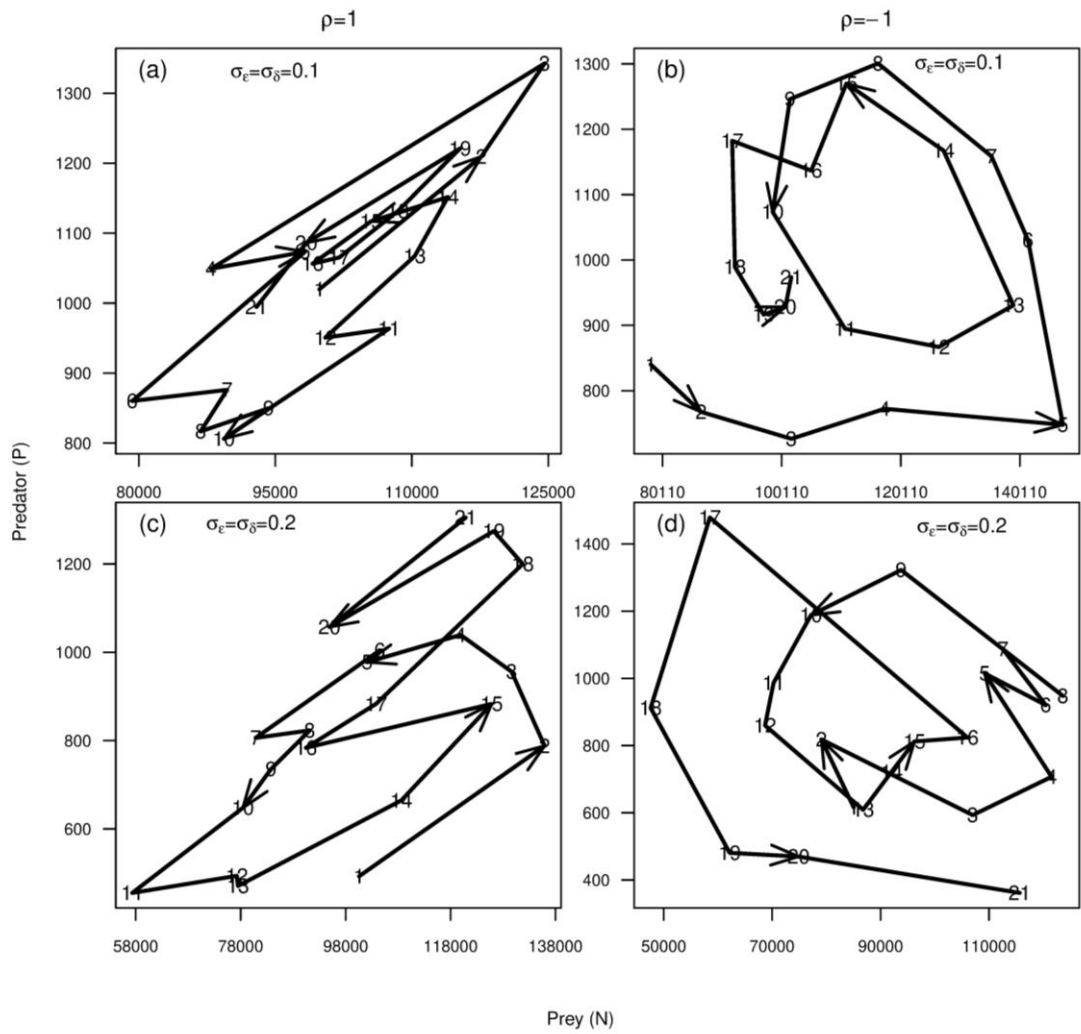


Figure 2

$$\sigma_\varepsilon = \sigma_\delta = 0.1$$

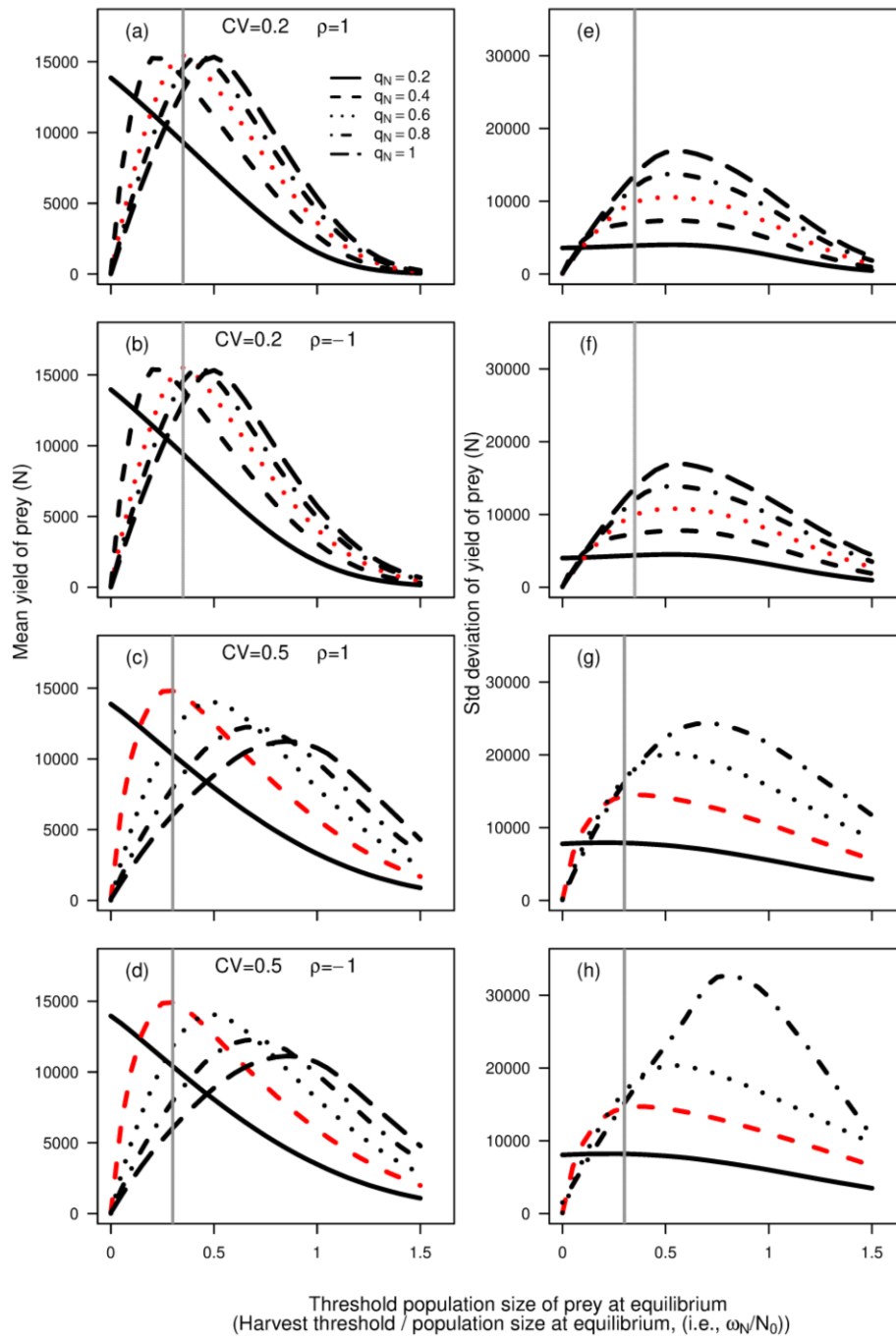


Figure 3

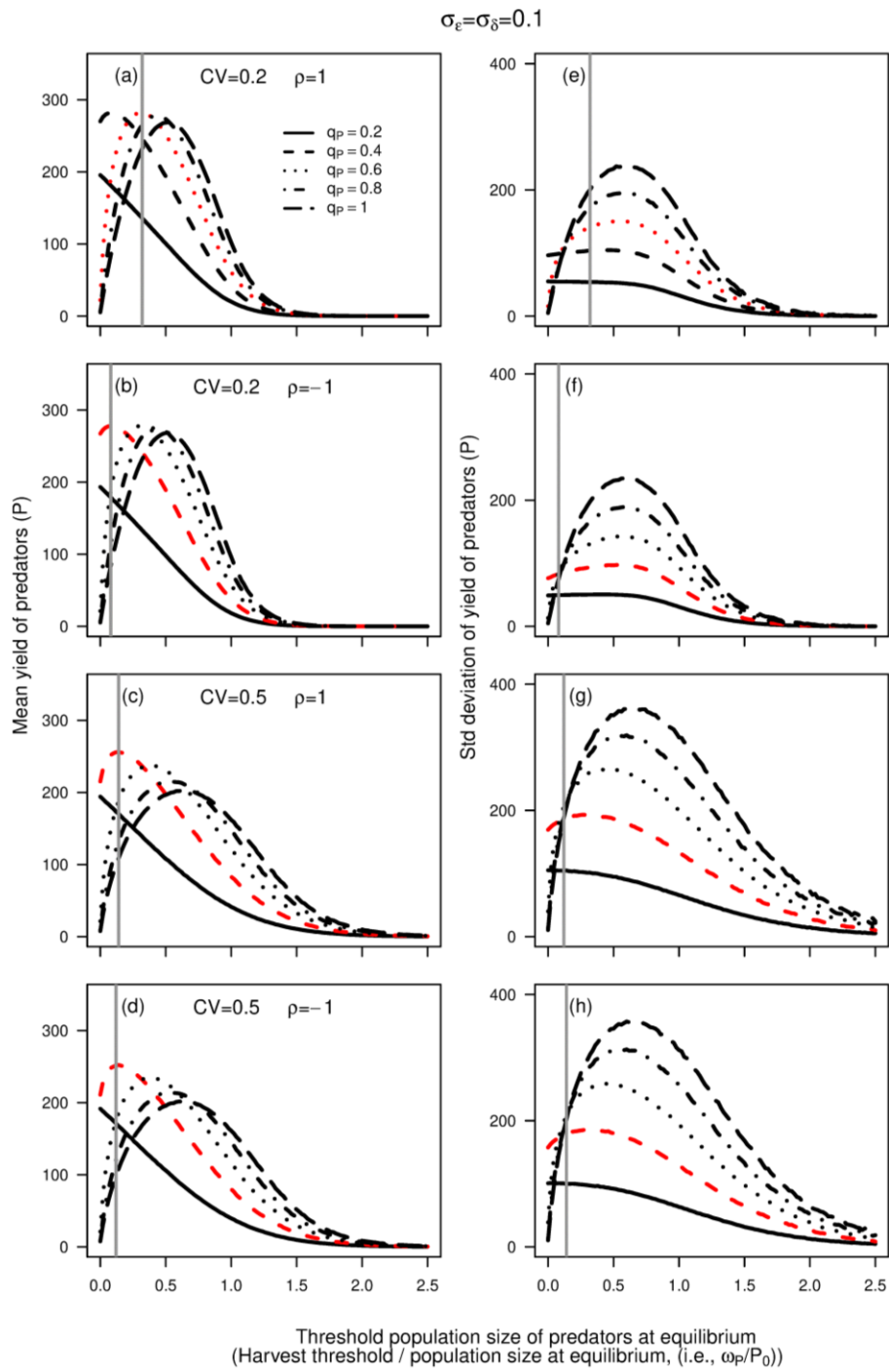


Figure 4

$$\sigma_\epsilon = \sigma_\delta = 0.1$$

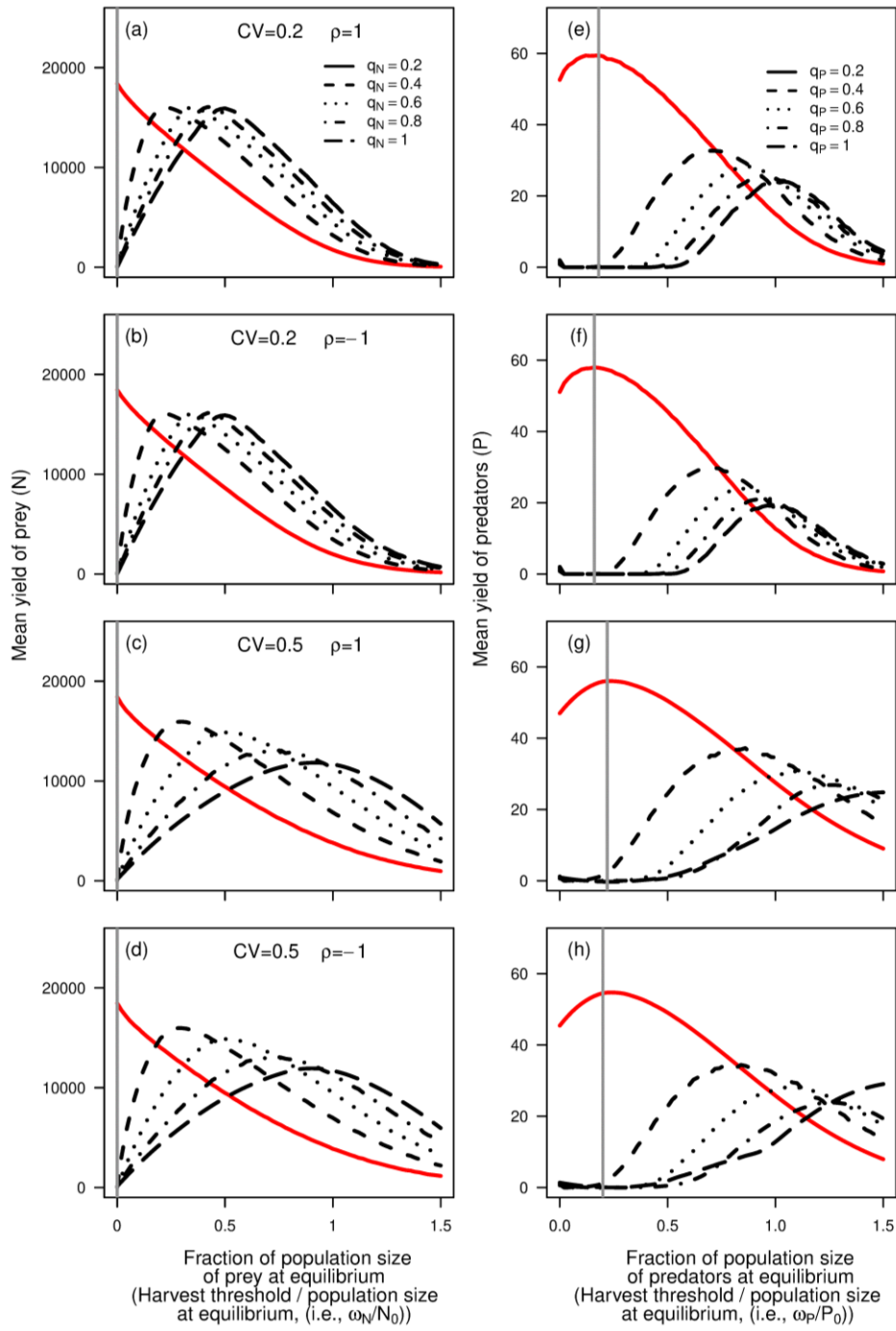


Figure 5

$$\sigma_\varepsilon = \sigma_\delta = 0.1$$

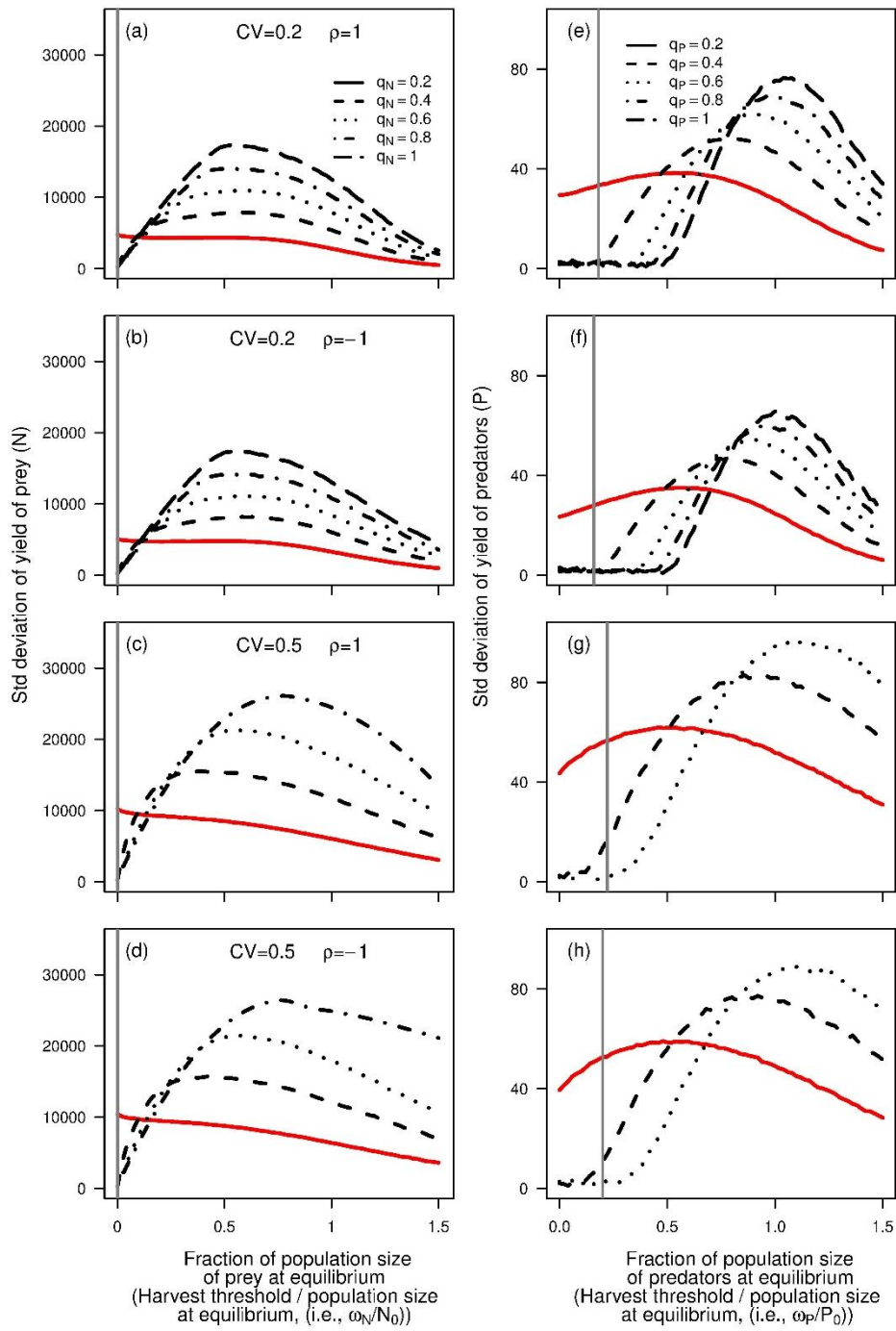


Figure 6

Appendix A

Bellier et al. Sustainable strategies for harvesting predators and prey in a fluctuating environment

The proportional threshold harvesting strategy and predator-prey dynamics at equilibrium

The proportional threshold harvesting strategy

If a population process can be approximated by a Markov process (i.e., a process with the probability that each event depends only on the state of the previous event), harvesting strategies can be some function of the population size expressing how much should be harvested each season. If the population estimates are uncertain, harvesting should be based on the estimates and the uncertainty in the estimates should be taken into account. Initially, we assume that the population size is known. We write $\mu_0(n) = E(\Delta N | N = n)$ and $v_0(n) = \text{var}(\Delta N | N = n)$ for the expectation and variance of the change in population size in the absence of harvesting. Writing $y(N)$ for the yield at population size N , the diffusion approximation has infinitesimal mean and variance,

$$\mu(n) = \mu_0(n) - \mu(n)$$

$$v(n) = v_0(n)$$

In this study, we assume that the annual change in population size ΔN is not too large relative to N so that the process may be approximated by a diffusion process (Engen et al., 1997; Karlin and Taylor, 1981; Lande et al., 1995; Turelli, 1977). When the proportional threshold harvesting strategy is considered, such that only a fraction q of the excess of the estimated population size above a threshold ω is harvested (Eq. (4) in the main text), the infinitesimal mean and variance in the diffusion approximation for N is then,

$$\mu(n) = \mu_0(n) - E \left[y(\hat{N}) | N = n \right] \tag{A.1}$$

$$v(n) = v_0(n) - \text{var} \left[y(\hat{N}) | N = n \right]. \tag{A.2}$$

For a given distribution of the estimator \hat{N} , say $f(\hat{n} | n)$, the above mean and variance are given by

$$E \left[y(\hat{N}) | N = n \right] = q \int_{\omega}^{\infty} (\hat{n} - \omega) f(\hat{n} | n) d\hat{n} \tag{A.3}$$

