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**Appendix A: The effects of a type III predator functional  
response on the effectiveness of reserve networks.**

## Predator-prey model with a type III functional response

The results presented in the main text were generated for metacommunities consisting of a prey and a specialist predator with a type II functional response. To determine the sensitivity of these results to the functional response of the predator, we now amend the Rosenzweig-MacArthur predator-prey model (1963) by using a type III functional response to model the dynamics of a prey and a generalist predator:

$$\begin{aligned}\frac{dN_1}{dt} &= rN_1 \left(1 - \frac{N_1}{K}\right) - \frac{aN_1^2 N_2}{1 + avN_1^2} - h_1 N_1 \\ \frac{dN_2}{dt} &= \frac{aN_1^2 N_2}{1 + avN_1^2} - mN_2 - h_2 N_2\end{aligned}\tag{A.1}$$

Where  $r=0.25$ ,  $K$ , and  $h_1$  represent respectively the intrinsic rate of growth, the carrying capacity and the harvesting rate of the prey  $N_1$  and  $a=0.9$ ,  $v=1$ ,  $m=0.6$ , and  $h_2$  represent respectively the attack rate, prey handling time, mortality and harvesting rate of the predator  $N_2$ . We now reproduce the analyses presented in the main text and in appendix B for this new model.

## Local stability analysis

The local stability analysis was performed by evaluating the following Jacobian matrix at each equilibrium solution and finding the eigenvalues:

$$J = \begin{pmatrix} r - h_1 - \frac{2N_1 r}{K} - \frac{2aN_1 N_2}{avN_1^2 + 1} + \frac{2a^2 v N_1^3 N_2}{(avN_1^2 + 1)^2} & -\frac{aN_1^2}{avN_1^2 + 1} \\ \frac{2N_1 N_2 a}{avN_1^2 + 1} & \frac{aN_1^2}{avN_1^2 + 1} - m - h_2 \end{pmatrix}\tag{A.2}$$

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., real and non-negative) 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  $(\hat{N}_1 = 0, \hat{N}_2 = 0)$  is locally unstable as long as the prey’s intrinsic rate of growth  $r$  is larger than its harvesting rate  $(r > h_1)$ . The prey solution

$(\hat{N}_1 = \frac{K}{r}(r - h_1), \hat{N}_2 = 0)$  is stable as long as the prey’s intrinsic rate of growth is larger than its

harvesting rate  $(r > h_1)$  and  $h_2 + m - \frac{a\left(K\left(1 - \frac{h_1}{r}\right)\right)^2}{av\left(K\left(1 - \frac{h_1}{r}\right)\right)^2 + 1} > 0$ . The stability of the coexistence

solution  $\left(\hat{N}_1 = (m + h_2) \sqrt{\frac{-1}{a(h_2 + m)(v(h_2 + m) - 1)}}, \hat{N}_2 = \frac{r}{Ka(v(h_2 + m) - 1)} - h_1 B + r_1 B\right)$

where  $B = \sqrt{\frac{-1}{a(h_2(v(h_2 + 2m) - 1) + m(mv - 1))}}$ , which is a double root (we only present the

positive root), was determined by deriving the zero net growth isoclines (ZNGI) of the predator and the prey, just like in appendix B. Note that this solution is only biologically relevant (i.e., real and non-negative) if  $v(h_2 + m) < 1$ . When  $v(h_2 + m) > 1$ , the equilibrium abundance of the prey becomes complex and the solution thus becomes biologically irrelevant.

For the parameter values used in this appendix, closed predator-prey communities reach a stable point equilibrium when productivity is low ( $K=5$ ) and exhibit limit cycles when

productivity is high ( $K=20$ ) as long as the harvesting rate of both species is smaller than  $\sim 0.2$  (Fig. D1). Below, we present results from simulations of the spatially-explicit metacommunity model with a constant mean harvesting rate of  $\bar{h}_i = 0.07$  with each community having either low productivity ( $K=5$  for equilibrium metacommunities) or high productivity ( $K=20$  for non-equilibrium metacommunities) to determine how changes in the underlying dynamical regime affect the performance of different reserve network designs.

## The effects of harvesting on closed communities

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

$$\hat{N}_1 = (m + h_2) \sqrt{\frac{-1}{a(h_2 + m)(v(h_2 + m) - 1)}} \quad (\text{A.3})$$

$$\hat{N}_2 = \frac{r}{Ka(v(h_2 + m) - 1)} - h_1 B + r_1 B, \text{ where } B = \sqrt{\frac{-1}{a(h_2(v(h_2 + 2m) - 1) + m(mv - 1))}}$$

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:

$$\begin{aligned} \frac{\partial \hat{N}_1}{\partial h_1} &= 0 \\ \frac{\partial \hat{N}_1}{\partial h_2} &= \frac{1}{2a(h_2 + m)(v(h_2 + m) - 1)^2 \sqrt{\frac{-1}{a(h_2 + m)(v(h_2 + m) - 1)}}} > 0 \end{aligned} \quad (\text{A.4})$$

Because of the 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 derivative of the predator abundance yields:

$$\frac{\partial \hat{N}_2}{\partial h_1} = -\sqrt{\frac{-1}{a(h_2 + m)(v(h_2 + m) - 1)}} \quad (\text{A.5})$$

Increasing the harvesting rate of the prey ( $h_1$ ) decreases predator abundance when  $v(h_2 + m) < 1$  and increases it otherwise because of the handling time  $v$  in the type III functional response (i.e., handling time  $v > 0$ ). Since  $v(h_2 + m) < 1$  is necessary for this equilibrium solution to be biologically relevant (i.e., real and non-negative), increasing the prey harvesting rate will always decrease the predator abundance. Unfortunately, the effect of the predator harvesting rate ( $h_2$ ) on the predator equilibrium abundance (i.e.,  $\frac{\partial \hat{N}_2}{\partial h_2}$ ) is too complex for simple interpretation.

