



# Classification of global dynamics of a periodic diffusive consumer-resource model

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## Abstract

In [40], a biological experiment with yeast was successfully designed to verify a seemingly counterintuitive mathematical phenomenon: in a heterogeneous environment, dispersal can allow a species' total population to exceed its carrying capacity. A key finding of [40] highlights the critical role of resource dynamics in shaping population dynamics. To shed light on this striking biological insight, a novel consumer-resource model was proposed in [40]. This paper aims to analyze this consumer-resource system, which incorporates resource decay and consumer loss, under conditions where the resource input rate may exhibit spatial heterogeneity and temporal periodicity. We characterize the persistence or extinction of both consumer and resource populations based on their dispersal rates and a relaxation-time parameter. Additionally, we derive the asymptotic profiles of positive periodic solutions as the resource dispersal rate becomes sufficiently small or large. Our results reveal several notable insights: (a) resource decay, even when slight, acts as a decisive factor preventing unlimited growth of resource abundance; (b) the consumer mortality rate is a key determinant of the consumer population's persistence or extinction; (c) when the consumer mortality rate is moderate, a temporally homogeneous resource input may be more advantageous for the consumer population than a temporally periodic one. We employ a variety of methods to establish our results, including the parabolic comparison principle, the upper-lower solution method for mixed quasi-monotone systems, the theory of asymptotically periodic systems, the uniform persistence theory for infinite-dimensional dynamical systems, and the principal eigenvalue theory.

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## 1 Introduction

Despite the extensive theoretical studies on diffusive logistic models (cf. [2, 4, 5, 7, 19, 20, 23, 29, 31, 36] and references therein), experimental validations of these theoretical findings are scarce. Notable exceptions include recent works by Zhang et al. [40] and Zhang et al. [41]. One central issue concerned in the experiment by Zhang et al. [40] is that the available resources are influenced by the feedback from the exploitation by consumers. Consequently the population parameters such as the carrying capacity and growth rate emerge from the interaction of consumers with exploited renewable resources. To investigate the effect of such feedback on the consumer and resource population dynamics, Zhang et al. [40] proposed the following consumer-resource model

$$\begin{cases} Z_t = \mu \Delta Z + Z \left( \frac{r(x)N}{k+N} - c(x) - g(x)Z \right), & x \in \Omega, t > 0, \\ N_t = N_R(x) - \sigma(x)N - \frac{r(x)NZ}{\gamma(k+N)}, & x \in \Omega, t > 0, \\ \partial_{\vec{n}} Z = 0, & x \in \partial\Omega, t > 0, \\ Z(x, 0) = Z_I(x) \geq, \neq 0, N(x, 0) = N_I(x) \geq 0, & x \in \Omega, \end{cases} \quad (1.1)$$

where  $Z(x, t)$  and  $N(x, t)$  denote the densities of the consumer population and the renewable resource (nutrient) at position  $x$  and time  $t$ , respectively,  $\Omega \subset \mathbb{R}^m$  ( $m \geq 1$ ) is a bounded domain with smooth boundary. Here  $\Delta = \sum_{i=1}^m \frac{\partial^2}{\partial x_i^2}$  is the usual Laplace operator and the constant  $\mu > 0$  denotes the dispersal rate of the consumer population;  $r$ ,  $c$  and  $g$  represent, respectively, the growth rate, mortality rate and loss rate due to the self-regulation of the consumer population; the function  $N_R$  stands for the resource input,  $\sigma$  is the decay/loss rate of resource from the system,  $k$  is the half-saturation constant,  $\gamma$  is the yield rate from the resource to the consumer population and  $\vec{n}(x)$  is the outward unit normal vector at  $x \in \partial\Omega$ . The global dynamics of (1.1) have been studied in [9, 11, 12, 38] for  $c = \sigma \equiv 0$ . When  $r$ ,  $g$  and  $N_R$  are spatially homogeneous (i.e. constant), He et al. [9] first showed that the large (resp. small) yield rate leads to the global stability of the constant steady state with unlimited (resp. limited) resource. When  $r$ ,  $g$  and  $N_R$  are spatially heterogeneous, He et al. [9] showed that there is a positive steady state with the partially limited resource in space for intermediate yield rate, which can not occur in the spatially homogeneous environment, and the resource-unlimited steady state is globally stable for large yield rate; He et al. [11] and Yao et al. [38] further obtained the global stability of resource-limited steady state for small yield rate; He et al. [12] studied the joint effects of the resource, the loss rate and the dispersal rate on total consumer populations for small yield rate. It was pointed out in [9] that the distinction between spatial homogeneity and heterogeneity for the intermediate yield rate is relevant to an experiment result of Zhang et al. [40] that spatially homogeneous resource distribution could produce higher population abundance than the spatially heterogeneous one. In addition to the afore-mentioned works, there are some results (cf. [33–35, 37]) concerning the dynamics of patched consumer-resource models which can be regarded as the discrete version of (1.1) in space.

As mentioned above, the current analytical results for the consumer-resource model (1.1) appear to be available only in the simplified case  $c = \sigma = 0$  (i.e. zero mortality for both consumer and resource populations). One purpose of this paper is to consider model (1.1)

with  $c > 0$  and  $\sigma > 0$ , investigating how the mortality rates of both consumer and resource impact the persistence or extinction of the consumer population. Moreover, we shall consider several other pertinent factors. These include the temporal variability of the resource and the resource dispersal. A notable example of this is the renowned laboratory experiment by Zhang et al. [40] with yeast diffusing in a heterogeneous environment containing exploitable and renewable nutrients (resources), where the nutrient was replenished at regular intervals (precisely every 24 hours). In the natural environment, temporal variability arising from climate change and anthropogenic activities can have profound implications for ecosystems. For example, it can change the environmental carrying capacity (cf. [28]) or affect the temporal average population size (cf. [39]). This is because the distribution of resources is significantly influenced by climate change and human activities. Another crucial factor that merits our attention is resource dispersal resulting from the non-uniform distribution of resources. In general, biological dispersal can be a strategy boosting population abundance in a single-species community [19, 40], or enhancing species fitness in a heterogeneous landscape [4, 6].

To take into account the factors mentioned above for the consumer-resource dynamics, we incorporate the resource dispersal and resource input periodicity into (1.1) to consider the following periodic diffusive consumer-resource model

$$\begin{cases} \tau Z_t = \mu \Delta Z + Z \left( \frac{rN}{k + N} - c - gZ \right), & x \in \Omega, t > 0, \\ N_t = d \Delta N + N_R(x, t) - \sigma N - \frac{rNZ}{\gamma(k + N)}, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} Z = \partial_{\bar{n}} N = 0, & x \in \partial\Omega, t > 0, \\ Z(x, 0) = Z_I(x) \geq, \neq 0, N(x, 0) = N_I(x) \geq 0, & x \in \Omega, \end{cases} \quad (1.2)$$

where  $\tau$  is the relaxation time representing the characteristic time for the consumer population to reach an equilibrium condition after a disturbance,  $\mu$  and  $d$  denote the dispersal rates of the consumer and the resource, respectively, the input rate  $N_R(x, t)$  is time-periodic with period  $\omega > 0$ , and all other variables and parameters have the same biological meanings as those in (1.1).

All parameters  $\tau, \mu, d, r, k, c, g, \sigma, \gamma$  are assumed to be nonnegative constants in this paper. Denote

$$C_{\omega}^{k,l}(\bar{\Omega} \times \mathbb{R}_+) = \{ \phi \in C^{k,l}(\bar{\Omega} \times \mathbb{R}_+) | \phi(x, t) = \phi(x, t + \omega), \forall (x, t) \in \bar{\Omega} \times \mathbb{R}_+ \},$$

where  $k, l \geq 0, \mathbb{R}_+ := [0, \infty)$  and  $\omega$  is a positive constant. The resource input rate function  $N_R(x, t)$  satisfies the following basic hypotheses:

- (H1)  $N_R(x, t)$  is spatially heterogeneous and strictly positive on  $\bar{\Omega} \times \mathbb{R}_+$ , and  $N_R(x, t) \in C_{\omega}^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R}_+)$  with  $\alpha \in (0, 1)$ .

In this paper, we primarily address the case that  $N_R$  is spatially heterogeneous, while our results remain valid for spatially homogeneous  $N_R$  with simpler conclusions (see Remark 1.4). Our first result concerns the global well-posedness and asymptotic behavior of solutions to (1.2) with  $\sigma, c, d \geq 0$ . To put our result into perspective, let us first recall a result of [9], which shows that model (1.2) with temporally homogeneous input  $N_R$  and  $\sigma = c = d = 0$  may lead to unlimited resource, namely  $N \rightarrow \infty$  uniformly as  $t \rightarrow \infty$  for large yield rate  $\gamma$ . In contrast, here we show the resource will be limited uniformly in time for all  $c, d \geq 0$  as long as  $\sigma > 0$ , as stated in the following theorem.

**Theorem 1.1** Assume that **(H1)** holds. Let  $\sigma, c, d \geq 0$  and all other parameters be positive. Then for any  $Z_I, N_I \in C(\overline{\Omega})$ , system (1.2) has a unique classical solution  $(Z, N)$  on  $\overline{\Omega} \times [0, \infty)$  satisfying

$$0 < Z \leq \rho_1 := \max \left\{ \max_{\overline{\Omega}} Z_I(x), \frac{r - c}{g} \right\} \text{ and } N > 0, \forall x \in \overline{\Omega}, t > 0. \tag{1.3}$$

Moreover, the following conclusions hold true:

- (i) If  $\sigma > 0$ , then  $0 < N \leq \rho_2 := \max \left\{ \max_{\overline{\Omega}} N_I(x), \frac{\max_{\overline{\Omega} \times [0, \omega]} N_R(x, t)}{\sigma} \right\}$  for  $x \in \overline{\Omega}, t > 0$ .
- (ii) If  $\sigma = 0$ , then

$$(Z, N) \rightarrow \begin{cases} (\frac{r-c}{g}, \infty) & \text{if } 0 \leq c < r \text{ and } \gamma > \gamma_0 := \frac{r(r-c)}{g \min_{\overline{\Omega} \times [0, \omega]} N_R}, \\ (0, \infty) & \text{if } c \geq r, \end{cases}$$

uniformly as  $t \rightarrow \infty$ .

Theorem 1.1 demonstrates that the resource decay (i.e.  $\sigma > 0$ ) can prevent the infinite-time blow-up of the resource (i.e., resource overabundance), whereas the resource dispersal fails to achieve this (for more detailed biological implications, refer to Remark 1.3-(3)). Nevertheless, the long-time behavior of the solution remains unknown. Hence, the second goal of this paper is to ascertain the global dynamics (persistence and extinction) of (1.2). It is well-known that the global dynamics of monotone dynamical systems can be derived from their local dynamics via monotone semi-flow theory [13, 30]; consequently, they can be fully characterized by leveraging principal eigenvalue theory. This approach is exemplified by competition systems in temporally homogeneous environments [10, 19] or temporally periodic environments [1, 14, 16]. However, this theoretical framework can not be applied to the non-monotone consumer-resource system (1.2) considered in the present study. The existing literature on the global dynamics of non-monotone time-periodic reaction-diffusion systems is rather scarce except for some notable works [18, 26] on the SIS epidemic models. Peng and Zhao [26] derived persistence and extinction results for certain specific classes of disease transmission and recovery rates, while Liu and Lou [18] extended these findings to more general transmission and recovery rates by introducing innovative contributions to the principal eigenvalue theory for linear time-periodic operators. It is worth mentioning that the analysis of [18] heavily relies on the distinctive structure of SIS epidemic models where the semi-trivial periodic solution is a constant. As a result, the coefficients of the linearized time-periodic parabolic eigenvalue problem of the SIS epidemic models are independent of the period. This is in contrast to the consumer-resource model (1.2), where the semi-trivial periodic solution is non-constant. This essential difference inspires us to leverage the relaxation time  $\tau$  to classify the persistence and extinction dynamics of (1.2), thereby enhancing our understanding of the complex behavior underlying the non-monotone consumer-resource system (1.2).

To state our results, we introduce some terminologies and notation. Clearly, (1.2) may have the following two classes of nonnegative periodic solutions when  $N_R(x, t)$  is temporally periodic with period  $\omega > 0$ :

- Semi-trivial  $\omega$ -periodic solution  $(0, \theta_d)$ ;
- Positive  $\omega$ -periodic solution  $(Z_*, N_*)$  with  $Z_*, N_* > 0$ .

Here  $\theta_d \in C_\omega^{2+\alpha, 1+\alpha/2}(\overline{\Omega} \times \mathbb{R}_+)$  denotes the unique positive  $\omega$ -periodic solution of the following periodic-parabolic equation

$$\begin{cases} \theta_t = d\Delta\theta + N_R(x, t) - \sigma\theta, & x \in \Omega, t > 0, \\ \partial_{\overline{n}}\theta = 0, & x \in \partial\Omega, t > 0, \\ \theta(x, t + \omega) = \theta(x, t), & x \in \overline{\Omega}, t \geq 0, \end{cases} \tag{1.4}$$

and  $(Z_*, N_*)$  satisfies

$$\begin{cases} \tau Z_t = \mu\Delta Z + Z \left( \frac{rN}{k+N} - c - gZ \right), & x \in \Omega, t > 0, \\ N_t = d\Delta N + N_R(x, t) - \sigma N - \frac{rNZ}{\gamma(k+N)}, & x \in \Omega, t > 0, \\ \partial_{\overline{n}}Z = \partial_{\overline{n}}N = 0, & x \in \partial\Omega, t > 0, \\ Z(x, t + \omega) = Z(x, t), N(x, t + \omega) = N(x, t), & x \in \overline{\Omega}, t \geq 0. \end{cases} \tag{1.5}$$

The existence and uniqueness of solutions to (1.4) have been obtained in [22, Proposition 4.4.8]. We say that  $(0, \theta_d)$  is *globally asymptotically stable* if the solution  $(Z, N)$  of (1.2) satisfies

$$\lim_{t \rightarrow \infty} \|(Z(\cdot, t), N(\cdot, t)) - (0, \theta_d(\cdot, t))\|_{[C(\overline{\Omega})]^2} = 0.$$

System (1.2) is said to be *uniformly persistent* if there is a constant  $\epsilon > 0$  so that the solution  $(Z, N)$  of (1.2) satisfies

$$\liminf_{t \rightarrow \infty} Z(x, t) \geq \epsilon \quad \text{and} \quad \liminf_{t \rightarrow \infty} N(x, t) \geq \epsilon \quad \text{uniformly on } \overline{\Omega}.$$

Our second result is concerned with the dynamics of (1.2) with temporally heterogeneous input  $N_R$ . Inspired by an idea of Liu and Lou [18], we define the following quantities

$$\begin{aligned} \ell_1 &:= \frac{1}{\omega|\Omega|} \int_\Omega \int_0^\omega \beta_d(x, t) dt dx, \quad \ell_2 := \max_{x \in \overline{\Omega}} \frac{1}{\omega} \int_0^\omega \beta_d(x, t) dt, \\ \ell_3 &:= \max_{\tilde{x} \in \mathcal{X}} \frac{1}{\omega} \int_0^\omega \beta_d(\tilde{x}(t), t) dt, \end{aligned} \tag{1.6}$$

where

$$\beta_d(x, t) := \frac{r\theta_d(x, t)}{k + \theta_d(x, t)}$$

and  $\mathcal{X} := \{\tilde{x} \in C(\mathbb{R}_+; \overline{\Omega}) | \tilde{x}(t) = \tilde{x}(t + \omega)\}$ . Here  $C(\mathbb{R}_+; \overline{\Omega})$  is the set of all continuous mappings from  $\mathbb{R}_+$  to  $\overline{\Omega} \subset \mathbb{R}^m (m \geq 1)$ . One can readily verify that  $\ell_1 \leq \ell_2 \leq \ell_3$ , where  $\ell_1 = \ell_2$  if and only if  $\int_0^\omega \beta_d(x, t) dt$  is independent of  $x$ , and  $\ell_2 = \ell_3$  if and only if  $\int_0^\omega \beta_d(\tilde{x}(t), t) dt$  reaches its maximum at  $\tilde{x}(t) \equiv x_1 \in \mathcal{X}$  for some point  $x_1 \in \overline{\Omega}$ . Since  $\theta_d$  is the  $\omega$ -periodic solution of (1.4) describing the resource dynamics in the absence of consumption,  $\beta_d$  is the optimal spatiotemporal growth rate of the consumer. Then  $\ell_1$  can be interpreted as the averaged optimal spatiotemporal growth rate across the entire habitat and full resource cycle;  $\ell_2$  denotes the spatial maximum of temporally averaged optimal growth rate;  $\ell_3$  is the maximum of temporally averaged optimal growth rate along all moving pathways followed by the resource.

Noticing that the consumer population will become extinct when  $(0, \theta_d)$  is globally asymptotically stable, we define the persistence region

$$\Lambda_p := \{(\mu, \tau) \in (0, \infty)^2 | \text{system (1.2) is uniformly persistent}\} \tag{1.7}$$

and the extinction region

$$\Lambda_e := \{(\mu, \tau) \in (0, \infty)^2 \mid (0, \theta_d) \text{ is globally asymptotically stable}\} \tag{1.8}$$

in terms of  $\mu$  and  $\tau$ . Then we have the following results.

**Theorem 1.2** *Assume that (H1) holds. Let  $c \geq 0$  and all other parameters be positive. By fixing all parameters except  $\mu$  and  $\tau$ , the following assertions hold.*

- (i) *If  $0 \leq c \leq \ell_1$ , then  $\Lambda_p = (0, \infty)^2$ .*
- (ii) *If  $\ell_1 < c < \ell_2$ , then there are two constants  $\mu_*, \mu^*$  with  $\mu^* \geq \mu_* > 0$  and a unique continuous function  $\tilde{\tau} : (\mu_*, \mu^*) \rightarrow [0, \infty)$  satisfying  $\tilde{\tau}(\mu) > 0$  for all  $\mu \in (\mu_*, \mu^*)$ ,  $\tilde{\tau}(\mu^*) = 0$ ,  $\lim_{\mu \rightarrow \mu_*} \tilde{\tau}(\mu) = \infty$ , such that*

$$\Lambda_p = [(0, \mu_*) \times (0, \infty)] \cup [(\mu_*, \mu^*) \times (0, \tilde{\tau}(\mu))] \text{ and } \Lambda_e = (0, \infty)^2 \setminus \Lambda_p.$$

*In particular, if  $\beta_d - \frac{1}{\omega} \int_0^\omega \beta_d dt$  is independent of  $x \in \Omega$ , then  $\mu_* = \mu^*$ ,  $\Lambda_p = (0, \mu^*) \times (0, \infty)$  and  $\Lambda_e = [\mu^*, \infty) \times (0, \infty)$ .*

- (iii) *If  $\ell_2 < c < \ell_3$ , then there is a unique continuous function  $\bar{\tau} : (0, \mu^*) \rightarrow [0, \infty)$  satisfying  $\bar{\tau}(\mu) > 0$  for  $\mu \in (0, \mu^*)$ ,  $\bar{\tau}(\mu^*) = 0$  and  $\lim_{\mu \rightarrow 0} \bar{\tau}(\mu) = 0$ , so that*

$$\Lambda_p = (0, \mu^*) \times (0, \bar{\tau}(\mu)) \text{ and } \Lambda_e = (0, \infty)^2 \setminus \Lambda_p.$$

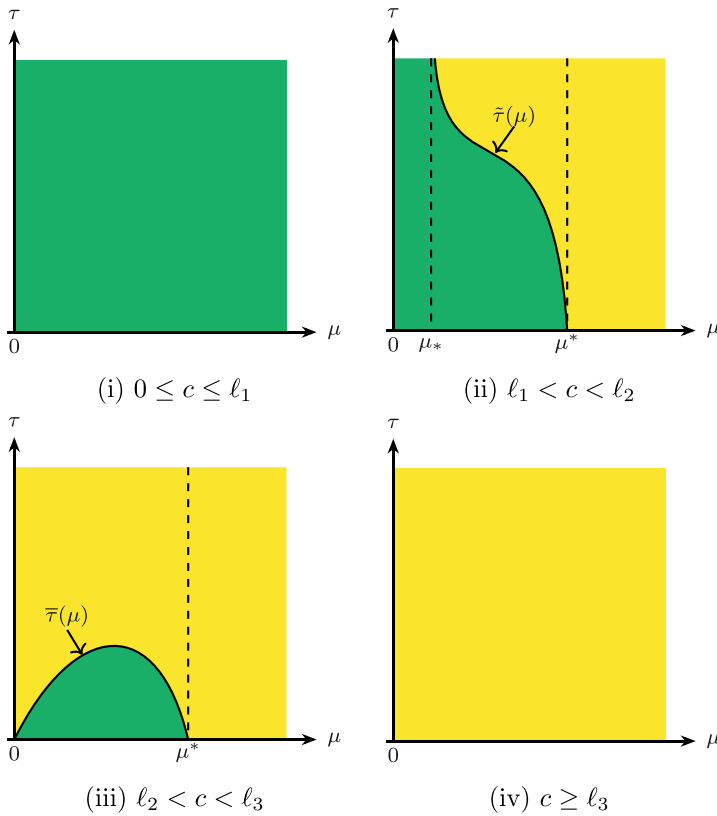
- (iv) *If  $c \geq \ell_3$ , then  $\Lambda_e = (0, \infty)^2$ .*

Moreover, system (1.2) admits a positive  $\omega$ -periodic solution if it is uniformly persistent.

**Remark 1.1** Theorem 1.2, as illustrated in Figure 1, classifies the persistence and extinction dynamics in terms of  $(\mu, \tau)$ . We give some further remarks on Theorem 1.2 and Figure 1.