$$\text{var} \left[y(\hat{N}) | N = n \right] = q \int_{\omega}^{\infty} (\hat{n} - \omega) f(\hat{n} | n) d\hat{n} - \left\{ E \left[y(\hat{N}) | N = n \right] \right\}^2. \tag{A.4}$$

Writing $\hat{n} = nZ$, an unbiased estimator with constant coefficient of variation requires that Z has distribution independent of n with mean 1. Then, if Z is approximately normally distributed the mean and variance can be expressed by the standard normal integral.

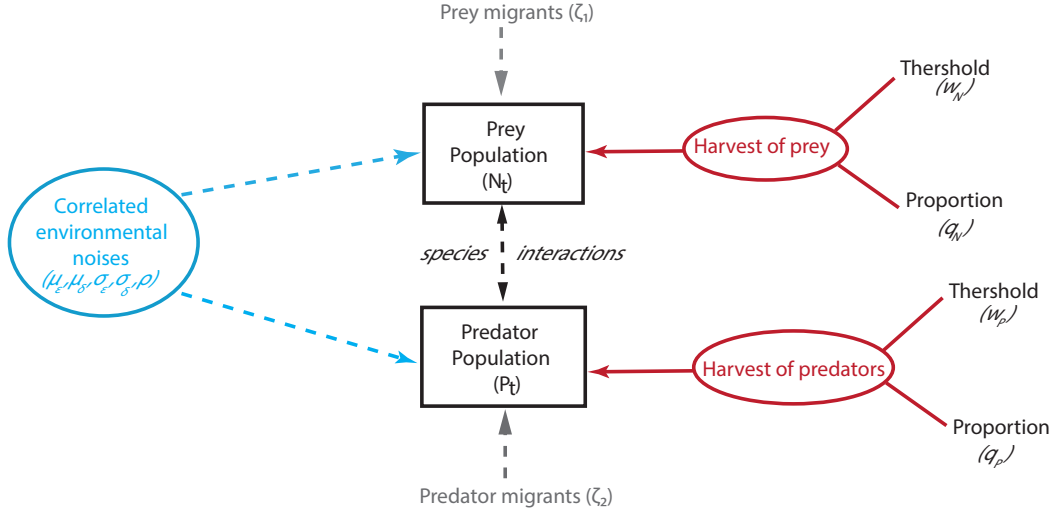


Figure A.1: Diagram of the predator-prey model with harvest as in Eqs. 5 and 6 in the main text.

Predator-prey dynamics at the equilibrium

The deterministic equilibrium (N^*, P^*) for $\sigma_\epsilon^2 = \sigma_\delta^2 = 0$ is given by

$$r \left[1 - \frac{N^*}{K} \right] - \frac{\alpha P^*}{1 + \beta N^*} = 0 \quad (\text{A.5})$$

$$c \frac{\alpha N^*}{1 + \beta N^*} e^{-\beta_1 P^*} = 1. \quad (\text{A.6})$$

Parameter of the predator-prey system at equilibrium

Table A.1: Values of dynamics parameters obtained from the deterministic equilibrium of the model Eqs. (A.5) and (A.6) in Appendix A.

Variable	Definition	Value at equilibrium
N_0	Number of prey	100000
P_0	Number of predators	1000
K	Carrying capacity of prey population	200000
r	Growth rate of prey population	0.5
α	Time to handle prey	5×10^{-4} unit time
β	Measure of time to handle each prey item	1×10^{-5}
β_1	Strength of density regulation of predators	5×10^{-4}
c	Impact of predators on prey	$0.04e^{0.5}$
Y_1	Mean of Poisson distribution for prey migrants	10
Y_2	Mean of Poisson distribution for predator migrants	5

Analyse of predators and prey without fluctuating environment

The predator-prey model without including the fluctuating environment (i.e., without the correlated environmental noises) which is expressed such as,

$$N_t = N_{t-1} + rN_{t-1} \left(1 - \frac{N_{t-1}}{K} \right) - \frac{\alpha N_{t-1}}{1 + \beta N_{t-1}} P_{t-1} + \zeta_{1,t} \quad (\text{A.7})$$

$$P_t = c' P_{t-1} e^{-\beta_1 P_{t-1}} + \zeta_{2,t} \quad (\text{A.8})$$

Based on our model, we analyzed the predator-prey dynamics without including the fluctuating environment (i.e., without the correlated environmental noises) as given by Eqs. (A.7) and (A.8) in Appendix A. The equilibrium values (i.e., parameters obtained from the deterministic equilibrium) given in Table A.1 in Appendix A were used to initiate the simulations (see Fig. A.2 in Appendix A).

