# Migration effects on population dynamics of the honeybee-mite interactions

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**Abstract.** Honeybees are an amazing and highly beneficial insect species that play important roles in undisturbed and agricultural ecosystems. Unfortunately, honeybees are increasingly threatened by numerous factors, most notably the parasitic varroa mite (*Varroa destructor* Anderson and Trueman). A recent field study showed that migrations of mites into hives on foraging bees greatly contributes to the rapid growth of mite population in colonies, and increases the mortality of honeybees. Motivated by this, we propose a simple two-patch honeybee-varroa model to explore how foraging behavior of honeybees in the presence of varroa mite infestations affect the population dynamics of honeybees and mites, respectively. We provide a full analysis on the local and global dynamics of our proposed two-patch model, which incorporates mite migration generated by honeybee foraging activities. Our analytical and numerical studies reveal the dynamical outcomes of migration including: (a) Mite's extinction cannot be prevented by mite migration when mite population in each patch goes extinct in the absence of mite migration, however, mite migration could drive mite extinct under proper conditions. (b) Under proper conditions, high rates of mite migration could have the following effects: (1) save one honeybee colony from collapsing when both honeybee colonies are going extinct without migration; (2) drive honeybee extinct in at least one patch. (c) Intermediate migration rate could generate multiple locally stable honeybee-mite coexistence equilibria, and drive mite's extinction under proper environments. (d) An increase in migration rate causes a growth of the varroa population, which in return has a negative feedback on the colony population. (e) Increasing mite migration from a healthy patch to a collapsing patch could reduce the extinction time in the collapsing patch. Our results provide novel insights on the effects of foraging and Varroa migration on colony survival.

**Keywords and phrases:** migration, honeybee, mite, colony loss, extinction

**Mathematics Subject Classification:** 37G35, 34C23, 92D25, 92D40

## 1. Introduction

The importance of honeybees in sustaining ecosystems, regional, national and global food supplies, and various agricultural industries cannot be underestimated. Today, the majority of food consumed by human relies on bees' pollination (increases in abundance yields and quality) [30,35,49]. Further,

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honeybees efficiency in pollination has made it possible to expand various agricultural industries such as vegetables, nuts, sunflowers, cocoa beans, or coffee that are extremely valuable for many national economies (see [7,22]). In [45], they estimated the economic value of honeybees as agricultural pollinators in United States and pointed out that the annual social gains range between \$1.6 to \$5.7 billion. The gross revenue from bees' pollination services in 2012 is estimated at \$655.6 million with almond pollination representing 45 percent of the total fees collected during the same year [6]. Aside from their monetary values, bees supply berries, seeds, and fruits to birds and various mammals via pollination, and thus, their impact on sustaining biodiversity is incalculable. And so, sharp declines in honeybee populations is a concern. There are many reasons for colony losses, but the major cause worldwide is varroa mites [3,13,21,23,25,46,48].

While Varroa reproductive rates are relatively low, the data in [12] show that mite populations can increase at unexpected rates late in the fall [19,33] even when miticides are applied in the late summer. It was reported in [40] that robbing behavior by bees tends to be at its peak during August and September when there is almost no nectar flow. Foragers from more populous colonies will rob weak hives. If the hives are weak due to Varroa, the mites will attach to the robbing bees and be transported to the robbers' colony. Varroa also will migrate to other hives on foragers from colonies infested with Varroa that drift into hives that are not their own [18,44]. During swarming seasons, Varroa often attach to the abdomen of forager bees facilitating their transport to other colonies. Occasionally, workers from Varroa infested colonies erroneously enter foreign nests in response to the effects caused by parasitism [43]. Understanding the dynamics of Varroa mites migration across colonies may elucidate the sudden increase in mite populations in the late fall, which may be a key contributing factor to the collapsing of honeybee colonies. This hypothesis is supported by the work of [13] where the proportion of foragers carrying mites entering and leaving colonies was measured while the appropriate relationship between the growth of the varroa population at two apiary sites was established. In [13], it was found that the degree of mite population growth was connected to the growth in the population of foragers with mites at *both* sites.

Mathematical models have been introduced in order to explore the existing relationship between foraging activities and the collapse of honeybee colonies. In [39], a nonlinear dynamical system was introduced to study the effect of Acute Bee Paralysis Virus (ABPV) carried by parasitic varroa mites to an uninfected population of honeybees. They found conditions under which bee colonies can avoid an ABPV epidemic (the linkage between ABPV, varroa mites, and honeybees can be found in [16]). In [19], the author developed a mite model to understand the population dynamics of mites and they determined the invasion rate of mites into brood cells by a mean length of the phoretic period. [9] extended the work of [19] and use it to estimate the values of parameters needed for the reproductive success of the mites in brood cells, which have a large impact on the mite population. Models were developed that combined colony population dynamics with Varroa population growth alone [14] and with viruses transmitted by Varroa [25,34]. The models predict colony collapse with Varroa alone due to reduced longevity of workers that ultimately affect brood rearing. If viruses are included, the models reveal that viruses initially have little effect on colony survival, but as the population of mites and viral transmission rates increase (particularly in the fall) there is a reduction in the number of healthy young bees entering the overwintering population. In [3], the authors created a model that describes how the presence of the mite affects the epidemiology of many viruses on adult bees. Their analysis reveals that the disease could become endemic and wipe out either the mite or the bee population. Finally both honeybee and mite could coexist under certain conditions. The work of [32] took into accounts the healthy hive dynamics and its extinction illustrating colony loss via a transmissible infection brought to hives by foragers. Further, there is a fair amount of mathematical and simulation models studying the effects of stresses, nutritional or pathogenesis, on colony development [27,28,38,41,42] or the role of dispersal in metapopulation studies [5,11,26,36,50]. These models have provided valuable insights on the population dynamics of honeybees and some of the mechanisms may facilitate colony loss or the role of dispersal in metapopulation studies. Despite the recent field work of [13] that suggests that mite migration via their attachments to forager bees may play a critical role on the rapid population growth of mites, a contributing factor in the collapse of honeybee colonies, this mechanism has not been fully explored. And so, there is a need to develop models that incorporate the migration of