However, for our particular parameterization of the model ( $m=0.6$ ,  $v=1$ ,  $h_1 = h_2$ ), it is sufficient to note that increasing the harvesting rate of the predator always reduces its abundance (Fig. A1). Overall, the effects of prey and predator harvesting on equilibrium abundance for communities characterized by type II (appendix A and main text) and type III functional responses are thus qualitatively identical.

## **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 predator handling time common to both the type II (main text and appendix B, Equ. B7-B8) and the type III (Equ. A4-A5) functional responses, mean predator abundance is a decelerating function of harvesting whereas prey abundance is an accelerating function of harvesting (Fig. A2 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. A2 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. A2 b). Therefore, the effects of harvesting on closed equilibrium communities do not depend on the specifics of the nonlinear functional response (i.e., type II vs. III). These effects merely require that the functional response be nonlinear because of non-zero predator handling time.

In enriched communities undergoing limit cycles ( $K=20$ ), increasing the harvesting rate reduces the amplitude (or power) and reduces the frequency of population fluctuations (Fig. A3 a, c). Because population fluctuations are bounded by zero and have asymmetrical shapes, decreasing their frequency and amplitude will tend to decrease mean abundance (Fig. A3 b, d). These 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. A4 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. A4 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. A4 b,d).

These are largely the same qualitative results obtained with the type II functional response used in the main text and in appendix B (Fig. B4). The only difference is that the type II functional response leads to higher prey abundance outside rather than within reserves because the specialist predator exerts a strong top-down effect on the prey within reserves (i.e., strong trophic cascades; Fig. B4 b), whereas the type III functional response leads to higher prey abundance within rather than outside reserves because the generalist predator exerts a weaker top-down effect on the prey (i.e., weak trophic cascades; Fig. A4 b). Hence, although the type II generates stronger trophic cascades than the type III, the effects of both functional responses on the mean abundance of the prey and the predator in closed communities are qualitatively identical (compare Fig. B4 b, d and A4 b, d).

## **The effects of reserve networks on equilibrium metacommunities with a type III functional response**

Under equilibrium conditions, the effects of reserve networks on metacommunities characterized by type II (Fig. 3, Table 1) and type III (Fig. A5, table A1) functional responses are qualitatively identical. Networks of small and aggregated reserves promote the mean abundance of the predator and reduce that of the prey globally and within reserves because of trophic cascades (Fig. A5 a-d). Conversely, networks of large and isolated reserves increase the global mean abundance of the prey and reduce that of the predator (Fig. A5 a, b). Here, lower connectivity between reserves and unprotected sites leads to reduced predator spillover into unprotected areas and thus weaker trophic cascades. This allows prey abundance to build-up in unprotected areas

faster than it decreases in reserves, and global mean prey abundance thus increases (Fig. A5 c, e). Predator global mean abundance decreases because limited spillover from reserves to unprotected areas causes predator abundance to decrease faster outside reserves than it increases within reserves (Fig. A5 d, f). As with the type II functional response, prey total yield is maximized for networks of large and isolated reserves because those same networks promote the mean abundance of the prey outside reserves where it can be harvested by reducing predator spillover and thus trophic cascades (Fig. A5 g). However, predator total yield never increases with reserves because the gains achieved in predator abundance occur primarily within reserves where harvesting is either limited or completely prohibited (Fig. A5 h; Table A1, A2).

Overall, these simulations show that the community-level tradeoff inherent to the design of reserve networks for equilibrium metacommunities does not depend on the specifics of the functional response (i.e., type II vs. type III). Whether species are trophically coupled via a specialist or a generalist predator, the potential for cascades greatly complicates the use of reserve networks to protect entire equilibrium (meta)communities.

