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Appendix B: The effects of harvesting on closed predator–prey communities with a type II functional response**.**

Local stability analysis of closed predator–prey communities

We start by performing a local stability analysis on the closed Rosenzweig-MacArthur predator–prey model (1963) with harvesting:

$$\begin{aligned} \frac{\mathrm{d}N_1}{\mathrm{d}t} &= rN_1\left(1-\frac{N_1}{K}\right)-\frac{aN_1N_2}{1+avN_1}-h_1N_1 \\ \frac{\mathrm{d}N_2}{\mathrm{d}t} &= \frac{aN_1N_2}{1+avN_1}-mN_2-h_2N_2 \end{aligned} \tag{B.1}$$

Where r, K and h_1 represent respectively the intrinsic rate of growth, the carrying capacity and the harvesting rate of the prey N_1 and a, v, m and h_2 represent respectively the attack rate, prey handling time, mortality and harvesting rate of the predator N_2. The local stability analysis was performed by evaluating the following Jacobian matrix at each equilibrium solution and finding the eigenvalues:

$$J=\begin{pmatrix} r-h_1-\dfrac{aN_2}{avN_1+1}-\dfrac{2rN_1}{K}+\dfrac{a^2vN_1N_2}{\left(avN_1+1\right)^2} & -\dfrac{aN_1}{avN_1+1} \\ -\dfrac{N_2a}{\left(avN_1+1\right)^2} & \dfrac{aN_1}{avN_1+1}-m-h_2 \end{pmatrix} \tag{B.2}$$

If the real part of the eigenvalues is smaller than zero then the equilibrium solution is locally stable. The model has three biologically-relevant (i.e., nonnegative and real) solutions: (1) the "extinction" solution where the abundance of both the predator and the prey is zero, (2) the "prey" solution, where the prey persists and the predator goes extinct and (3) the "coexistence" solution, where both the predator and the prey persist.

The extinction solution $\left(\hat{N}_1 = 0, \hat{N}_2 = 0\right)$ is locally unstable as long as the prey's intrinsic rate of growth r is larger than its harvesting rate $\left(r > h_1\right)$. The prey solution $\left(\hat{N}_1 = \frac{K}{r}\left(r - h_1\right), \hat{N}_2 = 0\right)$ is stable as long as the prey's intrinsic rate of growth is larger than its harvesting rate $\left(r > h_1\right)$ and $h_2 + m + \frac{h_1 - r_1}{\frac{r}{aK} - v\left(h_1 - r\right)} > 0$. The stability of the coexistence solution $\left(\hat{N}_1 = \frac{m + h_2}{a\left(1 - v\left(h_2 + m\right)\right)}, \hat{N}_2 = \frac{1}{a\left(v\left(h_2 + m\right) - 1\right)}\left(h_1 - r - \frac{r\left(h_2 + m\right)}{aK\left(v\left(h_2 + m\right) - 1\right)}\right)\right)$ can be determined by deriving the zero net growth isoclines (ZNGI) of the predator and the prey respectively:

$$
\begin{aligned}
N_1 &= \frac{m + h_2}{a\left(1 - v\left(h_2 + m\right)\right)} \\
N_2 &= \frac{1}{aK}\left(K\left(r - h_1\right) - arvN_1^2 + N_1\left(r\left(avK - 1\right) - h_1\right)\right)
\end{aligned}
\tag{B.3}
$$

The predator-prey system will undergo limit cycles if the ZNGIs intersect in the ascending section of the prey isocline $\left(\frac{\mathrm{d}N_2}{\mathrm{d}N_1} > 0\right)$. However, if the ZNGIs intersect in the descending section of the prey isocline $\left(\frac{\mathrm{d}N_2}{\mathrm{d}N_1} < 0\right)$, the dynamics will reach a point equilibrium (May 1973). Hence, we can determine the conditions under which the system will transition from a point equilibrium to a limit cycle (i.e., the Hopf bifurcation point) by solving:

$$
\left.\frac{\mathrm{d}N_2}{\mathrm{d}N_1}\right|_{N_1 = \hat{N}_1} = \frac{r}{aK}\left[avK - 1 - \frac{h_1}{r} + \frac{2\left(h_2 + m\right)}{\left(h_2 + m\right) - \frac{1}{v}}\right] = 0 \tag{B.4}
$$

