Received: 27 January 2018 | Accepted: 4 April 2018

DOI: 10.1111/nrm.12168

WILEY Natural Resource Modeling

Effects of harvesting mediated by dispersal traits

R. S. Cantrell | C. Cosner

Department of Mathematics, University of Miami, Coral Gables, FL, USA
(Email: rsc@math.miami.edu)

Correspondence
C. Cosner, Department of Mathematics, University of Miami, 1365 Memorial Dr., Ungar 515, Coral Gables, FL 33146, USA.
Email: gcc@math.miami.edu

Funding information
National Science Foundation, Grant/Award Number: DMS -1514752

Research partially supported by NSF Grant DMS 1514752.

Abstract

Trait-mediated behavioral responses to other species, especially predators, can have important effects on the dynamics of populations. One effect is to modify dispersal patterns, which in turn can modify population dynamics and species interactions. We model a situation where a focal population responds to disturbances created by the harvesting of another population by increasing the rate of random dispersal by individuals. The model shows that in some situations this effect can result in the extinction of the focal population, even if it is not itself subject to harvesting. This observation suggests that it may be desirable to consider trait-mediated effects when assessing the possible impacts of harvesting on conservation.

Recommendations for Resource Managers

- Be aware that harvesting a given crop or population can affect other populations because of their behavioral responses to the harvesting activity, even if it does not directly impose mortality on those populations or change their interactions with other species.
- A way that harvesting activity can affect nonharvested populations is to increase their dispersal rate. Managers should be aware that this has the potential to cause extinction in some situations even if no other effects of harvesting are present.
- For some populations, harvesting resources with which they interact or share an environment could in principle cause both direct and indirect effects, which could combine to have a different, perhaps greater, impact than either one would have separately.

KEYWORDS
dispersal, harvesting, reaction–diffusion, trait-mediated effects

1 | INTRODUCTION

The way that harvesting of particular species influences communities and ecosystems via the effects of direct interactions between species, and how direct interactions in turn influence the results of harvesting, has been studied fairly extensively; see, for example, Chakraborty, Pal, and Bairagi (2012), Chaudhuri (1986), Dunn, Baskett, and Hovel (2017), and Kar (2006). However, trait-mediated interactions based on indirect effects arising from behavioral responses can also be important (Schmitz, Křivan, & Ovadia, 2004; Werner & Peacor, 2003). This idea has been studied to a considerable extent in the context of predator–prey systems, where prey responses to the presence of predators can have significant indirect effects (Brown, Laundré, & Gurung, 1999; Peacor & Werner, 2001). Harvesting is in some sense a version of predation, and can have both direct and indirect effects on populations other than those being harvested (Grüebler, Schuler, Spaar, & Naef-Daenzer, 2015). In particular, in Grüebler et al. (2015), it was found that harvesting fields could harm grassland birds directly by increasing mortality and destroying nests and could also increase their rates of dispersal. Here, we consider the possibility that harvesting a given population may cause indirect effects on other populations, and how such indirect effects of harvesting might influence population persistence and species interactions. The particular scenario we explore is one where harvesting efforts targeting one species have the effect of disturbing individuals of another, unharvested, species so that they increase their rate of random (diffusive) movement. It is well known that in some situations, specifically in the case of populations inhabiting bounded habitats with lethal boundaries, populations cannot persist if their diffusion rates are too high. This can also occur in closed habitats containing both source and sink regions (see the discussion in Cantrell & Cosner, 1991, and Cantrell & Cosner, 2003, chapter 3) In fact, even if the habitat is closed and is heterogeneous but favorable everywhere, for competing species that have different diffusion rates but are otherwise ecologically identical, the slower diffuser will exclude the faster diffuser (see Dockery, Hutson, Mischaikow, & Pernarowski, 1998). For specificity, we will consider a situation where there are two species where the first has a negative effect on the second, the first is harvested and the second is not, but the random movement rate of the second species increases with the amount of effort used in harvesting the first species. Without this last trait-mediated effect, harvesting the first population would be expected to benefit the second by reducing the negative impact from the first. However, when the effect is present, it turns out that it can have a detrimental effect, even to the point of causing the extinction of the second, unharvested, species.