mites in order to study how bee foraging behavior can impact the health and survival of honeybee colonies.

Motivated by the work of [13], a two-patch honeybee-mite model that includes mite migration via their attachment to forager bees (*Apis Mellifera*), is introduced and analyzed in order to study the dynamical outcomes of mite migration on the survival of honeybee population and host-mite co-existence. The modeling framework used is inspired and influenced by the work of [13,15,29,31]. Specifically, we are interested in honeybee *Apis Mellifera* foragers which are required to return to their own colony after collecting nectar or pollen. However, this may not be the case for the mites attached to honeybee foragers, that is, mites could use their rides to migrate from Patch $i$ to Patch $j$ by attaching themselves to Patch $i$ honeybee foragers, then dropped in Patch $j$ while Patch $i$ honeybee foragers rob honey or pollen from Patch $j$. Or mites may be dropped by Patch $i$ honeybee foragers at resource sites while collecting nectar or pollen and are then picked up by Patch $j$ honeybee foragers that visit the same resource sites.

The remainder of the manuscript is organized as follows: Section 2 provides details on model derivations and the analysis of the dynamics of the related single patch model. Section 3 includes a detailed mathematical analysis of the *single patch* model, illustrating biological interpretations of the theoretical results. Section 4 investigates the dynamical outcomes of mite migrations patterns through the use of bifurcation diagrams. Section 5 discusses the findings, related biological interpretations, and final thoughts. The detailed proofs of the theoretical results are collected in the last section.

## 2. Model derivations

Let $H_i$ and $M_i$ be the total population of honeybees and mites in the colony (patch) $i$ at time $t$ respectively. Following the recent work of [25], the population dynamics of varroa mites and honeybees in a single colony $i$ could be described by the following set of nonlinear equations:

$$\frac{dH_i}{dt} = \frac{r_i H_i^2}{K_i + H_i^2} - d_{h_i} H_i - \alpha_i H_i M_i$$
$$\frac{dM_i}{dt} = c_i \alpha_i H_i M_i - d_{m_i} M_i \tag{2.1}$$

where $r_i$ is the egg laying rate of queen; $\sqrt{K_i}$ is the colony size at which the term $\frac{H_i^2}{K_i + H_i^2}$ achieves half of its maximum value; $d_{h_i}$ and $d_{m_i}$ are respectively the natural average death rate of the adult honey bees and mites population in colony $i$; $\alpha_i$ measures the parasitism rate of varroa mites; and $c_i$ is the conversion rate from the parasitism of honeybees to the reproduction of newborn mites. All the parameters are positive and [25] provided a great detail for the derivation of Model (2.1). The realistic ranges of these parameters can be found in Table 1 and are used for future numerical simulations including bifurcation diagrams.

Specifically, the single patch model (2.1) has the following assumptions:

1. The successful survivability of an egg into an adult bee in colony $i$ is represented by the term $\frac{H_i^2}{K_i + H_i^2}$, which incorporates the collaborative efforts of adult workers, via division of labor. This term assumes that successful colonies produce more brood and efficient workers, an assumption supported by the literature work [17,25,42].
2. From the reference [25], Model (2.1) assumes the implicit stage structure of both the bee population and the mite population where the ratio of different stages are constants. For instance, if we define $\xi_h \in [0,1]$ the percentage of brood population, then $(1 - \xi_h)H$ is the adult honeybee population (i.e the foragers). Therefore the honeybee model in (2.1) could be described as

$$\frac{dH_i}{dt} = \frac{r_i H_i^2}{K_i + H_i^2} - d_{h_i}(1 - \xi_{h_i})H_i - \alpha_i H_i M_i = \frac{r_i H_i^2}{K_i + H_i^2} - \hat{d}_{h_i} H_i - \alpha_i H_i M_i$$

with $\hat{d}_{h_i} = d_{h_i}(1 - \xi_{h_i})$. Similarly, if $\xi_m \in [0,1]$ is the percentage of mites at the non-phoretic stage, then $(1 - \xi_m)M$ is the phoretic mite population. Thus we denote $\hat{d}_{m_i} = d_{m_i}(1 - \xi_{m_i})$ and the mite model in (2.1) becomes

$$\frac{dM_i}{dt} = c_i \alpha_i H_i M_i - d_{m_i}(1 - \xi_{m_i})M_i = c_i \alpha_i H_i M_i - \hat{d}_{m_i} M_i.$$