The sign of the derivative and the stability of the coexistence solution depend on the term in squared brackets. By solving for any of the parameters in the bracketed term, we can determine the critical value at which the coexistence solution shifts from a point equilibrium to a limit cycle. Here, we solve for h_1:

$$h_1\big|_{\text{critical}} = r + \frac{r\left(1 + v\left(h_2 + m\right)\right)}{aKv\left(v\left(h_2 + m\right) - 1\right)} \tag{B.5}$$

The system will undergo limit cycles when $h_1 < h_1\big|_{\text{critical}}$ and reach a point equilibrium when $h_1 > h_1\big|_{\text{critical}}$.

For the parameter values used in this appendix and in the main text, closed predator-prey communities reach a stable point equilibrium when productivity is low (K=7) and exhibit limit cycles when productivity is high (K=40) as long as the harvesting rate of both species $h_i < 0.2$ (Fig. B1). In the main text, we present results from simulations of the spatially-explicit metacommunity model with a constant mean harvesting rate of $\bar{h}_i = 0.1$ with each community having either low productivity (K=7 for equilibrium metacommunities) or high productivity (K=40 for non-equilibrium metacommunities) to determine how changes in the underlying dynamical regime affect the performance of different marine reserve network designs.

The effects of harvesting in closed communities

We now assess the effects of harvesting on the (coexistence) equilibrium abundances of the prey and the predator:

$$\hat{N}_1 = \frac{m + h_2}{a\left(1 - v\left(h_2 + m\right)\right)}$$
$$\hat{N}_2 = \frac{1}{a\left(v\left(h_2 + m\right) - 1\right)}\left(h_1 - r - \frac{r\left(h_2 + m\right)}{aK\left(v\left(h_2 + m\right) - 1\right)}\right) \tag{B.6}$$

To determine the effects of changing the harvesting rates by establishing reserve networks, we can take the partial derivatives of the equilibrium abundance of the prey with respect to the harvesting rates:

$$\frac{\partial \hat{N}_1}{\partial h_1} = 0$$
$$\frac{\partial \hat{N}_1}{\partial h_2} = \frac{1}{a\left(v\left(h_2 + m\right) - 1\right)^2} > 0 \tag{B.7}$$

Because of the strong top-down control exerted by the predator (N_2), the abundance of the prey (N_1) grows in response to increases in the harvesting rate of the predator (h_2) but remains insensitive to changes in its own harvesting rate (h_1). Taking the partial derivatives of the predator abundance yields:

$$\frac{\partial \hat{N}_2}{\partial h_1} = \frac{1}{a\left(v\left(h_2 + m\right) - 1\right)}$$
$$\frac{\partial \hat{N}_2}{\partial h_2} = \frac{a^2 K v\left(r - h_1\right) + r\left(\left(v\left(h_2 + m\right)\right)^2 - 1\right)}{a^2 K\left(v\left(h_2 + m\right) - 1\right)^2} \tag{B.8}$$

Increasing the harvesting rate of the prey (h_1) increases predator abundance when $v\left(h_2 + m\right) > 1$ and decreases it otherwise because of the type II functional response (i.e., handling time v>0). When the mortality and harvesting rates of the predator are high, the predator's

abundance is depressed and so is its control over the prey. The prey is able to reach high densities that reduce the predator's overall efficiency because of the (proportional) increase in handling time. Hence, increasing the prey harvesting rate (h_1) will reduce prey abundance, increase the predator's efficiency and, ultimately, its abundance. For our particular parameterization of the model (m=0.2, v=1, $h_2 \in [0, 0.2]$), increasing the harvesting rate of the prey (h_1) always reduces predator abundance (Fig. B1).