Our modeling approach is based on a system of reaction–diffusion equations. We believe that the scenario we describe and the details of the models are new, but the analysis of the models is a fairly straightforward application of reaction–diffusion theory. In the second section of the paper, we describe the models and state some background results on reaction–diffusion equations. In the third section, we state and prove the main results about the models, then in the last section we discuss their implications.

2 | MODELS AND BACKGROUND RESULTS

2.1 | Models

Suppose that two species inhabit a bounded region $\Omega \subseteq \mathbb{R}^n$ (where $n = 1, 2, \text{or } 3$). We will assume that both species disperse by diffusion. For technical reasons we will assume that $\partial\Omega$ is smooth. We will focus on the case where the region includes both sources and sinks but is closed so that there is no loss of individuals by dispersal across the boundary. The case where the interior of Ω is locally a source everywhere but there is a loss of individuals across the boundary is similar. Suppose further that the first species, with density denoted by u, is subjected to constant effort harvesting at a rate h but that harvesting does not affect its dispersal rate, while the second species, with density denoted by v, is not harvested but reacts to the harvesting of the first competitor by increasing its diffusion rate by an amount proportional to h. The key idea is that the activities associated with harvesting the first species disturb individuals of the second species in a way that causes them to scatter, for example, to avoid what they may perceive as a danger even though it does not pose an actual threat. This is an example of a type of trait-mediated effect (see Brown et al., 1999; Peacor & Werner, 2001; Schmitz et al., 2004; Werner & Peacor, 2003). A simple model describing such a situation is

$$\begin{aligned} \frac{\partial u}{\partial t} &= D_u \Delta u + (a(x) - bu - cv)u - hu, \\ \frac{\partial v}{\partial t} &= (D_v + gh)\Delta v + (d(x) - eu - fv)v \quad \text{in} \quad \Omega \times (0, \infty), \\ \frac{\partial u}{\partial n} &= \frac{\partial v}{\partial n} = 0 \quad \text{on} \quad \partial\Omega \times (0, \infty). \end{aligned} \tag{1}$$

We assume that D_u, D_v, b, f, g, and h are positive constants and e is a nonnegative constant. We assume that the functions $a(x)$ and $d(x)$ are smooth and are positive on some subsets of Ω with positive measure, but the spatial average of $d(x)$ is negative. The functions $a(x)$ and $d(x)$ represent the local per capita rates of population growth or decline at location x. The interpretation of the constants in (1) is that D_u and D_v are the diffusion rates of the first and second species, respectively, h is the rate of constant effort harvesting of the first species, g represents the sensitivity of the diffusion rate of the second species to the rate of harvesting h of the first, b and f describe intraspecific competition leading to logistic self-limitation, and c represents the impact of the second species on the first. If $c > 0$ the interaction between the two species is competitive; if $c < 0$ then the first species would be an omnivore or generalist predator that preys on the second; if $c = 0$ the second species has no impact on the first. For our present purposes, it does not matter which of those cases occurs.

Reaction–diffusion models for interacting population with the general structure of (1) have been widely studied; see, for example, Cantrell and Cosner (2003) and the references therein. Spatially explicit models for harvesting based on reaction–diffusion equations have been studied from the viewpoint of optimal control by Suzanne Lenhart and her students and other collaborators (see Ding & Lenhart, 2009; Joshi, Herrera, Lenhart, & Neubert, 2009; Kelly, Xing, & Lenhart, 2016).

In the model (1) the diffusion rate of the second species is increased by an amount proportional to the harvesting rate h for the first species. The point of the model is that since $e \geq 0$, if harvesting the first species had no effect on the movement of the second, then it would benefit the second species by reducing the density of the first in the case $e > 0$ and would have no impact at all on the second if $e = 0$. However, we shall see that if harvesting the first species causes an increase in random movement by the second species then harvesting the first species may be detrimental to the second, to the point of causing its extinction. Another situation where a similar effect could occur without the presence of sink habitats in Ω for the second species (i.e., $d(x) > 0$) would be when there is a loss of individuals of the second species across $\partial\Omega$. In that case the density of the second species would satisfy a Dirichlet or Robin boundary condition ($u = 0$ or $\partial u / \partial n + \alpha u = 0$ with $\alpha > 0$, respectively) instead of the no-flux boundary condition shown in (1). The mathematical analysis and results in those cases would be similar to those for (1).