Since $\xi_h \in [0,1]$ is the percentage of brood population and $(1-\xi_h)H$ is the adult honeybee population, then $\frac{\xi_h}{1-\xi_h}$ is the ratio of the brood to the adult honeybee in a colony. Similarly, $\frac{\xi_m}{1-\xi_m}$ is the ratio of the mites at the non-phoretic stage to the mites at the phoretic stage. We note that $\xi_m$ and $\xi_h$ should normally vary with time (or season). Instead of utilizing an explicit age structure model in our current manuscript, we assume $\xi_m$ and $\xi_h$ are constant parameters. In reality, we should expect due to seasonality that the ratio of brood to adult bees or ratio of mites at the non-phoretic stage to the mites at the phoretic stage varies. As we point out earlier, our current model is motivated by the field work of [13] and follows the recent work of [25], thus our model does not include seasonality and assumes the constant ratios. In addition, the work of [24] suggests that the brood to adult bee ratio changes slightly from spring to fall; and the ratio of phoretic and non-phoretic mites changes throughout the season with the availability of brood.

3. The direct impact of the parasitism on honeybees is modeled by the term $\alpha_i H_i M_i$ that accounts for decreases in fitness due to mite parasitism; reductions on the average life span of bees. The use of Holling Type I functional response to model the direct impact of mite on the bees population follow the fact that mites have devastating effects on bee colonies (e.g transmission of viruses or other parasitism effects from [13]). While we are only referring to parasitism here, we assume that the rate of parasitism by the mite is proportional to the rate of encounter between the varroa mites and the honeybees in order to take into account the severity of mite infestation.

4. The survival of mites depends on the honeybee population (the life of the mite is intimately connected to the life of the honeybee) with the term $c_i \alpha_i H_i M_i$ representing the successful reproduction and maturation of mites via the consumption/parasitism of honeybees.

Let $N_{h_i}^c = \dfrac{\frac{r_i}{d_{h_i}} - \sqrt{\left(\frac{r_i}{d_{h_i}}\right)^2 - 4K_i}}{2}$, $N_{h_i}^* = \dfrac{\frac{r_i}{d_{h_i}} + \sqrt{\left(\frac{r_i}{d_{h_i}}\right)^2 - 4K_i}}{2}$, $H_i^* = \frac{d_{m_i}}{c_i \alpha_i}$, and $M_i^* = \frac{1}{\alpha_i}\left[\frac{r_i H_i^*}{H_i^{*2} + K_i} - d_{h_i}\right]$ where $N_{h_i}^c$ is the critical population in order for a honeybee colony to survive in the absence of mites (could also refer to an *Allee threshold*); $N_{h_i}^*$ is the population size of a healthy honeybee colony that could attain without mites; and $(H_i^*, M_i^*)$ are population size of honeybees and mites when they coexist in (2.1). The full dynamics of Model (2.1) can be summarized from [25] as follow:

1. Model (2.1) always has the extinction equilibrium $(0,0)$ which is always locally asymptotically stable and globally stable if $\frac{r_i}{2\sqrt{K_i}} < d_{h_i}$.

2. If $\frac{r_i}{2\sqrt{K_i}} > d_{h_i}$, then the system has additional two mite-free equilibria $(N_{h_i}^c, 0)$ and $(N_{h_i}^*, 0)$ which stability are as follow:
   - The equilibrium $(N_{h_i}^c, 0)$ is a saddle if $N_{h_i}^c < H_i^*$ and it is a source (i.e an unstable focus or an unstable node depending on parameter values) when $N_{h_i}^c > H_i^*$.
   - $(N_{h_i}^*, 0)$ is a sink for $N_{h_i}^* < H_i^*$ and a saddle when $N_{h_i}^* > H_i^*$. If $N_{h_i}^* < H_i^*$, the trajectory of Model (2.1) converges to the equilibrium $(0,0)$ or $(N_{h_i}^*, 0)$ depending on the initial conditions.

3. If $N_{h_i}^c < H_i^* < N_{h_i}^*$, then the unique interior equilibrium $(H_i^*, M_i^*)$ emerges, which is locally asymptotically stable when $H_i^* > \sqrt{K_i}$. In this case, initial conditions are important for the survival of the colony. Model (2.1) undergoes a supercritical Hopf-bifurcation at $H_i^* = \sqrt{K_i}$; and it has a unique unstable limit cycle around the co-existence equilibrium $(H_i^*, M_i^*)$ (which is a source) when $H_i^* < \sqrt{K_i}$ where the periodic orbits expand until it touches the stable manifold of the boundary equilibrium $(\bar{H}_h^c, 0)$ which lead to the extinction of both honeybees and parasitic mites. Under this condition, extinction of honeybees and mites occurs globally independently of initial conditions. We refer to the colony in the latter case as *the collapsing colony*. To further illustrate the dynamics of the single patch Model (2.1), we provide the bifurcation diagram in Figures 1(a) and 1(b) by letting