- (i) When  $N_R$  is temporally homogeneous, we have  $\beta_d - \frac{1}{\omega} \int_0^\omega \beta_d dt = 0$  and  $\ell_1 < \ell_2 = \ell_3$ . In this case, the assertion (iii) in Theorem 1.2 will not occur, and for all  $\ell_1 < c < \ell_3$ ,  $\Lambda_p = (0, \mu^*) \times (0, \infty)$  and  $\Lambda_e = [\mu^*, \infty) \times (0, \infty)$ .
- (ii) When  $N_R$  is temporally heterogeneous, we have the following clarifications.
  - (ii.1) For the critical case  $c = \ell_2$ , we can use Theorem A.1 and Theorem A.2 (i) with  $B = B^*$  to obtain a critical curve  $\bar{\tau}(\mu)$  separating the persistence and extinction regions for  $\mu \in (0, \mu^*)$ , which satisfies  $v_1(\bar{\tau}(\mu), \mu, \beta_d - c) \equiv 0$  and  $\bar{\tau}(\mu^*) = 0$  (see the definition of  $v_1$  in Sect. 3.1). But the behavior of  $\bar{\tau}(\mu)$  as  $\mu \rightarrow 0$  remains unknown since the hypothesis (H) in Theorem A.2 (i) is not imposed in our paper and hence we can not draw a precise graph for  $\bar{\tau}(\mu)$  when  $c = \ell_2$ . We do not know whether  $b_* = -\beta_d + \ell_2$  satisfies the hypothesis (H) in Theorem A.2 (i). If it does, then the graph in Figure 1 (iii) includes the case  $c = \ell_2$ .
  - (ii.2) The value  $\mu_*$  in Theorem 1.2 (ii) satisfies  $\mu_* \rightarrow 0$  as  $c \nearrow \ell_2$  (see the proof of Theorem 1.2 and Remark A.1). However, when  $c \in (\ell_1, \ell_2)$ , the curve  $\tau = \tilde{\tau}(\mu)$  satisfies  $\lim_{\mu \rightarrow \mu_*} \tilde{\tau}(\mu) = \infty$ , while when  $c \in (\ell_2, \ell_3)$ , the curve  $\bar{\tau}(\mu)$  satisfies  $\lim_{\mu \rightarrow 0} \bar{\tau}(\mu) = 0$ , which gives rise to a sharp transition between  $c \in (\ell_1, \ell_2)$  and  $c \in (\ell_2, \ell_3)$  (see Figure 1 (ii), (iii)).

Next we proceed to consider the global dynamics of (1.2) for the case where  $N_R$  is temporally homogeneous (i.e.,  $N_R(x, t) = N_R(x)$  on  $\bar{\Omega} \times \mathbb{R}_+$ ). In this case,  $\theta_d(x, t) = \theta_d(x)$  and we will classify the persistence and extinction dynamics of the consumer population in terms of  $(d, \mu)$ . To present our result, we introduce three quantities



**Fig. 1** Illustration of Theorem 1.2, where the consumer population is uniformly persistent in the green region while becomes extinct in the yellow region

$$c_1 := \frac{1}{|\Omega|} \int_{\Omega} \frac{rN_R(x)}{k\sigma + N_R(x)} dx, \quad c_2 := \frac{r \int_{\Omega} N_R(x) dx}{k\sigma|\Omega| + \int_{\Omega} N_R(x) dx}, \quad c_3 := \frac{r \max_{\overline{\Omega}} N_R}{k\sigma + \max_{\overline{\Omega}} N_R}, \tag{1.9}$$

and define

$$h(d) := \frac{1}{|\Omega|} \int_{\Omega} \frac{r\theta_d(x)}{k + \theta_d(x)} dx, \tag{1.10}$$

where  $c_1 < c_2 < c_3$  (see Lemma 4.2). Note that  $\ell_i = c_i$  for  $i = 1, 2, 3$  when  $N_R$  is a constant. We note that by the asymptotic properties of  $\theta_d$  established in Lemmas 3.5-3.6,  $c_1$  and  $c_3$  can be interpreted as the spatially averaged and maximal consumer growth rate for the slow resource diffusion (i.e.  $0 < d \ll 1$ ), respectively;  $c_2$  is the consumer growth rate for the rapid resource diffusion ( $d \gg 1$ ), where rapid diffusion homogenizes the resource into a spatially uniform state.

Define the persistence region

$$\Gamma_p := \{(d, \mu) \in (0, \infty)^2 \mid \text{system (1.2) is uniformly persistent}\} \tag{1.11}$$

and the extinction region

$$\Gamma_e := \{(d, \mu) \in (0, \infty)^2 \mid (0, \theta_d) \text{ is globally asymptotically stable}\} \tag{1.12}$$

in terms of  $d$  and  $\mu$ . Then we can completely classify the global dynamics of system (1.2), as stated below.

**Theorem 1.3** *Assume that (H1) holds and  $N_R$  is temporally homogeneous. Let  $c \geq 0$  and all other parameters be positive. Fixing all parameters except  $\mu$  and  $d$ , we have the following conclusions.*

- (i) *If  $0 \leq c \leq c_1$ , then  $\Gamma_p = (0, \infty)^2$ .*
- (ii) *If  $c = c_2$ , then there is a continuous function  $\mathcal{U} : [0, \infty) \rightarrow (0, \infty)$  satisfying  $\mathcal{U}(d) \rightarrow \infty$  as  $d \rightarrow \infty$ , such that  $\Gamma_p = (0, \infty) \times (0, \mathcal{U}(d))$  and  $\Gamma_e = (0, \infty) \times [\mathcal{U}(d), \infty)$ .*
- (iii) *If  $c \geq c_3$ , then  $\Gamma_e = (0, \infty)^2$ .*
- (iv) *If  $c_1 < c < c_2$ , then there is a constant  $\check{\mu} > 0$  and a continuous function  $\mathcal{U}_1 : [0, d_{h_1}) \rightarrow [\check{\mu}, \infty)$  satisfying  $\lim_{d \nearrow d_{h_1}} \mathcal{U}_1(d) = \infty$  such that*

$$[(0, d_{h_1}) \times [\check{\mu}, \mathcal{U}_1(d))] \cup [(0, d_{h_2}) \times (0, \check{\mu})] \cup [d_{h_2}, \infty) \times (0, \infty)] \subset \Gamma_p$$

*and  $(0, d_{h_1}) \times [\mathcal{U}_1(d), \infty) \subset \Gamma_e$ , where  $d_{h_1}$  and  $d_{h_2}$  are the smallest and largest positive roots of  $h(d) = c$ , respectively. If  $d_{h_1} \neq d_{h_2}$  (i.e.  $h(d) = c$  has at least two roots), then there are two constants  $l_{\check{h}}, r_{\check{h}}$  with  $l_{\check{h}} < r_{\check{h}}$  and  $h(l_{\check{h}}) = h(r_{\check{h}}) = c$ , such that either*

$$[l_{\check{h}}, r_{\check{h}}] \subset \{d \in [d_{h_1}, d_{h_2}] \mid h(d) \geq c\}, \tag{1.13}$$

*or*

$$(l_{\check{h}}, r_{\check{h}}) \subset \{d \in (d_{h_1}, d_{h_2}) \mid h(d) < c\}. \tag{1.14}$$

*If the case (1.13) occurs, then  $[l_{\check{h}}, r_{\check{h}}] \times [\check{\mu}, \infty) \subset \Gamma_p$ ; if the case (1.14) occurs, then there is a continuous function  $\mathcal{U}_{\check{h}} : (l_{\check{h}}, r_{\check{h}}) \rightarrow [\check{\mu}, \infty)$  with  $\lim_{d \searrow l_{\check{h}}} \mathcal{U}_{\check{h}}(d) = \lim_{d \nearrow r_{\check{h}}} \mathcal{U}_{\check{h}}(d) = \infty$  such that  $(l_{\check{h}}, r_{\check{h}}) \times [\check{\mu}, \mathcal{U}_{\check{h}}(d)) \subset \Gamma_p$ , and  $(l_{\check{h}}, r_{\check{h}}) \times [\mathcal{U}_{\check{h}}(d), \infty) \subset \Gamma_e$ .*

- (v) *If  $c_2 < c < c_3$ , then there is a constant  $\hat{\mu} > 0$  and a continuous function  $\tilde{\mathcal{U}}_1 : [0, d_{\beta_1}] \rightarrow [0, \hat{\mu}]$  satisfying  $\tilde{\mathcal{U}}_1(d_{\beta_1}) = 0$  and  $\tilde{\mathcal{U}}_1(d) > 0$  for  $d \in [0, d_{\beta_1})$  such that*

$$[(0, d_{\beta_1}) \times [\tilde{\mathcal{U}}_1(d), \hat{\mu}]] \cup [(0, d_{\beta_2}) \times (\hat{\mu}, \infty)] \cup [d_{\beta_2}, \infty) \times (0, \infty)] \subset \Gamma_e$$

*and  $(0, d_{\beta_1}) \times (0, \tilde{\mathcal{U}}_1(d)) \subset \Gamma_p$ , where  $d_{\beta_1}$  and  $d_{\beta_2}$  are the smallest and largest positive roots of  $\max_{x \in \bar{\Omega}} \beta_d(x) = c$ , respectively. If  $d_{\beta_1} \neq d_{\beta_2}$  (i.e.  $\max_{\bar{\Omega}} \beta_d = c$  has at least two roots), then there are two constants  $l_{\hat{\beta}}, r_{\hat{\beta}}$  with  $l_{\hat{\beta}} < r_{\hat{\beta}}$  and  $\max_{\bar{\Omega}} \beta_{l_{\hat{\beta}}} = \max_{\bar{\Omega}} \beta_{r_{\hat{\beta}}} = c$  such that either*

$$(l_{\hat{\beta}}, r_{\hat{\beta}}) \subset \left\{d \in (d_{\beta_1}, d_{\beta_2}) \mid \max_{x \in \bar{\Omega}} \beta_d(x) > c\right\}, \tag{1.15}$$

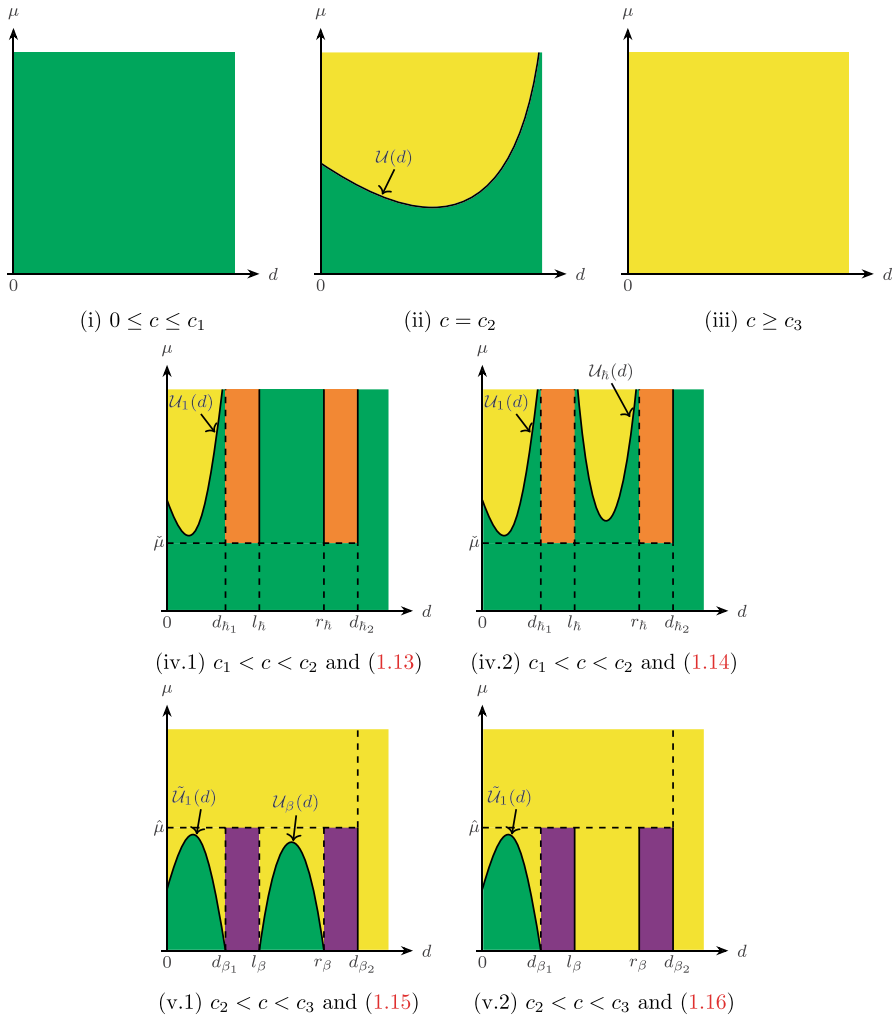
*or*

$$[l_{\hat{\beta}}, r_{\hat{\beta}}] \subset \left\{d \in [d_{\beta_1}, d_{\beta_2}] \mid \max_{x \in \bar{\Omega}} \beta_d(x) \leq c\right\}. \tag{1.16}$$

*If the case (1.15) occurs, then there is a continuous function  $\mathcal{U}_{\hat{\beta}} : [l_{\hat{\beta}}, r_{\hat{\beta}}] \rightarrow [0, \hat{\mu}]$  satisfying  $\mathcal{U}_{\hat{\beta}}(l_{\hat{\beta}}) = \mathcal{U}_{\hat{\beta}}(r_{\hat{\beta}}) = 0$  and  $\mathcal{U}_{\hat{\beta}}(d) > 0$  for  $d \in (l_{\hat{\beta}}, r_{\hat{\beta}})$  such that  $(l_{\hat{\beta}}, r_{\hat{\beta}}) \times (0, \mathcal{U}_{\hat{\beta}}(d)) \subset \Gamma_p$  and  $(l_{\hat{\beta}}, r_{\hat{\beta}}) \times [\mathcal{U}_{\hat{\beta}}(d), \hat{\mu}] \subset \Gamma_e$ ; if the case (1.16) occurs, then  $[l_{\hat{\beta}}, r_{\hat{\beta}}] \times (0, \hat{\mu}] \subset \Gamma_e$ .*

*Moreover, system (1.2) admits a positive steady state as long as it is uniformly persistent.*

**Remark 1.2** Theorem 1.3 is illustrated in Figure 2. We give some further remarks on Theorem 1.3 and Figure 2.



**Fig. 2** Illustration of Theorem 1.3, where the consumer population is uniformly persistent in the green region while becomes extinct in the yellow region. In the orange (resp. violet) region, the persistence and extinction of the consumer population is determined by the sign of  $h(d) - c$  (resp.  $\max_{x \in \bar{\Omega}} \beta_d(x) - c$ ), as demonstrated for  $d \in (l_h, r_h)$  (resp.  $d \in (l_\beta, r_\beta)$ )

- (i) When  $c_1 < c < c_2$ , the number of roots of  $h(d) = c$  is unknown. It follows from the proof of Theorem 1.3 (iv) that

$$\lim_{d \rightarrow 0} h(d) = c_1 < h(d) < c_2 = \lim_{d \rightarrow \infty} h(d), \quad \forall d > 0.$$

This means that  $h(d) = c$  has at least one positive root for any  $c \in (c_1, c_2)$ . In general,  $h(d) = c$  may have multiple (possibly infinitely many) roots.

- (ii) When  $c_2 < c < c_3$ , the number of roots of  $\max_{x \in \bar{\Omega}} \beta_d(x) = c$  remains unknown. But the proof of Theorem 1.3 (v) indicates

$$\lim_{d \rightarrow 0} \max_{x \in \bar{\Omega}} \beta_d(x) = c_3 > \max_{x \in \bar{\Omega}} \beta_d(x) > c_2 = \lim_{d \rightarrow \infty} \max_{x \in \bar{\Omega}} \beta_d(x), \quad \forall d > 0,$$

which implies that  $\max_{x \in \overline{\Omega}} \beta_d(x) = c$  has at least one positive root for any  $c \in (c_2, c_3)$ . We further show in Lemma 4.3 that if

$\Omega$  is a bounded interval in  $\mathbb{R}$ ,  $N_R \in C^1(\overline{\Omega})$  and  $N_R$  is monotonic in  $x \in \overline{\Omega}$ ,

then  $\max_{x \in \overline{\Omega}} \theta_d(x)$  is strictly decreasing in  $d$ , which implies that  $\max_{x \in \overline{\Omega}} \beta_d(x) = c$  has exactly one positive root for any  $c \in (c_2, c_3)$ . But generally,  $\max_{x \in \overline{\Omega}} \beta_d(x) = c$  may have multiple (possibly infinitely many) roots. In addition, the smallest positive root  $d_{\beta_1}$  of  $\max_{x \in \overline{\Omega}} \beta_d(x) = c$  tends to  $\infty$  as  $c \searrow c_2$ . We note that  $\lim_{d \rightarrow \infty} \mathcal{U}(d) = \infty$  for  $c = c_2$ , whereas  $\lim_{d \nearrow d_{\beta_1}} \tilde{\mathcal{U}}_1(d) = 0$  for  $c \in (c_2, c_3)$ . This leads to a sharp transition from Theorem 1.3 (ii) to Theorem 1.3 (v) (see Figure 2 (ii), (v.1) and (v.2)).

- (iii) Figure 2 is just a schematic illustration. The curves  $\mathcal{U}_1(d)$ ,  $\mathcal{U}(d)$  and  $\tilde{\mathcal{U}}(d)$  exist for  $c \in (c_1, c_2)$ ,  $c = c_2$  and  $c \in (c_2, c_3)$ , respectively, but their monotonicity with respect to  $d$  remains unknown.

**Remark 1.3** As recalled in Section 1, the global dynamics of model (1.2) with temporally homogeneous input  $N_R$  and  $\sigma = c = d = 0$  has been extensively studied in [9, 11, 38]. This paper primarily focuses on the scenario where  $N_R$  exhibits spatial heterogeneity,  $\sigma$ ,  $c$  and  $d$  are nonzero and nonnegative. Based on our results, we have the following observations.

- (1) When the resource does not decay ( $\sigma = 0$ ), an infinite-time blow-up of the resource population will occur irrespective of the resource dispersal under two scenarios: large mortality rate of the consumer (i.e.  $c \geq r$ ) or small mortality rate (i.e.  $c < r$ ) but large yield rate (i.e.  $\gamma > \gamma_0$ ), as stated in Theorem 1.1 (ii). As long as the resource decays ( $\sigma > 0$ ), the blow-up of the resource is prevented regardless of the influence of other factors such as the yield rate or the resource dispersal, as described in Theorem 1.1 (i). Remarkably, these results hold true for both temporally homogeneous and heterogeneous resource inputs. *This indicates that the resource decay emerges as a decisive factor that prevents the resource abundance from escalating to an explosive or overly abundant level.*
- (2) For both temporally heterogeneous and homogeneous resource inputs, regardless of whether the resource decays (i.e.  $\sigma \geq 0$ ), a high consumer mortality rate (specifically  $c > r$  in the case  $\sigma = 0$  and  $c \geq \max\{\ell_3, c_3\}$  in the case  $\sigma > 0$ ) results in the extinction of the consumer population. This conclusion aligns with Theorem 1.1 (ii), Theorem 1.2 (iv) and Theorem 1.3 (iii) (see also Figure 1-(iv) and Figure 2-(iii)). Conversely, when the consumer mortality rate is suitably low, the consumer population persists regardless of the resource decay rate  $\sigma > 0$ , as illustrated in Figure 1-(i) and Figure 2-(i). *Therefore, the consumer mortality rate is a crucial factor in determining the persistence or extinction of the consumer population.*
- (3) When the resource undergoes decays (i.e.  $\sigma > 0$ ) and the consumer mortality rate is at a moderate level (specifically  $\ell_1 < c < \ell_3$ ), a clear difference is observed between temporally heterogeneous and homogeneous resource inputs for  $(\mu, \tau) \in (0, \mu^*) \times (0, \infty)$ . Precisely, when  $N_R$  is temporally heterogeneous, the consumer population may either persist or go extinct, depending upon the value of the relaxation time  $\tau$  (as detailed in Theorem 1.2 (ii) and (iii) or illustrated in Figure 1-(ii) and (iii)). Conversely, when  $N_R$  is temporally homogeneous, the consumer population persists irrespective of the value of relaxation time  $\tau$  (see Remark 1.1). *This finding suggests that, when the consumer mortality rate is moderate, a temporally homogeneous resource input may be more advantageous for the consumer population than a temporally heterogeneous one.*

**Remark 1.4** Theorem 1.2 and Theorem 1.3 classify the global dynamics of (1.2) when  $N_R$  is spatially heterogeneous. When  $N_R$  is spatially homogeneous, i.e.,  $N_R(x, t) = N_R(t)$  on  $\bar{\Omega} \times \mathbb{R}_+$ , the solution of the following ODE problem

$$\begin{cases} \Theta_t = N_R(t) - \sigma\Theta, & t > 0, \\ \Theta(t + \omega) = \Theta(t), & t \geq 0, \end{cases}$$

is the unique solution of (1.4). In this case,

$$v_1\left(\tau, \mu, \frac{r\Theta}{k + \Theta} - c\right) = c - \frac{1}{\omega} \int_0^\omega \frac{r\Theta(t)}{k + \Theta(t)} dt = c - \ell_1,$$

where  $v_1\left(\tau, \mu, \frac{r\Theta}{k + \Theta} - c\right)$  is the principal eigenvalue of the linearized eigenvalue problem of (1.2) at  $(0, \Theta)$ . Then by Proposition 3.8, we can directly get the following results.

- (i) If  $0 \leq c < \ell_1$ , then system (1.2) is uniformly persistent for all  $\tau, \mu, d > 0$ .
- (ii) If  $c \geq \ell_1$ , then  $(0, \theta_d)$  is globally asymptotically stable for all  $\tau, \mu, d > 0$ .

The effect of the resource dispersal can be discerned from Theorem 1.3 for  $d \in (0, \infty)$ . Below we explore the asymptotic profiles of positive  $\omega$ -periodic solutions as  $d \rightarrow 0$  and  $d \rightarrow \infty$ .

**Theorem 1.4** (Asymptotics as  $d \rightarrow 0$ ) Assume that (H1) holds and  $c \in [0, c_*]$ , where

$$c_* = \frac{1}{\omega|\Omega|} \int_0^\omega \int_\Omega \frac{rp(x, t)}{k + p(x, t)} dx dt$$

with

$$p(x, t) = e^{-\sigma t} \left( \frac{\int_0^\omega e^{\sigma \zeta} N_R(x, \zeta) d\zeta}{e^{\sigma\omega} - 1} + \int_0^t e^{\sigma \zeta} N_R(x, \zeta) d\zeta \right), \quad x \in \bar{\Omega}, t \geq 0.$$

Then for fixed  $\mu > 0$  and sufficiently small  $d > 0$ , system (1.2) admits at least one positive  $\omega$ -periodic solution, and as  $d \rightarrow 0$  (passing to a subsequence of  $d$  if necessary), any positive  $\omega$ -periodic solution  $(Z, N)$  of (1.2) satisfies

$$(Z, N) \rightarrow (Z_0, N_0) \text{ in } [C(\bar{\Omega} \times [0, \omega])]^2,$$

where  $(Z_0, N_0)$  is a positive solution of

$$\begin{cases} \tau \frac{\partial Z_0}{\partial t} = \mu \Delta Z_0 + Z_0 \left( \frac{rN_0}{k + N_0} - c - gZ_0 \right), & x \in \Omega, t > 0, \\ \frac{\partial N_0}{\partial t} = N_R(x, t) - \sigma N_0 - \frac{rN_0 Z_0}{\gamma(k + N_0)}, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} Z_0 = 0, & x \in \partial\Omega, t > 0, \\ Z_0(x, t + \omega) = Z_0(x, t), N_0(x, t + \omega) = N_0(x, t), & x \in \Omega, t \geq 0. \end{cases} \tag{1.17}$$

For  $d \rightarrow \infty$  (fast resource dispersal), we have the following result.

