How predator evolution to lethal and sublethal toxicant effects alters the dynamics of a discrete-time predator-prey model

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Outline

1 Motivation

2 A Discrete-Time Predator-Prey Model

3 Evolutionary Predator-Prey Model with Sublethal Effects

4 Evolutionary Predator-Prey Model with Lethal Effects

5 Numerical Results
- Bistablity of the Lethal Model
- Comparison Between Lethal and Sublethal Model

6 Conclusion

Motivation

- Environmental toxicity is becoming a global concern for the biological population.
- Toxicants, including pesticides, heavy metals, and industrial chemicals disrupt the natural dynamics of ecosystems by interfering with species' survival, reproduction, and behavior.
- Predator-prey systems are highly vulnerable to such disruptions.
- This project analyzes the case of **predator evolution** considering two different toxicant effects.
    (i) **Sublethal effects, where toxicant impacts the fecundity of the predator.**
    (ii) **Lethal effects, where toxicant directly influences the predator's survival in a trait-dependent manner.**

The Main Model: Nonevolutionary Model

Model: A Discrete-time Predator-Prey Model (Ackleh et al., 2019)

$$\begin{aligned} n(t+1) &= \phi(n(t))\,(1 - f(p(t))p(t))\,n(t), \\ p(t+1) &= (s + b(n(t))n(t)f(p(t)))\,p(t), \end{aligned}$$

where

$$\phi(n) = \frac{r_0}{1+mn},\ b(n) = \frac{b_0}{1+\gamma n},\ \text{and } f(p) = \frac{c}{1+cp},$$

- $n(t), p(t)$ are densities of prey & predator population at time t.
- $\phi(n)$ is nonlinear growth rate of prey.
- s is the survival probability (density independent) of the predator.
- $0 \le f(p) \le 1$ is the probability that an individual prey is consumed by an individual predator when p predators are present.

Evolutioanry Model: Sublethal Effects

Model: Sublethal Effects (Ackleh et al., 2025)

$$
\begin{aligned}
n(t+1) &= \phi(n(t))n(t)(1-f(p(t),v)p(t))|_{v=u},\\
p(t+1) &= s_0 p(t) + (1-\epsilon(v))b(v)\bar{b}(n(t))n(t)f(p(t),v)p(t)|_{v=u},\\
u(t+1) &= u(t) + \nu\partial_v \ln[R(n(t),p(t),v]|_{v=u},
\end{aligned}
$$

where

- $R(n,p,v) = s_0 + (1-\epsilon(v))b(v)\bar{b}(n)nf(p,v)$ is the growth rate of a predator individual with trait v.
- $b(v) = b_0 e^{-w_b v^2}$, $\epsilon(v) = \epsilon_0 e^{-w_\epsilon v^2}$, and $f(p,v) = \frac{c(v)}{1+c(v)p}$; $c(v) = c_0 e^{-w_c v^2}$ are the trait-dependent **exponential nonlinearities**.
- In this case, the density dependent term $\bar{b}(n)$ is normalized to be one at zero density, where $\bar{b}(n) = \frac{1}{1+\gamma n}$.

Predator-Free Subsystem (P=0)

$$n(t+1) = \phi(n(t))n(t), \tag{1a}$$
$$u(t+1) = u(t) + \nu h(n, 0, u), \tag{1b}$$

where

$$h(n,0,u) = \frac{2u\left(\epsilon_0\left(w_b + w_c + w_\epsilon\right) - \left(w_b + w_c\right)e^{u^2 w_\epsilon}\right)}{\left(e^{u^2 w_\epsilon} - \epsilon_0\right) + \frac{s_0}{b_0 c_0 n \bar{b}(n)} e^{u^2\left(w_b + w_c + w_\epsilon\right)}}. \tag{2}$$

From equation (1a), we have a positive equilibrium $\bar{n} = \phi^{-1}(1) = \frac{r_0 - 1}{m}$, which exists when $r_0 > 1$ and is globally asymptotically stable. Plugging $\bar{n}$ in equation (1b) yields

$$u(t+1) = u(t) + \nu h(\bar{n}, 0, u(t)). \tag{3}$$

Dynamics of the Predator-Free Subsystem

Lemma

Assume $\nu < \frac{1}{2(w_b+w_c)}$ *and* $r_0 > 1$.

(a) *There is a unique positive equilibrium* $u^\diamond := \frac{\sqrt{\ln\left(\frac{\epsilon_0(w_b+w_c+w_\epsilon)}{w_b+w_c}\right)}}{\sqrt{w_\epsilon}}$ *for* (3) *if and only if* $\epsilon_0 > \frac{w_b+w_c}{w_b+w_c+w_\epsilon}$.