## **The effects of reserve networks on non-equilibrium metacommunities with a type III functional response**

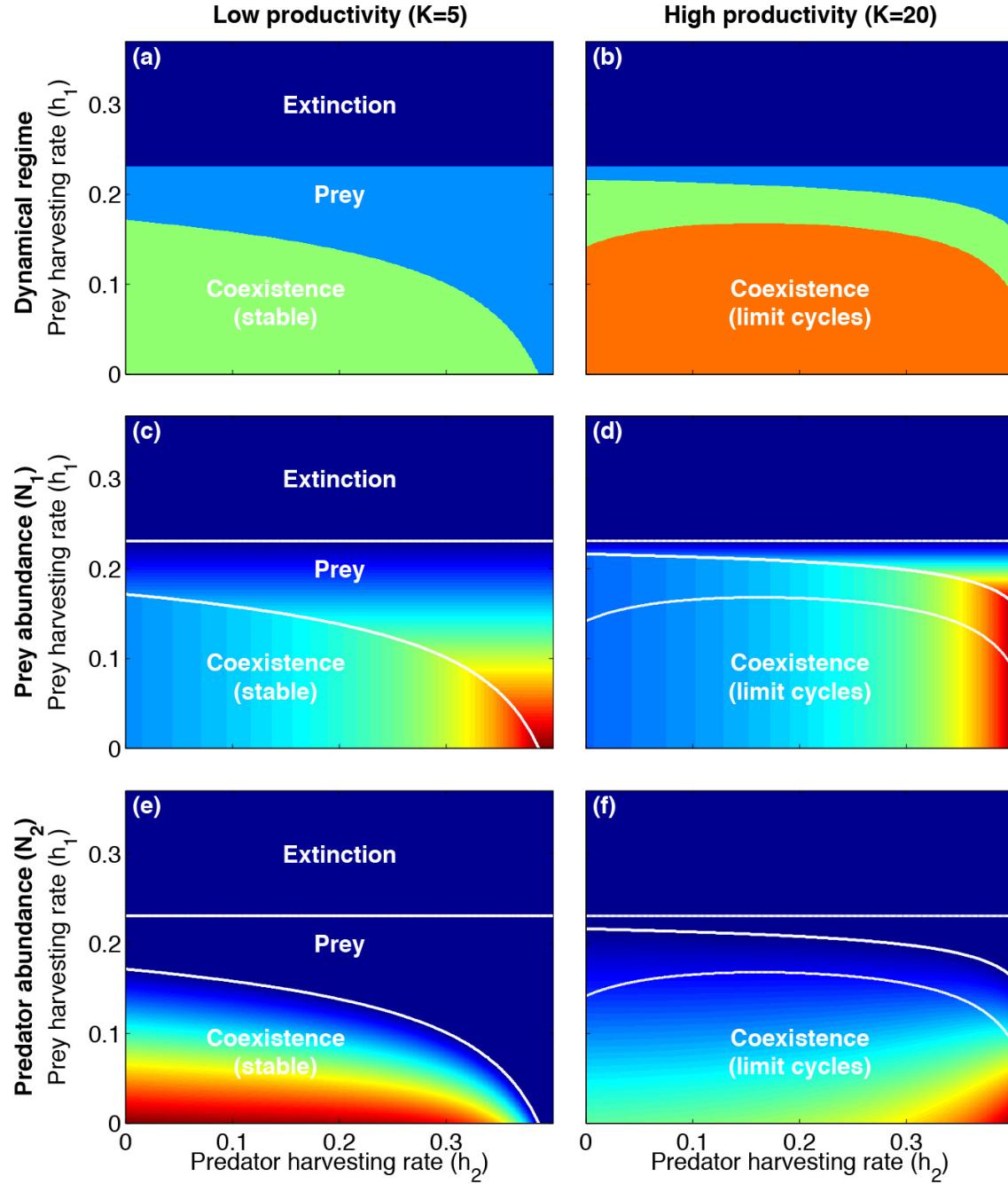
As with the type II functional response, reserve networks based on extent of patchiness (dispersal) maximize (minimize) the global mean abundance and the persistence of the predator and the prey for non-equilibrium metacommunities with a type III functional response (Fig. A6 a-b, Fig. A7). However, because the type III functional response leads to weaker trophic coupling, both prey and predator abundance vary in a unimodal manner with the size and spacing of reserves (Fig. A6). Here, because the intraspecific benefits associated with increased