2.2 | Background results

The general theory for reaction–diffusion models such as those appearing in (1) under classical boundary conditions is well established; see, for example, Cantrell and Cosner (2003) and Cantrell, Cosner, and Hutson (1993). In particular, solutions with nonnegative initial data remain nonnegative by the comparison principle for single equations, and because we assume $e \geq 0$ and $f > 0$ the comparison principle for single equations implies that v remains bounded as $t \to \infty$, and then since $b > 0$ a similar argument implies that u remains bounded as $t \to \infty$, so that solutions exist globally in time (see Cantrell et al., 1993, for a detailed discussion). The predictions of persistence or extinction in reaction–diffusion equations and systems with logistic self-limitation such as (1) are determined largely by the stability of the trivial equilibrium 0 or $(0,0)$ and, in the case of systems, of semitrivial equilibria of the form $(u^*, 0)$ and $(0, v^*)$. The stability or instability of those equilibria in turn is generally determined by the size or sign of principal eigenvalues of their linearizations at the trivial or semitrivial equilibria. We will state the key results, which are needed for the analysis of (1). For more details, see Cantrell and Cosner (2003) and Cantrell et al. (1993) and their references. We start with eigenvalue problems for a single linear equation, then turn to diffusive logistic equations, then systems.

Lemma 2.1. *Assume that* Ω *is bounded,* $D > 0$*, and* $\partial\Omega$ *and* $m(x)$ *are smooth.*

1. *The eigenvalue problem*

$$D\Delta\psi + m(x)\psi = \sigma\psi \text{ in } \Omega \tag{2}$$

with homogeneous classical (i.e., Neumann, Dirichlet, or Robin) boundary conditions has a principal eigenvalue σ_0*, which is the smallest eigenvalue and is characterized by having a positive eigenfunction* ψ_0.

2. *Suppose* $m(x) > 0$ *on some open subset of* Ω*. Then, the eigenvalue problem*

$$\Delta\phi + \lambda m(x)\phi = 0 \text{ in } \Omega \tag{3}$$

has a positive principal eigenvalue λ_0*, which is characterized by having a positive eigenfunction* ϕ_0 *if either the boundary conditions for* (3) *are Dirichlet or Robin, or they are Neumann and* $\int_\Omega m(x)dx < 0$.

3. *Suppose* $m(x) > 0$ *on some open subset of* Ω *and the boundary conditions for* (2) *and* (3) *are the same, and either they are Dirichlet or Robin, or they are Neumann and* $\int_\Omega m(x)dx < 0$*. Then* $\sigma_0 > 0$ *if and only if* $D < 1/\lambda_0$.

Lemma 2.1 summarizes a number of results that are stated in Cantrell and Cosner (2003), chapter 2, specifically theorems 2.4, 2.5, and 2.6, where they are discussed in more detail, with references.

Lemma 2.2. *Assume that* Ω *is bounded,* $D > 0$*, and* $\partial\Omega$ *and* $m(x), p(x)$*, are smooth with* $p(x) \geq p_0 > 0$*. The diffusive logistic equation*

$$\frac{\partial u}{\partial t} = D\Delta u + m(x)u - p(x)u^2 \text{ in } \Omega \times (0, \infty) \tag{4}$$

with homogeneous classical (i.e., Neumann, Dirichlet, or Robin) boundary conditions and nonnegative initial data $u(x,0)$ *has a bounded nonnegative global solution. If the principal eigenvalue* σ_0 *in* (2) *(discussed in part 1 of Lemma 2.1) is positive then* (4) *has a unique equilibrium* $u^*(x)$*, which is positive* *on* Ω *and is globally asymptotically stable among solutions with* $u(x,0) > 0$ *on an open subset of* Ω*. If* $\sigma_0 \leq 0$ *then the equilibrium* 0 *is globally asymptotically stable.*

This lemma follows from results in Cantrell and Cosner (2003), section 3.2.

Corollary 2.1. *If the hypotheses of part 3 of Lemma 2.1 are satisfied then* 0 *is globally asymptotically stable among nonnegative solutions of* (4) *if* $D \geq 1/\lambda_0$ *and* u^* *is globally asymptotically stable among positive solutions of* (4) *if* $D < 1/\lambda_0$.

The following is a standard comparison result based on the maximum principle. There are more general results of this type but this one is adequate for our current purposes. Results of this type are discussed in Cantrell and Cosner (2003), section 1.6.7.