$$r = 1500, \ c = 0.01, \ d_h = 0.15, \ dm = 0.095, \ \alpha = 0.005.$$

The scenario that we consider here is that the extinction equilibrium $(0,0)$ and the honeybee-only equilibrium $(N_h^*, 0)$ are both locally stable, i.e., they are the only two attractors of the system where the interior equilibrium $(H^*, M^*)$ is unstable and the system (2.1) undergoes a supercritical Hopf-bifurcation at $H^* = \frac{d_m}{\alpha c} = K$. Thus, initial conditions are important as both the bees and mites could be driven to extinction or only bee population can survive depending on initial condition. Initial condition is hence important for the survival of the colony. These dynamics are illustrated in Figures 1(a) and 1(b).
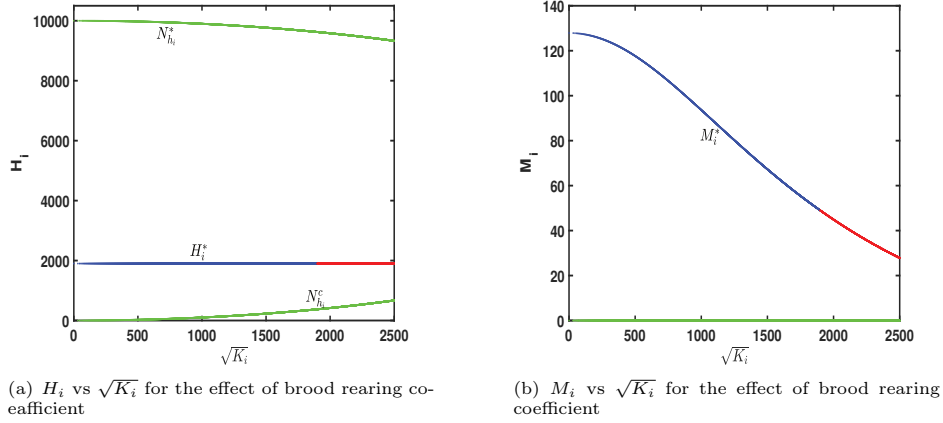
(a) $H_i$ vs $\sqrt{K_i}$ for the effect of brood rearing co-eafficient

(b) $M_i$ vs $\sqrt{K_i}$ for the effect of brood rearing coefficient

Figure 1: One parameter bifurcation diagrams of the single patch Model (2.1) when $r = 1500, c = 0.01, d_h = 0.15, \alpha = 0.005,$ $d_m = .095$. The notations $H_i^*$ and $M_i^*$ represent the population of honeybee and mite at Patch $i$, respectively. $N_{h_i}^*$ and $N_{h_i}^c$ are the honeybee population at the boundary equilibrium $E_{N_{h_i}^* 0}$ and $E_{N_{h_2}^c 0}$ respectively. The blue line represents sink, the green line a saddle, and the red line a source.

| Parameter | Description | Estimate/Units | Reference |
|:---:|:---:|:---:|:---:|
| $r$ | maximum birth rate | 0, 500, 1500 bees/day (depending on season) | see [16,46] |
| $d_h$ | average death rate of honeybee forager | (0.24-0.4) or (0.114-0.154) day$^{-1}$ | [27,28] |
| $d_m$ | average death rate of phoretic mite | (0.016-0.45) or 0.002(winter), 0.006(summer) day$^{-1}$ | [8,33] |
| $c$ | conversion rate from honeybee consumption to mite reproduction | 0-1 | N/A |
| $a$ | size of honeybee population at which rate of attachment is half maximal | 1000-1000000 bees | assumption |
| $\alpha$ | parasitism rate | ‡ (0.000556-0.00833) day$^{-1}$ | [20] |
| $\sqrt{K}$ | colony size at which the birth rate is half maximal | $\leq$ 22007(fall, spring), and $\leq$ 37500(summer) bees/day (upper bound values) | [39] |
| $\rho$ | relative dispersal rate of honeybee | varied | assumption |

Table 1: Standard parameters values used for simulation of honeybee and mite population of Model (2.2). Daily mortality of ‡ is calculated from the winter mortality rate 0.05-0.75 in [20] divided by the 90 winter days.

Varroa mites attached to honeybee foragers could move among colonies by direct transfer between foragers or by robbing nectar and pollen from highly infested colonies. Thus, varroa mites population could increase through reproduction, parasitising honeybees or, immigrating into the colonies by attaching to honeybee foragers [14]. To incorporate the behavior of mite migration, we define $\rho_{ij}$ as the average foraging rate of the honeybee foragers visiting colony $j$ from colony $i$ (for robbing) or the average connecting rate from colony $i$ to colony $j$ during the visitations of the same resource sites. More specifically, this average rate includes the potential events such as honeybee foragers from colony $i$ rubbing colony $j$; honeybee foragers from both colony $i$ and $j$ visiting a common resource such that the mites transfer between foragers. We do not model resource dynamics explicitly, however, the likelihood of bees visiting colonies that optimize resource consumption is implicitly incorporated into $\rho_{ij}$. The probability of the mites $M_j$ attaching to forager bees $H_j$ at colony $j$ is modeled by $\frac{H_j}{a_j + H_j}$, where $a_j$ is the size of the bee population at which the rate of attachment is half maximal (see the similar approach in [4,46]). Motivated by the importance of ensuring the "conservation of mass" in population modeling by [42] but perhaps a