In order to analyze the fluctuations of the population of predators and prey and make the populations of both species comparable, the population size of prey is reduced-centered (i.e., standardized) such as,

$$n_t = \frac{N_t - \bar{N}}{\sigma_N}, \quad (\text{A.9})$$

where n is the standardized densities of prey at time t , the mean population size of prey over time is \bar{N} and σ_N is the standardized deviation of the population size of prey over time.

The population size of predators is reduced-centered (i.e., standardized) such as,

$$p_t = \frac{P_t - \bar{P}}{\sigma_P}, \quad (\text{A.10})$$

where p is the standardized densities of predator at time t , the mean population size of predator over time is \bar{P} and σ_P is the standardized deviation of the population size of predators over time.

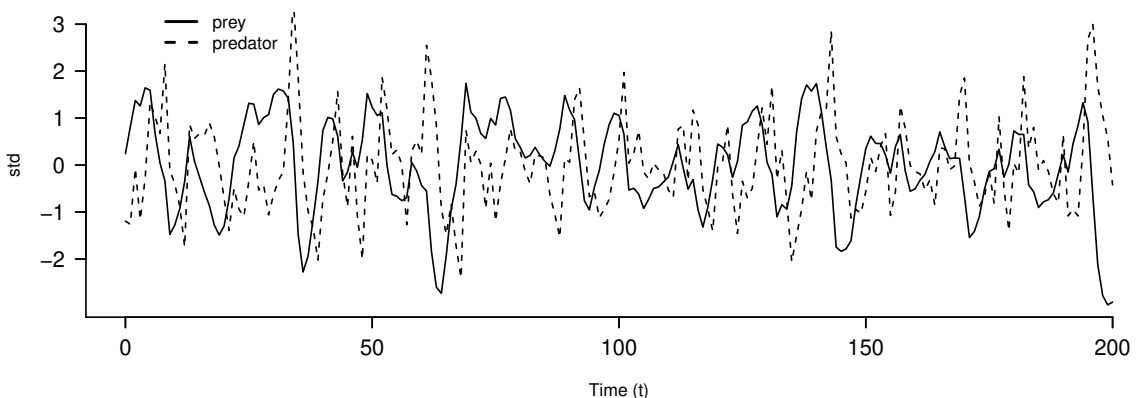


Figure A.2: Standardized densities of prey (Eq. A.9, plain line) and predators (Eq. A.10, dotted line) as a function of time (t) without fluctuating environment (Eqs. A.7 and A.8) with parameters values obtained from the deterministic equilibrium as given in Table A.1 in Appendix A.

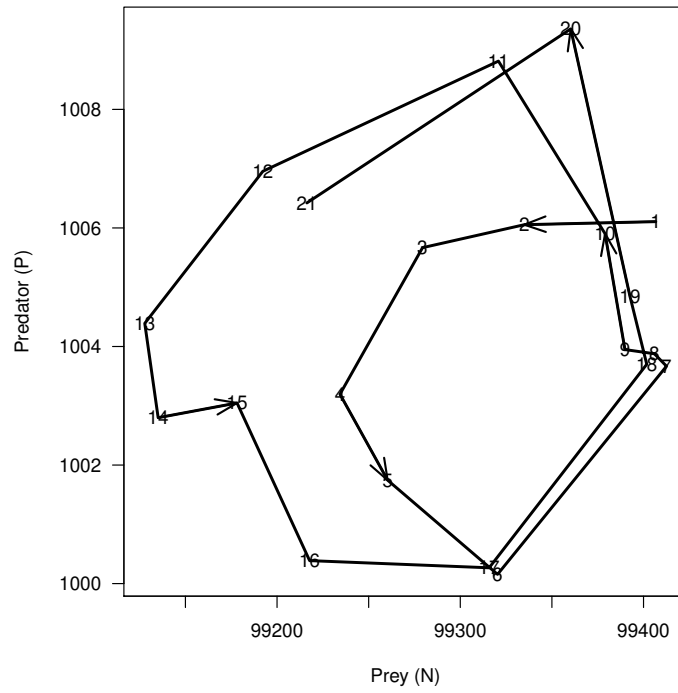


Figure A.3: The predators densities as a function of the prey densities (i.e., phase plane) without fluctuating environment (Eqs. A.7 and A.8) with parameters values obtained from the deterministic equilibrium as given in Table A.1 in Appendix A.

Analyse of predators and prey without migration

In order to show that our predator-prey system can sustain itself in isolation over the time period considered in the study; In other word, that our predator-prey model does not go to extinction without immigration (i.e., migration), we analyzed the dynamics of the model without migrants, which is written such as,

$$N_t = N_{t-1} + rN_{t-1} \left(1 - \frac{N_{t-1}}{K} \right) - \frac{\alpha N_{t-1}}{1 + \beta N_{t-1}} P_{t-1} + N_{t-1} \varepsilon_{t-1} \quad (\text{A.11})$$

$$P_t = c' P_{t-1} e^{-\beta_1 P_{t-1}} \Lambda_{t-1} \quad (\text{A.12})$$

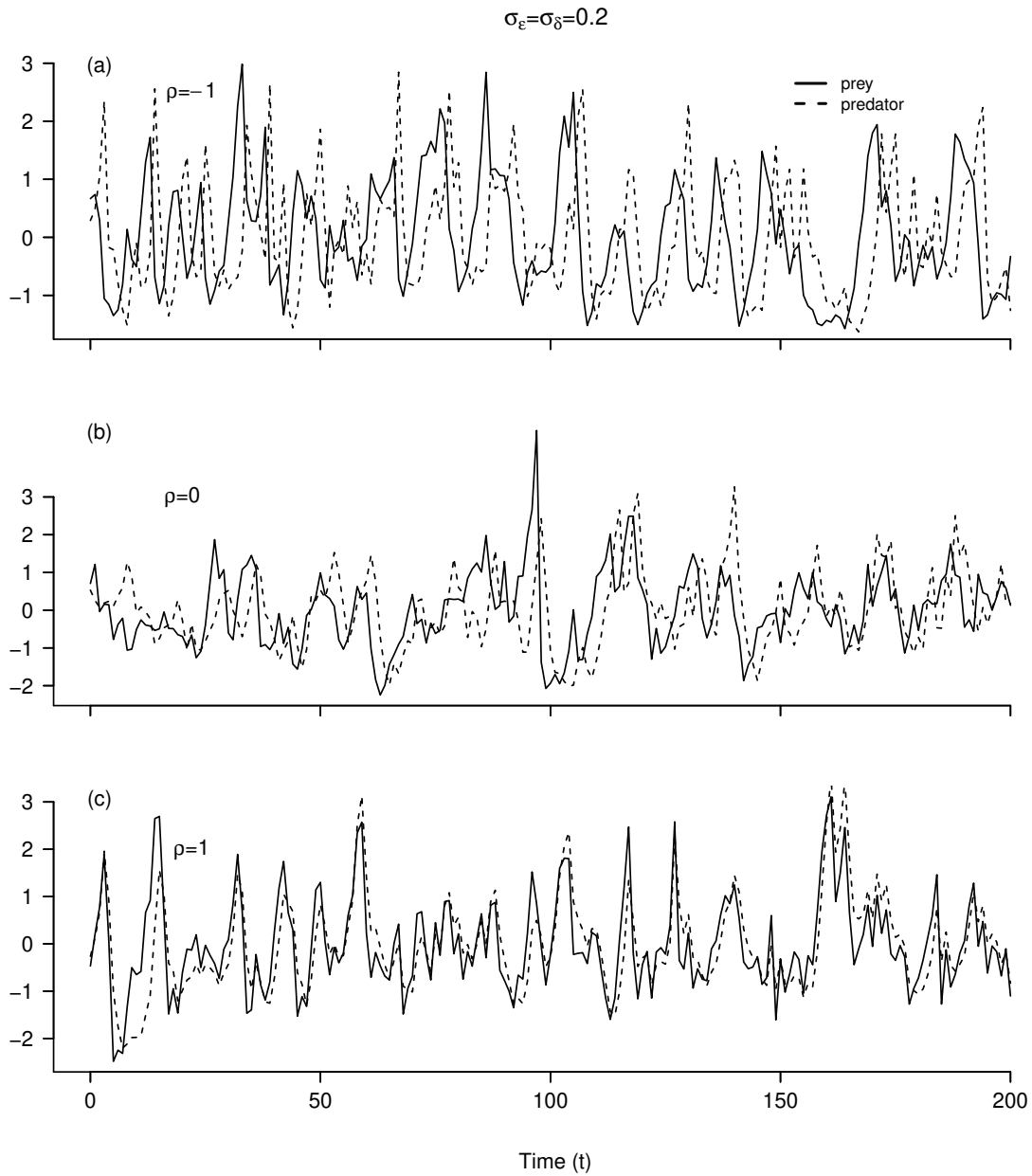


Figure A.4: Standardized densities of prey (Eq. A.9, plain line) and predators (Eq. A.10, dotted line) as a function of time (t) without migration (Eqs. A.11 and A.12) with parameters values obtained from the deterministic equilibrium as given in Table A.1 in Appendix A.

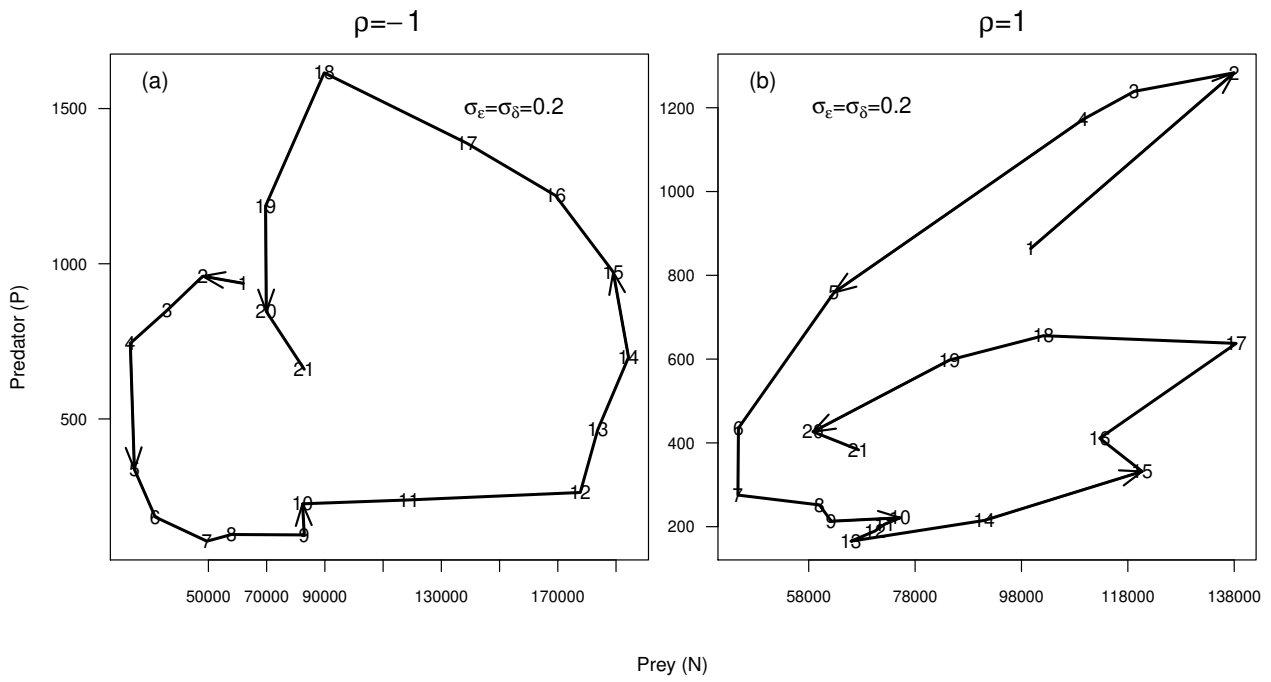


Figure A.5: The predators densities as a function of the prey densities (i.e., phase plane) without migration (Eqs. A.7 and A.8) with parameters values obtained from the deterministic equilibrium as given in Table A.1 in Appendix A.