Lemma 2.3. *Suppose that the hypotheses of Lemma 2.2 hold and that* u_1, u_2 *are nonnegative functions that satisfy the same homogeneous classical boundary conditions and*

$$\frac{\partial u_1}{\partial t} - D\Delta u_1 - m(x)u_1 + p(x)u_1^2 \leq \frac{\partial u_2}{\partial t} - D\Delta u_2 - m(x)u_2 + p(x)u_2^2 \text{ in } \Omega \times (0,\infty) \tag{5}$$

with $u_1(x,0) \leq u_2(x,0)$ *in* Ω*. Then* $u_1(x,t) \leq u_2(x,t)$ *for* $t > 0$.

Finally, for the system (1), we have the following condition for persistence of both populations:

Lemma 2.4. *The model* (1) *has a global nonnegative solution for any nonnegative initial data. If it admits semitrivial equilibria* $(u^*,0)$ *and* $(0,v^*)$ *and the semitrivial equilibria are both linearly unstable then the system* (1) *is permanent and thus predicts that both populations will persist if their initial densities* $u(x,0)$ *and* $v(x,0)$ *are both positive on open subsets of* Ω.

This lemma follows from results in Cantrell et al. (1993); see also Cantrell and Cosner (2003), chapter 4.

3 | MAIN RESULTS

In this section, we will show that under suitable assumptions on the coefficients model (1) predicts that both populations will persist if there is no harvesting but the second population will decline to extinction if the indirect effect of harvesting on the dispersal of the second species (measured by the product gh in the model) is sufficiently large, even though there is no harvesting of the second species.

Theorem 3.1. *Suppose that in the model* (1) *the local growth rates* $a(x)$ *and* $d(x)$ *are positive on open subsets of* Ω *but* $\int_\Omega d(x)dx < 0$*. Suppose further that the principal eigenvalues of the problems*

$$D_u\Delta\psi + a(x)\psi = \sigma_a\psi \text{ in } \Omega \tag{6}$$

and

$$D_v\Delta\psi + d(x)\psi = \sigma_d\psi \text{ in } \Omega \tag{7}$$

with homogeneous Neumann boundary conditions are both positive, so that the semitrivial equilibria $(u^*,0)$ *and* $(0,v^*)$ *exist for* (1) *when* $h = 0$*. Suppose further that the principal eigenvalues of the problems*

$$D_u\Delta\psi + (a(x) - cv^*)\psi = \tau_a\psi \text{ in } \Omega \tag{8}$$

and

$$D_v \Delta \psi + (d(x) - eu^*)\psi = \tau_d \psi \text{ in } \Omega \tag{9}$$

with homogeneous Neumann boundary conditions are both positive. Then model (1) *predicts persistence of both populations when* $h = 0$ *(no harvesting) but extinction of the second population if* gh *(the strength of the indirect effect of harvesting on the second population) is sufficiently large.*

Proof. If the principal eigenvalues of (6) and (7) are both positive then Lemma 2.2 implies the existence of semitrivial equilibria of (1) when $h = 0$. If the principal eigenvalues of (8) and (9) are both positive then Lemma 2.4 implies the persistence of both populations when $h = 0$. Under the assumptions on $d(x)$, by Lemma 2.1 with $m(x) = d(x)$ the eigenvalue problem (3) has a positive principal eigenvalue $\lambda_0(d(x))$, and if

$$D_v + gh > 1/\lambda_0(d(x)) \tag{10}$$

then the principal eigenvalue σ_0 of

$$(D_v + gh)\Delta\psi + d(x)\psi = \sigma\psi \text{ in } \Omega \tag{11}$$

with homogeneous Neumann boundary conditions is negative. It then follows from Lemma 2.2 that if (10) holds then $w = 0$ is globally asymptotically stable among nonnegative solutions of

$$\frac{\partial w}{\partial t} = (D_v + gh)\Delta u + d(x)w - fw^2 \text{ in } \Omega \times (0, \infty) \tag{12}$$

under homogeneous Neumann boundary conditions. Since we assume $e \geq 0$, for any nonnegative solutions (u, v) of (1) and w of (12) we have

$$\begin{aligned} &\frac{\partial v}{\partial t} - (D_v + gh)\Delta v - d(x)v + fv^2 = -euv \\ &\leq 0 = \frac{\partial w}{\partial t} - (D_v + gh)\Delta w - d(x)w + fw^2 \quad \text{in } \Omega \times (0, \infty). \end{aligned} \tag{13}$$