(b) *If* $\epsilon_0 < \frac{w_b+w_c}{w_b+w_c+w_\epsilon}$, *then equation* (3) *has one equilibrium,* $u = 0$, *which is globally asymptotically stable.*

(c) *Assume* $\epsilon_0 > \frac{w_b+w_c}{w_b+w_c+w_\epsilon}$. *The equilibrium* $u = 0$ *is unstable and the equilibrium* $u^\diamond$ *is globally asymptotically stable.*

Existence and Stability of Boundary Equilibria

Theorem

Assume ν is sufficiently small

(a) *Boundary equilibria with zero trait value:*

  (i) *The predator-free equilibrium* $(\bar{n}, 0, 0)$, *where* $\bar{n} := \phi^{-1}(1) = \frac{r_0 - 1}{m}$ *exists if* $r_0 > 1$ *and is globally asymptotically stable if* $\epsilon_0 < \frac{w_b + w_c}{w_b + w_c + w_\epsilon}$ *and* $s_0 + \bar{b}(\bar{n})\bar{n} b_0 c_0 (1 - \epsilon_0) < 1$.

  (ii) *The equilibrium* $(n^*, p^*, 0)$ *with* $n^*, p^* > 0$ *exists if* $r_0 > 1$ *and* $s_0 + (1 - \epsilon_0)\bar{b}(\bar{n})\bar{n} b_0 c_0 > 1$. *Moreover,* $(n^*, p^*, 0)$ *is locally asymptotically stable if* $\epsilon_0 < \frac{w_b + w_c(1 - p^* f(p^*, 0))}{w_b + w_\epsilon + w_c(1 - p^* f(p^*, 0))}$.

(b) *Boundary equilibrium with positive trait value:*

  (i) *The predator-free equilibrium* $(\bar{n}, 0, u^\diamond)$ *exists if* $r_0 > 1$ *and* $\epsilon_0 > \frac{w_b + w_c}{w_b + w_c + w_\epsilon}$ *and is locally asymptotically stable if* $s_0 + (1 - \epsilon(u^\diamond)) b(u^\diamond) \bar{b}(\bar{n}) \bar{n} c(u^\diamond) < 1$.

Persistence Analysis

Theorem

Assume $\nu < \frac{1}{2(w_b+w_c)}$. *Suppose that*

$$\epsilon_0 > \frac{w_b + w_c}{w_b + w_c + w_\epsilon}, \quad r_0 > 1, \quad \textit{and} \quad s_0+(1-\epsilon(u^\diamond))b(u^\diamond)\bar{b}(\bar{n})\bar{n}c(u^\diamond) > 1.$$

Then sublethal model is uniformly persistent, i.e., there exists an $\epsilon > 0$ *such that*

$$\min\left\{\liminf_{t\to\infty} n(t), \liminf_{t\to\infty} p(t), \liminf_{t\to\infty} u(t)\right\} > \epsilon$$

for any initial condition with $n(0), p(0), u(0) > 0$.

Interior Dynamics

Theorem

Let $(\hat{n}, \hat{p}, \hat{u})$ *be an interior equilibrium of the sublethal model. If* $\frac{\partial}{\partial u}\left(\left.\frac{\partial \ln R}{\partial v}\right|_{v=u}\right)\Big|_{(n,p,u)=(\hat{n},\hat{p},\hat{u})} < 0$, *then* $(\hat{n}, \hat{p}, \hat{u})$ *is locally asymptotically stable for sufficiently small* ν.

Evolutionary Model: Lethal Effects

Model: Lethal Effects (Ackleh et al., 2025)

$$\begin{aligned} n(t+1) &= \phi(n(t))n(t)(1-f(p(t),v)p(t))|_{v=u}, \\ p(t+1) &= s(v)(1-\epsilon(v))p(t) + b(n(t))n(t)f(p(t),v)p(t)|_{v=u}, \\ u(t+1) &= u(t) + \nu\partial_v \ln[R(n(t),p(t),v]|_{v=u}, \end{aligned}$$

where

- v is the predator's individual trait, and u is the mean trait of predators.
- $R(n,p,v) = s(v)(1-\epsilon(v)) + b(n)nf(p,v)$ is the growth rate of a predator individual with trait v.
- $s(v) = s_0 e^{-w_s v^2}$, $\epsilon(v) = \epsilon_0 e^{-w_\epsilon v^2}$, and $f(p,v) = \frac{c(v)}{1+c(v)p}$; $c(v) = c_0 e^{-w_c v^2}$ are the trait-dependent **exponential nonlinearities**.