**Theorem 1.5** (Asymptotics as  $d \rightarrow \infty$ ) Assume that (H1) holds and  $c \in [0, c^*]$ , where

$$c^* = \frac{1}{\omega} \int_0^\omega \frac{r\xi(t)}{k + \xi(t)} dt \quad \text{with} \quad \xi(t) = \frac{1}{|\Omega|} \int_\Omega p(x, t) dx.$$

Then for fixed  $\mu > 0$  and sufficiently large  $d > 0$ , system (1.2) admits at least one positive  $\omega$ -periodic solution, and as  $d \rightarrow \infty$  (passing to a subsequence of  $d$  if necessary), any positive  $\omega$ -periodic solution  $(Z, N)$  to (1.2) satisfies

$$(Z, N) \rightarrow (Z_\infty, N_\infty) \text{ in } [C(\bar{\Omega} \times [0, \omega])]^2,$$

where  $N_\infty$  is independent of  $x$ , and  $(Z_\infty, N_\infty)$  is a positive solution of

$$\begin{cases} \tau \frac{\partial Z_\infty}{\partial t} = \mu \Delta Z_\infty + Z_\infty \left( \frac{rN_\infty}{k+N_\infty} - c - gZ_\infty \right), & x \in \Omega, t > 0, \\ \frac{dN_\infty}{dt} = \frac{1}{|\Omega|} \int_\Omega N_R(x, t) dx - \sigma N_\infty - \frac{rN_\infty \int_\Omega Z_\infty(x, t) dx}{\gamma(k+N_\infty)|\Omega|}, & t > 0, \\ \partial_{\bar{n}} Z_\infty = 0, & x \in \partial\Omega, t > 0, \\ Z_\infty(x, t + \omega) = Z_\infty(x, t), N_\infty(t + \omega) = N_\infty(t), & x \in \Omega, t \geq 0. \end{cases} \tag{1.18}$$

The global dynamics and precise profiles of solutions to the limiting systems (1.17) and (1.18) are interesting questions left open for future effort.

**Sketch of proof ideas.** We employ the comparison principle and method of upper-lower solutions to get the uniform-in-time boundedness and time-asymptotics of solutions of (1.2), which establish Theorem 1.1 along with the local existence of solutions. To show Theorem 1.2 and Theorem 1.3, using the comparison principle, theory for asymptotically periodic parabolic systems and uniform persistence theory for infinite-dimensional dynamical systems, we first establish a key threshold criterion determining the persistence and extinction dynamics by the sign of the principal eigenvalue to the linearized eigenvalue problem of (1.2) at the semi-trivial periodic solution (see Proposition 3.8). For the case of temporally periodic resource input  $N_R(x, t)$ , we derive the upper and lower bounds of the principal eigenvalue and utilize the ingenious ideas of classifying the level set of principal eigenvalue for time-periodic parabolic operators in [18] to find conditions determining the sign of the principal eigenvalue as a function of the relaxation time  $\tau$  and diffusion rate  $\mu$ . Then an application of Proposition 3.8 yields Theorem 1.2. For the case of temporally homogeneous resource input  $N_R(x)$ , the principal eigenvalue of the time-periodic parabolic operator reduces to a corresponding elliptic eigenvalue problem of which the principal eigenvalue is monotonic in  $\mu$ . Using this monotonicity along with suitable asymptotic property in  $d$ , we can determine the sign of the principal eigenvalue and hence prove Theorem 1.3 by Proposition 3.8. Finally we employ the  $L^p$  estimates of the time-periodic parabolic equations, Sobolev embedding theorem and comparison principle to establish the asymptotic property of solutions as  $d \rightarrow 0$  (or  $\infty$ ) (i.e. Theorem 1.4 and Theorem 1.5).

The rest of the paper is organized as follows. In Section 2, we prove the global well-posedness of solutions to (1.2) (Theorem 1.1). In Section 3, we show some qualitative properties of the semi-trivial  $\omega$ -periodic solution, and establish a key dichotomous criterion determining the persistence and extinction dynamics of model (1.2) by the sign of the principal eigenvalue of the linearized eigenvalue problem at the semi-trivial  $\omega$ -periodic solution. Theorems 1.2 and 1.3 are established in Section 4. Section 5 is devoted to the proofs of Theorems 1.4 and 1.5. Finally we give a brief summary and discuss some open problems in Section 6.

## 2 Global well-posedness

In this section, we shall establish the global existence of classical solutions to (1.2) with boundedness and blow-up property. We start by giving the definition of classical solutions to (1.2) with  $d = 0$  and  $d > 0$ .

**Definition 2.1** (Classical solutions of (1.2))

- (i) Let  $\mu > 0, d = 0$ . For given  $Z_I, N_I \in C(\bar{\Omega})$  and  $T \in (0, \infty]$ ,  $(Z(x, t), N(x, t))$  is called a *classical solution* of (1.2) on  $\bar{\Omega} \times [0, T)$  if the following conditions hold:

- (i.1) for every  $p > m$ ,  $Z \in C([0, T], C(\overline{\Omega})) \cap C^1((0, T), C(\overline{\Omega})) \cap C([0, T], W^{2,p}(\Omega))$ ,
- (i.2)  $N \in C([0, T], C(\overline{\Omega})) \cap C^1((0, T), C(\overline{\Omega}))$  satisfies the second equation of (1.2),
- (i.3)  $\lim_{t \rightarrow 0} (\|Z(\cdot, t) - Z_0(\cdot)\|_{L^\infty(\Omega)} + \|N(\cdot, t) - N_0(\cdot)\|_{L^\infty(\Omega)}) = 0$ ,
- (i.4)  $Z(x, t)$  satisfies

$$Z(x, t) = Q(t)Z_0(x) + \int_0^t Q(t - \varsigma) \left( \frac{rN(x, \varsigma)Z(x, \varsigma)}{k + N(x, \varsigma)} - gZ(x, \varsigma)^2 \right) d\varsigma,$$

where  $Q(t) = e^{(-c+\mu\Delta)t}$  denotes the solution semigroup of the linear equation  $u_t = \mu\Delta u - cu$  in  $\Omega$  with the homogeneous Neumann boundary condition.

- (ii) Let  $\mu, d > 0$ . For given  $Z_I, N_I \in C(\overline{\Omega})$  and  $T \in (0, \infty)$ ,  $(Z(x, t), N(x, t))$  is called a *classical solution* of (1.2) on  $\overline{\Omega} \times [0, T)$  if  $(Z, N) \in [C(\overline{\Omega} \times [0, T)) \cap C^{2,1}(\overline{\Omega} \times (0, T))]^2$  satisfies (1.2).

The definition of classical solutions of (1.2) for  $d = 0$  follows from [21, Definition 1.1]. Below we prove Theorem 1.1.

**Proof of Theorem 1.1** Let  $Z_I, N_I \in C(\overline{\Omega})$ . The proof is divided into two cases: (a)  $d = 0$ ; (b)  $d > 0$ .

**Case (a):**  $d = 0$ . Similar to the proof of [21, Lemma 3.1], by the contraction mapping theorem, we obtain a constant  $T_{\max} > 0$  so that (1.2) admits a unique classical solution  $(Z(x, t), N(x, t))$  on  $\overline{\Omega} \times [0, T_{\max})$ . Moreover, if  $T_{\max} < \infty$ , then

$$\lim_{t \rightarrow T_{\max}^-} (\|Z(\cdot, t)\|_{L^\infty(\Omega)} + \|N(\cdot, t)\|_{L^\infty(\Omega)}) = \infty. \tag{2.1}$$

Next, we show that  $T_{\max} = \infty$ . Notice that  $N(x, 0) = N_I(x) \geq 0$  on  $\overline{\Omega}$ . Define

$$\Omega_1 := \{x \in \overline{\Omega} | N_I(x) > 0\} \quad \text{and} \quad \Omega_2 := \{x \in \overline{\Omega} | N_I(x) = 0\}.$$

Then for  $x \in \Omega_1$ ,  $N(x, t) > 0$  for  $t \in (0, T_0)$  with sufficiently small  $T_0 > 0$ , while for  $x \in \Omega_2$ , it follows from the second equation in (1.2) that  $N_t(x, 0) = N_R(x, 0) > 0$  and thus  $N(x, t) > 0$  for  $t \in (0, T_0)$  with sufficiently small  $T_0 > 0$ . We claim that  $N(x, t) > 0$  on  $\overline{\Omega} \times (0, T_{\max})$ . Indeed, otherwise, there is  $(x_0, T_1) \in \overline{\Omega} \times [T_0, T_{\max})$  such that  $N(x, t) > 0$  on  $\overline{\Omega} \times (0, T_1)$  and  $N(x_0, T_1) = 0$  yielding that  $N_t(x_0, T_1) = N_R(x_0, T_1) \leq 0$ , which is impossible. Notice that

$$\tau Z_t \leq \mu\Delta Z + Z(r - c - gZ), \quad \forall x \in \Omega, t \in (0, T_{\max}). \tag{2.2}$$

Then by the standard comparison argument and maximum principle, we obtain (1.3) on  $\overline{\Omega} \times [0, T_{\max})$ . This together with the equation of  $N(x, t)$  gives that

$$N_t \leq N_R(x, t) - \sigma N, \quad \forall x \in \overline{\Omega}, t \in (0, T_{\max}),$$

which implies that

$$N(x, t) \leq \max_{\overline{\Omega} \times [0, \omega]} N_R(x, t) \cdot \int_0^t e^{\sigma(\varsigma-t)} d\varsigma + e^{-\sigma t} N_I(x) \quad \text{on } \overline{\Omega} \times (0, T_{\max}), \tag{2.3}$$

and (2.1) cannot occur when  $T_{\max}$  is finite. Hence  $T_{\max} = \infty$  by (2.1), that is, system (1.2) has a unique global classical solution  $(Z, N)$  on  $\overline{\Omega} \times [0, \infty)$ .

In the following, we show the boundedness or the blow-up property of  $N(x, t)$ . For  $\sigma > 0$ , we infer from (2.3) that

$$N \leq \rho_2 = \max \left\{ \max_{\overline{\Omega}} N_I(x), \frac{\max_{\overline{\Omega} \times [0, \omega]} N_R(x, t)}{\sigma} \right\}, \quad \forall x \in \overline{\Omega}, t > 0. \tag{2.4}$$

While for  $\sigma = 0$ , we have the following two cases to consider.

Case 1.  $0 \leq c < r$  and  $\gamma > \frac{r(r-c)}{g \min_{\overline{\Omega} \times [0, \omega]} N_R(x, t)}$ . By (2.3), we have that  $N(x, t) \leq t \cdot \max_{\overline{\Omega} \times [0, \omega]} N_R(x, t) + \max_{\overline{\Omega}} N_I(x)$  on  $\overline{\Omega} \times \mathbb{R}_+$ , and hence

$$\begin{aligned} \frac{N(x, t)}{k + N(x, t)} &\leq 1 - \frac{k}{k + t \cdot \max_{\overline{\Omega} \times [0, \omega]} N_R(x, t) + \max_{\overline{\Omega}} N_I(x)} \\ &\leq 1 - \frac{C_1}{1 + t}, \quad \forall x \in \overline{\Omega}, t \geq 0, \end{aligned}$$

where  $C_1 = \max \left\{ \frac{k}{k + \max_{\overline{\Omega}} N_I(x)}, \frac{k}{\max_{\overline{\Omega} \times [0, \omega]} N_R(x, t)} \right\}$ . Let  $U = 1 - \frac{g}{r-c} Z$ . Then  $U$  satisfies  $U \leq 1$  and

$$\tau U_t - \mu \Delta U = (1 - U) \left( c + gZ - \frac{rN}{k + N} \right) \geq F(t, U), \quad \forall x \in \Omega, t > 0,$$

where

$$F(t, \varsigma) := (r - c)(1 - \varsigma) \left( \frac{C_1}{1 + t} - \varsigma \right).$$

Defining  $C_2 := \frac{1}{2} \min\{1, C_1\}$  and  $C_3 := \frac{C_1(r-c)}{4}$ , we obtain that

$$F(t, \varsigma) \geq (r - c) \cdot \frac{1}{2} \cdot \frac{C_1}{2(1 + t)} = \frac{C_3}{1 + t} \quad \text{for } t \geq 0, \varsigma \leq \frac{C_2}{1 + t}.$$

Thus, it follows from [9, Lemma 1] that there is  $T_2 > 0$  so that

$$U(x, t) > \frac{C_2}{1 + t} \quad \text{for } x \in \overline{\Omega}, t \geq T_2.$$

That is,

$$Z(x, t) < \frac{r - c}{g} \left( 1 - \frac{C_2}{1 + t} \right) \quad \text{for } x \in \overline{\Omega}, t \geq T_2.$$

This together with the equation of  $N$  in (1.2) implies that

$$N_t \geq \min_{\overline{\Omega} \times [0, \omega]} N_R(x, t) - \frac{r(r - c)}{\gamma g} \left( 1 - \frac{C_2}{1 + t} \right) \quad \text{for } x \in \overline{\Omega}, t \geq T_2,$$

and hence,

$$N(x, t) \geq N_I(x) + \left( \min_{\overline{\Omega} \times [0, \omega]} N_R(x, t) - \frac{r(r - c)}{\gamma g} \right) t + \int_0^t \frac{r(r - c)C_2}{\gamma g(1 + \varsigma)} d\varsigma \quad \text{for } x \in \overline{\Omega}, t \geq T_2.$$

When  $\gamma > \frac{r(r-c)}{g \min_{\overline{\Omega} \times [0, \omega]} N_R}$ , one immediately obtains that  $\lim_{t \rightarrow \infty} N(x, t) = \infty$  uniformly for  $x \in \overline{\Omega}$ . By the theory of asymptotically periodic system [43, Proposition 3.2.1], we derive that  $\lim_{t \rightarrow \infty} Z(x, t) = \frac{r-c}{g}$  uniformly on  $\overline{\Omega}$ .

Case 2.  $c \geq r$ . It follows from (2.2) and a comparison principle that  $\lim_{t \rightarrow \infty} Z(x, t) = 0$  uniformly on  $\overline{\Omega}$ . Then for any  $\varepsilon \in \left( 0, \frac{\gamma \min_{\overline{\Omega} \times [0, \omega]} N_R}{2r} \right)$ , there is  $T_3 > 0$  large enough such that  $0 < Z < \varepsilon$  for all  $x \in \overline{\Omega}$  and  $t > T_3$ , which yields that

$$N_t \geq \min_{\overline{\Omega} \times [0, \omega]} N_R(x, t) - \frac{r\varepsilon}{\gamma} > \frac{1}{2} \min_{\overline{\Omega} \times [0, \omega]} N_R(x, t) > 0 \quad \text{for } x \in \overline{\Omega}, t \geq T_3,$$

and hence,  $\lim_{t \rightarrow \infty} N(x, t) = \infty$  uniformly on  $\overline{\Omega}$ .

**Case (b):**  $d > 0$ . To prove the global existence and uniqueness of classical solutions to (1.2), we use the method of upper-lower solutions (cf. [24, 32]). We first note that problem (1.2) is a mixed quasi-monotone system in the set  $\{(Z, N) | Z \geq 0, N \geq 0\}$ . Let  $(\underline{Z}(x, t), \underline{N}(x, t)) = (0, 0)$  and  $(\tilde{Z}(x, t), \tilde{N}(x, t)) = (u^*(t), v^*(t))$ , where  $(u^*(t), v^*(t))$  is the unique solution of

$$\begin{cases} \tau u_t^* = u^*(r - c - gu^*), & t > 0, \\ v_t^* = \max_{\overline{\Omega} \times [0, \omega]} N_R(x, t) - \sigma v^*, & t > 0, \\ u^*(0) = \max_{\overline{\Omega}} Z_I(x), v^*(0) = \max_{\overline{\Omega}} N_I(x). \end{cases} \tag{2.5}$$

Then by a simple comparison, we immediately have  $0 < u^*(t) \leq \rho_1$  and  $v^*(t) > 0$  for all  $t > 0$ , where  $\rho_1$  is defined in (1.3). A direct calculation yields that

$$\begin{cases} \tau \tilde{Z}_t - \mu \Delta \tilde{Z} - \tilde{Z} \left( \frac{r \tilde{N}}{k + \tilde{N}} - c - g \tilde{Z} \right) \geq 0, & x \in \Omega, t > 0, \\ \tilde{N}_t - d \Delta \tilde{N} - N_R + \sigma \tilde{N} + \frac{r \tilde{N} \underline{Z}}{\gamma(k + \tilde{N})} \geq 0, & x \in \Omega, t > 0, \\ \tau \underline{Z}_t - \mu \Delta \underline{Z} - \underline{Z} \left( \frac{r \underline{N}}{k + \underline{N}} - c - g \underline{Z} \right) = 0, & x \in \Omega, t > 0, \\ \underline{N}_t - d \Delta \underline{N} - N_R + \sigma \underline{N} + \frac{r \underline{N} \tilde{Z}}{\gamma(k + \underline{N})} < 0, & x \in \Omega, t > 0, \\ \partial_{\tilde{n}} \underline{Z} = 0 = \partial_{\tilde{n}} \tilde{Z}, \partial_{\tilde{n}} \underline{N} = 0 = \partial_{\tilde{n}} \tilde{N}, & x \in \partial \Omega, t > 0, \\ \underline{Z}(x, 0) \leq Z_I(x) \leq \tilde{Z}(x, 0), \underline{N}(x, 0) \leq N_I(x) \leq \tilde{N}(x, 0), & x \in \overline{\Omega}, t > 0. \end{cases}$$

The above inequalities mean that  $(\tilde{Z}(x, t), \tilde{N}(x, t))$  and  $(\underline{Z}(x, t), \underline{N}(x, t))$  are a pair of upper-lower solutions to (1.2) (e.g., see [24, 32] for the definition of upper-lower solutions for mixed quasi-monotone systems). Hence, by the method of upper-lower solutions (cf. [32, Theorem 4.5]), problem (1.2) admits a unique global classical solution  $(Z(x, t), N(x, t))$  satisfying

$$0 \leq Z(x, t) \leq u^*(t) \leq \rho_1, \quad 0 \leq N(x, t) \leq v^*(t), \quad \forall x \in \overline{\Omega}, t \geq 0.$$

Since  $Z_I(x) \geq \neq 0$  and  $N_I(x) \geq 0$  on  $\overline{\Omega}$ , by the strong maximum principle,  $Z(x, t), N(x, t) > 0$  on  $\overline{\Omega} \times (0, \infty)$ .

It remains to show the boundedness or the blow-up property of  $N(x, t)$ . For the case (i):  $\sigma > 0$ , by a simple calculation from the equation of  $v^*$  in (2.5), we immediately have  $N \leq v^*(t) \leq \rho_2$  for all  $x \in \overline{\Omega}, t > 0$ , where the upper bound  $\rho_2$  is the same as one in (2.4). For the case (ii):  $\sigma = 0$ , we proceed with the following two scenarios.

Scenario 1:  $0 \leq c < r$  and  $\gamma > \frac{r(r-c)}{g \min_{\overline{\Omega} \times [0, \omega]} N_R(x, t)}$ . Since  $0 < N(x, t) \leq v^*(t)$  for all  $(x, t) \in \overline{\Omega} \times (0, \infty)$ , it follows from the equation of  $v^*$  in (2.5) that

$$N(x, t) \leq t \cdot \max_{\overline{\Omega} \times [0, \omega]} N_R(x, t) + \max_{\overline{\Omega}} N_I(x) \quad \text{on } \overline{\Omega} \times \mathbb{R}_+.$$

Similar to the argument in Case (a), one can find a sufficiently large  $\tilde{T}_2 > 0$  such that

$$N_t \geq d \Delta N + \min_{\overline{\Omega} \times [0, \omega]} N_R(x, t) - \frac{r(r-c)}{\gamma g} \left( 1 - \frac{C_2}{1+t} \right) \quad \text{for all } x \in \Omega, t \geq \tilde{T}_2,$$

where  $C_2$  is the same constant defined in Case (a). Notice that the following nonhomogeneous parabolic equation

$$\begin{cases} \hat{N}_t = d\Delta \hat{N} + \min_{\bar{\Omega} \times [0, \omega]} N_R(x, t) - \frac{r(r-c)}{\gamma g} \left(1 - \frac{C_2}{1+t}\right), & x \in \Omega, t > \tilde{T}_2, \\ \partial_{\bar{n}} \hat{N} = 0, & x \in \partial\Omega, t > \tilde{T}_2, \\ \hat{N}(x, \tilde{T}_2) = \min_{\bar{\Omega}} N(x, \tilde{T}_2), & x \in \bar{\Omega} \end{cases}$$

has a unique solution

$$\hat{N}(t) = \min_{\bar{\Omega}} N(x, \tilde{T}_2) + \left( \min_{\bar{\Omega} \times [0, \omega]} N_R(x, t) - \frac{r(r-c)}{\gamma g} \right) (t - \tilde{T}_2) + \int_{\tilde{T}_2}^t \frac{r(r-c)C_2}{\gamma g(1+s)} d_s, \quad t \geq \tilde{T}_2.$$

By the comparison principle, we have that  $N(x, t) \geq \hat{N}(t)$  for  $x \in \bar{\Omega}, t \geq \tilde{T}_2$ . Therefore, if  $\gamma > \frac{r(r-c)}{g \min_{\bar{\Omega} \times [0, \omega]} N_R}$ , then  $\lim_{t \rightarrow \infty} N(x, t) = \infty$  uniformly for  $x \in \bar{\Omega}$ .

**Scenario 2:**  $c \geq r$ . It follows from (2.2) and a comparison principle that  $\lim_{t \rightarrow \infty} Z(x, t) = 0$  uniformly on  $\bar{\Omega}$ . Then for any  $\varepsilon \in \left(0, \frac{\gamma \min_{\bar{\Omega} \times [0, \omega]} N_R}{2r}\right)$ , there is  $\tilde{T}_3 > 0$  large enough such that  $0 < Z < \varepsilon$  for  $x \in \bar{\Omega}, t > \tilde{T}_3$ , which causes that

$$N_t \geq d\Delta N + \min_{\bar{\Omega} \times [0, \omega]} N_R(x, t) - \frac{r\varepsilon}{\gamma} > d\Delta N + \frac{1}{2} \min_{\bar{\Omega} \times [0, \omega]} N_R(x, t) \quad \text{for } x \in \bar{\Omega}, t \geq \tilde{T}_3.$$

It follows from a comparison principle that  $\lim_{t \rightarrow \infty} N(x, t) = \infty$  uniformly on  $\bar{\Omega}$ .