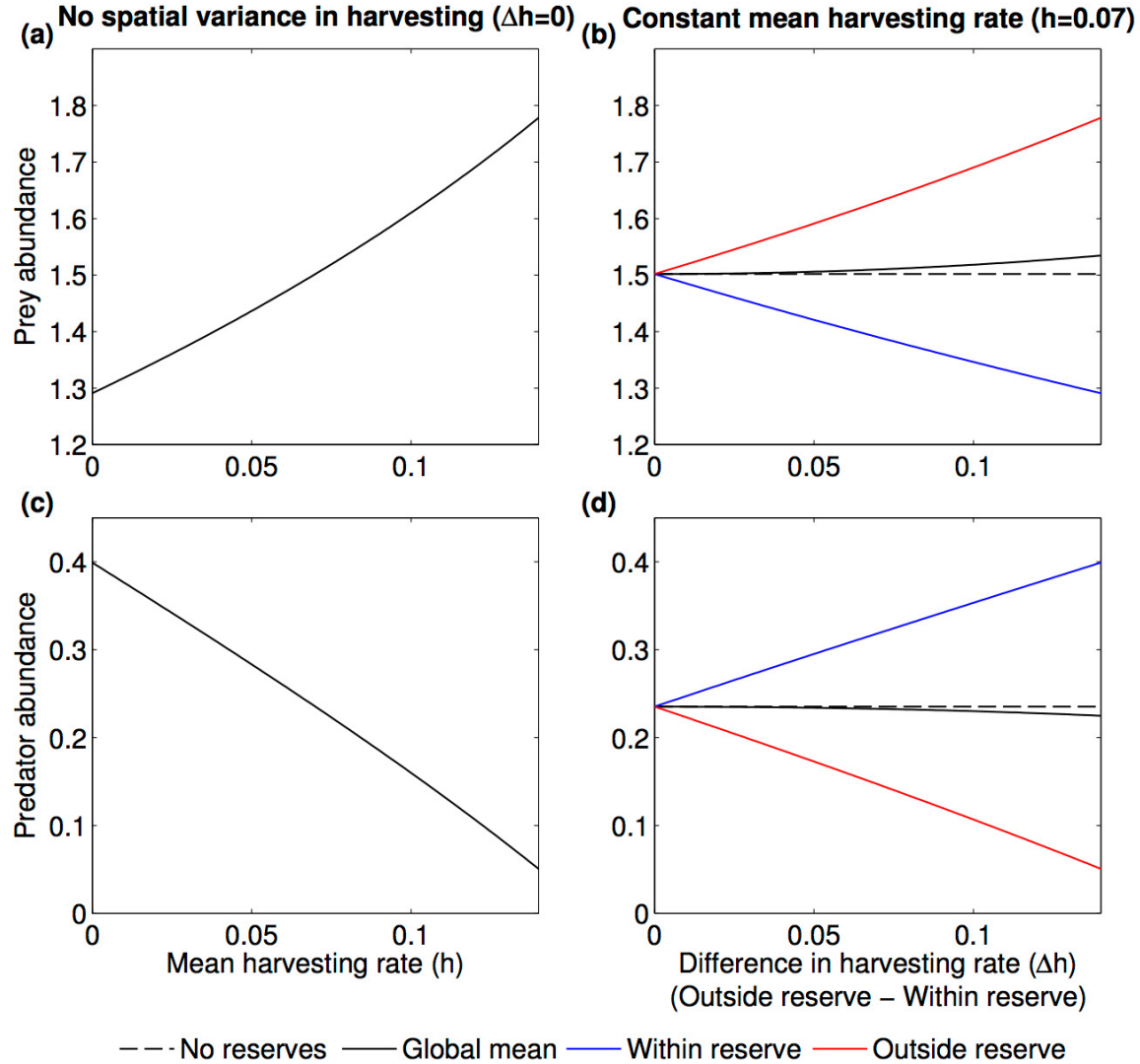
connectivity are more important than the interspecific costs associated with stronger trophic cascades, prey abundance is maximized globally, within and outside reserves for networks based on the extent of patchiness (Fig. A6 a, c, e). Additionally, partially protected (~50%) reserve networks based on the extent of patchiness can simultaneously maximize both the abundance and the total yield of the prey and the predator in non-equilibrium metacommunities characterized by a type III functional response (Fig. A6, Table A2). Hence, when trophic coupling is relatively diffuse (e.g., via a generalist predator), reserve networks based on the extent of patchiness can serve both conservation and fishery objectives optimally for non-equilibrium (meta)communities. Overall, these simulations echo the findings based on the type II functional response and show that weaker trophic coupling between species can lead to even more desirable ecological outcomes than those presented in the main text when reserve networks are based on the extent of patchiness.