The effect of increasing the harvesting rate of the predator (h_2) depends on the level of harvesting. Specifically:

$$\frac{\partial \hat{N}_2}{\partial h_2} = 0 \text{ if } h_2^* = \frac{1}{v}\left(1 - \frac{2r}{r + aKv(r - h_1)}\right) - m \tag{B.9}$$

Hence, if $h_2 > h_2^*$ then $\frac{\partial \hat{N}_2}{\partial h_2} < 0$, and increasing the predator harvesting rate will reduce its abundance whereas the converse is true if $h_2 < h_2^*$ (Fig. B1). This effect is again linked to the predator's handling time. Increasing the predator harvesting rate when it is low will increase predator abundance because the indirect gains from increased prey abundance outweigh the direct losses from increased harvesting at relatively low prey densities. However, increasing the predator harvesting rate when it is already high (and thus prey abundance is also high) will reduce predator abundance because of the reduced efficiency of the predator at high prey densities (i.e., increased time spent handling prey). For our particular parameterization of the model (m=0.2, v=1, $h_1 = h_2$), increasing the harvesting rate always reduces predator abundance (Fig. B1).

The effects of spatial variance in harvesting in closed communities

Our conservative modeling approach assumes that marine reserves will alter the spatial distribution (and thus the spatial variance) of the harvesting rate without affecting its mean across the metacommunity. Jensen's inequality predicts that increasing the variance of an independent variable (i.e., harvesting rate) will tend to increase (decrease) the response variable (i.e., mean abundance) if the latter is an accelerating (decelerating) function of the former (Ruel and Ayres 1999). Because of the type II functional response (see Eqs. B.7–B.8), mean predator abundance is a decelerating function of harvesting whereas prey abundance is an accelerating function of harvesting (Fig. B2 a,c). Hence, increasing the spatial variance of the harvesting rate by implementing reserves will reduce the mean abundance of the predator because predator abundance will decrease more in unprotected sites than it will increase in protected sites (Fig. B2 d). Conversely, increasing the spatial variance of the harvesting rate will increase the mean abundance of the prey because prey abundance will increase more in unprotected sites (where predator abundance is low) than it will decrease in protected sites (where predator abundance is high; Fig. B2 b).

In enriched communities undergoing limit cycles (K=40), increasing the harvesting rate reduces the amplitude (or power) and increases the frequency of population fluctuations (Fig. B3a, c). Because population fluctuations are bounded by zero and have asymmetrical shapes, increasing their frequency will tend to increase mean abundance whereas reducing their amplitude will tend to decrease mean abundance (Fig. B3 b, d). These opposing effects of harvesting on the frequency and amplitude of population fluctuations cause mean predator (prey) abundance to be an accelerating (decelerating) function of harvesting (Fig. B4 a,c) because the increase (decrease) in predator (prey) abundance within reserves is larger than the decrease

(increase) in predator (prey) abundance outside reserves (Fig. B4 b,d). Hence, because of Jensen's inequality, increasing the spatial variance of the harvesting rate by implementing reserves will increase (decrease) mean predator (prey) abundance (Fig. B4 b,d).