Analyze of the predator-prey dynamics within a fluctuating environment

Based on our model, we analyzed the predator-prey dynamics with a fluctuating environment as given by Eq. 1 and Eq. 3 in the main text. The equilibrium values given in Table A.1 in Appendix A were used to initiate the simulations (see Fig. 1 in the main text and Fig. A.6 in Appendix A). Under weak environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.1$) and when there is no correlation in environmental noise ($\rho = 0$), the dynamics of predators and prey was cycling (see Fig. 1a in the main text), after the predator population declined below a given point the prey population began to increase again. An increase in the prey population came after an increase in predation. An increasing number of predators caused a decline in the prey population. As the predation fell, it supported fewer predators, and with fewer predators, the prey population rose again. Under strong environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.2$), the amplitude of the oscillations between prey and predators increased (Fig. A.7b in Appendix A).

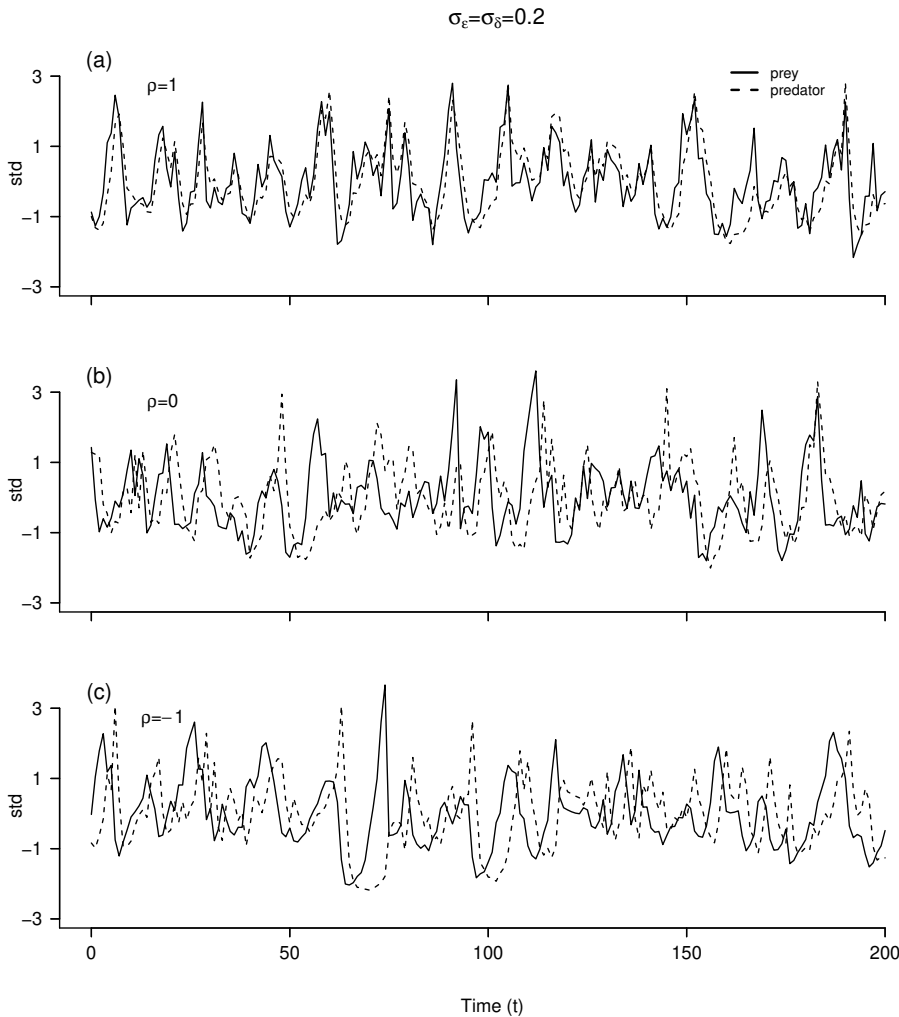


Figure A.6: Standardized densities of prey (Eq. A.9, plain line) and predators (Eq. A.10, dotted line) under strong environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.2$) as a function of time (t) for different correlation in environmental noises with parameters values as given in Table A.1 in Appendix A. (a), when the predators and prey responded similarly to the environment ($\rho = 1$); (b), when there were no correlation in the environmental noises ($\rho = 0$); (c), when the predators and prey responded differently to the environment ($\rho = -1$).

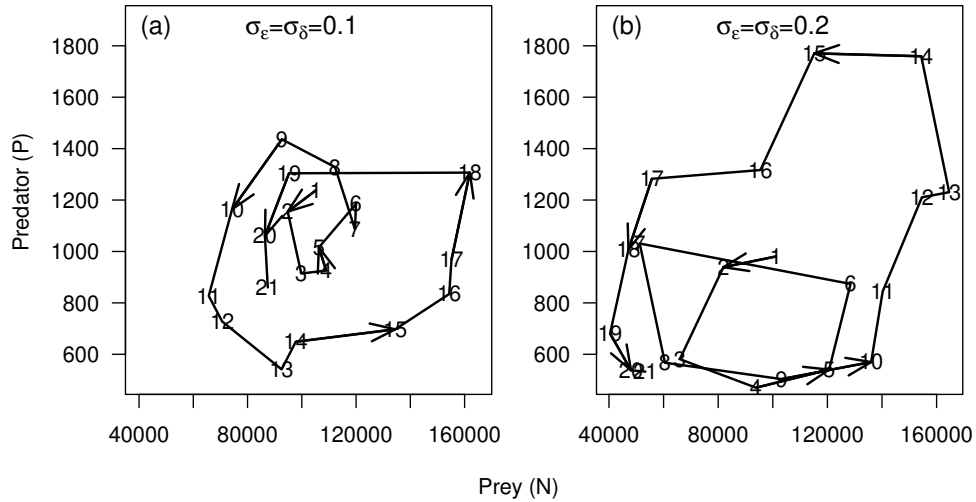


Figure A.7: The predators densities as a function of prey densities (i.e., phase plane) with environmental fluctuations with parameters values obtained from the deterministic equilibrium as given in Table A.1 in Appendix A when there were no correlation in environmental noises ($\rho = 0$). (a), when the environmental stochasticity was weak ($\sigma_\epsilon = \sigma_\delta = 0.1$); (b), when the environmental stochasticity was strong ($\sigma_\epsilon = \sigma_\delta = 0.2$).

References

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Appendix B

Bellier et al. Sustainable strategies for harvesting predators and prey in a fluctuating environment

Scenarios for analyzing the harvest of predators and prey without fluctuating environment

Table B.1: Parameters for scenarios of sustainable harvest of predators and prey without fluctuating environment. A (\times) shows for which fluctuating population size the predators and prey were harvested either separately or simultaneously with five different harvest fraction (q_N for the prey and q_P for the predator) ranging from 0.2 to 1 and increasing harvest threshold (ω_N for the prey and ω_P for the predator, see section *Harvest threshold of predators and prey* in Appendix B).

Fluctuating population size (CV)		Harvest		
		Prey	Predators	Predator-prey
1	$CV = 0.2$	\times	\times	\times
2	$CV = 0.5$	\times	\times	\times

Scenarios for analyzing the harvest of predators and prey in a fluctuating environmental

To make fluctuating the environment (see Table B.2 and Table B.3 in Appendix B), we defined a weak stochastic environment where the variance of the environmental noise of the prey σ_ϵ and predators σ_δ was 0.1 and a strong stochastic environment where the variance of the noise of the prey σ_ϵ and predators σ_δ was 0.2. Under each stochastic environment (i.e., weak and strong), we defined a correlated environment ($\rho = 1$) where both the predators and prey population growth are affected similarly by environmental fluctuations (Fig. 1 in the main text and Fig. A4 in Appendix A). At the opposite, when the correlation was negative ($\rho = -1$), the predators and prey population growth were affected differently by environmental fluctuations (Fig. 1 in the main text and Fig. A4 in Appendix A). We defined a low fluctuating state of the populations where the coefficient of variation (CV) was set at 0.2 and a high fluctuating state where the CV was set at 0.5.

The code of the simulation study has been developed in R (R Core Team 2019). The correlated environmental noises of prey and predators are generated from the mvtnorm library (Genz et al. 2020; Genz and Bretz 2009).

Table B.2: Parameters of each of the eight fluctuating environments for scenarios of sustainable harvest of predators and prey. Where σ_ϵ is the standard deviation of the environmental noise of the prey population (Eq. (1) in the main text), σ_δ is the standard deviation of the environmental noise of the predators population (Eq. (3) in the main text), ρ is the environmental correlation (Eq. (2) in the main text), and CV is the coefficient of variation of the prey and predators populations. A (\times) identifies the characteristic parameters of a given fluctuating environment. The features of each fluctuating environment are described in Table B.2 in Appendix B.

		$\sigma_\epsilon = \sigma_\delta$		0.1				0.2			
		ρ	CV	1		-1		1		-1	
				0.2	0.5	0.2	0.5	0.2	0.5	0.2	0.5
Environments	1		\times								
	2				\times						
	3					\times					
	4						\times				
	5							\times			
	6								\times		
	7									\times	
	8										\times

Table B.3: Characteristics of each of the eight fluctuating environments for scenarios of sustainable harvest (i.e., 120 scenarios) of predators and prey as described in the main text (i.e., section simulation study) and in Table B.2 in Appendix B. A (\times) shows in which environment the predators and prey were harvested either separately or simultaneously with five different harvest fraction (q_N for the prey and q_P for the predator) ranging from 0.2 to 1 and increasing harvest threshold (ω_N for the prey and ω_P for the predator, see section *Harvest threshold of predators and prey* in Appendix B).

Fluctuating environments		Harvest		
		Prey	Predators	Predator-prey
1	Weak stochastic environment, positive correlation, low population fluctuations.	\times	\times	\times
2	Weak stochastic environment, positive correlation, high population fluctuations.	\times	\times	\times
3	Weak stochastic environment, negative correlation, low population fluctuations.	\times	\times	\times
4	Weak stochastic environment, negative correlation, high population fluctuations.	\times	\times	\times
5	Strong stochastic environment, positive correlation, low population fluctuations.	\times	\times	\times
6	Strong stochastic environment, positive correlation, high population fluctuations.	\times	\times	\times
7	Strong stochastic environment, negative correlation, low population fluctuations.	\times	\times	\times
8	Strong stochastic environment, negative correlation, high population fluctuations.	\times	\times	\times

Harvest threshold of predators and prey

When the prey are harvested separately, the harvest threshold of the prey (ω_N) range from 0 to 120000 by 5000 prey's individuals; When the predators are harvested separately, the harvest threshold of the predator (ω_P) range from 0 to 2500 by 20 predator's individuals. When the prey and predators are harvested simultaneously, the harvest threshold of the prey (ω_N) range from 0 to 150000 by 5000 number of prey's individuals and the harvest threshold of the predators (ω_P) range from 0 to 1800 by 20 predator's individuals.

The expected mean yield

For each value of harvest fraction q and threshold ω over the time duration of the simulation (i.e., 1×10^6), we estimated the expected mean yield $E[Y(\hat{N})]$ such as,

$$E[Y(\hat{N})] = \frac{E[Y(\hat{N}_1) + \dots + Y(\hat{N}_n)]}{n} \quad (\text{B.1})$$

where n is the number of time step of the simulation which is equal to the time duration of the simulation (i.e., 1×10^6). The standard deviation of the yield is estimated such as,

$$s = \sqrt{\frac{1}{n-1} \sum_1^n (Y(\hat{N}_1) - E[Y(\hat{N})])^2}. \quad (\text{B.2})$$

References

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Appendix C

Bellier et al. Sustainable strategies for harvesting predators and prey in a fluctuating environment