## **LITERATURE CITED**

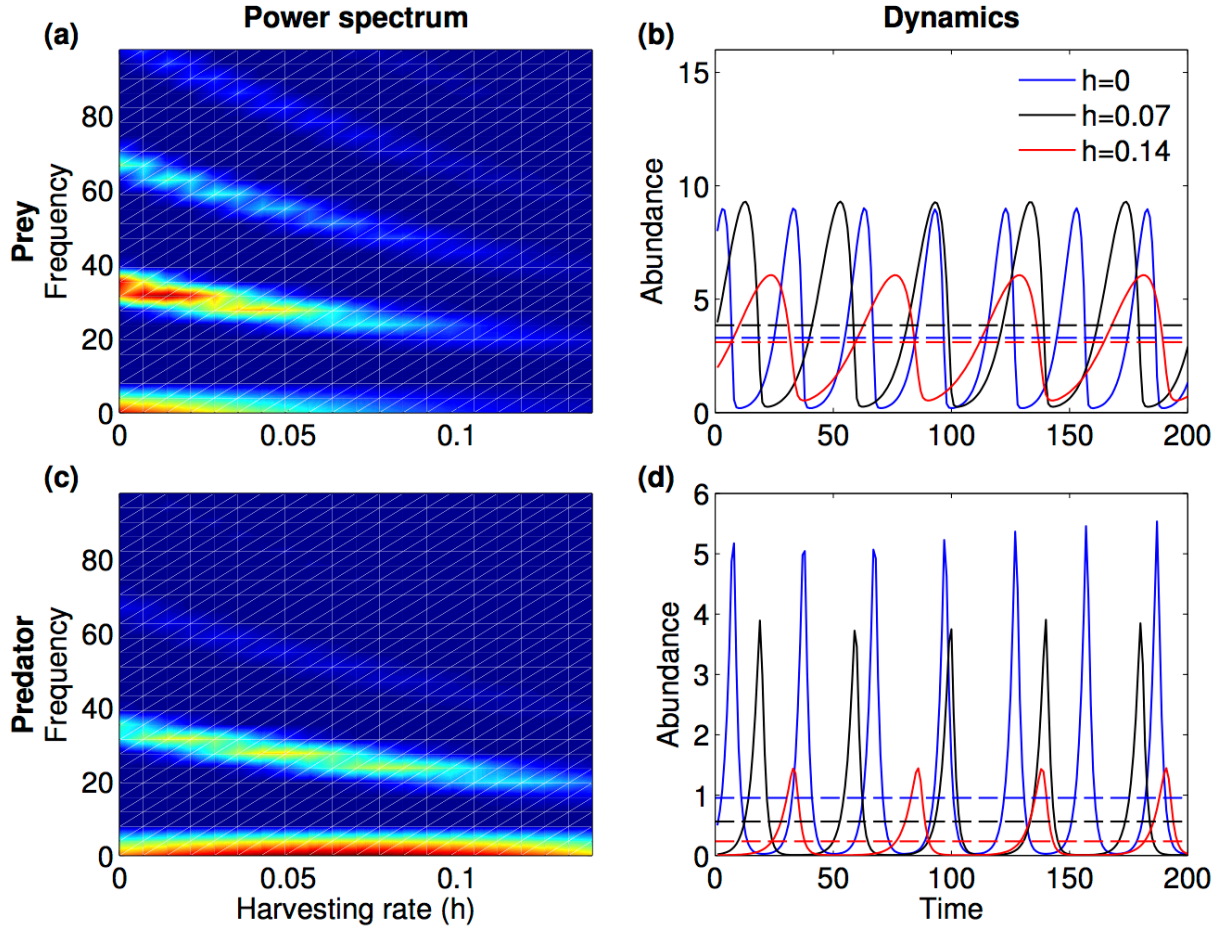
- Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical Representation and Stability Conditions of Predator-Prey Interactions. *American Naturalist* 97:209–223.
- Ruel, J. J., and M. P. Ayres. 1999. Jensen's inequality predicts effects of environmental variation. *Trends in Ecology & Evolution* 14:361–366.



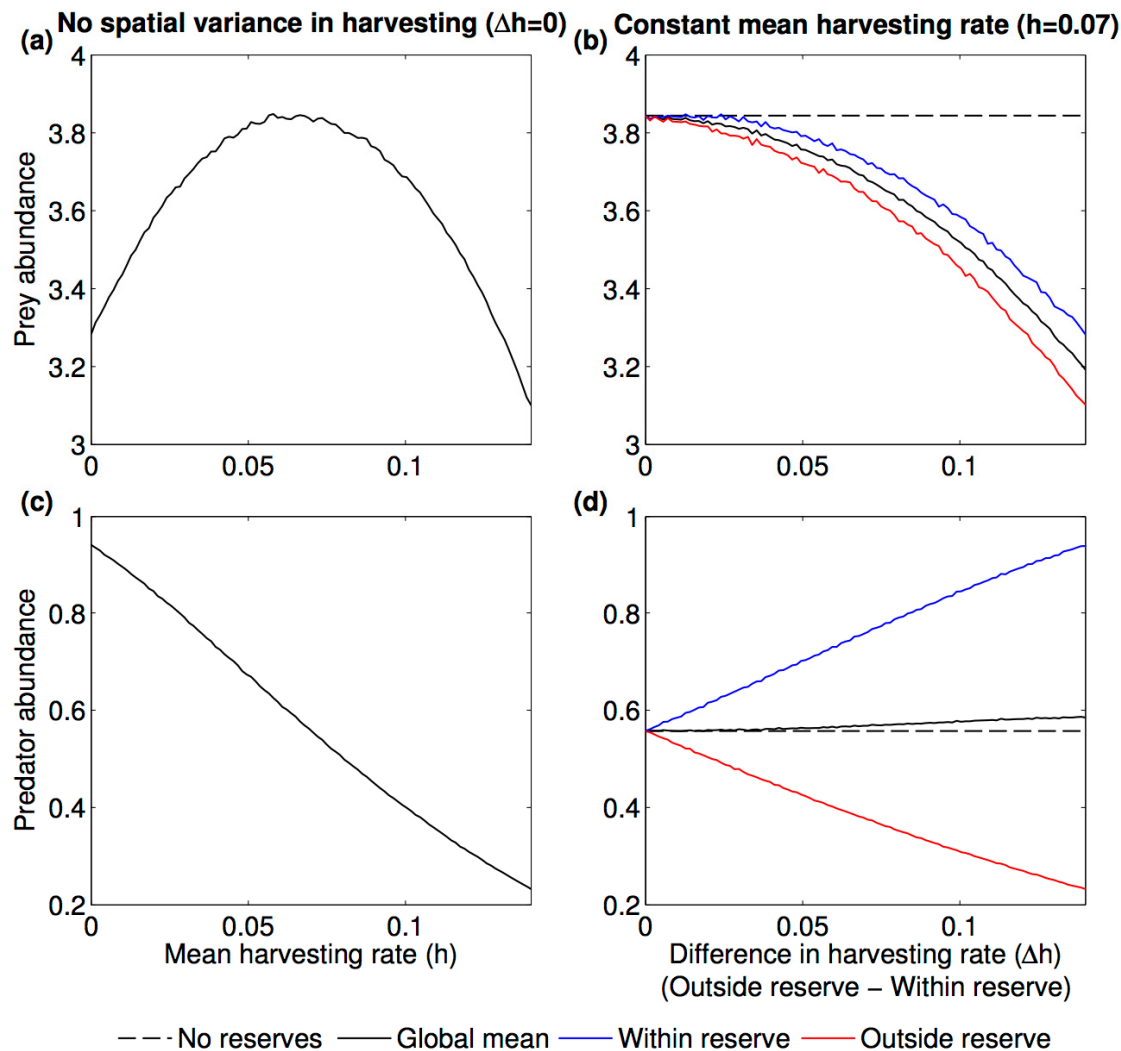
**FIG. A1.** The effect of increasing the harvesting rate on the dynamical regime (a, c) and the abundance of the prey (c, d) and the predator (e, f) in closed communities with a type III functional response and either low ( $K=5$ ; a, c, e) or high ( $K=20$ ; b, d, f) productivity.