It then follows from Lemma 2.3 that if we choose w to be a solution of (12) with $w(x, 0) = v(x, 0)$ then $v(x, t) \leq w(x, t)$ on $\Omega \times (0, \infty)$. Since we have $w = 0$ globally asymptotically stable in (12) it follows, by comparison, that $v \to 0$ as $t \to \infty$, implying the extinction of the second species when gh is large enough that (10) holds. ■

3.1 | Remarks

In the case treated by Theorem 3.1, we assumed that the environment Ω has a closed boundary but contains enough regions that are sinks for the second population that the average quality of habitat within Ω (measured by the integral of $d(x)/|\Omega|$) is negative. Analogous results follow by the same arguments in the case of homogeneous Dirichlet or Robin boundary conditions without the assumption that the average habitat quality is negative. In that case the mechanism leading to local extinction in Ω is increased loss of individuals through the boundary of Ω rather than increased dispersal into sink habitats. Since the mechanism leading to the prediction of extinction is trait based and does not involve trophic interactions, the effect of harvesting on the first population does not qualitatively affect the predictions of the model, although if there are interactions between the two species those might have quantitative effects on the levels of harvesting (described by h) and behavioral sensitivity to harvesting (described by g) required to cause extinction. Similarly, trophic interactions with the first species would only have quantitative effects on the results. The reason we assumed that the effect of the first population on the second is neutral or negative ($e \geq 0$) is to demonstrate that even in that situation, where harvesting the first population normally would be neutral or beneficial to the second, it could still result in extinction via a trait-mediated effect. In the case of mutualists, harvesting the first population would be directly harmful to the second, and we wanted to demonstrate that the trait-mediated effects of harvesting the first species could by themselves harm the second without any additional effects arising from species interactions. In fact, in real situations, harvesting one population may have both the indirect trait-mediated effect of increasing dispersal and the direct effects of increasing mortality and decreasing reproduction of other populations (see Grüebler et al., 2015).

In Theorem 3.1, we consider a situation where the overall environment for the second (focal) population has enough sink areas that the spatially averaged population growth rate for the second (focal) population is negative, so that excessive movement can result in extinction without competition or other interspecific effects. A more subtle way in which increased movement in response to harvesting might conceivably have a negative effect on a population might be by shifting the balance of competition. In the classic paper Dockery et al. (1998), it was shown that in the system

$$\begin{aligned}
&\frac{\partial u}{\partial t} = D_u \Delta u + (a(x) - u - v)u,\\
&\frac{\partial v}{\partial t} = D_v \Delta v + (a(x) - u - v)v \quad \text{in } \Omega \times (0, \infty),\\
&\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0, \infty),
\end{aligned} \tag{14}$$

where the competitors are ecologically identical except for diffusion rate, and where $a(x)$ is nonconstant, the slower diffuser excludes the faster diffuser. Suppose that the populations were harvested at an equal rate h, with $0 < a(x) - h$ everywhere so that either population could persist by itself even though it was harvested. If the one population reacts more strongly to harvesting by increasing its diffusion rate by a larger amount, that could shift the balance of competition. Specifically, in a system

$$\begin{aligned}
&\frac{\partial u}{\partial t} = D_u \Delta u + (a(x) - u - v)u - hu,\\
&\frac{\partial v}{\partial t} = (D_v + gh) \Delta v + (a(x) - u - v)v - hv \quad \text{in } \Omega \times (0, \infty),\\
&\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0, \infty),
\end{aligned} \tag{15}$$

with $D_u > D_v$ but with g large enough that $D_u < D_v + gh$, the results of Dockery et al. (1998) imply that the second species would exclude the first if there is no harvesting but the first species would exclude the second with harvesting at level h. The assumption that the two species are ecologically identical is too strong for most ecological situations, although it is plausible in the evolutionary setting in the context of pairwise invasibility analysis in adaptive dynamics as in Dockery et al. (1998). In more general settings, the relationships between diffusion rates and levels of competition and predictions of exclusion or coexistence have been studied in detail in He and Ni (2016). It might be possible to use the results of He and Ni (2016) to analyze the combined direct effects of harvesting and trait-mediated responses to harvesting on nonidentical competitors, but if so it would require another paper for the analysis.