Dynamics of the Pure Trait Equation

$$u(t+1) = u(t) + \nu \left[\frac{s'(u)}{s(u)} - \frac{\epsilon'(u)}{1-\epsilon(u)} \right] \quad (when \quad n = 0)$$

Lemma

Denote $\bar{u} := \sqrt{\frac{\ln\left(\frac{(w_s+w_\epsilon)\epsilon_0}{w_s}\right)}{w_\epsilon}}$ *and assume* $\nu < \frac{1}{2w_s}$.

(a) *If* $\epsilon_0 < \frac{w_s}{(w_s+w_\epsilon)}$, *then the pure trait equation has a one equilibrium* $u = 0$, *which is globally asymptotically stable.*

(b) *Assume* $\epsilon_0 > \frac{w_s}{(w_s+w_\epsilon)}$ *and* ν *is sufficiently small. Then the equilibrium* $u = 0$ *is unstable and the equilibrium* $\bar{u}$ *is globally asymptotically stable for* $\nu < \nu^*$.

Boundary Equilibria with Zero Trait Value

Denote $I(u) := s(u)(1-\epsilon(u)) + b(\bar{n})\bar{n}c(u)$ and $\tilde{\epsilon}_0(\bar{n}) := \frac{\bar{n}b(\bar{n})c_0 w_c + s_0 w_s}{(w_s+w_\epsilon)s_0}$.

Theorem

Assume ν is sufficiently small ($\nu < \frac{1}{2w_s}$).

(a) *(Boundary equilibria with zero trait value)*

  (i) *The extinction equilibrium $(0,0,0)$ is globally asymptotically stable if $r_0 < 1$ and $\epsilon_0 < \frac{w_s}{w_\epsilon + w_s}$.*

  (ii) *The predator-free equilibrium $(\bar{n},0,0)$, where $\bar{n} := \phi^{-1}(1)$, exists if $r_0 > 1$ and is locally asymptotically stable if $\epsilon_0 < \min\{\tilde{\epsilon}_0(\bar{n}), 1\}$ and $I(0) < 1$. If, in addition, $\epsilon_0 < \frac{w_s}{w_s+w_\epsilon}$ and $w_s + w_\epsilon \geq w_c$, then $(\bar{n},0,0)$ is globally asymptotically stable.*

  (iii) *A unique equilibrium of the form $(n^*, p^*, 0)$ with $n^*, p^* > 0$ exists if $r_0 > 1$ and $I(0) > 1$. Moreover, $(n^*, p^*, 0)$ is locally asymptotically stable if $\epsilon_0 < \min\left\{\frac{w_c \frac{n^* b(n^*) c_0}{s_0(1+p^* c_0)^2} + w_s}{w_s + w_\epsilon}, 1\right\}$.*

Boundary Equilibria with Positive Trait Value

Denote $C(u) := \left(\frac{\partial}{\partial u} \left(\frac{\partial \ln R}{\partial v} \Big|_{v=u} \right) \right) \Big|_{(\bar{n},0,u)}$ and $A := \frac{\bar{n} b(\bar{n}) c_0 w_c (w_c - (w_s + w_\epsilon))}{s_0 w_s w_\epsilon}$.

Theorem (Continued)

(b) *(Boundary equilibria with positive trait value)*

- (i) *The extinction equilibrium* $(0, 0, \bar{u})$ *exists if* $\epsilon_0 > \frac{w_s}{w_s + w_\epsilon}$*, and is globally asymptotically stable if* $r_0 < 1$ *.*
- (ii) *A unique predator-free equilibrium of the form* $(\bar{n}, 0, \tilde{u})$ *exists if* $r_0 > 1$ *and* $\epsilon_0 > \tilde{\epsilon}_0(\bar{n})$*, and is locally asymptotically stable if* $-2 < \nu C(\tilde{u}) < 0$ *and* $I(\tilde{u}) < 1$*.*
- (iii) *A unique predator-free equilibrium of the form* $(\bar{n}, 0, \tilde{u})$ *exists if* $r_0 > 1$*,* $\epsilon_0 = \tilde{\epsilon}_0(\bar{n}) < 1$*,* $w_s + w_\epsilon < w_c$*, and* $A > 1$*. Furthermore, it is locally asymptotically stable if* $-2 < \nu C(\tilde{u}) < 0$ *and* $I(\tilde{u}) < 1$*.*
- (iv) *If* $\epsilon_0 < \tilde{\epsilon}_0(\bar{n})$ *and* $r_0 > 1$*. Then two predator-free equilibria of the form* $(\bar{n}, 0, \tilde{u}_1)$ *and* $(\bar{n}, 0, \tilde{u}_2)$ *exist with* $\tilde{u}_1 < \tilde{u}_2$*, where the equilibrium* $(\bar{n}, 0, \tilde{u}_1)$ *is unstable and the equilibrium* $(\bar{n}, 0, \tilde{u}_2)$ *is locally asymptotically stable if* $-2 < \nu C(\tilde{u}_2) < 0$ *and* $I(\tilde{u}_2) < 1$*.*