Results on harvest of predators and prey without fluctuating environment

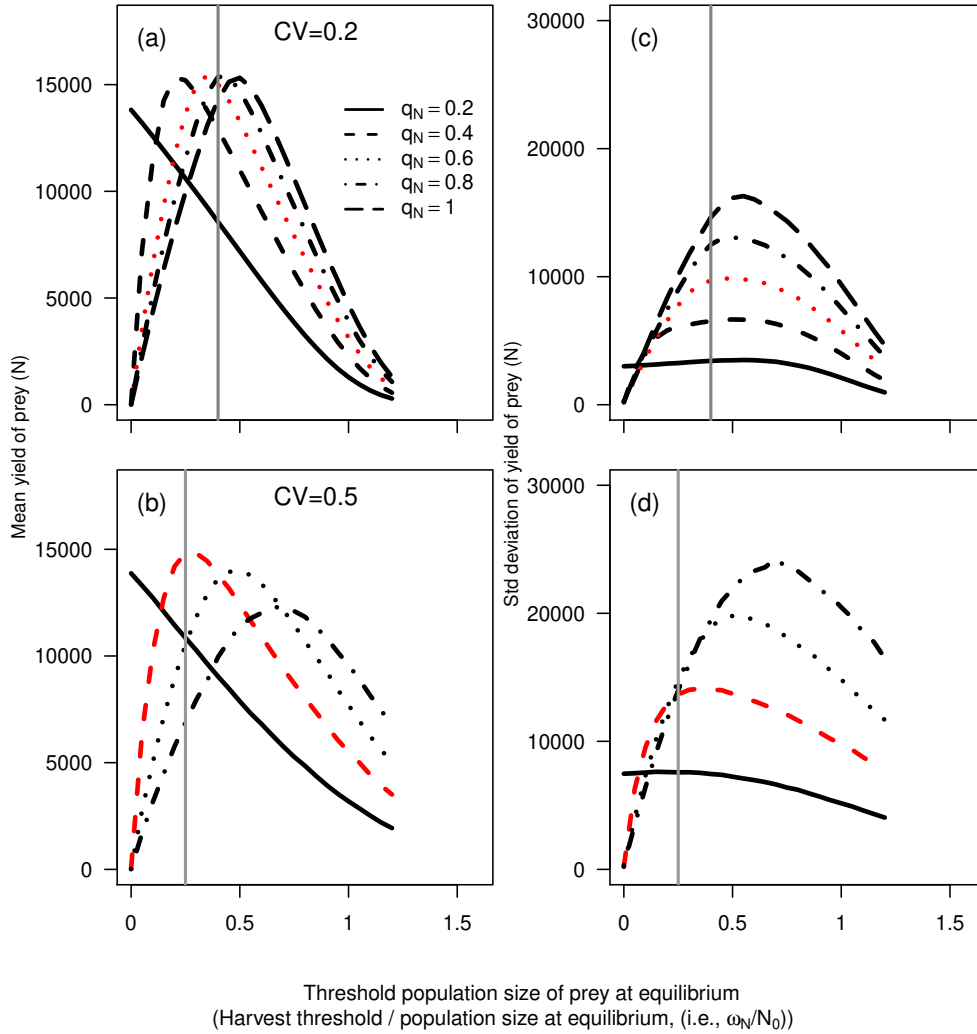


Figure C.1: Analyse of the yield of prey $y(\hat{N})$ over time, when only the prey were harvested, as a function of the fraction of population size of prey at equilibrium (i.e., harvest threshold of prey / population size of prey at equilibrium (ω_N/N_0)) and for different harvest fractions (q_N), for interacting predator-prey dynamics at the equilibrium (see Table A.1 in Appendix A for the values of the parameters at equilibrium); a-b, mean yield of prey $y(\hat{N})$ as a function of fraction of population size of prey at equilibrium (ω_N/N_0) with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$); c-d, variability of the yield of prey $y(\hat{N})$ as a function of fraction of population size of prey at equilibrium (ω_N/N_0) under the same conditions than a-b. Symbols are as for Fig. 3.

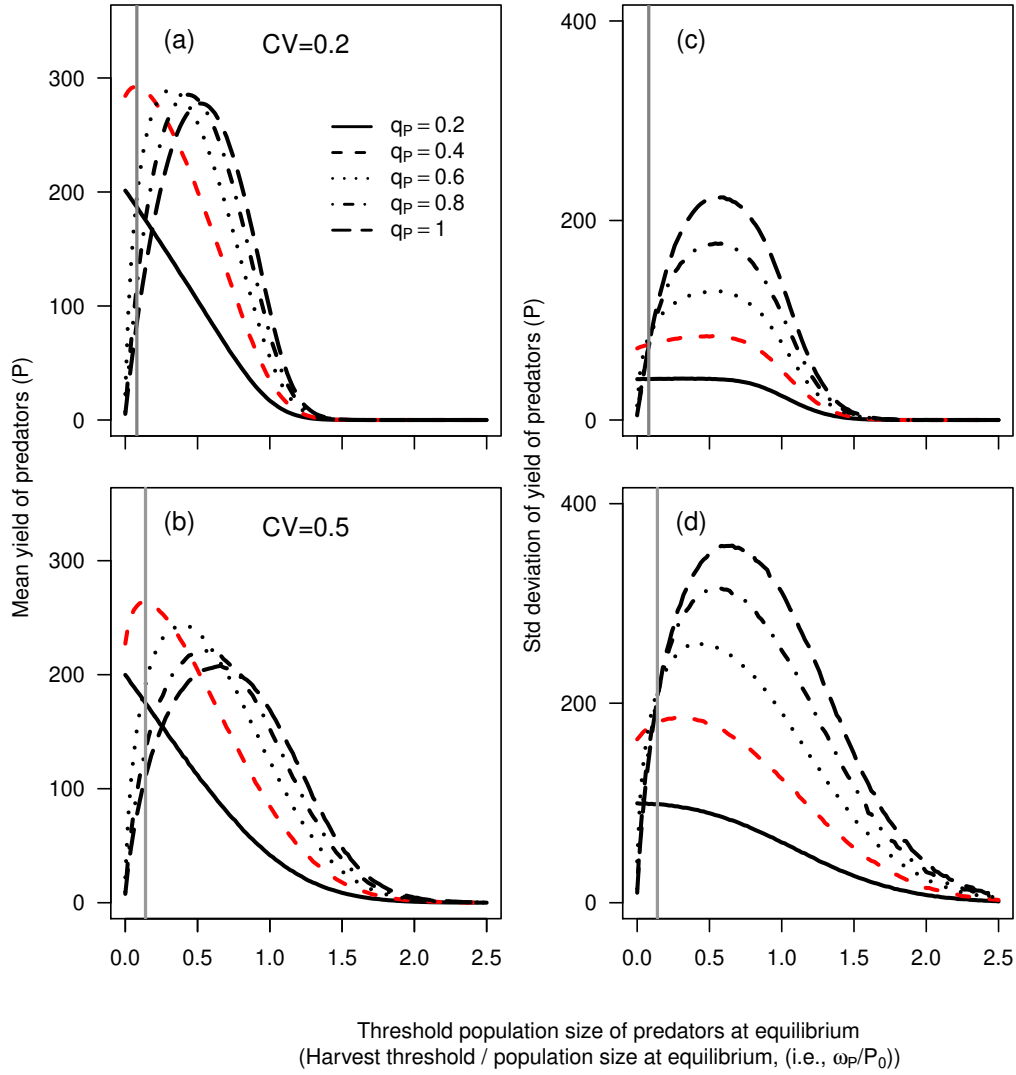


Figure C.2: Analyse of the yield of predators $y(\hat{P})$ over time, when only the predators were harvested, as a function of the fraction of population size of predators at equilibrium (i.e., harvest threshold of predators / population size of predators at equilibrium (ω_P/P_0)) and for different harvest fractions (q_P), for interacting predator-prey dynamics at the equilibrium (see Table A.1 in Appendix A for the values of the parameters at equilibrium); a-b, mean yield of predators $y(\hat{P})$ as a function of fraction of population size of predators at equilibrium (ω_P/P_0) with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$); c-d, variability of the yield of predators $y(\hat{P})$ as function of fraction of population size of predators at equilibrium (ω_P/P_0) under the same conditions than a-b. Symbols are as for Fig. 3.

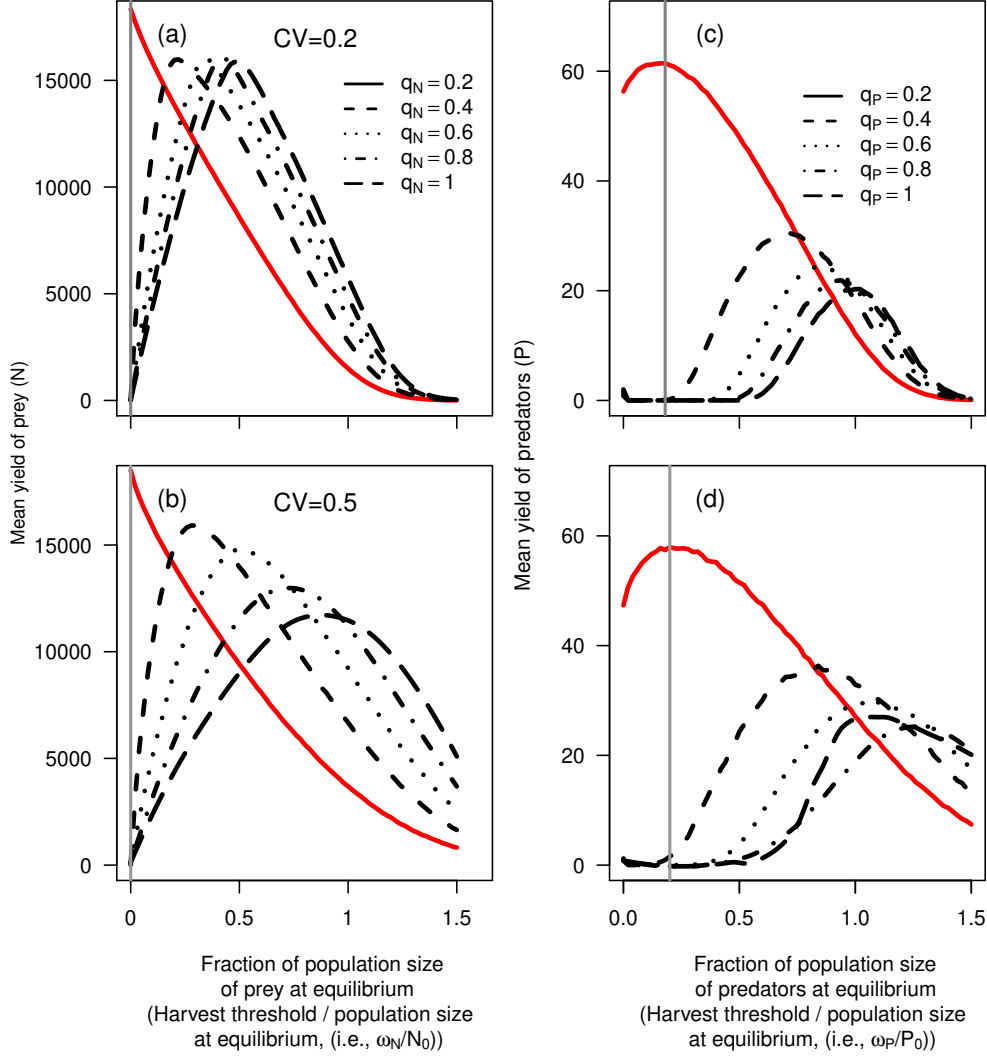


Figure C.3: Analyse of the yield of prey $y(\hat{N})$ (right column) and predators $y(\hat{P})$ (left column) when predators and prey were harvested simultaneously, as a function of threshold population size of prey (a-b) and predators (c-d) (i.e., fraction of population size at equilibrium of prey (a-b) and predators (c-d) (ω_N/N_0 and ω_P/P_0)) and for different harvest fractions (q_N and q_P), for interacting predator-prey dynamics at the equilibrium with dynamics parameters as in Table A.1 in Appendix A; a-b, mean yield of prey $y(\hat{N})$ as a function of fraction of population size of prey at equilibrium (ω_N/N_0), with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$); c-d, mean yield of predators $y(\hat{P})$ as a function of fraction of population size of predators at equilibrium (ω_P/P_0) under the same conditions than a-b. Symbols are as for Fig. 3.