bit unrealistically, our model ensures that no bees and mites are "lost". Thus, for a starting point, our model has the following net migration term at colony $i$ that conserves the mass:

$$\left( \rho_{ji} \overbrace{\frac{H_j}{a_j + H_j}}^{\text{probability of } M_j \text{ attaching to } H_j} M_j \underbrace{\phantom{xxxxxxxxxxxxxxxxx}}_{\text{mites entering colony i from colony j}} - \rho_{ij} \overbrace{\frac{H_i}{a_i + H_i}}^{\text{probability of } M_i \text{ attaching to } H_i} M_i \underbrace{\phantom{xxxxxxxxxxxxxxxxx}}_{\text{mites leaving colony i for colony j}} \right).$$

The population dynamics of varroa destructor and honeybees in a two-patch framework can be described by the following nonlinear equations:

$$\frac{dH_1}{dt} = \underbrace{\frac{r_1 H_1^2}{K_1 + H_1^2}}_{\text{successful reproduction at colony 1}} - \underbrace{d_{h_1} H_1}_{\text{mortality}} - \underbrace{\alpha_1 H_1 M_1}_{\text{parasitism effects}}$$

$$\frac{dM_1}{dt} = c_1 \alpha_1 H_1 M_1 - d_{m_1} M_1 + \underbrace{\left( \rho_{21} \overbrace{\frac{H_2}{a_2 + H_2}}^{\text{probability of } M_2 \text{ attaching to } H_2} M_2 - \rho_{12} \overbrace{\frac{H_1}{a_1 + H_1}}^{\text{probability of } M_1 \text{ attaching to } H_1} M_1 \right)}_{\text{Net dispersal effects at colony 1}}$$

$$\frac{dH_2}{dt} = \underbrace{\frac{r_2 H_2^2}{K_2 + H_2^2}}_{\text{successful reproduction at colony 2}} - \underbrace{d_{h_2} H_2}_{\text{mortality}} - \underbrace{\alpha_2 H_2 M_2}_{\text{parasitism effects}}$$

$$\frac{dM_2}{dt} = c_2 \alpha_2 H_2 M_2 - d_{m_2} M_2 + \underbrace{\left( \rho_{12} \overbrace{\frac{H_1}{a_1 + H_1}}^{\text{probability of } M_1 \text{ attaching to } H_1} M_1 - \rho_{21} \overbrace{\frac{H_2}{a_2 + H_2}}^{\text{probability of } M_2 \text{ attaching to } H_2} M_2 \right)}_{\text{Net dispersal effects at colony 2}}$$

(2.2)

where it is assumed that the single patch model (2.1) already includes the added mortality due to foraging behavior. Model (2.2) allows to address the following:

1. The migration effects on the population dynamics of honeybees versus Varroa mites by comparing the number of equilibria and their stability of the single patch model (2.1) to the corresponding two patch model (2.2) when $\rho_{12} = \rho_{21} = \rho$.
2. The dynamical effects of varied migration rates (i.e., $\rho_{12}$, $\rho_{21}$) on population outcomes of the two-patch model (2.2).
3. Identify conditions where migration rates could promote or suppress the collapse of a honeybee colony.

## 3. Mathematical analysis

The state space of the proposed two patch model (2.2) is $\{(H_1, M_1, H_2, M_2) \in \mathbb{R}_+^4\}$. Recall that

$$N_{h_i}^c = \frac{\frac{r_i}{d_{h_i}} - \sqrt{\left(\frac{r_i}{d_{h_i}}\right)^2 - 4K_i}}{2}, \quad N_{h_i}^* = \frac{\frac{r_i}{d_{h_i}} + \sqrt{\left(\frac{r_i}{d_{h_i}}\right)^2 - 4K_i}}{2}, \quad H_i^* = \frac{d_{m_i}}{c_i \alpha_i}, \text{ and } \quad M_i^* = \frac{1}{\alpha_i}\left[\frac{r_i H_i^*}{H_i^{*2} + K_i} - d_{h_i}\right] \text{ for }$$

$i = 1, 2$. We start with the basic dynamical properties of Model (2.2) as the following theorem:

**Theorem 3.1.** *Assume that all parameters are strictly positive. Model (2.2) is positively invariant and bounded in $\mathbb{R}_+^4$. Moreover, we have the following dynamics regarding Model (2.2):*

*1. The set $H_i = 0$ for $i = 1$ or 2 is invariant.*

2. The honeybee population in patch $i = 1, 2$ is bounded by $N_{h_i}^*$, i.e.,

$$\limsup_{t \to \infty} H_i(t) \leq N_{h_i}^*.$$

And the honeybee population $H_i(t)$ approaches to 0 if its initial population is less than the critical threshold, i.e., $H_i(0) < N_{h_i}^c$.

3. The extinction equilibrium $E_{0000} = (0, 0, 0, 0)$ is always locally asymptotically stable, and Model (2.2) converges to $E_{0000}$ locally if the initial honeybee population at both patches are less than the critical threshold, i.e., $H_i(0) < N_{h_i}^c$ $i = 1$ and 2.