The proof of Theorem 1.1 is completed. □

### 3 A dichotomous criterion for the global dynamics

To investigate the global dynamics of system (1.2), we first collect some known results on the principal eigenvalues of related eigenvalue problems, show some qualitative properties of the semi-trivial  $\omega$ -periodic solution, and then establish a dichotomous criterion for the global dynamics of (1.2).

#### 3.1 Eigenvalue problems

Consider the following time-periodic parabolic eigenvalue problem

$$\begin{cases} \chi \varphi_t - \kappa \Delta \varphi - f(x, t)\varphi = \nu \varphi, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} \varphi = 0, & x \in \partial\Omega, t > 0, \\ \varphi(x, t + \omega) = \varphi(x, t), & x \in \Omega, t \geq 0, \end{cases} \quad (3.1)$$

where  $\chi, \kappa > 0$  and  $f(x, t) \in C_{\omega}^{\alpha, \alpha/2}(\bar{\Omega} \times \mathbb{R}_+)$ . By the Krein-Rutman Theorem [15] and in [13, Theorem 7.2], problem (3.1) has a simple real principal eigenvalue, denoted by  $\nu_1 = \nu_1(\chi, \kappa, f)$ , with a positive eigenfunction  $\varphi_1 \in C_{\omega}^{2+\alpha, 1+\alpha/2}(\bar{\Omega} \times \mathbb{R}_+)$  satisfying  $\|\varphi_1\|_{L^2(\Omega \times (0, \omega))} = 1$ , while the real parts of all other eigenvalues of (3.1) are larger than  $\nu_1$ .

**Lemma 3.1** *The following results hold for the principal eigenvalue  $\nu_1$  of (3.1).*

- (i)  $-\frac{1}{\omega} \int_0^{\omega} \max_{x \in \bar{\Omega}} f(x, t) dt \leq \nu_1 \leq -\frac{1}{\omega} \int_0^{\omega} \int_{\Omega} f(x, t) dx dt$ , where the equality on the right-hand side holds if and only if  $f$  depends only on  $t$ .

- (ii)  $v_1$  is a smooth function of  $\kappa \in (0, \infty)$  and  $f(x, t) \in C^{\alpha, \alpha/2}(\bar{\Omega} \times \mathbb{R}_+)$ . Moreover, if  $f_1 \geq f_2$  then  $v_1(\chi, \kappa, f_1) \leq v_1(\chi, \kappa, f_2)$  with strict inequality if  $f_1 > f_2$ .
- (iii) For any  $\chi > 0$ ,

$$\lim_{\kappa \rightarrow 0} v_1(\chi, \kappa, f) = -\max_{x \in \bar{\Omega}} \frac{1}{\omega} \int_0^\omega f(x, t) dt \text{ and}$$

$$\lim_{\kappa \rightarrow \infty} v_1(\chi, \kappa, f) = -\frac{1}{\omega|\Omega|} \int_0^\omega \int_\Omega f(x, t) dx dt.$$

- (iv) For any  $\kappa > 0$ ,

$$\lim_{\chi \rightarrow 0} v_1(\chi, \kappa, f) = \underline{v}_1(\kappa) \text{ and } \lim_{\chi \rightarrow \infty} v_1(\chi, \kappa, f) = \bar{v}_1(\kappa), \tag{3.2}$$

where both  $\underline{v}_1(\kappa)$  and  $\bar{v}_1(\kappa)$  are non-decreasing in  $\kappa \in (0, \infty)$ ,

$$\lim_{\kappa \rightarrow 0} \underline{v}_1(\kappa) = -\max_{\tilde{x} \in \mathcal{X}} \frac{1}{\omega} \int_0^\omega f(\tilde{x}(t), t) dt, \quad \lim_{\kappa \rightarrow 0} \bar{v}_1(\kappa) = -\max_{x \in \bar{\Omega}} \frac{1}{\omega} \int_0^\omega f(x, t) dt,$$

and

$$\lim_{\kappa \rightarrow \infty} \underline{v}_1(\kappa) = \lim_{\kappa \rightarrow \infty} \bar{v}_1(\kappa) = -\frac{1}{\omega|\Omega|} \int_0^\omega \int_\Omega f(x, t) dx dt.$$

- (v) If  $f(x, t) := \tilde{f}(x)$  with  $\tilde{f} \in L^\infty(\Omega)$  is non-constant, then  $v_1(\chi, \kappa, \tilde{f})$  is strictly increasing in  $\kappa \in (0, \infty)$ , and has the following variational characterization

$$v_1(\chi, \kappa, \tilde{f}) = \inf_{0 \neq \varphi \in H^1(\Omega)} \frac{\kappa \int_\Omega |\nabla \varphi|^2 - \int_\Omega \tilde{f} \varphi^2}{\int_\Omega \varphi^2}.$$

**Proof** The proof for assertions (i)-(iii) can be found in [14, Theorem 2.4] and [2, Lemma 2.15] (see also [18]). Assertion (iv) comes from [18, Lemma 3.2]. Assertion (v) is a consequence of [2, Theorem 2.1 and Corollary 2.2]. □

Next, we consider a weighted elliptic eigenvalue problem

$$\begin{cases} \Delta \psi + \lambda w(x) \psi = 0, & x \in \Omega, \\ \partial_{\bar{n}} \psi = 0, & x \in \partial\Omega, \end{cases} \tag{3.3}$$

where  $w \in L^\infty(\Omega)$  is non-constant.  $\lambda$  is called a principal eigenvalue to (3.3) provided that (3.3) admits a positive solution. Clearly, 0 is a principal eigenvalue to (3.3). Then we have the following conclusion from [23, Theorem 4.2].

**Proposition 3.2** *Suppose that  $w \in L^\infty(\Omega)$ . Then problem (3.3) admits a nonzero real principal eigenvalue  $\lambda_1(w)$  if and only if  $w$  changes sign and  $\int_\Omega w \neq 0$ . Precisely, if  $w$  changes sign, then  $\text{sign} \lambda_1(w) = -\text{sign}(\int_\Omega w)$ . Moreover, for  $\int_\Omega w < 0$ ,  $\lambda_1(w)$  is continuous in  $w$  and has the following variational characterization:*

$$\lambda_1(w) = \inf \left\{ \frac{\int_\Omega |\nabla \psi|^2}{\int_\Omega w \psi^2} \mid \psi \in H^1(\Omega) \text{ and } \int_\Omega w \psi^2 > 0 \right\}.$$

The following results of [23, Proposition 4.4] show the relationship between  $v_1(\chi, \kappa, f)$  and  $\lambda_1(f)$  when  $f$  is independent of  $t$ .

**Proposition 3.3** *Suppose that  $f \in L^\infty(\Omega)$ . Then the following assertions are true.*

- (i) If  $f \not\equiv 0$  and  $\int_\Omega f \geq 0$ , then  $v_1(\chi, \kappa, f) < 0$  for all  $\kappa > 0$ .
- (ii) If  $f$  changes sign and  $\int_\Omega f < 0$ , then  $\text{sign} v_1(\chi, \kappa, f) = \text{sign}(\kappa - 1/\lambda_1(f))$ .

### 3.2 Qualitative properties of semi-trivial periodic solutions

For the unique solution  $\theta_d$  of (1.4), the following estimate holds.

**Lemma 3.4** *Assume that (H1) holds. Then  $d \mapsto \theta_d(x, t)$  is a smooth mapping from  $\mathbb{R}_+$  to  $C^{2,1}(\overline{\Omega} \times [0, \omega])$ , and*

$$\frac{\min_{\overline{\Omega} \times [0, \omega]} N_R(x, t)}{\sigma} < \theta_d(x, t) < \frac{\max_{\overline{\Omega} \times [0, \omega]} N_R(x, t)}{\sigma}, \quad \forall x \in \overline{\Omega}, t \geq 0.$$

**Proof** The smoothness of  $\theta_d$  with respect to  $d$  follows from the implicit function theorem (cf. [2, Proposition 3.6]). By the definitions of upper and lower solutions of periodic parabolic problem (cf. [13, Definition 21.1] and [32, Definition 7.2]),

$$\tilde{\theta} := \frac{\max_{\overline{\Omega} \times [0, \omega]} N_R(x, t)}{\sigma} \quad \text{and} \quad \underline{\theta} := \frac{\min_{\overline{\Omega} \times [0, \omega]} N_R(x, t)}{\sigma}$$

are upper and lower solutions to (1.4), respectively. Then the method of upper-lower solutions yields the existence of solution  $\theta$  to (1.4), which together with the strong maximum principle implies that  $\underline{\theta} < \theta < \tilde{\theta}$  on  $\overline{\Omega} \times \mathbb{R}_+$ . By the uniqueness of solutions to (1.4), we have that  $\underline{\theta} < \theta_d < \tilde{\theta}$  on  $\overline{\Omega} \times \mathbb{R}_+$ .  $\square$

A direct calculation can show that for each  $x \in \overline{\Omega}$ , the following ODE

$$\begin{cases} p_t = N_R(x, t) - \sigma p, & t > 0, \\ p(x, t + \omega) = p(x, t), & t \geq 0, \end{cases} \tag{3.4}$$

admits a unique solution

$$p(x, t) = e^{-\sigma t} \left( \frac{\int_0^\omega e^{\sigma \varsigma} N_R(x, \varsigma) d\varsigma}{e^{\sigma \omega} - 1} + \int_0^t e^{\sigma \varsigma} N_R(x, \varsigma) d\varsigma \right), \quad t \geq 0.$$

Then by [1, Lemma 4.2], one has the following result about the asymptotic behavior of  $\theta_d$  as  $d \rightarrow 0$ .

**Lemma 3.5** *Assume that (H1) holds. Then*

$$\lim_{d \rightarrow 0} \|\theta_d - p\|_{C(\overline{\Omega} \times [0, \omega])} = 0. \tag{3.5}$$

*If  $N_R$  is further independent of  $t$ , then it follows that*

$$\lim_{d \rightarrow 0} \|\theta_d - N_R/\sigma\|_{C(\overline{\Omega})} = 0. \tag{3.6}$$

Next, we study the asymptotic behavior of  $\theta_d$  as  $d \rightarrow \infty$ . Note that the following ODE

$$\begin{cases} \xi_t = \frac{1}{|\Omega|} \int_{\Omega} N_R(x, t) dx - \sigma \xi, & t > 0, \\ \xi(t) = \xi(t + T), & t \geq 0, \end{cases} \tag{3.7}$$

admits a unique solution  $\xi(t) = \frac{1}{|\Omega|} \int_{\Omega} p(x, t) dx$ . Then we have the following result by a similar argument to the proof of [14, Lemma 3.7].

**Lemma 3.6** *Assume that (H1) holds. Then*

$$\lim_{d \rightarrow \infty} \|\theta_d - \xi\|_{C(\overline{\Omega} \times [0, \omega])} = 0. \tag{3.8}$$

*Especially, if  $N_R$  is independent of  $t$ , then*

$$\lim_{d \rightarrow \infty} \left\| \theta_d - \frac{1}{\sigma |\Omega|} \int_{\Omega} N_R(x) dx \right\|_{C(\overline{\Omega})} = 0. \tag{3.9}$$

### 3.3 Stability of semi-trivial periodic solutions

For the time-periodic two-species competition system, the long-time behavior of its solutions depends closely on the linear stability of semi-trivial periodic solutions by the theoretical framework of monotone semi-flows [13]. Though system (1.2) is non-monotone, we still can derive the persistence and extinction of the consumer population by studying the linear stability of the semi-trivial  $\omega$ -periodic solution (see Proposition 3.8).

Let  $(\check{Z}, \check{N})$  denote a  $\omega$ -periodic solution of (1.2). Then linearizing system (1.2) at  $(\check{Z}, \check{N})$ , we obtain

$$\begin{cases} \tau Z_t = \mu \Delta Z + \left( \frac{r\check{N}}{k + \check{N}} - c - 2g\check{Z} \right) Z + \frac{kr\check{Z}}{(k + \check{N})^2} N, & x \in \Omega, t > 0, \\ N_t = d \Delta N - \frac{r\check{N}}{\gamma(k + \check{N})} Z - \left( \sigma + \frac{kr\check{Z}}{\gamma(k + \check{N})^2} \right) N, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} Z = \partial_{\bar{n}} N = 0, & x \in \partial\Omega, t > 0. \end{cases} \tag{3.10}$$

Following the definition of stability in [13], we say that  $(\check{Z}, \check{N})$  is *linearly stable* if the moduli of all eigenvalues of the  $\omega$ -periodic solution map of (3.10) are smaller than 1;  $(\check{Z}, \check{N})$  is *linearly unstable* if the  $\omega$ -periodic solution map of (3.10) has an eigenvalue with modulus larger than 1.

Let  $\Pi$  be the  $\omega$ -periodic solution map of (3.10) with  $(\check{Z}, \check{N}) = (0, \theta_d)$ . Suppose that  $\lambda$  is an eigenvalue of  $\Pi$  with eigenfunction  $(\phi, \psi)$ . When  $\phi \neq 0$ ,  $\lambda$  is an eigenvalue of the  $\omega$ -periodic solution map of

$$\begin{cases} \tau Z_t = \mu \Delta Z + \left( \frac{r\theta_d}{k + \theta_d} - c \right) Z, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} Z = 0, & x \in \partial\Omega, t > 0, \end{cases} \tag{3.11}$$

while when  $\phi \equiv 0$ ,  $\lambda$  is an eigenvalue of the  $\omega$ -periodic solution map of

$$\begin{cases} N_t = d \Delta N - \sigma N, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} N = 0, & x \in \partial\Omega, t > 0. \end{cases} \tag{3.12}$$

By [13, Proposition 14.4], one obtains that  $\exp(-\omega \cdot v_1(1, d, -\sigma))$  is the simple eigenvalue with maximal modulus of the  $\omega$ -periodic solution map of (3.12). Notice that  $v_1(1, d, -\sigma) = \sigma > 0$ . Then all eigenvalues of the  $\omega$ -period solution map of (3.12) have moduli smaller than 1. Since  $\exp(-\omega \cdot v_1(\tau, \mu, \frac{r\theta_d}{k + \theta_d} - c))$  is the simple eigenvalue with maximal modulus of the  $\omega$ -periodic solution map of (3.11) by [13, Proposition 14.4], the linear stability of the semi-trivial  $\omega$ -periodic solution  $(0, \theta_d)$  is determined by the sign of  $v_1(\tau, \mu, \frac{r\theta_d}{k + \theta_d} - c)$ . Precisely, there holds that

**Lemma 3.7** *Assume that (H1) holds and all parameters except  $c$  are positive. Then the semi-trivial  $\omega$ -periodic solution  $(0, \theta_d)$  is linearly stable if  $v_1(\tau, \mu, \frac{r\theta_d}{k + \theta_d} - c) > 0$  and linearly unstable if  $v_1(\tau, \mu, \frac{r\theta_d}{k + \theta_d} - c) < 0$ .*

Now we can prove the following key dichotomous criterion determining the long-time dynamics of the solutions to (1.2) based on the sign of the principal eigenvalue  $v_1(\tau, \mu, \frac{r\theta_d}{k + \theta_d} - c)$ .

**Proposition 3.8** *Assume that (H1) holds and all parameters except  $c$  are positive. Then the following conclusions hold for system (1.2).*

- (i) If  $v_1(\tau, \mu, \frac{r\theta_d}{k+\theta_d} - c) \geq 0$ , then the semi-trivial  $\omega$ -periodic solution  $(0, \theta_d)$  is globally asymptotically stable.
- (ii) If  $v_1(\tau, \mu, \frac{r\theta_d}{k+\theta_d} - c) < 0$ , then system (1.2) is uniformly persistent. Moreover, when  $N_R$  is temporally heterogeneous, (1.2) has a positive  $\omega$ -periodic solution, while when  $N_R$  is temporally homogeneous, (1.2) has a positive steady state.

**Proof** We start by proving the assertion (i) with the assumption  $v_1(\tau, \mu, \frac{r\theta_d}{k+\theta_d} - c) \geq 0$ . Recall that  $\theta_d$  is defined by (1.4). Let  $\mathcal{N}(x, t)$  denote the unique solution of the following parabolic problem

$$\begin{cases} \mathcal{N}_t = d\Delta\mathcal{N} + N_R(x, t) - \sigma\mathcal{N}, & x \in \Omega, t > 0, \\ \partial_{\bar{n}}\mathcal{N} = 0, & x \in \partial\Omega, t > 0, \\ \mathcal{N}(x, 0) = N_I(x) \geq 0, & x \in \bar{\Omega}, \end{cases} \tag{3.13}$$

and define

$$\bar{U}(x, t) := \theta_d(x, t) + \eta e^{-\sigma t} \quad \text{and} \quad \underline{U}(x, t) := \theta_d(x, t) - \eta e^{-\sigma t}, \quad \forall x \in \bar{\Omega}, t \geq 0,$$

where  $\eta$  is a constant satisfying  $\eta \geq \max_{x \in \bar{\Omega}} |\theta_d(x, 0) - N_I(x)|$ . One can check that  $\bar{U}$  and  $\underline{U}$  are upper and lower solutions of (3.13), respectively. An application of the method of upper-lower solutions gives that  $\underline{U}(x, t) \leq \mathcal{N}(x, t) \leq \bar{U}(x, t)$  on  $\bar{\Omega} \times \mathbb{R}_+$ , which implies that

$$\lim_{t \rightarrow \infty} \|\mathcal{N}(x, t) - \theta_d(x, t)\|_{C(\bar{\Omega})} = 0. \tag{3.14}$$

The comparison principle also indicates that  $N(x, t) \leq \mathcal{N}(x, t)$  for all  $(x, t) \in \bar{\Omega} \times \mathbb{R}_+$ . Then  $Z$  satisfies

$$\begin{cases} \tau Z_t \leq \mu \Delta Z + Z \left( \frac{r\mathcal{N}}{k + \mathcal{N}} - c - gZ \right), & x \in \Omega, t > 0, \\ \partial_{\bar{n}} Z = 0, & x \in \partial\Omega, t > 0. \end{cases} \tag{3.15}$$

Let  $\mathcal{Z}(x, t)$  be the solution of

$$\begin{cases} \tau \mathcal{Z}_t = \mu \Delta \mathcal{Z} + \mathcal{Z} \left( \frac{r\mathcal{N}}{k + \mathcal{N}} - c - g\mathcal{Z} \right), & x \in \Omega, t > 0, \\ \partial_{\bar{n}} \mathcal{Z} = 0, & x \in \partial\Omega, t > 0, \\ \mathcal{Z}(x, 0) = Z_I(x, t_0), & x \in \bar{\Omega}. \end{cases} \tag{3.16}$$

Thus, we obtain from the comparison principle that  $Z(x, t) \leq \mathcal{Z}(x, t)$  for  $(x, t) \in \bar{\Omega} \times [t_0, \infty)$ . By (3.14), the parabolic problem (3.16) is asymptotically periodic (cf. [43, Section 3.2]), and its limit equation is

$$\begin{cases} \tau \tilde{\mathcal{Z}}_t = \mu \Delta \tilde{\mathcal{Z}} + \tilde{\mathcal{Z}} \left( \frac{r\theta_d}{k + \theta_d} - c - g\tilde{\mathcal{Z}} \right), & x \in \Omega, t > 0, \\ \partial_{\bar{n}} \tilde{\mathcal{Z}} = 0, & x \in \partial\Omega, t > 0, \\ \tilde{\mathcal{Z}}(x, 0) = Z_I(x, t_0), & x \in \bar{\Omega}. \end{cases}$$

This, along with the theory for asymptotically periodic systems [43, Proposition 3.2.1], gives that

$$\lim_{t \rightarrow \infty} \|\mathcal{Z}(\cdot, t) - \tilde{\mathcal{Z}}(\cdot, t)\|_{C(\bar{\Omega})} = 0. \tag{3.17}$$

Since  $v_1(\tau, \mu, \frac{r\theta_d}{k+\theta_d} - c) \geq 0$ , by the criterion determining the persistence and extinction of periodic-parabolic logistic equation given in [13, Theorem 28.1], we have  $\lim_{t \rightarrow \infty} \tilde{\mathcal{Z}}(x, t) =$

0 uniformly for  $x \in \overline{\Omega}$ , which combined with (3.17) and the fact that  $Z \leq \mathcal{Z}$  implies that  $\lim_{t \rightarrow \infty} Z(x, t) = 0$  uniformly for  $x \in \overline{\Omega}$ . This yields that  $\frac{rNZ}{\gamma(k+N)} \rightarrow 0$  uniformly in  $\overline{\Omega}$  as  $t \rightarrow \infty$ . Then we conclude from the theory for asymptotically periodic systems [43, Proposition 3.2.1] that

$$\lim_{t \rightarrow \infty} \|N(\cdot, t) - \mathcal{N}(\cdot, t)\|_{C(\overline{\Omega})} = 0,$$

which along with (3.14) indicates that  $|N(x, t) - \theta_d(x, t)| \rightarrow 0$  uniformly in  $x \in \overline{\Omega}$  as  $t \rightarrow \infty$ . Hence,  $(0, \theta_d)$  is globally asymptotically stable. This finishes the proof of assertion (i).

Now we prove the assertion (ii) by assuming  $v_1(\tau, \mu, \frac{r\theta_d}{k+\theta_d} - c) < 0$ . By the weakly repelling property for the periodic-parabolic system [43, Proposition 7.1.1], there exists  $\epsilon > 0$  such that

$$\limsup_{t \rightarrow \infty} \left( \|Z(\cdot, t)\|_{C(\overline{\Omega})} + \|N(\cdot, t) - \theta_d(\cdot, t)\|_{C(\overline{\Omega})} \right) \geq \epsilon$$

for all  $Z_I \geq, \neq 0$  and  $N_I \geq 0$ , which means that  $(0, \theta_d)$  is a weak repeller for system (1.2). Then by the theory of uniform persistence (cf. [43, Theorem 1.3.1 and Remark 1.3.1]), an argument similar to the proof of [25, Theorem 2.5] or [26, Theorem 3.3] can be carried out to assert that system (1.2) is uniformly persistent for all  $Z_I \geq, \neq 0$  and  $N_I \geq 0$ . Finally, it follows from the theory for periodic coexistence states in infinite-dimensional periodic semi-flows [42, Theorem 2.3] that (1.2) has a positive  $\omega$ -periodic solution when  $N_R$  is temporally heterogeneous, while has a positive steady state when  $N_R$  is temporally homogeneous.  $\square$

### 4 Proof of Theorem 1.2 and Theorem 1.3

Proposition 3.8 demonstrates that the sign of  $v_1(\tau, \mu, \frac{r\theta_d}{k+\theta_d} - c)$  determines the long-time behavior of solutions to (1.2). In this section, we will establish the global dynamics of (1.2) by examining how the relaxation time and the dispersal rates impact the sign of  $v_1(\tau, \mu, \frac{r\theta_d}{k+\theta_d} - c)$ . We will achieve this by considering two distinct cases: temporally periodic and homogeneous inputs.