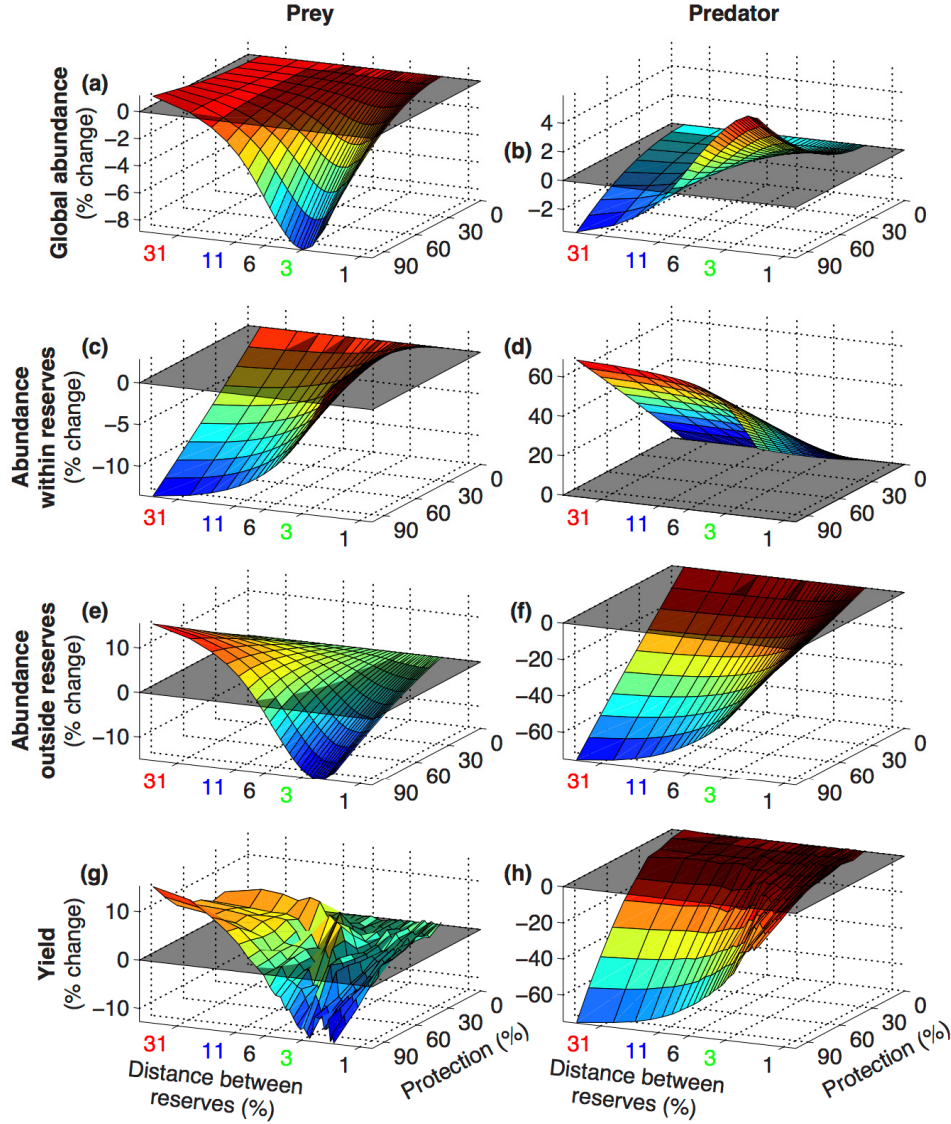
**FIG. A2.** The effect of increasing the mean (a, c) or the spatial variance (b, d) of the harvesting rate  $h$  on the global mean abundance of the prey (a, b) and the predator (c, d) in closed equilibrium metacommunities ( $K=5$ ) with a type III functional response and two isolated sites. (a, c) 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.,  $h=0.07$  for both sites).



**FIG. A3.** 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 ( $K=20$ ) and a type III functional response. 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.