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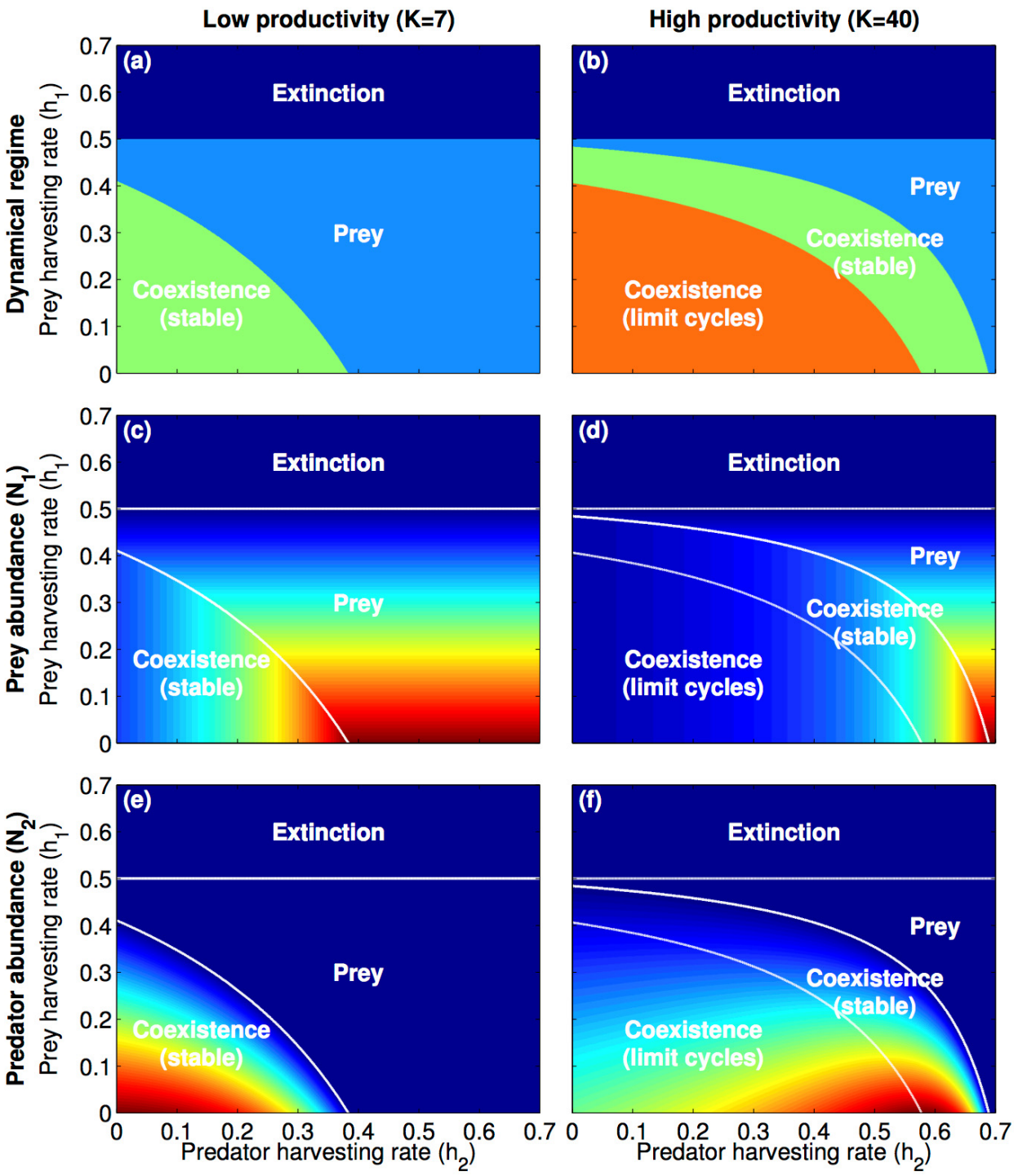

FIG. B1. The effect of increasing the harvesting rate on the dynamical regime (a, c) and the abundance of the prey (c, d) and the predator (e, f) in closed communities with either low (*K*=7; a, c, e) or high (*K*=40; b, d, f) productivity.