#### 4.1 Temporally periodic input (i.e. $N_R(x, t) = N_R(x, t + \omega)$ with $\omega > 0$ )

In this case, we investigate the effects of the relaxation time  $\tau$  and dispersal rate  $\mu$  on the sign of  $v_1(\tau, \mu, \frac{r\theta_d}{k+\theta_d} - c)$ . Define

$$\beta_d(x, t) := \frac{r\theta_d(x, t)}{k + \theta_d(x, t)}, \quad \forall x \in \overline{\Omega}, t \geq 0.$$

Let  $t = \omega s$  and  $\tilde{\beta}(x, s) = \beta_d(x, \omega s)$ . Note that the linear eigenvalue problem

$$\begin{cases} \tau \varphi_t - \mu \Delta \varphi - \beta_d(x, t) \varphi = v \varphi, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} \varphi = 0, & x \in \partial \Omega, t > 0, \\ \varphi(x, t + \omega) = \varphi(x, t), & x \in \Omega, t \geq 0 \end{cases} \tag{4.1}$$

admits a unique principal eigenvalue  $v_1(\tau, \mu, \beta_d)$ , associated with a positive eigenfunction  $\varphi_1 \in C_\omega^{2+\alpha, 1+\alpha/2}(\overline{\Omega} \times \mathbb{R}_+)$  satisfying  $\|\varphi_1\|_{L^2(\Omega \times (0, \omega))} = 1$ . Then the Krein-Rutman Theorem (cf. [15]) implies that  $(v_1(\tau, \mu, \beta_d), \varphi_1(x, \omega s))$  is the principal eigen-pair to the linear eigenvalue problem

$$\begin{cases} \frac{\tau}{\omega} \phi_s - \mu \Delta \phi - \tilde{\beta}(x, s) \phi = \nu \phi, & x \in \Omega, s > 0, \\ \partial_{\bar{n}} \phi = 0, & x \in \partial \Omega, s > 0, \\ \phi(x, s + 1) = \phi(x, s), & x \in \Omega, s \geq 0. \end{cases} \tag{4.2}$$

Recalling the constants  $\ell_1, \ell_2$  and  $\ell_3$  defined in (1.6), there holds that

$$\ell_1 = \frac{1}{|\Omega|} \int_{\Omega} \int_0^1 \tilde{\beta}(x, s) ds dx, \quad \ell_2 = \max_{x \in \bar{\Omega}} \int_0^1 \tilde{\beta}(x, s) ds \quad \text{and} \quad \ell_3 = \max_{\tilde{x} \in \tilde{\mathcal{X}}} \int_0^1 \tilde{\beta}(\tilde{x}(t), t) ds,$$

where  $\tilde{\mathcal{X}} := \{\tilde{x} \in C(\mathbb{R}_+; \bar{\Omega}) | \tilde{x}(s) = \tilde{x}(s + 1)\}$ . These three quantities play an important role in identifying the sign of  $\nu_1(\tau, \mu, \beta_d)$ .

**Lemma 4.1** *Let  $N_R$  satisfy (H1). Then  $-\ell_3 < \nu_1(\tau, \mu, \beta_d) < -\ell_1$  for all  $\mu, \tau > 0$ .*

**Proof** By Lemma 3.1 (i), we directly obtain that  $-\ell_3 \leq \nu_1(\tau, \mu, \beta_d) \leq -\ell_1$  for all  $\mu, \tau > 0$ . Next, we prove that  $\nu_1(\tau, \mu, \beta_d) \neq -\ell_1$ . Dividing the first equation in (4.2) by  $\varphi_1(x, \omega s)$  and integrating the result over  $\Omega \times (0, 1)$  yields that

$$-\mu \int_0^1 \int_{\Omega} \left| \frac{\nabla_x \varphi_1(x, \omega s)}{\varphi_1(x, \omega s)} \right| dx ds - \int_0^1 \int_{\Omega} \tilde{\beta}(x, s) dx ds = \nu_1(\tau, \mu, \beta_d) |\Omega|.$$

If  $\nu_1(\tau, \mu, \beta_d) = -\ell_1 = -\int_0^1 \int_{\Omega} \tilde{\beta}(x, s) dx ds$  for some  $\mu, \tau > 0$ , then  $\nabla_x \varphi_1(x, \omega s) \equiv 0$  and thus,  $\varphi_1(x, \omega s)$  does not depend on  $x$ . This together with the first equation in (4.2) implies that  $\tilde{\beta}(x, s)$  is independent of  $x$ , which is impossible since  $\theta_d$  depends on  $x$ . Hence,  $\nu_1(\tau, \mu, \beta_d) \neq -\ell_1$ .

It remains to show that  $\nu_1(\tau, \mu, \beta_d) > -\ell_3$ . Noticing that  $\beta_d(x, t) - \frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt = \tilde{\beta}(x, s) - \int_0^1 \tilde{\beta}(x, s) ds$ , we need to consider two cases.

*Case 1.*  $\beta_d(x, t) - \frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt$  depends on  $x$ . In this case, we deduce from Theorem A.1 that for each  $\mu > 0$ ,  $\frac{\partial \nu_1(\tau, \mu, \beta_d)}{\partial \tau} > 0$  for all  $\tau > 0$ . It follows from Lemma 3.1 (iv) that

$$\lim_{\tau \rightarrow 0} \nu_1(\tau, \mu, \beta_d) = \underline{\nu}_1(\mu, \beta_d),$$

where  $\underline{\nu}_1(\mu, \beta_d)$  is non-decreasing in  $\mu$  and  $\lim_{\mu \rightarrow 0} \underline{\nu}_1(\mu, \beta_d) = -\ell_3$ . Then  $\nu_1(\tau, \mu, \beta_d) > \underline{\nu}_1(\mu, \beta_d) \geq -\ell_3$  for all  $\mu, \tau > 0$ .

*Case 2.*  $\beta_d(x, t) - \frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt$  is independent of  $x$ . Since  $\beta_d(x, t)$  depends on  $x$ ,  $\frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt$  is non-constant. Let  $F(t) := \beta_d(x, t) - \frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt$ . Then  $\beta_d(x, t) = \frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt + F(t)$  with  $\int_0^{\omega} F(t) dt = 0$ . This combined with [13, Lemma 15.3] implies that  $\nu_1(\tau, \mu, \beta_d) = \nu_1(\tau, \mu, \frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt)$ , which is strictly increasing in  $\mu$  and  $\lim_{\mu \rightarrow 0} \nu_1(\tau, \mu, \frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt) = -\ell_2$  by Lemma 3.1 (iii) and (v). Moreover, by [3, Lemma B.1], there holds that

$$\begin{aligned} \ell_3 &= \max_{\tilde{x} \in \tilde{\mathcal{X}}} \frac{1}{\omega} \int_0^{\omega} \beta_d(\tilde{x}(t), t) dt = \frac{1}{\omega} \int_0^{\omega} \max_{x \in \bar{\Omega}} \beta_d(x, t) dt \\ &= \frac{1}{\omega} \int_0^{\omega} \max_{x \in \bar{\Omega}} \left( \frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt + F(t) \right) dt = \max_{x \in \bar{\Omega}} \frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt = \ell_2. \end{aligned}$$

Hence,  $\nu_1(\tau, \mu, \beta_d) = \nu_1(\tau, \mu, \frac{1}{\omega} \int_0^{\omega} \beta_d(x, t) dt) > -\ell_2 = -\ell_3$  for all  $\mu, \tau > 0$ .

In both cases above, we derive that  $\nu_1(\tau, \mu, \beta_d) > -\ell_3$  for all  $\mu, \tau > 0$ . The proof is completed.  $\square$

In view of Proposition 3.8, we can prove Theorem 1.2 concerning the persistence and extinction of the consumer population with the help of some results of [18] placed in the Appendix.

**Proof of Theorem 1.2** It is straightforward to see that  $v_1(\tau, \mu, \beta_d - c) = v_1(\tau, \mu, \beta_d) + c$  for any  $c \geq 0$  from (4.1). Then we have

$$v_1(\tau, \mu, \beta_d - c) \begin{cases} < 0 & \text{if } v_1(\tau, \mu, \beta_d) < -c, \\ = 0 & \text{if } v_1(\tau, \mu, \beta_d) = -c, \\ > 0 & \text{if } v_1(\tau, \mu, \beta_d) > -c. \end{cases} \tag{4.3}$$

Suppose that  $0 \leq c \leq \ell_1$ . Then we derive from Lemma 4.1 that  $v_1(\tau, \mu, \beta_d) < -\ell_1 \leq -c$  for all  $\mu, \tau > 0$ . Hence system (1.2) is uniformly persistent by (4.3) and Proposition 3.8 (ii), and  $\Lambda_p = (0, \infty)^2$ . Part (i) is proved.

Suppose that  $\ell_1 < c < \ell_2$ , that is,  $-\ell_2 < -c < -\ell_1$ . Then we obtain from Theorem A.2 (ii) (see Appendix) that there are two constants  $\mu_*, \mu^*$  with  $\mu^* \geq \mu_* > 0$  and a unique continuous function  $\tilde{\tau} : (\mu_*, \mu^*) \rightarrow [0, \infty)$  so that  $v_1(\tilde{\tau}(\mu), \mu, \beta_d) \equiv -c$ , where  $\mu^*$  satisfies  $\mu^* \rightarrow \infty$  as  $c \rightarrow \ell_1, \mu^* \rightarrow 0$  as  $c \rightarrow \ell_3$  and  $v_1(\tau, \mu^*, \beta_d) \rightarrow -c$  as  $\tau \rightarrow 0$ , and  $\tilde{\tau}$  satisfies  $\tilde{\tau}(\mu^*) = 0, \tilde{\tau}(\mu) > 0$  for  $\mu \in (\mu_*, \mu^*)$  and  $\tilde{\tau}(\mu) \rightarrow \infty$  as  $\mu \rightarrow \mu_*$ . Especially, if  $\beta_d(x, t) - \frac{1}{\omega} \int_0^\omega \beta_d(x, t) dt = \tilde{\beta}(x, s) - \int_0^1 \tilde{\beta}(x, s) ds$  is independent of  $x \in \Omega$ , then  $v_1(\tau, \mu^*, \beta_d) \equiv -c$  for all  $\tau > 0$ , i.e.,  $\mu_* = \mu^*$ . It follows from Theorem A.1 that for each  $\mu > 0, v_1(\tau, \mu, \beta_d)$  is non-decreasing with respect to  $\tau$ , and either  $\frac{\partial v_1(\tau, \mu, \beta_d)}{\partial \tau} > 0$  for all  $\tau > 0$ , or  $\frac{\partial v_1(\tau, \mu, \beta_d)}{\partial \tau} \equiv 0$ . Moreover,  $\frac{\partial v_1(\tau, \mu, \beta_d)}{\partial \tau} \equiv 0$  if and only if  $\tilde{\beta} - \int_0^1 \tilde{\beta} ds$  does not depend on  $x$ . Thus, we deduce that  $v_1(\tau, \mu, \beta_d) < -c$  if  $(\mu, \tau) \in [(0, \mu_*] \times (0, \infty)] \cup [(\mu_*, \mu^*) \times (0, \tilde{\tau}(\mu))]$ , and  $v_1(\tau, \mu, \beta_d) \geq -c$  if  $(\mu, \tau) \in [(\mu_*, \mu^*) \times [\tilde{\tau}(\mu), \infty)] \cup [(\mu^*, \infty) \times (0, \infty)]$ . Then by (4.3) and Proposition 3.8, we obtain

$$\Lambda_p = [(0, \mu_*] \times (0, \infty)] \cup [(\mu_*, \mu^*) \times (0, \tilde{\tau}(\mu))]$$
 and  $\Lambda_e = (0, \infty)^2 \setminus \Lambda_p$ ,

where  $\Lambda_p$  and  $\Lambda_e$  are defined in (1.7) and (1.8), respectively. Part (ii) is proved. Similarly, part (iii) can be obtained by Theorem A.1, Theorem A.2 (i) and Proposition 3.8.

Suppose that  $c \geq \ell_3$ . Then we see from Lemma 4.1 that  $v_1(\tau, \mu, \beta_d) > -\ell_3 \geq -c$  for all  $\mu, \tau > 0$ . This together with (4.3) shows that  $v_1(\tau, \mu, \beta_d - c) > 0$ . Hence  $(0, \theta_d)$  is globally asymptotically stable by Proposition 3.8 (i), and  $\Lambda_e = (0, \infty)^2$ .

Finally, the theory for periodic coexistence state in infinite-dimensional periodic semi-flows [42, Theorem 2.3] implies that system (1.2) has a positive  $\omega$ -periodic solution as long as it is uniformly persistent. This completes the proof of Theorem 1.2. □

### 4.2 Temporally homogeneous input (i.e. $N_R$ is independent of $t$ )

In this case, we simply write  $N_R(x, t) \equiv N_R(x)$ . Then  $\theta_d := \theta_d(x)$  is independent of  $t$  and satisfies the elliptic equation

$$\begin{cases} d\Delta\theta + N_R(x) - \sigma\theta = 0, & x \in \Omega, \\ \partial_{\bar{n}}\theta = 0, & x \in \partial\Omega. \end{cases} \tag{4.4}$$

Moreover,  $\beta_d(x, t) = \beta_d(x) = \frac{r\theta_d(x)}{k + \theta_d(x)}, \forall x \in \bar{\Omega}, t \geq 0$ .

We first prove the following simple fact.

**Lemma 4.2** For the constants  $c_1, c_2$  and  $c_3$  defined in (1.9), we have  $c_1 < c_2 < c_3$ .

**Proof** Since  $N_R$  is spatially heterogeneous, it holds that  $\frac{1}{|\Omega|} \int_{\Omega} N_R < \max_{\overline{\Omega}} N_R$  and hence  $c_2 < c_3$ . Noticing that

$$\begin{aligned} & \int_{\Omega} \frac{N_R}{k\sigma + N_R} - \int_{\Omega} \frac{\bar{N}_R}{k\sigma + \bar{N}_R} = \int_{\Omega} \frac{k\sigma(N_R - \bar{N}_R)}{(k\sigma + N_R)(k\sigma + \bar{N}_R)} \\ & = \frac{k\sigma}{k\sigma + \bar{N}_R} \int_{\Omega} \frac{(N_R - \bar{N}_R)(k\sigma + \bar{N}_R)}{(k\sigma + N_R)(k\sigma + \bar{N}_R)} - \frac{k\sigma}{k\sigma + \bar{N}_R} \int_{\Omega} \frac{(k\sigma + N_R)(N_R - \bar{N}_R)}{(k\sigma + N_R)(k\sigma + \bar{N}_R)} \\ & = -\frac{k\sigma}{k\sigma + \bar{N}_R} \int_{\Omega} \frac{(N_R - \bar{N}_R)^2}{(k\sigma + N_R)(k\sigma + \bar{N}_R)} = -\frac{k\sigma}{(k\sigma + \bar{N}_R)^2} \int_{\Omega} \frac{(N_R - \bar{N}_R)^2}{k\sigma + N_R} < 0, \end{aligned} \tag{4.5}$$

where  $\bar{N}_R = \frac{1}{|\Omega|} \int_{\Omega} N_R(x)dx$  and the last inequality holds due to the spatial heterogeneity of  $N_R$ , we have  $c_1 < c_2$ . Hence,  $c_1 < c_2 < c_3$ .  $\square$

When  $N_R$  is temporally homogeneous (i.e.  $N_R(x, t) \equiv N_R(x)$ ), the principal eigenvalue  $v_1(\tau, \mu, \beta_d - c) = v_1(0, \mu, \beta_d - c) := \tilde{v}_1(\mu, \beta_d - c)$  is independent of  $\tau$  and strictly increases with respect to the dispersal rate  $\mu$  (see Lemma 3.1 (v)). With this property, we can explore the effects of  $\mu, d$  on the dynamics of (1.2). For simplicity, we shall drop the tilde from  $\tilde{v}_1$  in the rest of this subsection without ambiguity. Then we prove Theorem 1.3 on the persistence and extinction of the consumer population for the case  $N_R(x, t) \equiv N_R(x)$ .

**Proof of Theorem 1.3** We fix all parameters except  $\mu$  and  $d$ . For part (i), we suppose that  $c \in [0, c_1]$ . Dividing the equation of  $\theta_d$  (see (4.4)) by  $\sigma(k + \theta_d)^2$ , we obtain that

$$\frac{d\Delta\theta_d}{\sigma(k + \theta_d)^2} + \frac{k + N_R/\sigma}{(k + \theta_d)^2} - \frac{1}{k + \theta_d} = 0, \quad x \in \Omega.$$

Then integrating the above equality over  $\Omega$  and using the divergence theorem, we have

$$\int_{\Omega} \frac{2d}{\sigma(k + \theta_d)^3} |\nabla\theta_d|^2 + \int_{\Omega} \frac{k + N_R/\sigma}{(k + \theta_d)^2} - \int_{\Omega} \frac{1}{k + \theta_d} = 0.$$

Thus, there holds that

$$\int_{\Omega} \frac{k + N_R/\sigma}{(k + \theta_d)^2} < \int_{\Omega} \frac{1}{k + \theta_d}, \tag{4.6}$$

where the inequality is strict since  $\nabla\theta_d \neq 0$ . It follows from Hölder’s inequality that

$$\int_{\Omega} \frac{1}{k + \theta_d} \leq \left( \int_{\Omega} \frac{k + N_R/\sigma}{(k + \theta_d)^2} \right)^{\frac{1}{2}} \left( \int_{\Omega} \frac{1}{k + N_R/\sigma} \right)^{\frac{1}{2}} < \left( \int_{\Omega} \frac{1}{k + \theta_d} \right)^{\frac{1}{2}} \left( \int_{\Omega} \frac{1}{k + N_R/\sigma} \right)^{\frac{1}{2}},$$

where the last inequality results from (4.6). Hence,

$$\int_{\Omega} \frac{1}{k + \theta_d(x)} < \int_{\Omega} \frac{1}{k + N_R(x)/\sigma}, \quad \forall d > 0,$$

which implies that

$$c_1 < \frac{1}{|\Omega|} \int_{\Omega} \beta_d(x), \quad \forall d > 0. \tag{4.7}$$

By the assumption  $c \in [0, c_1]$  and Lemma 3.1 (iii) and (v), we conclude that

$$v_1(\mu, \beta_d - c) < c - \frac{1}{|\Omega|} \int_{\Omega} \beta_d(x) \leq c_1 - \frac{1}{|\Omega|} \int_{\Omega} \beta_d(x) < 0$$

for all  $\mu, d > 0$ . Therefore, system (1.2) is uniformly persistent for all  $\mu, d > 0$  by Proposition 3.8, i.e.,  $\Gamma_p = (0, \infty)^2$ . This proves part (i).

For part (ii), we suppose that  $c = c_2$ . Noting that  $\int_{\Omega} \theta_d(x) dx = \int_{\Omega} N_R(x) dx / \sigma$  for all  $d > 0$ , we deduce that  $\max_{\overline{\Omega}} \theta_d > \frac{1}{\sigma|\Omega|} \int_{\Omega} N_R$ , and hence

$$\max_{\overline{\Omega}} \beta_d = \frac{r \max_{\overline{\Omega}} \theta_d}{k + \max_{\overline{\Omega}} \theta_d} > \frac{r \int_{\Omega} N_R}{k\sigma|\Omega| + \int_{\Omega} N_R} = c_2 \quad \text{for all } d > 0.$$

Similar to (4.5), we have  $\bar{h}(d) < c_2$  for all  $d > 0$ , where  $\bar{h}(d)$  is defined in (1.10). Moreover,  $\lim_{d \rightarrow 0} \bar{h}(d) = c_1$  by Lemma 3.5, and  $\lim_{d \rightarrow \infty} \bar{h}(d) = c_2$  by Lemma 3.6. These results indicate that  $\beta_d - c$  changes sign in  $x \in \overline{\Omega}$  for all  $d \geq 0$ , which together with Proposition 3.2 implies that  $\lambda_1(\beta_d - c) > 0$  for  $d \in [0, \infty)$ ,  $\lim_{d \rightarrow \infty} \lambda_1(\beta_d - c) = 0$ , and  $\lambda_1(\beta_d - c)$  is a continuous function of  $d \in [0, \infty)$ . Define

$$\mathcal{U}(d) := \frac{1}{\lambda_1(\beta_d - c)}, \quad \forall d \in [0, \infty).$$

Then we obtain from Proposition 3.3 (ii) that for any  $d > 0$ ,

$$\text{sign } v_1(\mu, \beta_d - c) = \text{sign}(\mu - \mathcal{U}(d)). \tag{4.8}$$

Moreover,  $\lim_{d \rightarrow \infty} \mathcal{U}(d) = \infty$ . Therefore, by Proposition 3.8, system (1.2) is uniformly persistent for  $(d, \mu) \in (0, \infty) \times (0, \mathcal{U}(d))$ , and  $(0, \theta_d)$  is globally asymptotically stable for  $(d, \mu) \in (0, \infty) \times [\mathcal{U}(d), \infty)$ . That is,  $\Gamma_p = (0, \infty) \times (0, \mathcal{U}(d))$  and  $\Gamma_e = (0, \infty) \times [\mathcal{U}(d), \infty)$ . This proves part (ii).

For part (iii), we suppose that  $c \in [c_3, \infty)$ . Then Lemmas 3.1 and 3.4 indicate that

$$v_1(\mu, \beta_d - c) > c - \frac{r \max_{\overline{\Omega}} N_R}{k\sigma + \max_{\overline{\Omega}} N_R} = c - c_3 \geq 0, \quad \forall \mu, d > 0.$$

Hence,  $(0, \theta_d)$  is globally asymptotically stable for all  $\mu, d > 0$  by Proposition 3.8 (i), i.e.,  $\Gamma_e = (0, \infty)^2$ . This proves part (iii).