Persistence Analysis

Theorem

Assume $\nu < \frac{1}{2w_s}$ *and* $r_0 > 1$*. Suppose that*

$$\epsilon_0 > \tilde{\epsilon}_0(\bar{n}) \quad \text{and} \quad s(\tilde{u})\left(1 - \epsilon(\tilde{u})\right) + b(\bar{n})\bar{n}c(\tilde{u}) > 1.$$

Then the lethal model is uniformly persistent, i.e., there exists an $\epsilon > 0$ *such that*

$$\min\{\liminf_{t\to\infty} n(t), \liminf_{t\to\infty} p(t), \liminf_{t\to\infty} u(t)\} > \epsilon$$

for any initial condition with $n(0), p(0), u(0) > 0$*.*

Theorem

Suppose the assumptions of the above theorem hold. Then there exists at least one interior equilibrium $(\hat{n}, \hat{p}, \hat{u})$ *of the lethal model. If* $\frac{\partial}{\partial u}\left(\frac{\partial \ln R}{\partial v}|_{v=u}\right)|_{(n,p,u)=(\hat{n},\hat{p},\hat{u})} < 0$*, then there exists a positive number* δ *such that* $(\hat{n}, \hat{p}, \hat{u})$ *is locally asymptotically stable for* $\nu < \delta$*.*

Bistability of the Predator-Free Trait Equation

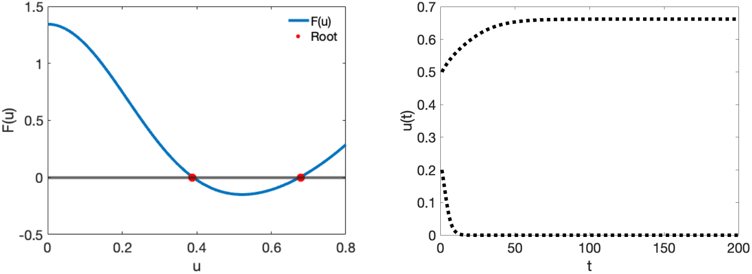

Figure: The left diagram shows the existence of two positive equilibria ($u = 0.3905$ and $u = 0.6759$) of a trait equation, while the right diagram exhibits the local stability of the trivial ($u = 0$) equilibrium and the equilibrium has a higher positive value ($u = 0.6759$).

Bistability Depending on the Initial Conditions

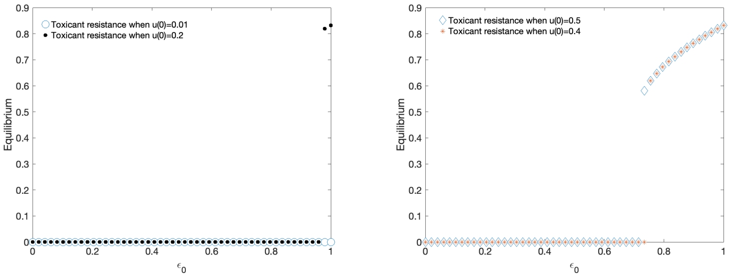

Figure: Both figures exhibit the local stability of the equilibria u=0 and u=0.6759 under both low and high initial trait conditions, but at different toxicant levels: lower initial conditions ensure the stability of the positive equilibrium in the higher toxic environment, while the scenario may reverse for the higher initial conditions of the initial trait conditons.

Impact of Bistability on the Lethal Model

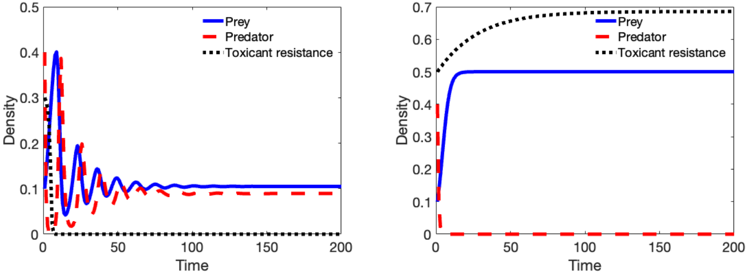

Figure: The time series solutions of the lethal model are presented for two different trait initial conditions (a) $u(0) = 0.3$ and (b) $u(0) = 0.5$.