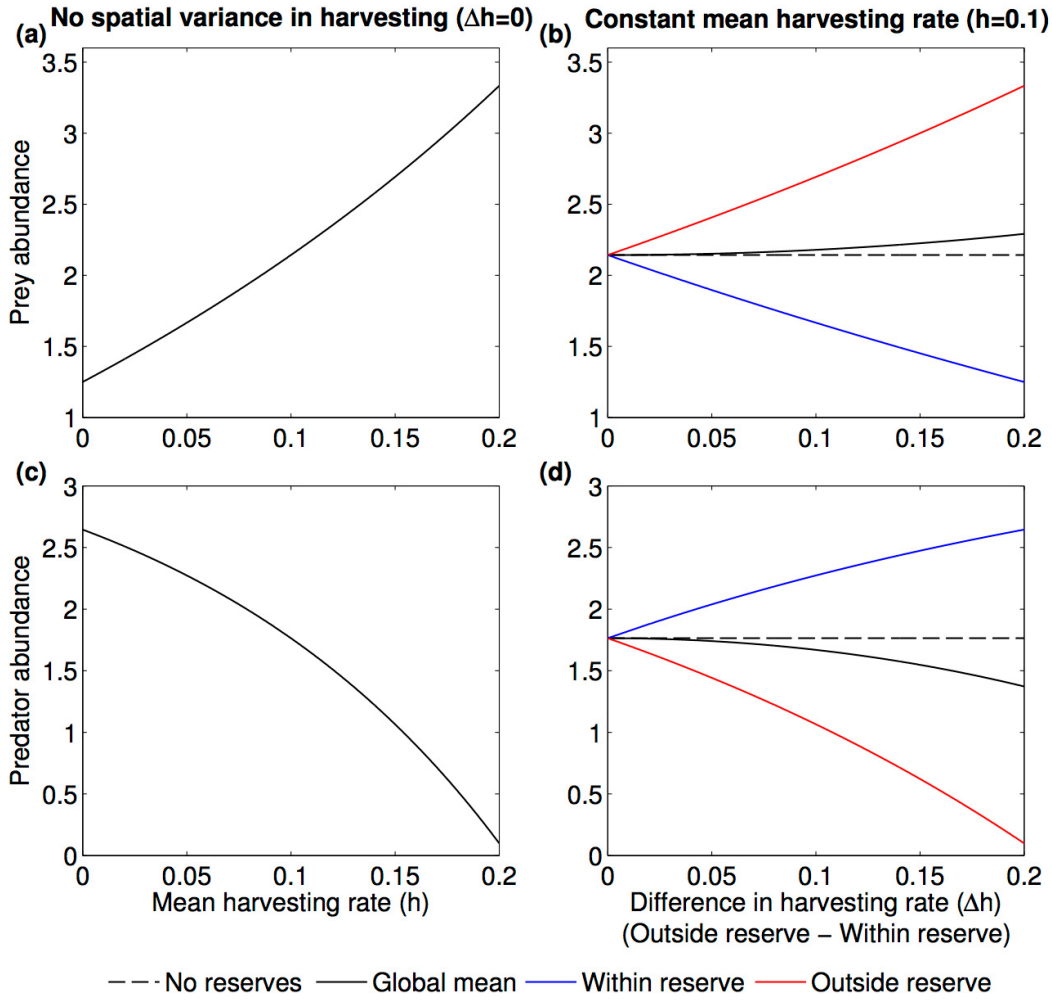

FIG. B2. The effect of increasing the mean (a, c) or the spatial variance (b, d) of the harvesting rate *h* on the global mean abundance of the prey (a, b) and the predator (c, d) in closed equilibrium metacommunities (*K*=7) consisting of two isolated sites. (a, c) The equilibrium abundance of the prey (predator) is an accelerating (decelerating) function of the mean harvesting rate *h*. (b, d) Because of Jensen's inequality, the global mean abundance (black) of the prey (predator) will increase (decrease) in response to spatial variance in the harvesting rate. Here, spatial variance in the harvesting rate is induced by increasing the difference in the harvesting rate between the protected site (blue) and the unprotected site (red). The horizontal dashed line indicates the global mean abundance in the absence of spatial variance in the harvesting rate (i.e., *h*=0.1 for both sites).