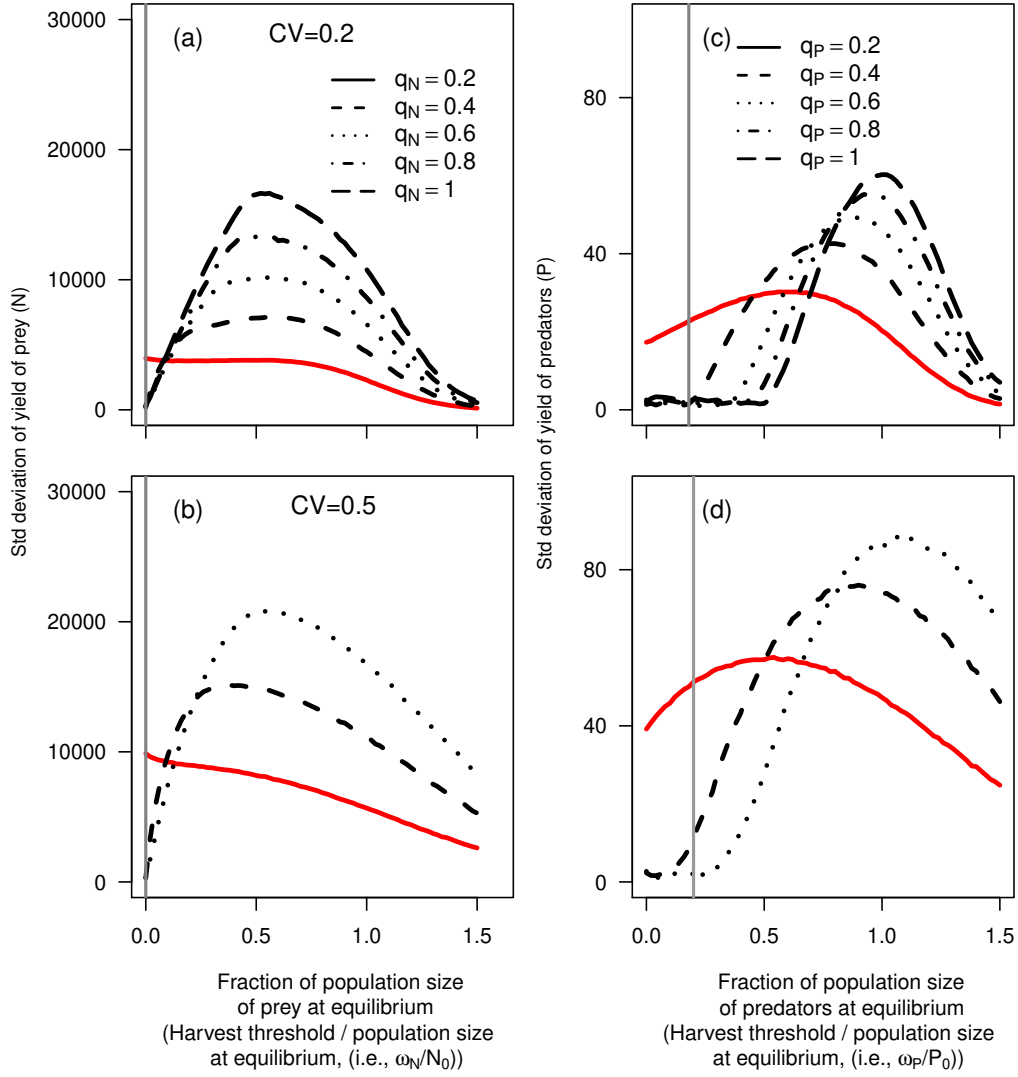


Figure C.4: Variability of the yield of prey $y(\hat{N})$ (right column) and predators $y(\hat{P})$ (left column) when predators and prey were harvested simultaneously, as a function of threshold population size of prey (a-b) and predators (c-d) (i.e., fraction of population size at equilibrium of prey (a-b) and predators (c-d) (ω_N/N_0 and ω_P/P_0)) and for different harvest fractions (q_N and q_P), for interacting predator-prey dynamics at the equilibrium with dynamics parameters as in Table A.1 in Appendix A; a-b, variability of the yield of prey $y(\hat{N})$ as a function of fraction of population size of prey at equilibrium (ω_N/N_0), with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$); c-d, mean yield of predators $y(\hat{P})$ as a function of fraction of population size of predators at equilibrium (ω_P/P_0) under the same conditions than a-b. Symbols are as for Fig. 3.

Table C.1: Optimal yields $y(\hat{N})$ of prey, when only the prey were harvested and the predator-prey dynamics was at equilibrium (Eqs. (A.5) and (A.6) in Appendix A), with dynamics parameters as in Table A.1 in Appendix A. The optimal yields of prey $y(\hat{N})$ were obtained for different intensities of population fluctuations (CV) and for different harvest fractions (q_N). The optimal yield of prey and its standard deviation $SD(\hat{N})$ are associated with an estimated harvest threshold for prey ($\hat{\omega}_N$). "—" denotes that the standard deviation of the optimal yield is too high to be considered.

CV	q_N	$\hat{\omega}_N$	$y(\hat{N})$	$SD(\hat{N})$
0.2	0.2	0	13816.85	3002.96
0.2	0.4	20000	15327.81	5810.72
0.2	0.6	35000	15434.03	9394.26
0.2	0.8	40000	15364.79	12509.35
0.2	1	50000	15320.66	16154.74
0.5	0.2	0	13872.57	7469.42
0.5	0.4	25000	14826.98	13655.16
0.5	0.6	50000	13955.43	19793.39
0.5	0.8	70000	12288.88	24316.84
0.5	1	"—"	"—"	"—"

Table C.2: Optimal yields $y(\hat{P})$ of predators, when only the predators were harvested and the predator-prey dynamics was at equilibrium (Eqs. (A.5) and (A.6) in Appendix A), with dynamics parameters as in Table A.1 in Appendix A. The optimal yields of prey $y(\hat{P})$ were obtained for different intensities of population fluctuations (CV) and for different harvest fractions (q_P). The optimal yield of predators and its standard deviation $SD(\hat{P})$ are associated with an estimated harvest threshold for predators ($\hat{\omega}_P$). "—" denotes that the standard deviation of the optimal yield is too high to be considered.

CV	q_P	$\hat{\omega}_P$	$y(\hat{P})$	$SD(\hat{P})$
0.2	0.2	0	201.23	40.97
0.2	0.4	80	292.37	75.88
0.2	0.6	320	289.40	122.37
0.2	0.8	440	285.34	172.94
0.2	1	520	277.67	222.91
0.5	0.2	0	199.82	99.68
0.5	0.4	140	263.84	180.58
0.5	0.6	380	243.54	257.38
0.5	0.8	540	221.12	314.39
0.5	1	660	207.82	358.00

Table C.3: Optimal yields $y(\hat{N})$ of prey when the predators and prey were harvested simultaneously and when the predator-prey dynamics was at equilibrium (Eqs. (A.5) and (A.6) in Appendix A), with dynamics parameters as in Table A.1 in Appendix A. The optimal yields of prey $y(\hat{N})$ were obtained for different intensities of population fluctuations (CV) for different harvest fractions (q_N). The optimal yield of prey and its standard deviation $SD(\hat{N})$ are associated with an estimated harvest threshold ($\hat{\omega}_N$). "—" denotes that the standard deviation of the optimal yield is too high to be considered.

CV	q_N	$\hat{\omega}_N$	$y(\hat{N})$	$SD(\hat{N})$
0.2	0.2	0	18332.90	3956.22
0.2	0.4	22000	15980.34	6132.54
0.2	0.6	34000	16012.06	9469.63
0.2	0.8	42000	16041.89	13115.88
0.2	1	50000	15899.79	16551.75
0.5	0.2	0	18496.02	9869.35
0.5	0.4	28000	15917.29	14749.85
0.5	0.6	48000	14756.77	20509.02
0.5	0.8	72000	13097.01	30802.14
0.5	1	84000	11987.97	" — "

Table C.4: Optimal yields $y(\hat{P})$ of predators when the predators and prey were harvested simultaneously and when the predator-prey dynamics was at equilibrium (Eqs. (A.5) and (A.6) in Appendix A), with dynamics parameters as in Table A.1 in Appendix A. The mean optimal yields of predators $y(\hat{P})$ were obtained for different intensities of population fluctuations (CV) for different harvest fractions (q_P). The optimal yield of predators and its standard deviation $SD(\hat{P})$ are associated with an estimated harvest threshold ($\hat{\omega}_P$). "—" denotes that the standard deviation of the optimal yield is too high to be considered.

CV	q_P	$\hat{\omega}_P$	$y(\hat{P})$	$SD(\hat{P})$
0.2	0.2	180	61.44	22.68
0.2	0.4	720	30.44	42.42
0.2	0.6	840	24.41	49.33
0.2	0.8	940	21.89	55.32
0.2	1	1020	20.29	60.29
0.5	0.2	200	57.93	51.23
0.5	0.4	840	36.33	75.95
0.5	0.6	1080	30.30	89.56
0.5	0.8	1320	25.67	" — "
0.2	1	920	108.24	" — "

Results on harvest of predators and prey under strong environmental stochasticity

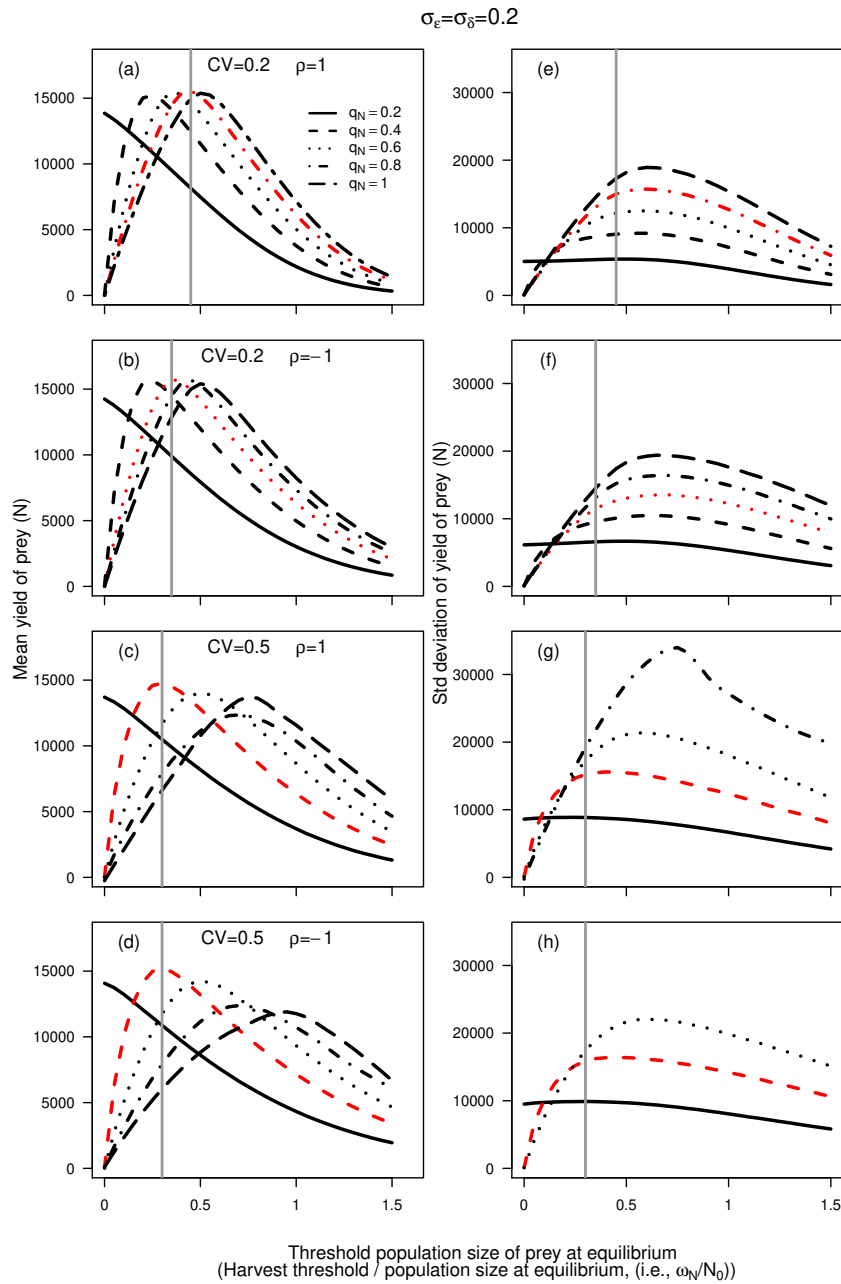


Figure C.5: Analysis of the yield of prey $y(\hat{N})$ over time, when only the prey were harvested, as a function of the fraction of population size of prey at equilibrium (i.e., harvest threshold of prey / population size of prey at equilibrium (ω_N/N_0)) and for different harvest fractions (q_N), for interacting predator-prey dynamics at the equilibrium (see Table A.1 in Appendix A for the values of the parameters at equilibrium); a-d, mean yield of prey $y(\hat{N})$ as a function of fraction of population size of prey at equilibrium (ω_N/N_0), under strong environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.2$) with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$) and opposite environmental correlations ($\rho = 1$ and $\rho = -1$). e-h, variability of the yield of prey $y(\hat{N})$ as a function of fraction of population size of prey at equilibrium (ω_N/N_0) under the same conditions than a-d. Symbols are as for Fig. 3.