4. If $\frac{r_i}{2\sqrt{K_i}} < d_{h_i}$ for either $i = 1$, or 2, the honeybee population $H_i(t)$ approaches to 0, i.e.,

$$\limsup_{t \to \infty} H_i(t) = 0.$$

Thus if $\frac{r_i}{2\sqrt{K_i}} < d_{h_i}$ for $i = 1$ and 2, then (2.2) converges to $E_{0000}$ globally.

5. If $N_{h_i}^* < H_i^* = \frac{d_{m_i}}{c_i \alpha_i}$ for both $i = 1, 2$, then the population of mites in both patches goes extinct.

**Biological Implications:** Theorem 3.1 implies that Model (2.2) is well-defined biologically. By comparison, with the dynamics of the single patch model (2.1), we observe that Model (2.2) inherits many dynamic properties from Model (2.1) including the importance of initial honeybee population and sufficient conditions that lead to the extinction of mites. For example, if mite population in each patch goes extinct in the absence of mite migration, then migration of mites can not prevent its extinction. However, if honeybee populations go extinct in one patch and survives in the other patch, then migration could potentially make mites survive in both patches. On the other hand, migration could also drive the extinction of mites in both patches (see our one dimensional bifurcation diagrams shown in Figures 2(a)-2(c)). In the case that honeybee colonies go extinct in both patches, the large migration rate in mites could save one honeybee colony from collapsing (see Figures 14 and 15).

In addition, Theorem 3.1 indicates that honeybee population at patch $i$ goes extinct when the inequality $\frac{r_i}{2\sqrt{K_i}} < d_{h_i}$ holds. Define $\hat{H}_j^* = \frac{\left(H_j^* - a_j + \frac{\rho_{ji}}{c_j \alpha_j}\right) + \sqrt{4 a_j H_j^* + \left(H_j^* - a_j + \frac{\rho_{ji}}{c_j \alpha_j}\right)^2}}{2}$ and

$$\hat{M}_j^* = \frac{1}{\alpha_j}\left[\frac{r_j \hat{H}_j^*}{(\hat{H}_j^*)^2 + K_j} - d_{h_j}\right], \quad \hat{M}_i^* = \frac{\rho_{ji} \hat{H}_j^* \hat{M}_j^*}{d_{m_i}(a_j + \hat{H}_j^*)}$$

for $i, j = 1, 2$, $i \neq j$. Then we have the following theorem regarding the dynamics when one of the two honeybee colonies collapses:
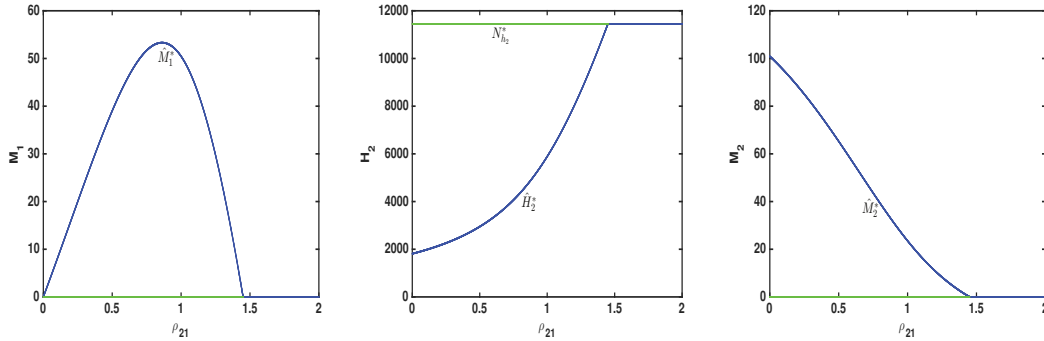


(a) $M_1$ vs $\rho_{21}$ for the effect of migrations (b) $H_2$ vs $\rho_{21}$ for the effect of migrations (c) $M_2$ vs $\rho_{21}$ for the effect of migrations

Figure 2: One parameter bifurcation diagrams of the subsystem Model (3.1) when $r_2 = 1500$, $c_2 = 0.01$, $d_{h_2} = 0.15$, $\alpha_2 = 0.005$, $a_2 = 23000$, $K_2 = 1000000$. Honeybees and mites population are extinct in patch 1 (i.e $(H_1^*, M_1^*) = (0, 0)$) and the interior equilibrium $(H_2^*, M_2^*) = (1812, 100.9)$ of the second patch is a sink in the absence of migration. The notations $\hat{H}_2^*$ and $\hat{M}_i^*$, $i = 12$ represent the population of honeybee and mite at the unique interior equilibrium. $N_{h_2}^*$ is the honeybee population at the boundary equilibrium $E_{0 N_{h_2}^* 0}$. The blue line represents sink and the green line a saddle.