4 | CONCLUSIONS

Model (1) shows that in principle it is possible that a trait-mediated effect of the harvesting of one population on a second population, specifically increased dispersal, could have a detrimental effect on the second population. We assumed that the trait-mediated effect was the only source of negative impact that harvesting the first species has on the second, and that the second is not harvested at all. In our modeling framework, we found that the detrimental effect could be strong enough to cause extinction of the second population, but we assumed the average local population growth rate of the second population was negative. We observed that in certain other special cases where the local population growth rates of both populations are positive it is plausible that a similar effect could occur. These results suggest that trait-mediated effects of harvesting may be significant even for those populations that are not being harvested. Perhaps those should be considered in assessing the effects of harvesting in the context of biological conservation. In our modeling approach, we did not try to study how trait-mediated effects of harvesting might combine with the direct effects of harvesting on population dynamics and species interactions. It would be interesting to study that topic further.

ORCID

C. Cosner http://orcid.org/0000-0001-5194-160X

REFERENCES

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, *80*(2), 385–399.

Cantrell, R. S., & Cosner, C. (1991). The effects spatial heterogeneity in population dynamics. *Journal of Mathematical Biology*, *29*, 315–338.

Cantrell, R. S., & Cosner, C. (2003). *Spatial ecology via reaction-diffusion equations*. Chichester, UK: John Wiley & Sons Ltd.

Cantrell, R. S., Cosner, C. & Hutson, V. (1993). Permanence in ecological systems with spatial heterogeneity, *Proceedings of the Royal Society of Edinburgh*, *123A*, 533–559.

Chakraborty, S., Pal, S. & Bairagi, N. (2012). Predator-prey interaction with harvesting: Mathematical study with biological ramifications. *Applied Mathematical Modelling*, *36*(9), 4044–4059.

Chaudhuri, K. (1986). A bioeconomic model of harvesting a multispecies fishery. *Ecological Modelling*, *32*(4), 267–279.

Ding, W., & Lenhart, S. (2009). Optimal harvesting of a spatially explicit fishery model. *Natural Resource Modeling*, *22*(2), 173–211.

Dockery, J., Hutson, V., Mischaikow, K., & Pernarowski, M. (1998). The evolution of slow dispersal rates: A reaction diffusion model. *Journal of Mathematical Biology*, *37*, 61–83.

Dunn, R. P., Baskett, M. L., & Hovel, K. A. (2017). Interactive effects of predator and prey harvest on ecological resilience of rocky reefs. *Ecological Applications*, *27*(6), 1718–1730.

Grüebler, M. U., Schuler, H., Spaar, R., & Naef-Daenzer, B. (2015). Behavioural response to anthropogenic habitat disturbance: Indirect impact of harvesting on Whinchat populations in Switzerland. *Biological Conservation*, *186*, 52–59.

He, X., & Ni, W.-M. (2016). Global dynamics of the Lotka-Volterra competition-diffusion system: Diffusion and spatial heterogeneity I. *Communications on Pure and Applied Mathematics*, *69*(5), 981–1014.

Joshi, H. R., Herrera, G. E., Lenhart, S., & Neubert, M. G. (2009). Optimal dynamic harvest of a mobile renewable resource. *Natural Resource Modeling*, *22*(2), 322–343.

Kar, T. K. (2006). Modelling and analysis of a harvested prey-predator system incorporating a prey refuge. *Journal of Computational and Applied Mathematics*, *185*(1), 19–33.

Kelly, M., Xing, Y., & Lenhart, S. (2016). Optimal fish harvesting for a population modeled by a nonlinear parabolic partial differential equation. *Natural Resource Modeling*, *29*(1), 36–70.

Peacor, S. D., & Werner, E. E. (2001). The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences USA*, *98*, 3904–3908

Schmitz, O. J., Křivan, V. & Ovadia, O. (2004). Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecology Letters*, *7*, 153–163.

Werner, E. E., & Peacor, S. D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, *84*, 1083–1100.

How to cite this article: Cantrell RS, Cosner C. Effects of harvesting mediated by dispersal traits. *Nat Resour Model*. 2018;e12168. https://doi.org/10.1111/nrm.12168