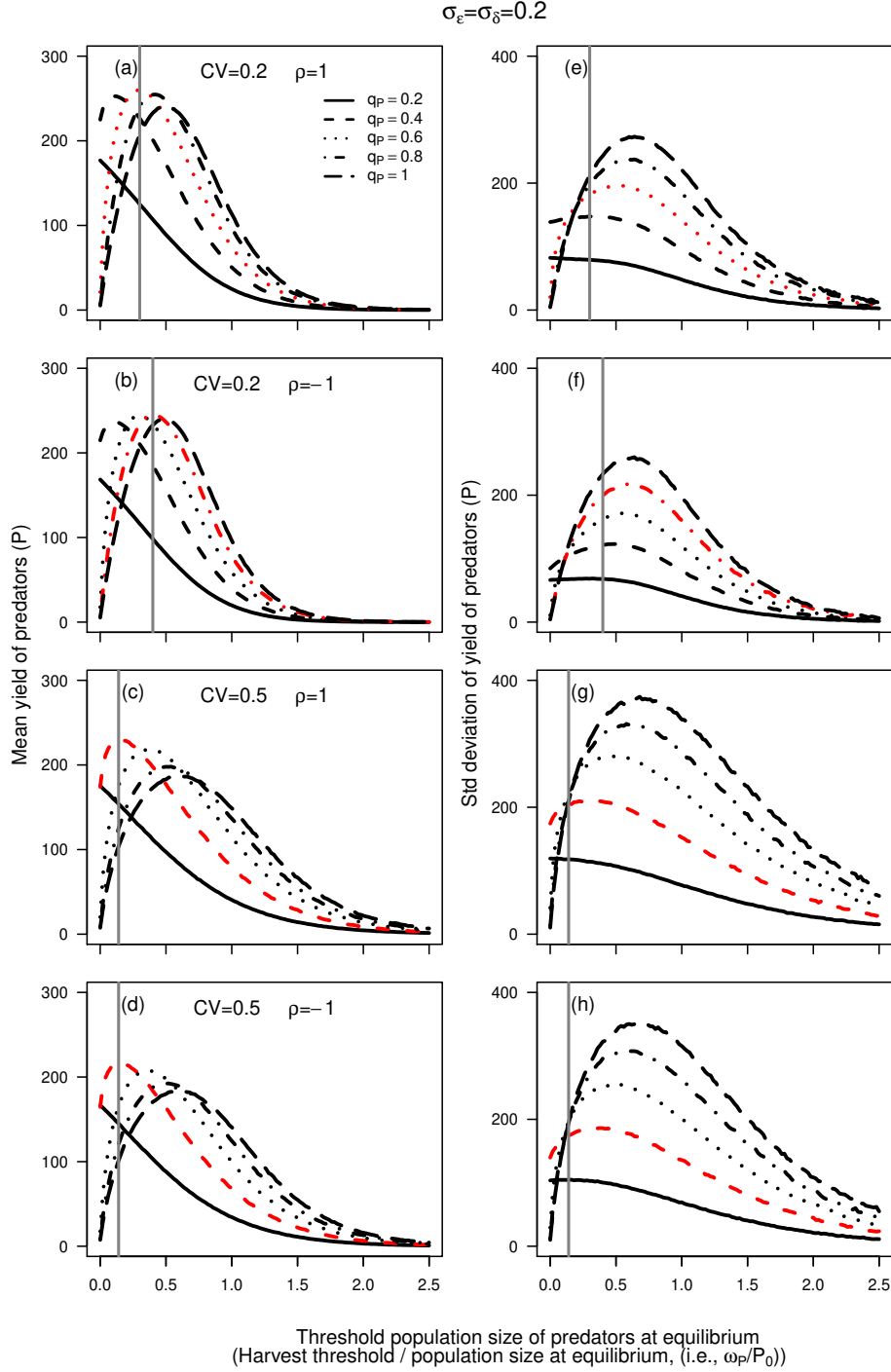


Figure C.6: Analyse of the yield of predators $y(\hat{P})$ over time, when only the predators were harvested, as a function of the fraction of population size of predators at equilibrium (i.e., harvest threshold of predators / population size of predators at equilibrium (ω_P/P_0)) and for different harvest fractions (q_P), for interacting predator-prey dynamics at the equilibrium (see Table A.1 in Appendix A for the values of the parameters at equilibrium); a-d, mean yield of predators $y(\hat{P})$ as a function of fraction of population size of predators at equilibrium (ω_P/P_0), under strong environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.2$) with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$) and opposite environmental correlations ($\rho = 1$ and $\rho = -1$); e-h, variability of the yield of predators $y(\hat{P})$ as a function of fraction of population size of predators at equilibrium (ω_P/P_0) under the same conditions than a-d. Symbols are as for Fig. 3.

$$\sigma_\epsilon = \sigma_\delta = 0.2$$

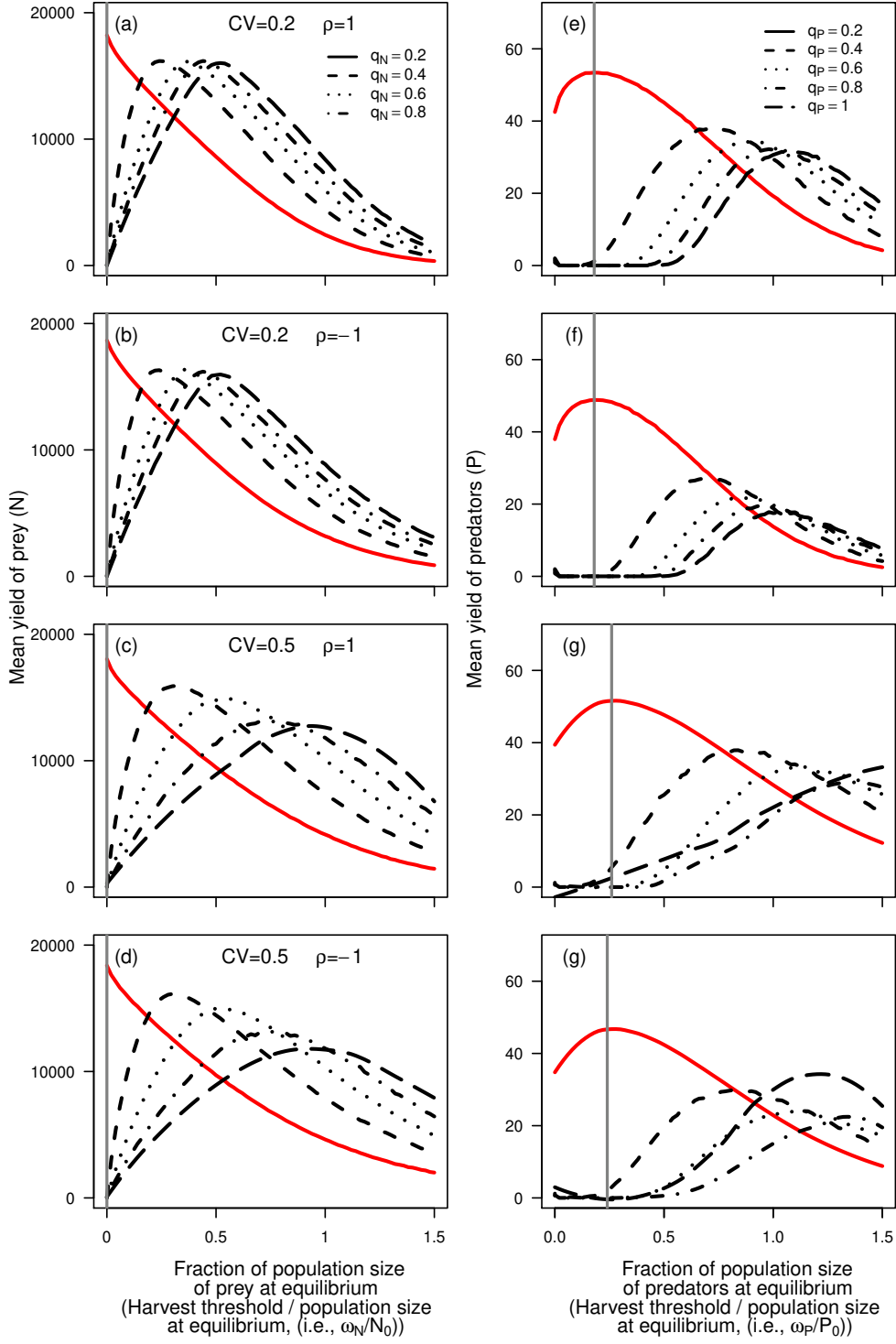


Figure C.7: Mean yield of prey $y(\hat{P})$ (right column) and predators $y(\hat{P})$ (left column) when predators and prey were harvested simultaneously, as a function of threshold population size (i.e., fraction of population size at equilibrium (ω_N/N_0 or ω_P/P_0)) and for different harvest fractions (q_N and q_P), for interacting predator-prey dynamics at the equilibrium with dynamics parameters as in Table A.1 in Appendix A; a-d, mean yield of prey $y(\hat{N})$ as a function of fraction of population size of prey at equilibrium (ω_N/N_0), under strong environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.2$) with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$) and opposite environmental correlations ($\rho = 1$ and $\rho = -1$). e-h, mean yield of predators $y(\hat{P})$ as a function of fraction of population size of predators at equilibrium (ω_P/P_0) under the same conditions than a-d. Symbols are as for Fig. 5.

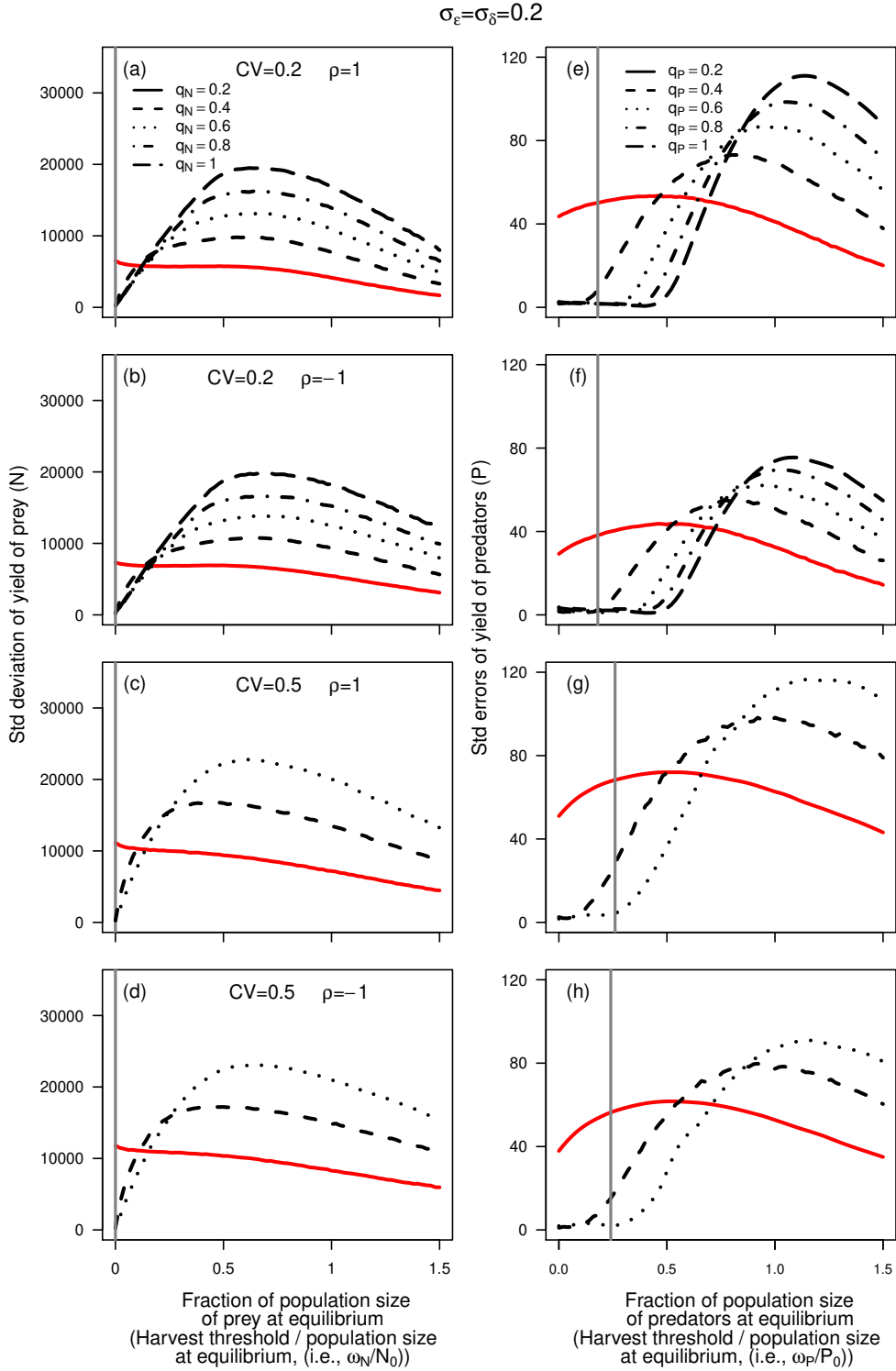


Figure C.8: Variability of the yield of prey $y(\hat{N})$ (right column) and predators $y(\hat{P})$ (left column) when predators and prey were harvested simultaneously, as a function of threshold population size (i.e., fraction of population size at equilibrium (ω_P/N_0 or ω_N/P_0)) and for different harvest fractions (q_N and q_P), for interacting predator-prey dynamics at the equilibrium with dynamics parameters as in Table A.1 in Appendix A; a-d, Variability of the yield of prey $y(\hat{N})$ as a function of fraction of population size of prey at equilibrium (ω_N/N_0), under strong environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.2$) with different intensities of population fluctuations ($CV = 0.2$ and $CV = 0.5$) and opposite environmental correlations ($\rho = 1$ and $\rho = -1$). e-h, Variability of the yield of predators $y(\hat{P})$ as a function of fraction of population size of predators at equilibrium (ω_P/P_0) under the same conditions than a-d. Symbols are as for Fig. 6.