**Theorem 3.2.** *[Dynamics of Model (3.1)] If the inequality $\frac{r_i}{2\sqrt{K_i}} < d_{h_i}$ holds, then Model (2.2) reduces to the following system:*

$$\frac{dM_i}{dt} = -d_{m_i} M_i + \rho_{ji} \frac{H_j}{a_j + H_j} M_j$$

$$\frac{dH_j}{dt} = \frac{r_j H_j^2}{K_j + H_j^2} - d_{h_j} H_j - \alpha_j H_j M_j \tag{3.1}$$

$$\frac{dM_j}{dt} = c_j \alpha_j H_j M_j - d_{m_j} M_j - \rho_{ji} \frac{H_j}{a_j + H_j} M_j$$

*whose dynamics can be summarized as follows:*

1. *If $\frac{r_j}{2\sqrt{K_j}} \geq d_{h_j}$, Model (3.1) has two boundary equilibria $(0, N_{h_j}^c, 0)$ and $(0, N_{h_j}^*, 0)$ where $(0, N_{h_j}^c, 0)$ is always saddle; and $(0, N_{h_j}^*, 0)$ is a sink if the following inequality holds*

$$N_{h_j}^* \left(1 - \frac{\rho_{ji}}{c_j \alpha_j (\alpha_j + N_{h_j}^*)}\right) < \frac{d_{m_j}}{c_j \alpha_j} = H_j^*$$

   *which is equivalent to (i) $H_j^* > N_{h_j}^*$ or (ii) $\rho_{ji} > \frac{c_j \alpha_j (N_{h_j}^* - H_j^*)(a_j + N_{h_j}^*)}{N_{h_j}^*} > 0$;*

   *otherwise, $(0, N_{h_j}^*, 0)$ is a saddle.*

2. *If $\frac{r_j}{2\sqrt{K_j}} \geq d_{h_j}$ and $N_{h_j}^c < \hat{H}_j^* < N_{h_j}^*$ hold, then Model (3.1) has a unique interior equilibrium $(\hat{M}_i^*, \hat{H}_j^*, \hat{M}_j^*)$ which is locally stable if $\hat{H}_j^* > \sqrt{K_j}$ otherwise it is saddle.*
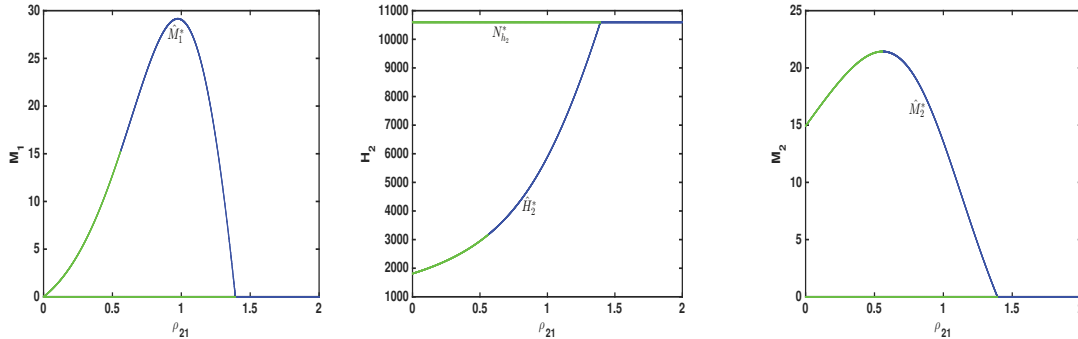


(a) $M_1$ vs $\rho_{21}$ for the effect of migrations    (b) $H_2$ vs $\rho_{21}$ for the effect of migrations    (c) $M_2$ vs $\rho_{21}$ for the effect of migrations

Figure 3: One parameter bifurcation diagrams of the subsystem Model (3.1) when $r_2 = 1500$, $c_2 = 0.01$, $d_{h_2} = 0.15$, $\alpha_2 = 0.005$, $a_2 = 23000$, $K_2 = 10000000$. Honeybees and mites population are extinct in patch 1 (i.e $(H_1^*, M_1^*) = (0, 0)$) and the interior equilibrium $(H_2^*, M_2^*) = (1812, 14.9)$ of the second patch is a saddle in the absence of migration. The notations $\hat{H}_2^*$ and $\hat{M}_i^*$, $i = 12$ represent the population of honeybee and mite at the unique interior equilibrium. $N_{h_2}^*$ is the honeybee population at the boundary equilibrium $E_{0N_{h_2}^* 0}$. The blue line represents sink and the green line a saddle.

**Biological Implications:** Theorem 3.2 is relevant where one colony is broken. However, from dynamical point of view, the results of Theorem 3.2 regarding Model (3.1) capture the role of migration on honeybee colonies collapsing in one patch while the other is healthy. The migration effects could hence be summarized as follows:

1. Migration has no effect when $H_j^* > N_{h_j}^* > \sqrt{K_j}$ hold as Model (3.1) approaches to $(0, N_{h_j}^*, 0)$ for any value of $\rho_{ji}$ (i.e., including $\rho_{ji} = 0$).

2. If there is no migration (i.e., $\rho_{ji} = 0$) and the inequalities $N_{h_j}^* > \max\left\{\sqrt{K_j}, H_j^*\right\}$ hold, then Model (3.1) approaches $(0, H_j^*, M_j^*)$ when $N_{h_j}^* > H_j^* > \max\left\{\sqrt{K_j}, N_j^c\right\}$ while it approaches extinction when

$N_{h_j}^* > \sqrt{K_j} > H_j^*$. However, if there is a large migration rate (i.e., $\rho_{ji} > \frac{c_j \alpha_j (N_{h_j}^* - H_j^*)(a_j + N_{h_j}^*)}{N_{h_j}^*} > 0$), then Model (3.1) can have locally stability at $(0, N_{h_j}^*, 0)$. This implies that the large migration can drive mite extinct when $N_{h_j}^* > H_j^* > \max\left\{\sqrt{K_j}, N_j^c\right\}$ hold (see Figures 2(a)-2(c) for this case); and it could also save honeybee colonies from collapsing if $N_{h_j}^* > \sqrt{K_j} > H_j^*$ hold. See bifurcation diagrams in Figures 3(a)-3(c) for this case.