For part (iv), we suppose that  $c \in (c_1, c_2)$ . The proof of part (ii.b) gives that

$$\max_{x \in \overline{\Omega}} \beta_d(x) > c_2 > \bar{h}(d), \quad \forall d > 0.$$

Then by (4.7) and Lemmas 3.4-3.6, we get

$$\lim_{d \rightarrow 0} \bar{h}(d) = c_1 < \bar{h}(d) < c_2 = \lim_{d \rightarrow \infty} \bar{h}(d), \quad \forall d > 0,$$

which implies that for any  $c \in (c_1, c_2)$ ,  $\bar{h}(d) = c$  has at least one positive root. Let  $d_{\bar{h}_1}$  and  $d_{\bar{h}_2}$  denote the smallest and largest positive roots of  $\bar{h}(d) = c$ , respectively. Thus,  $\bar{h}(d) < c$  for  $d \in (0, d_{\bar{h}_1})$  and  $\bar{h}(d) > c$  for  $d \in (d_{\bar{h}_2}, \infty)$ . When  $d \geq d_{\bar{h}_2}$ , by Lemma 3.1 (iii) and (v), there holds that

$$v_1(\mu, \beta_d - c) < c - \bar{h}(d) \leq 0, \quad \forall \mu > 0, \tag{4.9}$$

which implies that  $(0, \theta_d)$  is linearly unstable for all  $\mu > 0$  and  $d \geq d_{\bar{h}_2}$ .

When  $d \in (0, d_{\bar{h}_1})$ ,  $\bar{h}(d) < c$  and  $\beta_d - c$  changes sign in  $x \in \overline{\Omega}$ . Then by Lemma 3.1 and Proposition 3.2, we infer that  $\lambda_1(\beta_d - c)$  is a continuous function of  $d \in [0, \infty)$ ,  $\lambda_1(\beta_{d_{\bar{h}_1}} - c) = 0$  and  $\lambda_1(\beta_d - c) > 0$  for all  $d \in [0, d_{\bar{h}_1})$ . Define

$$\mathcal{U}_1(d) := \frac{1}{\lambda_1(\beta_d - c)}, \quad \forall d \in [0, d_{\bar{h}_1}). \tag{4.10}$$

From Proposition 3.3 (ii), we obtain that when  $d \in (0, d_{h_1})$ ,

$$\text{sign } v_1(\mu, \beta_d - c) = \text{sign}(\mu - \mathcal{U}_1(d)). \tag{4.11}$$

Moreover,  $\mathcal{U}_1(d) > 0$  for  $d \in [0, d_{h_1})$  and  $\lim_{d \nearrow d_{h_1}} \mathcal{U}_1(d) = \infty$ . Denote

$$\check{\mu} := \frac{1}{\sup_{d>0} \lambda_1(\beta_d - c)}.$$

Here  $0 < \check{\mu} \leq \mathcal{U}_1(d) < \infty$  for  $d \in (0, d_{h_1})$  by the previous argument. For  $0 < \mu < \check{\mu}$ , we define two sets

$$\mathcal{U}_1 := \{d > 0 | h(d) \geq c\} \quad \text{and} \quad \mathcal{U}_2 := \{d > 0 | h(d) < c\}.$$

Since  $\max_{x \in \bar{\Omega}} \beta_d - c > 0$  for all  $d > 0$ , it follows from Proposition 3.3 (i) that for  $d \in \mathcal{U}_1$ ,  $v_1(\mu, \beta_d - c) < 0$  for all  $\mu > 0$ , while for  $d \in \mathcal{U}_2$ ,  $\beta_d - c > 0$  changes sign and  $v_1(\mu, \beta_d - c) < 0$  for  $0 < \mu < \check{\mu} \leq \frac{1}{\lambda_1(\beta_d - c)}$ . Hence, when  $0 < \mu < \check{\mu}$ ,  $v_1(\mu, \beta_d - c) < 0$  for all  $d > 0$ . Therefore, it follows from Proposition 3.8 that system (1.2) is uniformly persistent for  $(d, \mu) \in \Gamma_1$ , where

$$\Gamma_1 := [(0, d_{h_1}) \times [\check{\mu}, \mathcal{U}_1(d)]] \cup [(0, d_{h_2}) \times (0, \check{\mu})] \cup [d_{h_2}, \infty) \times (0, \infty)],$$

and  $(0, \theta_d)$  is globally asymptotically stable for  $(d, \mu) \in \Gamma_2 := (0, d_{h_1}) \times [\mathcal{U}_1(d), \infty)$ . That is,  $\Gamma_1 \subset \Gamma_p$  and  $\Gamma_2 \subset \Gamma_e$ .

To prove the remainder of part (iv), we need to consider the positive roots of  $h(d) = c$ . If  $d_{h_1} = d_{h_2}$  (i.e.,  $h(d) = c$  has only one root), then we immediately obtain that

$$\Gamma_1 \cup \Gamma_2 = (0, \infty)^2.$$

If  $d_{h_1} \neq d_{h_2}$  (i.e.  $h(d) = c$  has at least two roots), then there are two constants  $l_{\bar{h}}, r_{\bar{h}}$  with  $l_{\bar{h}} < r_{\bar{h}}$  and  $h(l_{\bar{h}}) = h(r_{\bar{h}}) = c$ , such that either (1.13) holds, or (1.14) holds. Next, we consider two cases.

Case 1. (1.13) holds. In this case, we derive from Lemma 3.1 (iii) and (v) that (4.9) still holds for  $d \in [l_{\bar{h}}, r_{\bar{h}}]$ . Hence, by Proposition 3.8 (ii), system (1.2) is uniformly persistent for  $(d, \mu) \in [l_{\bar{h}}, r_{\bar{h}}] \times [\check{\mu}, \infty)$ , i.e.,  $[l_{\bar{h}}, r_{\bar{h}}] \times [\check{\mu}, \infty) \subset \Gamma_p$ .

Case 2. (1.14) holds. Since  $\max_{\bar{\Omega}} \beta_d > c_2 > c$  for all  $d > 0$ , we infer that  $\beta_d - c$  changes sign in  $x \in \bar{\Omega}$  for  $d \in (l_{\bar{h}}, r_{\bar{h}})$ . Then it follows from Proposition 3.2 that  $\lambda_1(\beta_{l_{\bar{h}}} - c) = \lambda_1(\beta_{r_{\bar{h}}} - c) = 0$  and  $\lambda_1(\beta_d - c) > 0$  for  $d \in (l_{\bar{h}}, r_{\bar{h}})$ . Define

$$\mathcal{U}_{\bar{h}}(d) := \frac{1}{\lambda_1(\beta_d - c)}, \quad \forall d \in (l_{\bar{h}}, r_{\bar{h}}).$$

From Proposition 3.3 (ii), we obtain that when  $d \in (l_{\bar{h}}, r_{\bar{h}})$ ,

$$\text{sign } v_1(\mu, \beta_d - c) = \text{sign}(\mu - \mathcal{U}_{\bar{h}}(d)).$$

Moreover,  $\mathcal{U}_{\bar{h}}(d) \geq \check{\mu}$  for  $d \in (l_{\bar{h}}, r_{\bar{h}})$  and  $\lim_{d \searrow l_{\bar{h}}} \mathcal{U}_{\bar{h}}(d) = \lim_{d \nearrow r_{\bar{h}}} \mathcal{U}_{\bar{h}}(d) = \infty$ . Therefore, we obtain from Proposition 3.8 that system (1.2) is uniformly persistent for  $(d, \mu) \in (l_{\bar{h}}, r_{\bar{h}}) \times [\check{\mu}, \mathcal{U}_{\bar{h}}(d))$ , and  $(0, \theta_d)$  is globally asymptotically stable for  $(d, \mu) \in (l_{\bar{h}}, r_{\bar{h}}) \times [\mathcal{U}_{\bar{h}}(d), \infty)$ . That is,  $(l_{\bar{h}}, r_{\bar{h}}) \times [\check{\mu}, \mathcal{U}_{\bar{h}}(d)) \subset \Gamma_p$  and  $(l_{\bar{h}}, r_{\bar{h}}) \times [\mathcal{U}_{\bar{h}}(d), \infty) \subset \Gamma_e$ . This proves part (iv).

For part (v), we suppose that  $c \in (c_2, c_3)$ . It follows from Lemmas 3.5 and 3.6 that

$$\begin{aligned} \lim_{d \rightarrow \infty} \max_{\bar{\Omega}} \beta_d(x) &= \lim_{d \rightarrow \infty} \frac{r \max_{\bar{\Omega}} \theta_d}{k + \max_{\bar{\Omega}} \theta_d} = \frac{r \int_{\Omega} N_R}{k\sigma + \int_{\Omega} N_R} = c_2, \\ \lim_{d \rightarrow 0} \max_{\bar{\Omega}} \beta_d(x) &= \lim_{d \rightarrow 0} \frac{r \max_{\bar{\Omega}} \theta_d}{k + \max_{\bar{\Omega}} \theta_d} = \frac{r \max_{\bar{\Omega}} N_R}{k\sigma + \max_{\bar{\Omega}} N_R} = c_3. \end{aligned} \tag{4.12}$$

By (4.12), we see that  $\max_{x \in \bar{\Omega}} \beta_d(x) = c$  admits at least one positive root. Let  $d_{\beta_1}$  and  $d_{\beta_2}$  denote the smallest and largest positive roots of  $\max_{\bar{\Omega}} \beta_d = c$ , respectively. Then  $\max_{\bar{\Omega}} \beta_d - c < 0$  for  $d > d_{\beta_2}$ , which combined with Lemma 3.1 (i) and (v) yields that

$$v_1(\mu, \beta_d - c) > c - \max_{\bar{\Omega}} \beta_d \geq 0 \quad \text{for all } \mu > 0, d \geq d_{\beta_2}. \tag{4.13}$$

Next, we discuss the sign of  $v_1(\mu, \beta_d - c)$  when  $0 < d < d_{\beta_2}$ . By Lemmas 3.1 and 3.5, we have that

$$\begin{aligned} \lim_{d \rightarrow 0} \lim_{\mu \rightarrow 0} v_1(\mu, \beta_d - c) &= c - \frac{r \max_{\bar{\Omega}} N_R}{k\sigma + \max_{\bar{\Omega}} N_R} = c - c_3 < 0, \\ \lim_{\mu \rightarrow 0} v_1(\mu, \beta_d - c) &= c - \max_{\bar{\Omega}} \beta_d > 0 \quad \text{for all } d > d_{\beta_2}, \end{aligned}$$

and

$$\lim_{\mu \rightarrow \infty} v_1(\mu, \beta_d - c) = c - \frac{1}{|\Omega|} \int_{\Omega} \beta_d(x) > c_2 - h(d) > 0 \quad \text{for all } d > 0. \tag{4.14}$$

Thus, there exists  $(d, \mu) \in (0, d_{\beta_2}] \times (0, \infty)$  such that  $v_1(\mu, \beta_d - c) = 0$ .

**Claim 4.1** Define

$$\hat{\mu} = \sup \left\{ \mu > 0 \mid d \in (0, d_{\beta_2}], v_1(\mu, \beta_d - c) = 0 \right\}. \tag{4.15}$$

Then  $\hat{\mu}$  is positive and finite.

The positivity of  $\hat{\mu}$  is obvious. It remains to prove the finiteness of  $\hat{\mu}$ . The variational characterization of  $v_1(\mu, \beta_d - c)$  gives that

$$\begin{aligned} v_1(\mu, \beta_d - c) &= \inf_{0 \neq \varphi \in H^1(\Omega)} \frac{\mu \int_{\Omega} |\nabla \varphi|^2 - \int_{\Omega} (\beta_d - c) \varphi^2}{\int_{\Omega} \varphi^2} \\ &= \inf_{0 \neq \varphi \in H^1(\Omega)} \left( \frac{\mu \int_{\Omega} |\nabla \varphi|^2 - \int_{\Omega} (\frac{rN_R}{k\sigma + N_R} - c) \varphi^2}{\int_{\Omega} \varphi^2} + \frac{\int_{\Omega} (\frac{rN_R}{k\sigma + N_R} - \beta_d) \varphi^2}{\int_{\Omega} \varphi^2} \right) \\ &\geq \inf_{0 \neq \varphi \in H^1(\Omega)} \frac{\mu \int_{\Omega} |\nabla \varphi|^2 - \int_{\Omega} (\frac{rN_R}{k\sigma + N_R} - c) \varphi^2}{\int_{\Omega} \varphi^2} - \sup_{0 \neq \varphi \in H^1(\Omega)} \left| \frac{\int_{\Omega} (\frac{rN_R}{k\sigma + N_R} - \beta_d) \varphi^2}{\int_{\Omega} \varphi^2} \right|. \end{aligned}$$

Denote

$$I_1 := \frac{\mu \int_{\Omega} |\nabla \varphi|^2 - \int_{\Omega} (\frac{rN_R}{k\sigma + N_R} - c) \varphi^2}{\int_{\Omega} \varphi^2} \quad \text{and} \quad I_2 := \left| \frac{\int_{\Omega} (\frac{rN_R}{k\sigma + N_R} - \beta_d) \varphi^2}{\int_{\Omega} \varphi^2} \right|.$$

Since  $\theta_d \rightarrow N_R/\sigma$  in  $C(\bar{\Omega})$  as  $d \rightarrow 0$  by Lemma 3.5, there holds that

$$I_2 \leq \max_{x \in \bar{\Omega}} \left| \frac{rN_R}{k\sigma + N_R} - \beta_d \right| \leq \max_{x \in \bar{\Omega}} \left| \frac{rk\sigma}{(k\sigma + N_R)(k + \theta_d)} \right| \cdot \max_{x \in \bar{\Omega}} |\theta_d - N_R/\sigma| \rightarrow 0$$

as  $d \rightarrow 0$  for any  $\varphi \in H^1(\Omega)$ , which implies that for any  $\varphi \in H^1(\Omega)$ ,  $I_2 < \frac{c_2 - c_1}{2}$  for  $0 < d < d_s$  with  $d_s > 0$  being a sufficiently small constant independent of  $\varphi$ . By Lemma 3.1, we have

$$\begin{aligned} \lim_{\mu \rightarrow \infty} \inf_{0 \neq \varphi \in H^1(\Omega)} I_1 &= \lim_{\mu \rightarrow \infty} v_1\left(\mu, \frac{rN_R}{k\sigma + N_R} - c\right) \\ &= c - \frac{1}{|\Omega|} \int_{\Omega} \frac{rN_R(x)}{k\sigma + N_R(x)} dx = c - c_1 > c_2 - c_1. \end{aligned}$$

Then there exists a constant  $\mu_1 > 0$  independent of  $d$  such that  $\inf_{0 \neq \varphi \in H^1(\Omega)} I_1 > c_2 - c_1 > 0$  for  $\mu > \mu_1$ . This means that for any  $d \in (0, d_s)$  and  $\mu > \mu_1$ , it holds that

$$v_1(\mu, \beta_d - c) \geq \inf_{0 \neq \varphi \in H^1(\Omega)} I_1 - \sup_{0 \neq \varphi \in H^1(\Omega)} I_2 \geq c_2 - c_1 - \frac{c_2 - c_1}{2} = \frac{c_2 - c_1}{2} > 0.$$

Thus, for any  $d \in (0, d_s)$ , the constant  $\mu(d)$  satisfying  $v_1(\mu(d), \beta_d - c) = 0$  is not greater than  $\mu_1$ . On the other hand, since  $v_1(\mu, \beta_d - c)$  is continuous in  $\mu$  and  $d$ , we infer from (4.14) that for any  $d \in [d_s, d_{\beta_2}]$ , the constant  $\mu(d)$  satisfying  $v_1(\mu(d), \beta_d - c) = 0$  is finite. Hence, the constant  $\hat{\mu}$  defined in (4.15) is finite. **Claim 4.1** is proved.

By (4.13), **Claim 4.1** and the monotonicity of  $v_1(\mu, \cdot)$  in  $\mu$ , we obtain that

$$v_1(\mu, \beta_d - c) > 0, \quad \forall (d, \mu) \in [(0, d_{\beta_2}) \times (\hat{\mu}, \infty)] \cup [[d_{\beta_2}, \infty) \times (0, \infty)]. \tag{4.16}$$

Next, we investigate the sign of  $v_1(\mu, \beta_d - c)$  when  $(d, \mu) \in (0, d_{\beta_1}) \times (0, \hat{\mu}]$ . As shown in part (ii.b), we have  $h(d) < c_2 < c$  for all  $d > 0$ . Notice that  $\lim_{d \rightarrow 0} h(d) = c_1 < c$  by Lemma 3.5. Since  $\max_{\bar{\Omega}} \beta_d - c > 0$  for  $0 \leq d < d_{\beta_1}$ , it follows from Proposition 3.2 that  $\lambda^*(d) := \lambda_1(\beta_d - c) > 0$  for each  $d \in [0, d_{\beta_1})$ . Next, we have the following claim.

**Claim 4.2**  $\lambda^*(d) \rightarrow \infty$  as  $d \nearrow d_{\beta_1}$ .

To prove **Claim 4.2**, by an argument of contradiction, we suppose that taking a subsequence of  $d$  if necessary, there exists a positive constant  $C$  such that  $\lambda^*(d) \leq C$  for all  $d \in (0, d_{\beta_1})$ . According to the definition of  $\lambda^*(d)$ , it corresponds to a positive function  $\psi \in C^2(\bar{\Omega})$  satisfying that  $\|\psi\|_{L^\infty(\Omega)} = 1$  and

$$\begin{cases} \Delta \psi + \lambda^*(d)(\beta_d - c)\psi = 0, & x \in \Omega, \\ \partial_{\bar{n}} \psi = 0, & x \in \partial\Omega. \end{cases}$$

Then by the  $L^p$  theory of elliptic equations and the embedding theorem, taking a subsequence of  $d$  if necessary, we suppose that  $\lambda^*(d) \rightarrow \check{\lambda}$  for some nonnegative constant  $\check{\lambda}$  and  $\psi \rightarrow \check{\psi}$  in  $C^1(\bar{\Omega})$  as  $d \nearrow d_{\beta_1}$ , where  $\check{\psi}$  satisfies (weakly)

$$\begin{cases} \Delta \check{\psi} + \check{\lambda}(\beta_{d_{\beta_1}} - c)\check{\psi} = 0, & x \in \Omega, \\ \partial_{\bar{n}} \check{\psi} = 0, & x \in \partial\Omega. \end{cases}$$

If  $\check{\lambda} > 0$ , then integrating the equation of  $\check{\psi}$  yields that

$$\int_{\Omega} (\beta_{d_{\beta_1}} - c)\check{\psi} = 0.$$

This identity contradicts the fact that  $\check{\psi} > 0$ ,  $\max_{\bar{\Omega}} \beta_{d_{\beta_1}} - c = 0$  and  $\beta_{d_{\beta_1}} - c \not\equiv 0$  on  $\bar{\Omega}$ . If  $\check{\lambda} = 0$ , then  $\check{\psi}$  is a constant. Integrating the equation of  $\psi$  gives that

$$\int_{\Omega} (\beta_d - c)\psi = 0.$$

Letting  $d \nearrow d_{\beta_1}$ , we obtain that

$$\int_{\Omega} (\beta_{d_{\beta_1}} - c) = 0,$$

which contradicts the fact that  $\bar{h}(d) < c$  for all  $d > 0$ . This finishes the proof of **Claim 4.2**.

Define

$$\tilde{\mathcal{U}}_1(d) := \frac{1}{\lambda_1(\beta_d - c)}, \quad \forall d \in [0, d_{\beta_1}).$$

Since  $\bar{h}(d) - c < 0$  for all  $d > 0$  and  $\max_{\bar{\Omega}} \beta_d - c > 0$  for  $0 < d < d_{\beta_1}$ , we deduce from Proposition 3.3 (ii) that when  $d \in (0, d_{\beta_1})$ ,

$$\text{sign } v_1(\mu, \beta_d - c) = \text{sign}(\mu - \tilde{\mathcal{U}}_1(d)). \tag{4.17}$$

Moreover,  $\tilde{\mathcal{U}}_1(0) > 0$  and  $\lim_{d \rightarrow d_{\beta_1}} \tilde{\mathcal{U}}_1(d) = 0$  by **Claim 4.2**. The definition of  $\hat{\mu}$  in (4.15) implies that  $\hat{\mu} \geq \sup_{d \in (0, d_{\beta_1})} \tilde{\mathcal{U}}_1(d)$ . Therefore, it follows from (4.16), (4.17) and Proposition 3.8 that  $(0, \theta_d)$  is globally asymptotically stable for  $(d, \mu) \in \tilde{\Gamma}_1$ , where

$$\tilde{\Gamma}_1 := [(0, d_{\beta_1}) \times [\tilde{\mathcal{U}}_1(d), \hat{\mu}]] \cup [(0, d_{\beta_2}) \times (\hat{\mu}, \infty)] \cup [d_{\beta_2}, \infty) \times (0, \infty)],$$

and system (1.2) is uniformly persistent for  $(d, \mu) \in \tilde{\Gamma}_2 := (0, d_{\beta_1}) \times (0, \tilde{\mathcal{U}}_1(d))$ . That is,  $\tilde{\Gamma}_1 \subset \Gamma_e$  and  $\tilde{\Gamma}_2 \subset \Gamma_p$ .

To prove the remainder of part (v), we need to consider the positive roots of  $\max_{x \in \bar{\Omega}} \beta_d(x) = c$ . If  $d_{\beta_1} = d_{\beta_2}$  (i.e.  $\max_{\bar{\Omega}} \beta_d = c$  has only one root), then we immediately obtain that

$$\tilde{\Gamma}_1 \cup \tilde{\Gamma}_2 = (0, \infty)^2.$$

If  $d_{\beta_1} \neq d_{\beta_2}$  (i.e.  $\max_{\bar{\Omega}} \beta_d = c$  has at least two roots), then there are two constants  $l_\beta, r_\beta$  with  $l_\beta < r_\beta$  and  $\max_{\bar{\Omega}} \beta_{l_\beta} = \max_{\bar{\Omega}} \beta_{r_\beta} = c$  such that either (1.15) holds, or (1.16) holds. Next, we consider two cases.