Optimal yield associated to its variability under the different fluctuating environments

Table C.5: Optimal yields $y(\hat{N})$ of prey, when only the prey were harvested and the predator-prey dynamics was at equilibrium (Eqs. (A.5) and (A.6) in Appendix A), with dynamics parameters as in Table A.1 in Appendix A. The optimal yields of prey $y(\hat{N})$ were obtained for different intensities of population fluctuations (CV), under weak environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.1$) and strong environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.2$), when the predators and prey responded similarly to environmental fluctuations ($\rho = 1$) or differently ($\rho = -1$) and for different harvest fractions (q_N). The optimal yield of prey and its standard deviation $SD(\hat{N})$ are associated with an estimated harvest threshold ($\hat{\omega}_N$). " -- " denotes that the standard deviation of the optimal yield is too high to be considered.

$\sigma_1 = \sigma_2$	CV	q_N	$\hat{\omega}_N$	$\rho = 1$		$\rho = -1$		
				$y(\hat{N})$	$SD(\hat{N})$	$\hat{\omega}_N$	$y(\hat{N})$	$SD(\hat{N})$
0.1	0.2	0.2	0	13871.70	3597.35	0	13964.67	4007.29
0.1	0.2	0.4	20000	15251.87	6309.00	20000	15378.74	6445.09
0.1	0.2	0.6	35000	15517.19	9957.35	35000	15441.18	9879.72
0.1	0.2	0.8	45000	15402.98	13520.22	45000	15435.77	13581.43
0.1	0.2	1	50000	15327.03	--	50000	15342.25	--
0.1	0.5	0.2	0	13865.84	7786.99	0	13967.13	8053.99
0.1	0.5	0.4	30000	14814.14	14366.31	30000	14926.76	14522.16
0.1	0.5	0.6	30000	14018.65	--	50000	14036.47	--
0.1	0.5	0.8	70000	12243.07	--	70000	12291.36	--
0.1	0.5	1	90000	11151.75	--	100000	11174.44	--
0.2	0.2	0.2	0	13864.15	5022.97	0	14236.51	6126.21
0.2	0.2	0.4	25000	15212.08	8109.77	25000	15682.24	8719.23
0.2	0.2	0.6	35000	15450.26	11209.43	35000	15727.58	11504.30
0.2	0.2	0.8	45000	15539.41	14987.60	45000	15698.59	15232.89
0.2	0.2	1	50000	15362.75	--	50000	15397.06	--
0.2	0.5	0.2	0	13709.19	8596.33	0	14076.48	9484.34
0.2	0.5	0.4	30000	14748.43	15209.85	30000	15174.94	15864.75
0.2	0.5	0.6	50000	14008.73	--	50000	14220.92	--
0.2	0.5	0.8	70000	12294.47	--	70000	12385.82	--
0.2	0.5	1	90000	11279.73	--	95000	11883.65	--

Table C.6: Optimal yields $y(\hat{P})$ of predators, when only the predators were harvested and the predator-prey dynamics was at equilibrium (Eqs. (A.5) and (A.6) in Appendix A), with dynamics parameters as in Table A.1 in Appendix A. The optimal yields of predators $y(\hat{P})$ were obtained for different intensities of population fluctuations (CV), under weak environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.1$) and strong environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.2$), when the predators and prey responded similarly to environmental fluctuations ($\rho = 1$) or differently ($\rho = -1$) for different harvest fractions (q_P). The optimal yield of predators and its standard deviation $SD(\hat{P})$ are associated with an estimated harvest threshold ($\hat{\omega}_P$).

		$\rho = 1$					$\rho = -1$		
$\sigma_\epsilon = \sigma_\delta$	CV	q_P	$\hat{\omega}_P$	$y(\hat{P})$	$SD(\hat{P})$	$\hat{\omega}_P$	$y(\hat{P})$	$SD(\hat{P})$	
0.1	0.2	0.2	0	193.26	48.99	0	195.48	54.98	
0.1	0.2	0.4	80	277.95	82.84	80	282.12	98.71	
0.1	0.2	0.6	320	277.99	130.77	320	281.81	141.21	
0.1	0.2	0.8	420	275.46	180.32	440	277.97	188.13	
0.1	0.2	1	520	268.33	231.55	520	268.48	237.40	
0.1	0.5	0.2	0	191.57	100.75	0	194.12	105.20	
0.1	0.5	0.4	140	252.16	179.23	120	255.71	186.80	
0.1	0.5	0.6	360	234.16	256.73	380	237.64	262.22	
0.1	0.5	0.8	520	214.79	313.14	520	215.48	317.51	
0.1	0.5	1	640	202.43	356.26	660	202.61	361.23	
0.2	0.2	0.2	0	176.85	82.33	0	168.52	66.40	
0.2	0.2	0.4	100	252.76	143.56	120	236.84	102.34	
0.2	0.2	0.6	300	259.67	182.49	300	244.32	149.46	
0.2	0.2	0.8	420	254.69	224.48	400	244.88	199.56	
0.2	0.2	1	480	241.05	259.55	480	240.07	249.50	
0.2	0.5	0.2	0	175.42	119.27	0	166.34	103.73	
0.2	0.5	0.4	140	229.86	204.18	140	216.77	174.52	
0.2	0.5	0.6	400	218.81	278.88	400	207.32	248.75	
0.2	0.5	0.8	540	197.97	328.83	520	192.38	305.11	
0.2	0.5	1	620	186.78	369.51	600	183.83	349.95	

Table C.7: Optimal yields $y(\hat{N})$ of prey when the predators and prey were harvested simultaneously and the predator-prey dynamics was at equilibrium (Eqs. (A.5) and (A.6) in Appendix A), with dynamics parameters as in Table A.1 in Appendix A. The optimal yields of prey $y(\hat{N})$ were obtained for different intensities of population fluctuations (CV), under weak environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.1$) and strong environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.2$), when the predators and prey responded similarly to environmental fluctuations ($\rho = 1$) or differently ($\rho = -1$) for different harvest fractions (q_N). The optimal yield of prey and its standard deviation $SD(\hat{N})$ are associated with an estimated harvest threshold ($\hat{\omega}_N$). " -- " denotes that the standard deviation of the optimal yield is too high to be considered.

$\sigma_\epsilon = \sigma_\delta$	CV	q_N	$\hat{\omega}_N$	$\rho = 1$		$\rho = -1$		
				$y(\hat{N})$	$SD(\hat{N})$	$\hat{\omega}_N$	$y(\hat{N})$	$SD(\hat{N})$
0.1	0.2	0.2	0	18404.47	4727.24	0	18462.41	5051.31
0.1	0.2	0.4	22000	16017.28	6701.84	22000	16084.75	6836.85
0.1	0.2	0.6	34000	16029.34	10010.29	34000	16061.47	10021.25
0.1	0.2	0.8	42000	16062.96	13515.03	42000	16136.46	13666.36
0.1	0.2	1	50000	15928.07	--	50000	15910.25	--
0.1	0.5	0.2	0	18433.17	10256.40	0	18474.18	10439.29
0.1	0.5	0.4	30000	15944.84	15226.06	30000	15971.67	15319.16
0.1	0.5	0.6	50000	14860.73	--	52000	14889.26	--
0.1	0.5	0.8	74000	13054.27	--	74000	13095.92	--
0.1	0.5	1	88000	12223.05	--	90000	13367.19	--
0.2	0.2	0.2	0	18213.90	6524.92	0	18657.50	7312.62
0.2	0.2	0.4	24000	16178.16	8397.36	24000	16308.26	8797.08
0.2	0.2	0.6	36000	16137.19	11632.17	36000	16367.85	11849.23
0.2	0.2	0.8	44000	16181.62	15203.52	44000	16193.66	15330.14
0.2	0.2	1	52000	16019.19	--	52000	15967.40	--
0.2	0.5	0.2	0	18038.31	11157.12	0	18380.39	11796.90
0.2	0.5	0.4	32000	15920.00	16366.39	30000	16139.91	16508.77
0.2	0.5	0.6	56000	14942.89	--	50000	14996.64	--
0.2	0.5	0.8	70000	13107.39	--	74000	13200.16	--
0.2	0.5	1	92000	28659.37	--	92000	11853.97	--

Table C.8: Optimal yields $y(\hat{P})$ of predators when the predators and prey were harvested simultaneously and the predator-prey dynamics was at equilibrium (Eqs. (A.5) and (A.6) in Appendix A), with dynamics parameters as in Table A.1 in Appendix A. The mean optimal yields of predators $y(\hat{P})$ were obtained for different intensities of population fluctuations (CV), under weak environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.1$) and strong environmental stochasticity ($\sigma_\epsilon = \sigma_\delta = 0.2$), when the predators and prey responded similarly to environmental fluctuations ($\rho = 1$) or differently ($\rho = -1$) for different harvest fractions (q_P). The optimal yield of predators and its standard deviation $SD(\hat{P})$ are associated with an estimated harvest threshold ($\hat{\omega}_P$). "—" denotes that the standard deviation of the optimal yield is too high to be considered.

$\sigma_\epsilon = \sigma_\delta$	CV	q_P	$\rho = 1$			$\rho = -1$		
			$\hat{\omega}_P$	$y(\hat{P})$	$SD(\hat{P})$	$\hat{\omega}_P$	$y(\hat{P})$	$SD(\hat{P})$
0.1	0.2	0.2	180	59.44	33.32	160	57.98	28.00
0.1	0.2	0.4	700	32.68	51.11	720	29.72	46.18
0.1	0.2	0.6	880	28.24	62.08	840	24.01	53.37
0.1	0.2	0.8	980	25.57	69.50	940	21.19	60.01
0.1	0.2	1	1040	24.05	76.51	1000	19.67	65.76
0.1	0.5	0.2	220	56.17	56.66	200	54.88	52.70
0.1	0.5	0.4	860	37.23	82.82	800	34.79	76.66
0.1	0.5	0.6	1080	31.13	96.57	1080	28.40	89.44
0.1	0.5	0.8	1140	31.41	—	1240	23.89	97.46
0.1	0.5	1	1140	26.62	—	1320	54.03	—
0.2	0.2	0.2	180	53.41	50.15	180	48.84	38.18
0.2	0.2	0.4	740	38.43	72.50	700	27.22	53.22
0.2	0.2	0.6	900	34.60	87.04	900	21.82	62.39
0.2	0.2	0.8	1020	32.61	98.99	940	19.61	68.94
0.2	0.2	1	1080	31.59	109.45	980	17.80	73.59
0.2	0.5	0.2	260	51.63	68.39	240	46.85	56.38
0.2	0.5	0.4	840	37.91	96.57	820	29.86	77.80
0.2	0.5	0.6	1120	33.50	117.57	1140	24.02	91.10
0.2	0.5	0.8	1440	32.53	1231.77	1400	43.64	—
0.2	0.5	1	1180	189.93	—	980	329.86	—

Sustainable strategies for harvesting predators and prey in a fluctuating environment

Edwige Bellier, Bernt-Erik Sæther and Steinar Engen

Highlights

An approach that provides theoretical scenarios of harvest of interacting species for a sustainable use of natural resources.

A harvest approach of interacting species that accounts for predators and prey's joint dynamics, natural fluctuations in abundances and consider varying environments.

Correlated environmental effects are included in the model and affect both species at the same time.

Strong environmental stochasticity increased the variance of predators and prey's yield, making the harvest of the interacting species less predictable.

Optimal yields for predators and prey can be obtained with different harvest strategies when both species are harvested simultaneously.