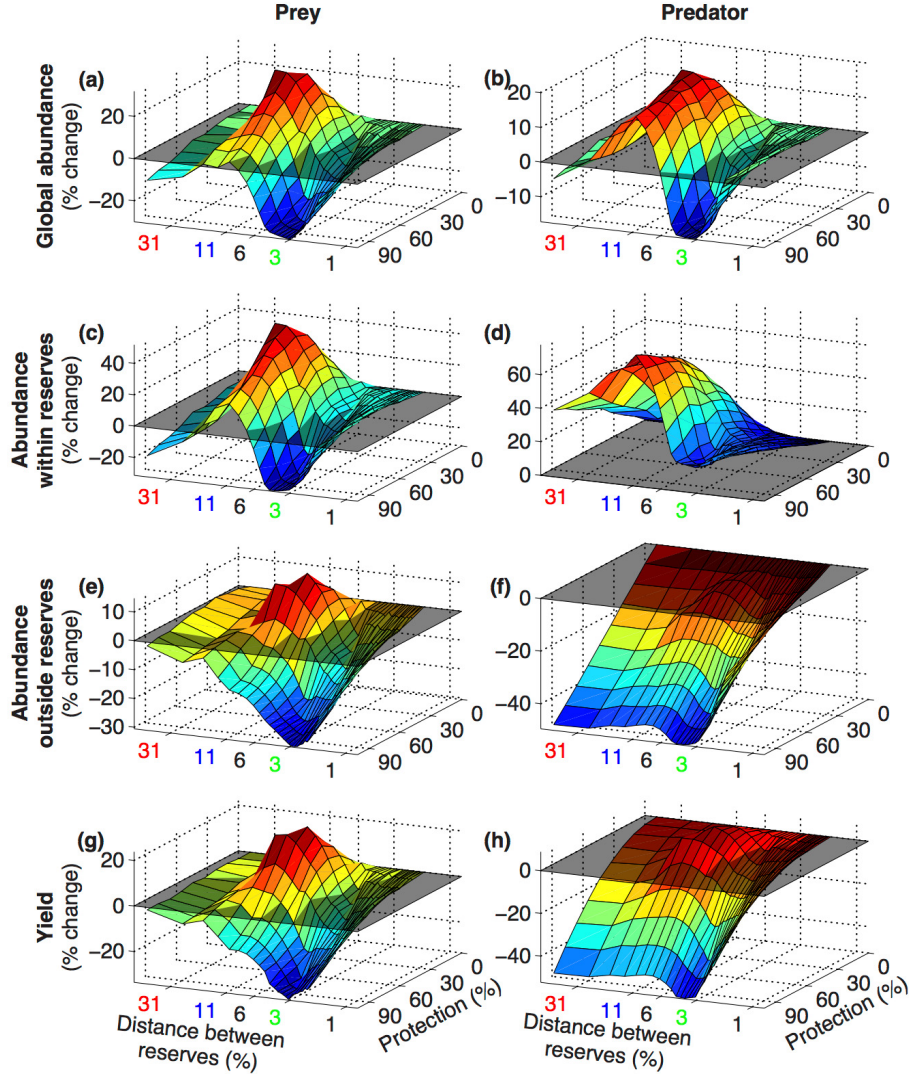


**FIG. A4.** The effect of increasing the mean (a, c) or the spatial variance (b, d) of the harvesting rate  $h$  on the global mean abundance of the prey (a, b) and the predator (c, d) in closed non-equilibrium metacommunities ( $K=20$ ) with a type III functional response and two isolated sites. (a, 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.,  $h=0.07$  for both sites).