Case 1. (1.15) holds. Since  $\bar{h}(d) < c_2 < c$  for all  $d > 0$ , we infer that  $\beta_d - c$  changes sign in  $x \in \bar{\Omega}$  for  $d \in (l_\beta, r_\beta)$ . Then it follows from Proposition 3.2 that  $\lambda_1(\beta_d - c) > 0$  for  $d \in (l_\beta, r_\beta)$ . In addition, by an argument similar to the proof of **Claim 4.2**, we deduce that  $\lim_{d \searrow l_\beta} \lambda_1(\beta_d - c) = \lim_{d \nearrow r_\beta} \lambda_1(\beta_d - c) = \infty$ . Define

$$\mathcal{U}_\beta(d) := \frac{1}{\lambda_1(\beta_d - c)}, \quad \forall d \in (l_\beta, r_\beta).$$

From Proposition 3.3 (ii), when  $d \in (l_\beta, r_\beta)$ , we obtain that

$$\text{sign } v_1(\mu, \beta_d - c) = \text{sign}(\mu - \mathcal{U}_\beta(d)).$$

Moreover,  $0 < \mathcal{U}_\beta(d) \leq \hat{\mu}$  for  $d \in (l_\beta, r_\beta)$  by **Claim 4.1**, and  $\mathcal{U}_\beta(l_\beta) = \mathcal{U}_\beta(r_\beta) = 0$ . Therefore, we obtain from Proposition 3.8 that system (1.2) is uniformly persistent for  $(d, \mu) \in (l_\beta, r_\beta) \times (0, \mathcal{U}_\beta(d))$ , and  $(0, \theta_d)$  is globally asymptotically stable for  $(d, \mu) \in (l_\beta, r_\beta) \times [\mathcal{U}_\beta(d), \hat{\mu}]$ . That is,  $(l_\beta, r_\beta) \times (0, \mathcal{U}_\beta(d)) \subset \Gamma_p$  and  $(l_\beta, r_\beta) \times [\mathcal{U}_\beta(d), \hat{\mu}] \subset \Gamma_e$ .  
Case 2. (1.16) holds. In this case, we obtain from Lemma 3.1 (iii) and (v) that

$$v_1(\mu, \beta_d - c) > c - \max_{\bar{\Omega}} \beta_d \geq 0 \quad \text{for all } (d, \mu) \in [l_\beta, r_\beta] \times (0, \hat{\mu}].$$

Hence, by Proposition 3.8 (i),  $(0, \theta_d)$  is globally asymptotically stable for  $(d, \mu) \in [l_\beta, r_\beta] \times (0, \hat{\mu}]$ , i.e.,  $[l_\beta, r_\beta] \times (0, \hat{\mu}] \subset \Gamma_e$ . This proves part (v).

Finally, the theory for periodic coexistence state in infinite-dimensional periodic semi-flows [42, Theorem 2.3] asserts that system (1.2) has a positive steady state as long as it is uniformly persistent. The proof of Theorem 1.3 is completed.  $\square$

We shall conclude this section by proving the following results which show some monotone properties for  $\theta_d(x)$  in  $x$  or  $d$ .

**Lemma 4.3** *Let  $N_R$  satisfies (H1) and  $N_R$  is temporally homogeneous, where  $\Omega$  is a bounded interval in  $\mathbb{R}$  and  $N_R(x) \in C^1(\overline{\Omega})$ . Then the unique solution  $\theta_d$  to (4.4) has the following property: if  $N_R(x)$  is non-decreasing (resp. non-increasing) in  $x \in \overline{\Omega}$ , then  $\theta_d(x)$  is strictly increasing (resp. decreasing) in  $x \in \Omega$ . Moreover,  $\max_{x \in \overline{\Omega}} \theta_d(x)$  is strictly decreasing in  $d \in (0, \infty)$ .*

**Proof** We only prove the case that  $N_R(x)$  is non-decreasing, and the other case can be proved similarly.

Without loss of generality, assume that  $\Omega = (0, 1)$  and  $N_R(x)$  is non-decreasing in  $x \in [0, 1]$ . To prove the monotonicity of  $\theta_d(x)$  with respect to  $x$ , by an argument of contradiction, we assume that there is a point  $x_* \in (0, 1)$  such that  $\partial_x \theta_d(x_*) \leq 0$ . It follows from the equation of  $\theta_d$  that

$$\partial_{xx} \theta_d(0) = \frac{\sigma \theta_d(0) - N_R(0)}{d}.$$

Due to the monotonicity of  $N_R$  in  $x$ , by Lemma 3.4, we have  $N_R(0)/\sigma = \min_{x \in [0,1]} N_R(x) < \theta_d(0)$ , which implies that  $\partial_{xx} \theta_d(0) > 0$ . Since  $\partial_x \theta_d(0) = 0$ ,  $\partial_x \theta_d(x) > 0$  for sufficiently small  $x > 0$ . Then by the hypothesis that  $\partial_x \theta_d(x_*) \leq 0$  for some  $x_* \in (0, 1)$ , we derive that  $\partial_x \theta_d(x_0)$  and  $\partial_x \theta_d(x) > 0$  in  $(0, x_0)$  for some  $x_0 \in (0, x_*]$ . Now, we look at the following equations

$$\begin{cases} d \partial_{xx} \theta_d + N_R(x) - \sigma \theta_d = 0, & x \in (0, x_0), \\ \partial_x \theta_d(0) = \partial_x \theta_d(x_0) = 0. \end{cases} \tag{4.18}$$

By the strong maximum principle, there holds that

$$\min_{x \in [0, x_0]} N_R(x)/\sigma < \theta_d(x) < \max_{x \in [0, x_0]} N_R(x)/\sigma, \quad \forall x \in [0, x_0].$$

Especially,  $\theta_d(x_0) < \max_{x \in [0, x_0]} N_R(x)/\sigma = N_R(x_0)/\sigma$ . Thus,  $\partial_{xx} \theta_d(x_0) < 0$  by (4.18), which together with the fact that  $\theta_d \in C^2([0, 1])$  causes that  $\partial_x \theta_d(x) < \partial_x \theta_d(x_0) = 0$  for  $x \in (x_0, x_0 + \varepsilon)$  with  $0 < \varepsilon \ll 1 - x_0$ . Since  $\partial_x \theta_d(1) = 0$ , we can find  $x_1 \in (x_0 + \varepsilon, 1)$  so that  $\partial_x \theta_d(x_1) = 0$  and  $\partial_x \theta_d(x) < 0$  in  $(x_0, x_1)$ . Recall that  $\partial_x N_R(x) > 0$  on  $[0, 1]$ . Then  $N_R(x) - \sigma \theta_d(x) > N_R(x_0) - \sigma \theta_d(x_0) > 0$  for  $x \in (x_0, x_1)$ . Hence,  $\partial_{xx} \theta_d(x) < 0$  and thus  $\partial_x \theta_d(x) < 0$  in  $(x_0, x_1]$ , contradicting the fact that  $\partial_x \theta_d(x_1) = 0$ . This proves that  $\theta_d(x)$  strictly increasing in  $(0, 1)$ .

In the following, we prove the monotonicity of  $\theta_d(1) = \max_{x \in [0,1]} \theta_d(x)$  with respect to  $d$ . Differentiating the equation of  $\theta_d$  with respect to  $d$ , we get

$$\begin{cases} d \partial_{xx} \theta'_d - \sigma \theta'_d = -\partial_{xx} \theta_d, & x \in (0, 1), \\ \partial_x \theta'_d(0) = \partial_x \theta_d(1) = 0, \end{cases} \tag{4.19}$$

where  $'$  denotes the differentiation with respect to  $d$ . Multiplying the first equation in (4.18) by  $\theta'_d$  and the first equation in (4.19) by  $\theta_d$ , and subtracting the results, one derives that

$$d(\theta_d \partial_{xx} \theta'_d - \theta'_d \partial_{xx} \theta_d) = \theta'_d N_R(x) - \theta_d \partial_{xx} \theta_d. \tag{4.20}$$

Then integrating (4.20) over  $(0, 1)$  gives that

$$\int_0^1 \theta'_d(x) N_R(x) dx = - \int_0^1 |\partial_x \theta_d(x)|^2 dx. \tag{4.21}$$

This means that  $\theta'_d(x^*) < 0$  for some  $x^* \in (0, 1)$  as  $\partial_x \theta_d \not\equiv 0$  in  $(0, 1)$ . By an argument of contradiction, we assume that  $\theta'_{d^0}(1) \geq 0$  for some constant  $d^0 > 0$ . If  $\theta'_{d^0}(1) > 0$ , then  $\theta'_{d^0}(x) > 0$  in a neighborhood left to  $x = 1$  by the continuity of  $\theta'_{d^0}$ . If  $\theta'_{d^0}(1) = 0$ , then it follows from (4.18) and (4.19) that

$$\partial_{xx} \theta'_{d^0}(1) = - \frac{\partial_{xx} \theta_{d^0}(1)}{d^0} = \frac{N_R(1) - \sigma \theta_{d^0}(1)}{d^0} > 0,$$

where the last inequality holds as  $\theta_{d^0}(1) = \max_{x \in [0,1]} \theta_{d^0}(x) < \max_{x \in [0,1]} N_R(x) / \sigma = N_R(1) / \sigma$ . Thus, in the above two cases,  $\theta'_{d^0}(x) > 0$  in a neighborhood left to  $x = 1$ . Suppose that there is  $x^0 \in [0, 1)$  so that

$$\theta'_{d^0}(x) > 0 \text{ in } (x^0, 1), \quad \theta'_{d^0}(x^0) = 0 \quad \text{and} \quad \partial_x \theta'_{d^0}(x^0) \geq 0.$$

Integrating (4.20) with  $d = d^0$  over  $(x^0, 1)$ , we obtain that

$$0 \geq -d \partial_x \theta'_{d^0}(x^0) \theta_{d^0}(x^0) = \theta_{d^0}(x^0) \partial_x \theta_{d^0}(x^0) + \int_{x^0}^1 [\theta'_{d^0}(x) N_R(x) + |\partial_x \theta_{d^0}(x)|^2] dx > 0,$$

which is a contradiction. Hence  $\theta'_{d^0}(x) > 0$  in  $[0, 1)$ , contradicting (4.21). Therefore,  $\theta_d(1) = \max_{x \in [0,1]} \theta_d(x)$  is strictly decreasing with respect to  $d > 0$ . The proof is completed.  $\square$

### 5 Proof of Theorems 1.4 and 1.5

By the theory for the periodic coexistence state in infinite-dimensional periodic semi-flows (cf. [42, 43]), there is at least one positive  $\omega$ -periodic solution to system (1.2) as long as system (1.2) is uniformly persistent (see Proposition 3.8). This fact indicates the conditions for the existence of positive  $\omega$ -periodic solutions to (1.2). In this section, we show some asymptotic profiles of positive  $\omega$ -periodic solutions to (1.2) as the resource dispersal rate tends to zero or infinity.

Any positive  $T$ -periodic solution of (1.2) satisfies (1.5). To show the asymptotic profiles of positive  $\omega$ -periodic solutions to (1.2) as  $d \rightarrow 0$  or  $d \rightarrow \infty$ , we first prepare the following two lemmas, which are concerned with the  $L^\infty$ -estimate and  $W_q^{2,1}$ -estimate for any positive solution to (1.5).

**Lemma 5.1** *Let  $(Z, N)$  denote a positive solution to (1.5). Assume that  $c < r$ . Then*

$$0 < Z < \frac{r - c}{g} \quad \text{and} \quad 0 < N < \max_{\Omega \times [0, \omega]} N_R / \sigma \quad \text{on } \overline{\Omega} \times \mathbb{R}_+.$$

Moreover, (1.5) has no positive solution when  $c \geq r$ .

**Proof** We omit the proof as it is standard by the maximum principle for time-periodic parabolic equations (cf. [32, Theorem 7.1]).  $\square$

**Lemma 5.2** *Let  $(Z, N)$  be a positive solution to (1.5). Then for  $\mu \geq \varepsilon$  (resp.  $d \geq \varepsilon$ ), where  $\varepsilon > 0$  is a small constant, there is a positive constant  $C$  depending on  $\varepsilon, m, r, c, g, N_R, \sigma, \gamma, k$  and  $\Omega$ , so that*

$$\|Z\|_{W_q^{2,1}(\Omega \times (0, \omega))} \leq C \quad (\text{resp. } \|N\|_{W_q^{2,1}(\Omega \times (0, \omega))} \leq C), \quad \forall q \in (1, \infty).$$

**Proof** This lemma is obtained by the  $L^p$  theory for time-periodic parabolic equations [17].  $\square$

Now, we are ready to prove Theorems 1.4 and 1.5.

**Proof of Theorem 1.4** Since  $c \in [0, c_*]$ , by Lemmas 3.1 and 3.5, we have

$$\lim_{d \rightarrow 0} v_1\left(\tau, \mu, \frac{r\theta_d}{k + \theta_d} - c\right) = v_1\left(\tau, \mu, \frac{rp}{k + p} - c\right) < c - c_* < 0$$

for all  $\mu \in (0, \infty)$ . Then by Proposition 3.8 (ii), system (1.2) possesses at least one positive  $\omega$ -periodic solution for sufficiently small  $\mu > 0$ . Assume that  $(Z_{(i)}, N_{(i)})$  is a positive  $\omega$ -periodic solution to (1.2) with  $d = d_{2,i}$  and  $d_{2,i} \rightarrow 0$  as  $i \rightarrow \infty$ . By Lemma 5.1,  $\|\frac{rN_{(i)}}{k+N_{(i)}} - c - gZ_{(i)}\|_{L^\infty(\Omega \times (0, \omega))}$  is uniformly bounded in  $i$ . It follows from Lemma 5.2 that  $\|Z_{(i)}\|_{W_q^{2,1}(\Omega \times (0, \omega))}$  is uniformly bounded in  $i$ . Thus, the embedding theorem implies that  $Z_{(i)} \rightarrow Z_0$  in  $C(\bar{\Omega} \times [0, \omega])$  as  $i \rightarrow \infty$ , by taking a subsequence of  $d_{2,i}$  if necessary, where  $Z_0$  is a nonnegative  $\omega$ -periodic function. For  $N_{(i)}$ , we derive from Lemma 5.1 that  $\lim_{i \rightarrow \infty} N_{(i)} = N_0$  weakly in  $L^q(\Omega \times (0, \omega))$  for any  $q > 1$ , where  $N_0$  is a nonnegative  $\omega$ -periodic function. Moreover,  $(Z_0, N_0)$  satisfies

$$\begin{cases} \partial_t Z_0 = \mu \Delta Z_0 + Z_0 \left( \frac{rN_0}{k+N_0} - c - gZ_0 \right), & x \in \Omega, t > 0, \\ \partial_{\bar{n}} Z_0 = 0, & x \in \partial\Omega, t > 0, \\ Z_0(x, t + \omega) = Z_0(x, t), N_0(x, t + \omega) = N_0(x, t), & x \in \Omega, t > 0. \end{cases}$$

Then by the maximum principle of time-periodic parabolic equations (cf. [32, Theorem 7.1]), we infer that either  $Z_0 \equiv 0$  on  $\bar{\Omega} \times \mathbb{R}_+$  or  $Z_0 > 0$  on  $\bar{\Omega} \times \mathbb{R}_+$ .

In the following, we prove that  $Z_0 > 0$  on  $\bar{\Omega} \times \mathbb{R}_+$ . Suppose, to the contrary, that  $Z_0 \equiv 0$  on  $\bar{\Omega} \times \mathbb{R}_+$ . Then for any  $\varepsilon \in (0, \min_{\bar{\Omega}} N_R/\sigma)$ , there is a large integer  $M_0 > 0$  so that  $0 \leq Z_{(i)} \leq \varepsilon$  on  $\bar{\Omega} \times \mathbb{R}_+$  for  $i > M_0$ . By the equation of  $N_{(i)}$ , we have that for  $i > M_0$ ,

$$\begin{cases} \partial_t N_{(i)} \geq d_{2,i} \Delta N_{(i)} + N_R(x, t) - \sigma N_{(i)} - \frac{r\varepsilon N_{(i)}}{\gamma(k+N_{(i)})}, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} N_{(i)} = 0, & x \in \partial\Omega, t > 0 \end{cases}$$

and

$$\begin{cases} \partial_t N_{(i)} \leq d_{2,i} \Delta N_{(i)} + N_R(x, t) - \sigma N_{(i)}, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} N_{(i)} = 0, & x \in \partial\Omega, t > 0. \end{cases}$$

**Claim 5.1** Let  $h \in C_\omega(\bar{\Omega} \times \mathbb{R}_+)$  be a positive function. For each  $i \in \{1, 2, 3, \dots\}$ , the following problem

$$\begin{cases} \partial_t N_{(i)} = d_{2,i} \Delta N_{(i)} + N_R(x, t) - \sigma N_{(i)} - \frac{rhN_{(i)}}{\gamma(k+N_{(i)})}, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} N_{(i)} = 0, & x \in \partial\Omega, t > 0 \end{cases} \tag{5.1}$$

possesses a unique  $\omega$ -periodic solution  $N_{h,i}$ . Moreover,  $N_{h,i} > 0$  on  $\bar{\Omega} \times \mathbb{R}_+$  for  $i \in \{1, 2, 3, \dots\}$ .

It is easy to verify that  $0$  and  $\max_{\bar{\Omega} \times [0, \omega]} N_R/\sigma$  are lower and upper solutions to (5.1), respectively. Then the method of upper-lower solutions for time-periodic parabolic equations (cf. [32, Theorem 7.3]) indicates that (5.1) possesses a  $\omega$ -periodic solution. Since  $f(x, t, N) = N_R(x, t) - \sigma N - \frac{r\varepsilon N}{k+N}$  is a concave function with respect to  $N$ , by [13,

Theorem 27.1], (5.1) has a unique  $\omega$ -periodic solution  $N_{h,i}$ . By the maximum principle for time-periodic parabolic equations (cf. [32, Theorem 7.1]),  $N_{h,i} > 0$  on  $\bar{\Omega} \times \mathbb{R}_+$ . This proves **Claim 5.1**.

**Claim 5.2** Let  $h \in C_\omega(\bar{\Omega} \times \mathbb{R}_+)$  be a positive function. Then  $N_{h,i} \rightarrow p_h$  in  $C(\bar{\Omega} \times [0, \omega])$  as  $i \rightarrow \infty$ , where for each  $x \in \bar{\Omega}$ ,  $p_h(x, t)$  denotes the unique positive  $\omega$ -periodic solution to the ODE

$$p_t = N_R(x, t) - \sigma p - \frac{rhp}{\gamma(k + p)}, \quad t > 0. \tag{5.2}$$

Let  $\rho_0$  be a constant with  $0 < \rho_0 \ll \min_{\bar{\Omega} \times [0, \omega]} N_R(x, t)$ . Similar to the proof of **Claim 5.1**, we find that for each  $x \in \bar{\Omega}$  and any  $\varrho \in (-\varrho_0, \varrho_0)$ , the perturbed equation

$$p_t = N_R(x, t) \pm \varrho - \sigma p - \frac{rhp}{\gamma(k + p)}, \quad t > 0 \tag{5.3}$$

admits a unique positive  $\omega$ -periodic solutions  $p_{h,\varrho}^\pm$ . Notice that  $\int_0^\omega (\sigma + \frac{r h k}{\gamma(k+p_h)^2}) dt > 0$  for all  $x \in \bar{\Omega}$ . Then for each  $x \in \bar{\Omega}$ ,  $p_{h,\varrho}^\pm$  is linearly stable for (5.3). Since  $N_R(x, t) \in C_\omega^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R}_+)$ , by the dependence of solutions of ODEs on the parameter (cf. [8]), we have  $p_{h,\varrho}^\pm \in C_\omega^{0,1}(\bar{\Omega} \times \mathbb{R}_+)$  and

$$\|p_{h,\varrho}^\pm - p_h\|_{C(\bar{\Omega} \times [0, \omega])} \rightarrow 0 \text{ as } \varrho \rightarrow 0, \tag{5.4}$$

where  $p_h$  is the unique positive  $\omega$ -periodic solution of (5.2) for each  $x \in \bar{\Omega}$ . By Lemma 4.1 in [1], for each  $\varrho \in (0, \varrho_0)$ , there are  $\tilde{p}_{h,\varrho}^\pm \in C_\omega^{2,1}(\bar{\Omega} \times \mathbb{R}_+)$  so that

$$\|\tilde{p}_{h,\varrho}^\pm - p_{h,\varrho}^\pm\|_{C^{0,1}(\bar{\Omega} \times [0, \omega])} < \frac{\varrho}{4 \cdot \max\{1, \sigma, \frac{r h}{\gamma k}\}}, \quad \frac{\partial \tilde{p}_{h,\varrho}^\pm}{\partial \bar{n}} = 0 \text{ on } \partial\Omega \times \mathbb{R}_+. \tag{5.5}$$

Note that  $p_{h,\varrho}^- < p_{h,\varrho}^+$  by the comparison principle. Then  $\tilde{p}_{h,\varrho}^- < \tilde{p}_{h,\varrho}^+$  for  $\varrho \in (0, \varrho_0)$ . In the following, we prove the convergence of  $N_{h,i}$  as  $i \rightarrow \infty$ . For this aim, we show that for any  $\varrho \in (0, \varrho_0)$ , there is a small constant  $d_0$  so that when  $0 < d_{2,i} < d_0$ , the functions  $\tilde{p}_{h,\varrho}^-$  and  $\tilde{p}_{h,\varrho}^+$  are lower and upper solutions of (5.1), respectively. Fixing  $\varrho \in (0, \varrho_0)$  and using (5.3) and (5.5), we find that

$$\begin{aligned} & \frac{\partial \tilde{p}_{h,\varrho}^+}{\partial t} - d_{2,i} \Delta \tilde{p}_{h,\varrho}^+ - N_R + \sigma \tilde{p}_{h,\varrho}^+ + \frac{r h \tilde{p}_{h,\varrho}^+}{\gamma(k + \tilde{p}_{h,\varrho}^+)} \\ &= \left( \frac{\partial \tilde{p}_{h,\varrho}^+}{\partial t} - \frac{\partial p_{h,\varrho}^+}{\partial t} \right) - d_{2,i} \Delta \tilde{p}_{h,\varrho}^+ + \varrho + \sigma (\tilde{p}_{h,\varrho}^+ - p_{h,\varrho}^+) + \frac{r h \gamma k (\tilde{p}_{h,\varrho}^+ - p_{h,\varrho}^+)}{\gamma^2 (k + \tilde{p}_{h,\varrho}^+) (k + p_{h,\varrho}^+)} \\ &\geq \varrho/4 - d_{2,i} \Delta \tilde{p}_{h,\varrho}^+ + \varrho - \varrho/4 - \varrho/4 \\ &= \varrho/4 - d_{2,i} \Delta p_{h,\varrho}^+ > 0, \quad x \in \Omega, t > 0 \end{aligned}$$

for  $0 < d_{2,i} < d_0$  with sufficiently small  $d_0 > 0$ . Hence,  $\tilde{p}_{h,\varrho}^+$  is an upper-solution to (5.1) for  $0 < d_{2,i} < d_0$ . Similarly,  $\tilde{p}_{h,\varrho}^-$  is a lower-solution to (5.1) for  $0 < d_{2,i} < d_0$ . Then an application of the method of upper-lower solutions for time-periodic parabolic equations [32, Theorem 7.3] indicates that (5.1) possesses a  $\omega$ -periodic solution  $N$  with  $0 < \tilde{p}_{h,\varrho}^- < N < \tilde{p}_{h,\varrho}^+$ . By the uniqueness of solutions to (5.1),  $0 < \tilde{p}_{h,\varrho}^- < N_{h,i} < \tilde{p}_{h,\varrho}^+$  for  $0 < d_{2,i} < d_0$ . Finally, by (5.4) and (5.5),  $N_{h,i} \rightarrow p_h$  in  $C(\bar{\Omega} \times [0, \omega])$  as  $i \rightarrow \infty$ . This proves **Claim 5.2**.