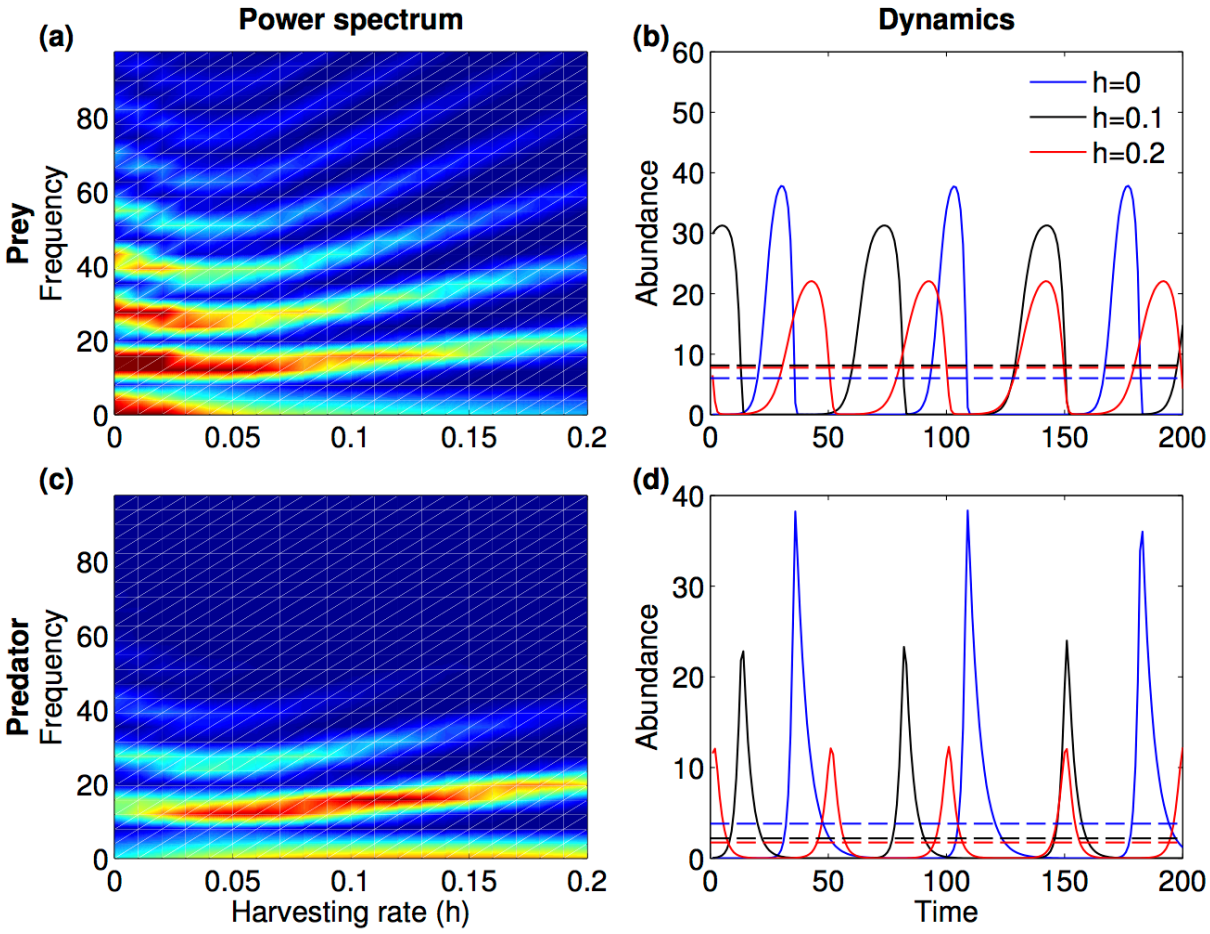

FIG. B3. The effect of increasing the harvesting rate on the power spectrum (a, b) and the dynamics (c, d) of the prey (a, b) and the predator (c, d) in closed communities with high productivity (K=40). We used Welch's method to obtain the power spectrum of each species' abundance at each harvesting rate. The power spectrum describes the contribution of each frequency to the total variability (or power) of a time series (color bar: warmer [colder] colors represent higher [lower] power). The horizontal dashed lines in (b, d) represent time-averaged abundance.