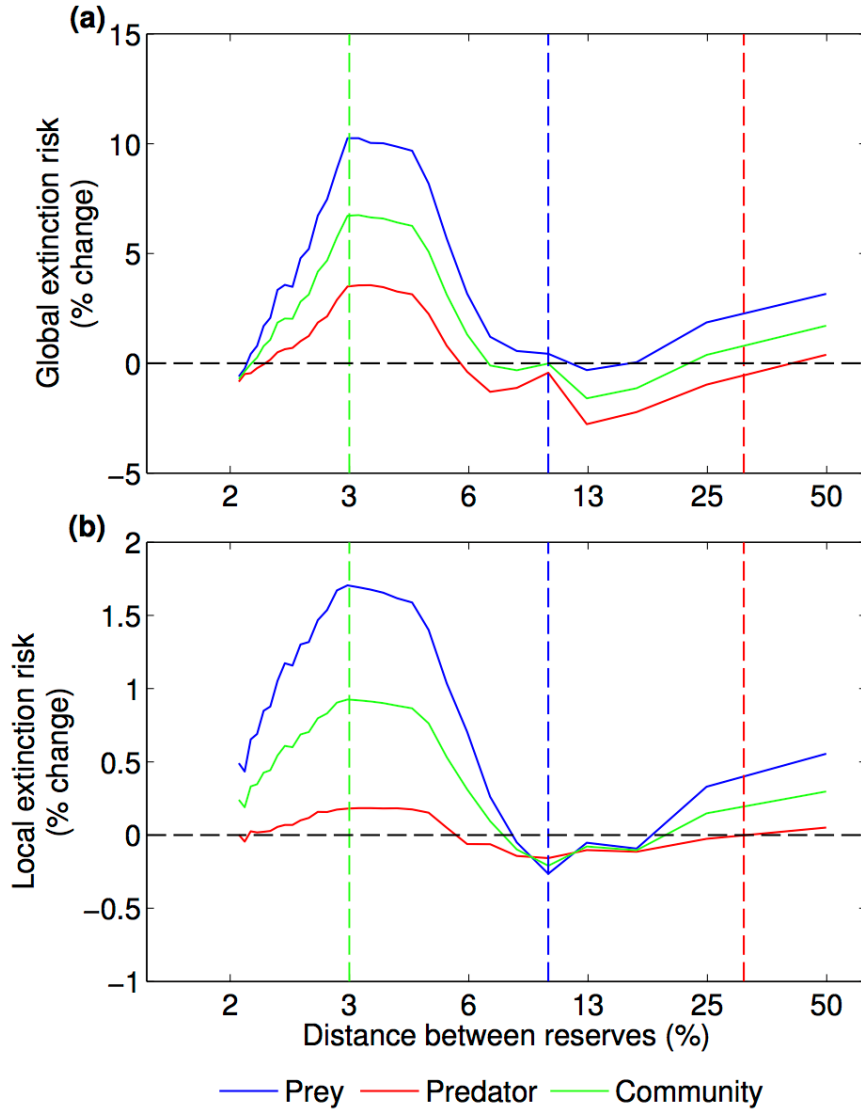


**FIG. A5.** The effect of varying the level of protection and the distance between reserves (expressed as % of spatial extent) on prey and predator (a, b) global mean abundance, (c, d) mean abundance within reserves, (e, f) mean abundance outside reserves and (g, h) total yield for equilibrium metacommunities ( $K=5$ ) with full dispersal and a type III functional response. Each metric is measured in percent change relative to baseline scenarios without reserves (i.e., spatially uniform harvesting rate) represented by the semi-transparent black horizontal surface. The mean predator and prey harvesting rates are set to 0.07. The green, blue, and red axis tick labels represent respectively the extent of dispersal, the extent of patchiness, and the scale of coupling. Results represent means from 10 replicate simulations.





**FIG. A6.** The effect of varying the level of protection and the distance between reserves (expressed as % of spatial extent) on prey and predator (a, b) global mean abundance, (c, d) mean abundance within reserves, (e, f) mean abundance outside reserves and (g, h) total yield for non-equilibrium metacommunities ( $K=20$ ) with full dispersal and a type III functional response. Each metric is measured in percent change relative to baseline scenarios without reserves (i.e., spatially uniform harvesting rate) represented by the semi-transparent black horizontal surface. The mean predator and prey harvesting rates are set to 0.07. The green, blue, and red axis tick labels represent respectively the extent of dispersal, the extent of patchiness, and the scale of coupling. Results represent means from 10 replicate simulations.



**FIG. A7.** The effect of varying the distance between no-take marine reserves (expressed as % of spatial extent) on global (a) and local (b) extinction risk for the prey (blue), the predator (red), and entire communities (green) in non-equilibrium metacommunities ( $K=20$ ) with a type III functional response. The vertical dashed lines represent the extent of dispersal (green), the extent of patchiness (blue) and the scale of coupling (red). The extinction risk is measured in percent change relative to baseline scenarios without reserves (i.e., spatially uniform harvesting rate) represented by the horizontal dashed line. The mean predator and prey harvesting rates are set to 0.07. Results represent means from 10 replicate simulations.



**TABLE A1.** The performance of different no-take (100% protected) marine reserve designs based on their effect on global mean abundance and total yield for equilibrium ( $K=5$ ) and non-equilibrium metacommunities ( $K=20$ ) with a type III functional response. The values represent the percent change of each metric for marine reserve designs described in rows relative to baseline simulations of metacommunities with no reserves.

		Percent change in equilibrium metacommunities		Percent change in non-equilibrium metacommunities	
		Prey	Predator	Prey	Predator
Global mean abundance	Extent of dispersal	-9	5	-30	-17
	Extent of patchiness	-2	-0.6	3	16
	Scale of coupling	0.3	-3	-6	2
Total yield	Extent of dispersal	-10	-41	-31	-48
	Extent of patchiness	6	-66	-15	-44
	Scale of coupling	14	-72	-6	-47

**TABLE A2.** The performance of different partially-protected (45%) marine reserve designs based on their effect on global mean abundance and total yield for equilibrium ( $K=5$ ) and non-equilibrium metacommunities ( $K=20$ ) with a type III functional response. The values represent the percent change of each metric for marine reserve designs described in rows relative to baseline simulations of metacommunities with no reserves.

		Percent change in equilibrium metacommunities		Percent change in non-equilibrium metacommunities	
		Prey	Predator	Prey	Predator
Global mean abundance	Extent of dispersal	-2	1	-9	-3
	Extent of patchiness	-0.3	-0.3	31	20
	Scale of coupling	0.1	-0.6	-0.7	0.8
Total yield	Extent of dispersal	-1	-8	-11	-10
	Extent of patchiness	4	-11	23	5
	Scale of coupling	5	-12	-0.9	-9