By Lemma 3.5, Claim 5.1 and Claim 5.2, using the comparison principle, we see that

$$p_\varepsilon \leq \liminf_{i \rightarrow \infty} N_{(i)} \leq \limsup_{i \rightarrow \infty} N_{(i)} \leq p \text{ on } \overline{\Omega} \times [0, \omega],$$

where  $p(x, t)$  is the unique positive  $\omega$ -periodic solution of (3.4) for each  $x \in \overline{\Omega}$ . Taking  $\varepsilon \rightarrow 0$  gives that

$$N_{(i)} \rightarrow p \text{ in } C(\overline{\Omega} \times [0, \omega]) \text{ as } i \rightarrow \infty.$$

Let  $\tilde{Z}_{(i)} = Z_{(i)} / \|Z_{(i)}\|_{L^\infty(\Omega \times (0, \omega))}$ . Then  $\tilde{Z}_{(i)}$  satisfies

$$\begin{cases} \tau \frac{\partial \tilde{Z}_{(i)}}{\partial t} = \mu \Delta \tilde{Z}_{(i)} + \tilde{Z}_{(i)} \left( \frac{rN_{(i)}}{k+N_{(i)}} - c - gZ_{(i)} \right), & x \in \Omega, t > 0, \\ \partial_{\bar{n}} \tilde{Z}_{(i)} = 0, & x \in \partial\Omega, t > 0. \end{cases}$$

By the regularity theory and Harnack's inequality for parabolic equations, up to a subsequence of  $d_{2,i}$  if necessary,  $\tilde{Z}_{(i)} \rightarrow \tilde{Z}_0 > 0$  in  $C(\overline{\Omega} \times [0, \omega])$  as  $i \rightarrow \infty$ , where  $\tilde{Z}_0$  satisfies (weakly)

$$\begin{cases} \tau \frac{\partial \tilde{Z}_0}{\partial t} = \mu \Delta \tilde{Z}_0 + \tilde{Z}_0 \left( \frac{rp}{k+p} - c \right), & x \in \Omega, t > 0, \\ \partial_{\bar{n}} \tilde{Z}_0 = 0, & x \in \partial\Omega, t > 0. \end{cases}$$

Since  $\tilde{Z}_0 > 0$ , the above equation combined with the Krein-Rutman theorem yields that  $v_1(\tau, \mu, \frac{rp}{k+p} - c) = 0$ . By the assumption  $c \in [0, c_*]$ , we derive from Lemma 3.1 that

$$v_1 \left( \tau, \mu, \frac{rp}{k+p} - c \right) < -\frac{1}{\omega|\Omega|} \int_0^\omega \int_\Omega \left( \frac{rp}{k+p} - c \right) = c - c_* \leq 0,$$

which is a contradiction. Hence,  $Z_0 > 0$  on  $\overline{\Omega} \times \mathbb{R}_+$ .

In the following, we consider the convergence of  $N_{(i)}$  as  $i \rightarrow \infty$ . Since  $Z_{(i)} \rightarrow Z_0$  in  $C(\overline{\Omega} \times [0, \omega])$  as  $i \rightarrow \infty$ , for sufficiently small  $\varepsilon > 0$ , there exists a large integer  $M > 0$  so that

$$0 < Z_0 - \varepsilon < Z_{(i)} < Z_0 + \varepsilon \text{ on } \overline{\Omega} \times \mathbb{R}_+ \text{ for } i > M. \tag{5.6}$$

The equation of  $N_{(i)}$  and (5.6) give that

$$\begin{cases} \partial_t N_{(i)} \leq d_{2,i} \Delta N_{(i)} + N_R(x, t) - \sigma N_{(i)} - \frac{rN_{(i)}(Z_0 - \varepsilon)}{\gamma(k + N_{(i)})}, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} N_{(i)} = 0, & x \in \partial\Omega, t > 0 \end{cases}$$

and

$$\begin{cases} \partial_t N_{(i)} \geq d_{2,i} \Delta N_{(i)} + N_R(x, t) - \sigma N_{(i)} - \frac{rN_{(i)}(Z_0 + \varepsilon)}{\gamma(k + N_{(i)})}, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} N_{(i)} = 0, & x \in \partial\Omega, t > 0. \end{cases}$$

By Claim 5.1 and Claim 5.2, the following equation

$$\begin{cases} \partial_t N_{(i)} = d_{2,i} \Delta N_{(i)} + N_R(x, t) - \sigma N_{(i)} - \frac{rN_{(i)}(Z_0 - \varepsilon)}{\gamma(k + N_{(i)})}, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} N_{(i)} = 0, & x \in \partial\Omega, t > 0 \end{cases}$$

possesses a unique positive  $\omega$ -periodic solution  $\tilde{N}_{(i)}$  for  $i > M$ , and  $\tilde{N}_{(i)} \rightarrow p_{Z_0 - \varepsilon}$  in  $L^\infty(\Omega \times (0, \omega))$  as  $i \rightarrow \infty$ . By the same way, the following equation

$$\begin{cases} \partial_t N_{(i)} = d_{2,i} \Delta N_{(i)} + N_R(x, t) - \sigma N_{(i)} - \frac{rN_{(i)}(Z_0 + \varepsilon)}{\gamma(k + N_{(i)})}, & x \in \Omega, t > 0, \\ \partial_{\bar{n}} N_{(i)} = 0, & x \in \partial\Omega, t > 0 \end{cases}$$

has a unique positive  $\omega$ -periodic solution  $\underline{N}_{(i)}$  for  $i > M$ , and  $\underline{N}_{(i)} \rightarrow p_{Z_0+\varepsilon}$  in  $L^\infty(\Omega \times (0, \omega))$  as  $i \rightarrow \infty$ . A comparison argument gives that  $\underline{N}_{(i)} \leq N_{(i)} \leq \tilde{N}_{(i)}$  on  $\bar{\Omega} \times \mathbb{R}_+$  for  $i > M$ . Therefore,

$$p_{Z_0+\varepsilon} \leq \liminf_{i \rightarrow \infty} N_{(i)} \leq \limsup_{i \rightarrow \infty} N_{(i)} \leq p_{Z_0-\varepsilon}.$$

Sending  $\varepsilon \rightarrow 0$  in the above inequalities yields that

$$N_{(i)} \rightarrow p_{Z_0} = N_0 \text{ in } C(\bar{\Omega} \times [0, \omega]) \text{ as } i \rightarrow \infty.$$

Finally, by the regularity theory of parabolic PDEs, the equation of  $Z_{(i)}$  indicates that  $Z_0$  satisfies the first equation in (1.17). This means that  $(Z_0, N_0)$  is a positive solution to (1.17). This completes the proof of Theorem 1.4.  $\square$

**Proof of Theorem 1.5** Let  $c \in [0, c^*)$ . Then we obtain from Lemma 3.1 (ii) and Lemma 3.6 that

$$\lim_{d \rightarrow \infty} v_1\left(\tau, \mu, \frac{r\theta_d}{k + \theta_d} - c\right) = v_1\left(\tau, \mu, \frac{r\xi}{k + \xi} - c\right) = c - c^* < 0$$

for all  $\mu \in (0, \infty)$ . By Proposition 3.8 (ii), system (1.2) possesses at least one positive  $\omega$ -periodic solution for sufficiently large  $d > 0$ . Assume that  $(Z, N)$  is any positive  $\omega$ -periodic solution to (1.2) with  $d > 0$  large enough. We see from Lemma 5.1 that  $Z$  and  $N$  are uniformly bounded in  $d$ . Then by an argument similar to [14, Lemma 3.7], we derive that by taking a subsequence of  $d$  if necessary,  $(Z, N)$  converges to  $(Z_\infty, N_\infty)$  in  $[C(\bar{\Omega} \times [0, \omega])]^2$  as  $d \rightarrow \infty$ , where  $N_\infty$  does not depend on  $x$ , and  $(Z_\infty, N_\infty)$  is a nonnegative  $\omega$ -periodic solution to the shadow system (1.18).

We first prove that  $N_\infty$  is a positive function. Since  $N_\infty$  is  $\omega$ -periodic in  $t$ , without losing generality, we suppose that  $N_\infty(0) = 0$ . Then  $\frac{dN_\infty}{dt}(0) = \frac{1}{|\Omega|} \int_\Omega N_R(x, 0)dx > 0$ , which leads to that  $N_\infty(t) > 0$  in a right neighborhood of  $t = 0$ . Suppose that there is a constant  $t_1 > 0$  so that  $t_1 = \min\{t > 0 | N_\infty(t) = 0\}$ . Then  $\frac{dN_\infty}{dt}(t_1) = \frac{1}{|\Omega|} \int_\Omega N_R(x, t_1)dx > 0$ , which is impossible. Thus,  $N_\infty(t) > 0$  for  $t > 0$ . According to the periodicity of  $N_\infty$ , we have  $N_\infty(0) = N_\infty(\omega) > 0$ , a contradiction. Hence,  $N_\infty(t) > 0$  for all  $t \geq 0$ .

Next, we verify that  $Z_\infty$  is a positive function. On the contrary, suppose that there is  $(x_0, t_0) \in \bar{\Omega} \times \mathbb{R}_+$  such that  $Z_\infty(x_0, t_0) = 0$ . Then the Harnack inequality of parabolic equations indicates that  $Z_\infty(x, t) \equiv 0$  on  $\bar{\Omega} \times [0, t_0]$ . By the periodicity of  $Z_\infty$  and the Harnack inequality of parabolic equations, there holds that  $Z_\infty(x, t) \equiv 0$  on  $\bar{\Omega} \times \mathbb{R}_+$ , which gives rise to  $N_\infty(t) = \xi(t)$  on  $[0, \infty)$ . Let  $\tilde{Z} = \frac{Z}{\|Z\|_{L^\infty(\Omega \times (0, \omega))}}$ . Then  $\|\tilde{Z}\|_{L^\infty(\Omega \times (0, \omega))} = 1$  and  $\tilde{Z}$  satisfies

$$\begin{cases} \tau \tilde{Z}_t = \mu \Delta \tilde{Z} + \tilde{Z} \left( \frac{rN}{k+N} - c - gZ \right), & x \in \Omega, t > 0, \\ \partial_{\tilde{n}} \tilde{Z} = 0, & x \in \partial\Omega, t > 0, \\ \tilde{Z}(x, t + \omega) = \tilde{Z}(x, t), & x \in \Omega, t \geq 0. \end{cases}$$

By Lemma 5.2,  $\|\tilde{Z}\|_{W_p^{2,1}(\Omega \times (0, \omega))}$  is uniformly bounded for large  $d$ , which together with the embedding theorem indicates that taking a subsequence of  $d$  if necessary,  $\tilde{Z} \rightarrow \tilde{Z}_\infty$  in  $C(\bar{\Omega} \times [0, \omega])$  as  $d \rightarrow \infty$ , where  $\tilde{Z}_\infty$  satisfies  $\|\tilde{Z}_\infty\|_{L^\infty(\Omega \times (0, \omega))} = 1$  and

$$\begin{cases} \tau \partial_t \tilde{Z}_\infty = \mu \Delta \tilde{Z}_\infty + \tilde{Z}_\infty \left( \frac{r\xi}{k+\xi} - c \right), & x \in \Omega, t > 0, \\ \partial_{\tilde{n}} \tilde{Z}_\infty = 0, & x \in \partial\Omega, t > 0, \\ \tilde{Z}_\infty(x, t + \omega) = \tilde{Z}_\infty(x, t), & x \in \Omega, t \geq 0. \end{cases}$$

Since  $\|\tilde{Z}_\infty\|_{L^\infty(\Omega \times (0, \omega))} = 1$ , by the Harnack inequality, we have  $\tilde{Z}_\infty > 0$  on  $\bar{\Omega} \times \mathbb{R}_+$ . Then the Krein-Rutman theorem implies that

$$v_1\left(\tau, \mu, \frac{r\xi}{k + \xi} - c\right) = c - \frac{1}{\omega} \int_0^\omega \frac{r\xi(t)}{k + \xi(t)} dt = 0,$$

which contradicts the assumption that  $c \in [0, c^*)$ . Therefore,  $(Z_\infty, N_\infty)$  is a positive solution to (1.18). The proof of Theorem 1.5 is completed.  $\square$

## 6 Conclusions and remarks

This paper establishes the global dynamics of the consumer-resource model (1.2) with temporal variability as well as resource dispersal and decay. Our results demonstrate how these factors affect the persistence and extinction of the consumer populations jointly with other factors like the relaxation time and dispersal rates.

First it is shown in Theorem 1.1 (ii) that if there is no resource decay (i.e.  $\sigma = 0$ ), then the resource abundance will have infinite-time blow-up for large yield rate irrespective of consumer mortality rate or resource dispersal. As long as the resource decays (i.e.  $\sigma > 0$ ), the resource remains limited regardless of other factors such as the yield rate, consumer mortality, resource dispersal, and so on (see Theorem 1.1 (i)), but the persistence and extinction dynamics depend on various factors as shown in Theorem 1.2 and Theorem 1.3. Specifically the persistence and extinction of the consumer population for the temporally periodic resource input  $N_R(x, t)$  and the temporally homogeneous resource input  $N_R(x)$  are classified, respectively, in Theorem 1.2 in terms of  $(\mu, \tau)$  and in Theorem 1.3 in terms of  $(d, \mu)$ , where  $\tau > 0$  is the relaxation time of the consumer and  $\mu, d$  denote the dispersal rates of the consumer and resource, respectively. We find that both temporally periodic and temporally homogeneous cases will lead to the same persistence or extinction dynamics when the consumer mortality rate is small or large (see Theorem 1.2 (i) and (iv), and Remark 1.1). However, when the consumer mortality rate is moderate, the dynamics may be different (see Theorem 1.2, Remark 1.1, and Remark 1.3 (3)). All these findings predict the possible consumer-resource dynamics.

In Theorem 1.4 and Theorem 1.5, we also show that any positive  $\omega$ -periodic solution of (1.2) converges to an  $\omega$ -periodic solution of (1.17) (resp. (1.18)) as the resource dispersal rate  $d \rightarrow 0$  (resp.  $d \rightarrow \infty$ ). The global dynamics with possible solution profiles for the limiting systems (1.17) and (1.18) is worthy of consideration in the future. In addition to this, we mention several other questions to be pursued.

- The result of Theorem 1.1 finds that the resource decay (i.e.  $\sigma > 0$ ) is a predominant factor precluding the resource abundance from blowing up. When the consumer is uniformly persistent in the case  $\sigma > 0$ , we show there is a positive periodic (resp. steady-state) solution when  $N_R$  is temporally heterogeneous (resp. temporally homogeneous). However, the stability and number of positive periodic (or steady-state) solutions remain unknown in this paper. Therefore investigating the properties of positive periodic (or steady-state) solutions such as the multiplicity, uniqueness and stability is an inherently interesting problem.
- The current paper assumes that all coefficients  $r, c, g, \sigma$  in the system (1.2) are constant. For a realistic ecological system in a heterogeneous environment, they may also vary spatially or temporally. Hence, it would be relevant to explore the global dynamics of the consumer-resource system (1.2) with spatially or temporally variable coefficients.

Of particular interest is when some of these variable coefficients (e.g.,  $\sigma$  or  $g$ ) degenerate in space, the solution may blow up at the degenerate points/sets and consequently the dynamics become very subtle. We shall investigate such a delicate problem in a forthcoming paper.

### Appendix. On a weighted time-periodic parabolic problem

In this appendix, we list some results for the principal eigenvalue of a weighted time-periodic parabolic eigenvalue problem:

$$\begin{cases} \varpi \varphi_s - d \Delta \varphi + \zeta(x, s) \varphi = \lambda \eta(x, s) \varphi, & x \in \Omega, s > 0, \\ \partial_{\bar{n}} \varphi = 0, & x \in \partial \Omega, s > 0, \\ \varphi(x, s + 1) = \varphi(x, s), & x \in \Omega, s \geq 0, \end{cases} \tag{A.1}$$

where  $\varpi, d$  are two positive constant,  $\zeta, \eta \in C^{\alpha, \alpha/2}(\bar{\Omega} \times \mathbb{R}_+)$  are periodic in  $s$  with period 1, and  $\eta > 0$  on  $\bar{\Omega} \times \mathbb{R}_+$ . According to the Krein-Rutman theorem, problem (A.1) possesses a principal eigenvalue  $\lambda(\varpi, d)$ , which is real and simple, and has a positive eigenfunction.

The following result [18, Theorems 1.1] asserts the monotonicity of  $\lambda(\varpi, d)$  with respect to  $\varpi$ .

**Theorem A.1** *Let  $\lambda(\varpi, d)$  be the principal eigenvalue of (A.1). Then for each fixed  $d > 0$ , either  $\frac{\partial \lambda(\varpi, d)}{\partial \varpi} > 0$  for any  $\varpi > 0$ , or  $\frac{\partial \lambda(\varpi, d)}{\partial \varpi} \equiv 0$ . Particularly,  $\frac{\partial \lambda(\varpi, d)}{\partial \varpi} \equiv 0$  if and only if  $\zeta - \int_0^1 \zeta ds - \lambda_*(\eta - \int_0^1 \eta ds)$  is independent of  $x \in \Omega$ , where  $\lambda_* = \lambda_*(d)$  is the principal eigenvalue of*

$$\begin{cases} -d \Delta \phi + \int_0^1 \zeta ds \phi = \lambda_* \int_0^1 \eta ds \phi, & x \in \Omega, \\ \partial_{\bar{n}} \phi = 0, & x \in \partial \Omega. \end{cases}$$

Denote

$$\underline{B} := \min_{\tilde{x} \in \tilde{\mathcal{X}}} \frac{\int_0^1 \zeta(\tilde{x}(t), t) ds}{\int_0^1 \eta(\tilde{x}(t), t) ds}, \quad B_* := \min_{x \in \bar{\Omega}} \frac{\int_0^1 \zeta(x, s) ds}{\int_0^1 \eta(x, s) ds}, \quad \bar{B} := \frac{\int_{\Omega} \int_0^1 \zeta(x, s) ds dx}{\int_{\Omega} \int_0^1 \eta(x, s) ds dx},$$

where  $\tilde{\mathcal{X}} = \{\tilde{x} \in C(\mathbb{R}_+; \bar{\Omega}) | \tilde{x}(s) = \tilde{x}(s + 1)\}$ . Note that  $\underline{B} \leq B_* \leq \bar{B}$ . Then the following results follow from [18, Theorems 1.3].

**Theorem A.2** *If  $\bar{B} = \underline{B}$ , then  $\lambda(\varpi, d) \equiv \bar{B}$  for all  $\varpi, d > 0$ ; If  $\underline{B} < \bar{B}$ , then for each  $B \in (\underline{B}, \bar{B})$ , there exists a unique constant  $d_B > 0$  satisfying  $\lambda(\varpi, d_B) \rightarrow B$  as  $\varpi \rightarrow 0$ ,  $d_B \rightarrow 0$  as  $B \searrow \underline{B}$  and  $d_B \rightarrow \infty$  as  $B \nearrow \bar{B}$ , such that the following statements for  $\lambda(\varpi, d)$  hold.*

- (i) *For  $B \in (\underline{B}, B_*]$ , there exists a unique continuous function  $\varpi_B(d) : (0, d_B] \rightarrow [0, \infty)$  so that  $\lambda(\varpi_B(d), d) \equiv B$  for  $d \in (0, d_B]$ ,  $\varpi_B(d_B) = 0$  and  $\varpi_B(d) > 0$  for all  $d \in (0, d_B)$ . Moreover, for  $B < B_*$ ,  $\varpi_B(d) \rightarrow 0$  as  $d \rightarrow 0$ ; for  $B = B_*$ , if the following hypothesis holds:*

**(H)**  *$b_* := \zeta - B_* \eta \in C^{2,0}(\bar{\Omega} \times \mathbb{R}_+)$  and there are finite number of points  $x_j \in \Omega$  ( $1 \leq j \leq M$ ) so that  $\int_0^1 b_*(x_j, s) ds = 0$  and  $\int_0^1 b_*(x, s) ds > 0$  for all  $x \in \bar{\Omega} \setminus \{x_1, \dots, x_M\}$ , where the Hessian matrix of  $\int_0^1 b_*(x, s) ds$  at  $x = x_j$  is invertible,*

then  $\varpi_{B_*}(d) \rightarrow 0$  as  $d \rightarrow 0$ .

- (ii) For  $B \in (B_*, \bar{B})$ , if  $\xi - \int_0^1 \xi ds - B(\eta - \int_0^1 \eta ds)$  does not depend on  $x \in \Omega$ , then  $\lambda(\varpi, d_B) \equiv B$  for all  $\varpi > 0$ ; otherwise, there is a unique constant  $\underline{d}_B \in (0, d_B)$  and a unique continuous function  $\underline{\varpi}_B(d) : (\underline{d}_B, d_B] \rightarrow [0, \infty)$ , where  $\lambda(\underline{d}_B) = B$  with  $\bar{\lambda}(d) := \lim_{\varpi \rightarrow \infty} \lambda(\varpi, d)$ , so that  $\lambda(\underline{\varpi}_B(d), d) \equiv B$  for all  $d \in (\underline{d}_B, d_B]$ ,  $\underline{\varpi}_B(d_B) = 0$ ,  $\underline{\varpi}_B(d) > 0$  for all  $d \in (\underline{d}_B, d_B)$ , and  $\underline{\varpi}_B(d) \rightarrow \infty$  as  $d \searrow \underline{d}_B$ .

**Remark A.1** For the situation  $\eta \equiv 1$ , we see from Lemma 3.1 (iv) that  $\bar{\lambda}(d) := \lim_{\varpi \rightarrow \infty} \lambda(\varpi, d)$  is non-decreasing in  $d \in (0, \infty)$ ,  $\lim_{d \rightarrow 0} \bar{\lambda}(d) = B_*$  and  $\lim_{d \rightarrow \infty} \bar{\lambda}(d) = \bar{B}$ . Then when  $\eta \equiv 1$ , the constant  $\underline{d}_B$  in Theorem A.2 (ii) satisfies  $\underline{d}_B \rightarrow 0$  as  $B \searrow B_*$ , while  $\underline{d}_B \rightarrow \infty$  as  $B \nearrow \bar{B}$ .

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## Declarations

**Conflicts of Interest** The authors declare that they have no competing interests.

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