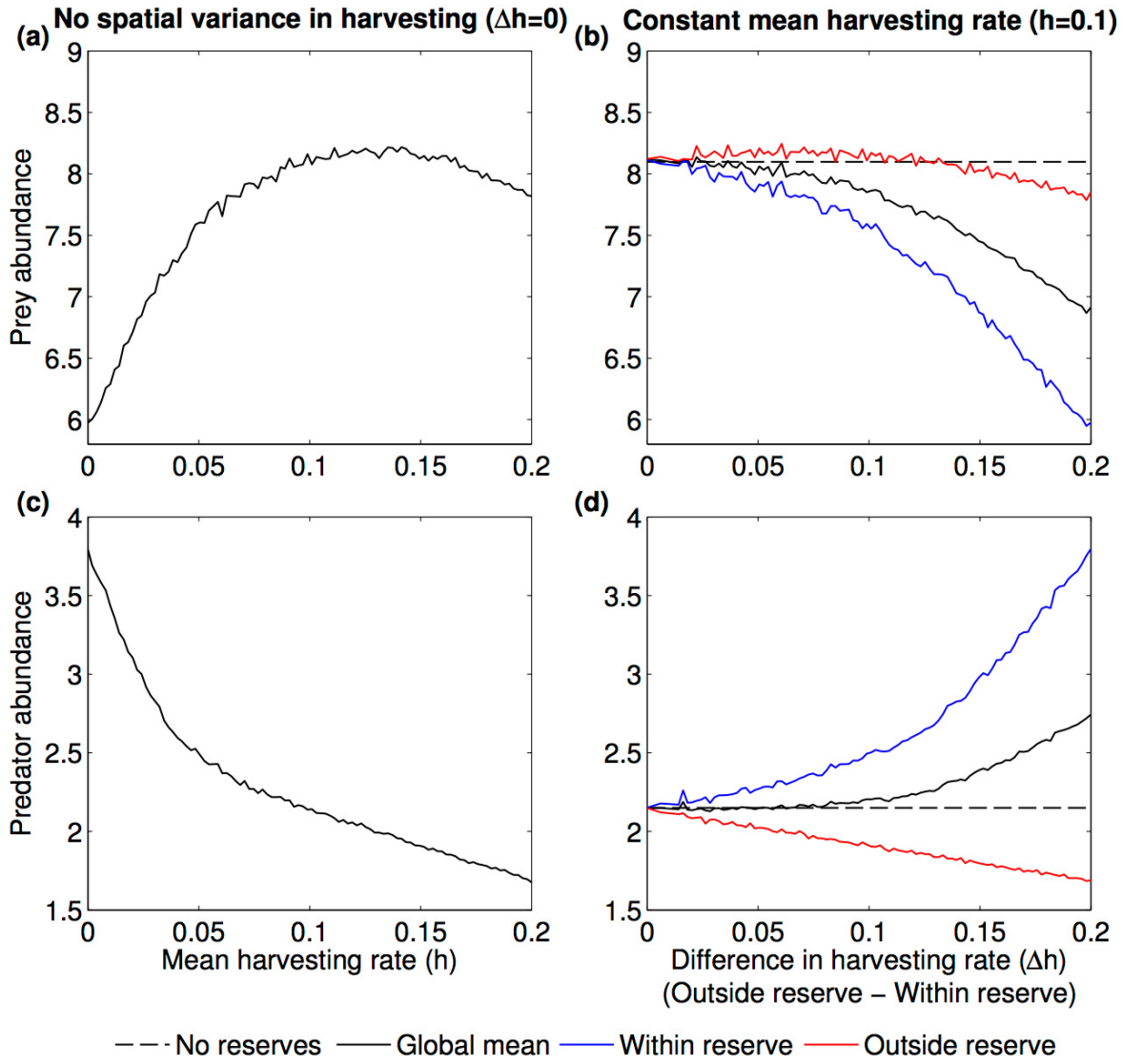

FIG. B4. The effect of increasing the mean (a, c) or the spatial variance (b, d) of the harvesting rate *h* on the global mean abundance of the prey (a, b) and the predator (c, d) in closed non-equilibrium metacommunities (*K*=40) consisting of two isolated sites. (a, c) The mean abundance of the prey (predator) is a decelerating (accelerating) function of the mean harvesting rate *h*. (b, d) Because of Jensen's inequality, the global mean abundance (black) of the prey (predator) will decrease (increase) in response to spatial variance in the harvesting rate. Here, spatial variance in the harvesting rate is induced by increasing the difference in the harvesting rate between the protected site (blue) and the unprotected site (red). The horizontal dashed line indicates the global mean abundance in the absence of spatial variance in the harvesting rate (i.e., *h*=0.1 for both sites).