Notice that here we observe that predator survival is dependent on the initial trait value, with smaller initial trait values resulting in predator survival, but larger initial values resulting in predator extinction despite the evolution of toxicant resistance.

Lethal and Sublethal Effects Comparison

Here we choose the predator reproduction $b_0 = 3$ and $s_0 = 0.9$.

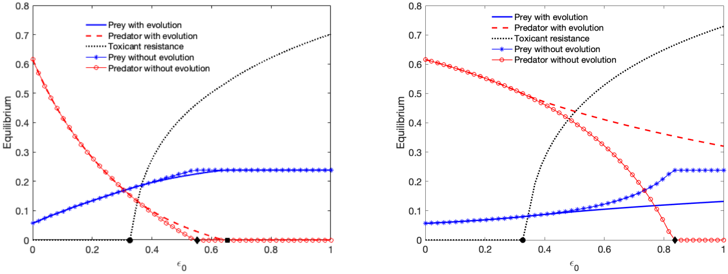

Figure: Shown are the bifurcation diagrams for the equilibria of the prey and predator, both with and without evolution, and the mean trait for the bifurcation parameter $0 \le \epsilon_0 \le 1$ when toxicant effects are lethal (left) or sublethal (right).

Lethal and Sublethal Effects Comparison (continued)

Here we choose $b_0 = 5$ and $s_0 = 0.9$.

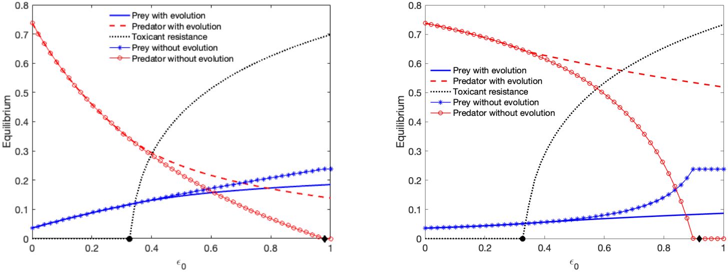

Figure: Shown are the bifurcation diagrams for the equilibria of the prey and predator, both with and without evolution, and the mean trait for the bifurcation parameter $0 \leq \epsilon_0 \leq 1$ when toxicant effects are lethal (left) or sublethal (right).

Lethal and Sublethal Effects Comparison (continued)

Here we choose $b_0 = 5$and $s_0 = 0.5$.

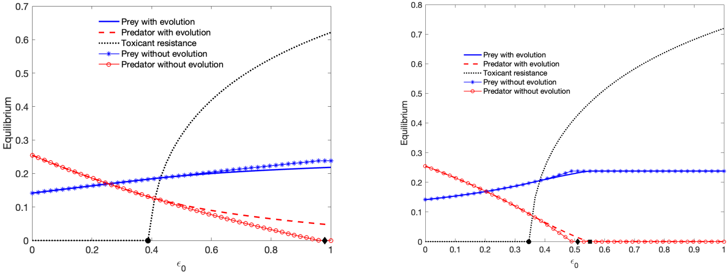

Figure: Shown are the bifurcation diagrams for the equilibria of the prey and predator, both with and without evolution, and the mean trait for the bifurcation parameter $0 \leq \epsilon_0 \leq 1$ when toxicant effects are lethal (left) or sublethal (right).

Key Outcomes

- In the lethal effects scenario, toxicant resistance can evolve even below the threshold level, leading to bistability with two predator-free equilibria, $u = 0$ and a positive value, both locally stable. Predator survival then depends on the initial trait: low values lead to survival, while high values result in extinction despite resistance evolution.
- In the non-evolutionary scenario, when fecundity is lower, the predator goes extinct at a lower toxicant level in the lethal case compared to the sublethal case. In contrast, when fecundity is higher, this scenario is reversed. Thus, lethal effects are greater when fecundity is low, but sublethal effects become greater when fecundity is high.
- Compared with lethal and sublethal models, the toxicant threshold level is the same for all scenarios from which the predator begins to evolve in response to toxicants.
- When predator survival is higher, sublethal effects produce higher predator densities. However, the scenario is reversed when predator survival is low.
- Finally, in all scenarios, evolution produces higher predator densities in the toxic environment.

Future Work

- **Frequency-dependent evolution:** Frequency-dependent evolution occurs when an individual's fitness is impacted by the traits of others in the population.
- **Evolution in structured predator-prey models:** The impact of evolution in either the predator or prey when the prey is structured, or the predator is structured.

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Thanks for your attention!