3. Notice that $\hat{H}_j^* = \frac{\left(H_j^* - a_j + \frac{\rho_{ji}}{c_j \alpha_j}\right) + \sqrt{4 a_j H_j^* + \left(H_j^* - a_j + \frac{\rho_{ji}}{c_j \alpha_j}\right)^2}}{2}$, an increasing function of the migration rate $\rho_{ji}$, requires the need of an intermediate value of the migration rate to ensure $\max\left\{\sqrt{K_j}, N_{h_j}^c\right\} < \hat{H}_j^* < N_j^*$. In short, the proper migration rate could save honeybee colonies from collapsing especially when $H_j^* < \sqrt{K_j} < \hat{H}_j^*$. For instance, when

$$r_2 = 1500, \ c_2 = 0.01, \ d_{h_2} = 0.15, \ \alpha_2 = 0.005, \ a_2 = 23000,$$

with $K_2 = 4000000$, $\max\left\{\sqrt{K_j}, N_{h_j}^c\right\} < \hat{H}_j^* < N_j^* \Leftrightarrow 1812 < 2000 < 5888$, and the equilibrium $(\hat{M}_i^*, \hat{H}_j^*, \hat{M}_j^*) = (42.21, 5888.97, 19.67)$ is locally stable for $\rho_{21} = 1$ while $(0, N_{h_j}^*, 0) = (0, 11180.7, 0)$ is saddle. When $\rho_{21} = 5$ under the same parameters, then Model (3.1) has no interior equilibrium and $(0, N_{h_j}^*, 0)$ is locally stable.

The dynamics generated by migration in the subsystem Model (3.1) are better understood via the use of the following bifurcation diagrams (see Figures 2(a)-2(c) and Figures 3(a)-3(a)), which provide direct illustrations of the effects of migration on mites.

## 3.1. Boundary equilibria and their stability

Model (2.2) is capable of supporting the following boundary equilibria under additional conditions:

$$E_{0000} = (0, 0, 0, 0), \quad E_{N_{h_1}^c 000} = (N_{h_1}^c, 0, 0, 0), \quad E_{N_{h_1}^* 000} = (N_{h_1}^*, 0, 0, 0), \quad E_{00 N_{h_2}^c 0} = (0, 0, N_{h_2}^c, 0)$$

$$E_{00 N_{h_2}^* 0} = (0, 0, N_{h_2}^*, 0), \quad E_{N_{h_1}^c 0 N_{h_2}^c 0} = (N_{h_1}^c, 0, N_{h_2}^c, 0), \quad E_{N_{h_1}^* 0 N_{h_2}^c 0} = (N_{h_1}^*, 0, N_{h_2}^c, 0),$$

$$E_{N_{h_1}^c 0 N_{h_2}^* 0} = (N_{h_1}^c, 0, N_{h_2}^*, 0), \quad E_{N_{h_1}^* 0 N_{h_2}^* 0} = (N_{h_1}^*, 0, N_{h_2}^*, 0),$$

$$E_{H_1, M_1, 0, M_2} = (\hat{H}_1^*, \hat{M}_1^*, 0, \hat{M}_2^*), \quad E_{0, M_1, H_2, M_2} = (0, \check{M}_1^*, \check{H}_2^*, \check{M}_2^*).$$

where $\check{H}_j^* = \frac{\left(H_j^* - a_j + \frac{\rho_{ji}}{c_j \alpha_j}\right) + \sqrt{4 a_j H_j^* + \left(H_j^* - a_j + \frac{\rho_{ji}}{c_j \alpha_j}\right)^2}}{2}$ and $\check{M}_j^* = \frac{1}{\alpha_j}\left[\frac{r_j \check{H}_j^*}{(\check{H}_j^*)^2 + K_j} - d_{h_j}\right]$, $\check{M}_i^* = \frac{\rho_{ji} \check{H}_j^* \hat{M}_j^*}{d_{m_i}(a_j + \hat{H}_j^*)}$ for $i, j = 1, 2, \ i \neq j$. It would be interesting to explore how migration rates affect the local stability of the following boundary equilibria

$$E_{N_{h_1}^* 000}, \ E_{00 N_{h_2}^* 0}, \ E_{N_{h_1}^* 0 N_{h_2}^* 0}, \ E_{H_1, M_1, 0, M_2} \text{ and } E_{0, M_1, H_2, M_2}.$$

The conditions on the existence and stability of these boundary equilibria are illustrated in the following theorem:

**Theorem 3.3.** *[Boundary equilibria of Model (2.2)] Let $i, j = 1, 2$ and $i \neq j$. The existence and stability conditions of the boundary equilibria of Model (2.2) are provided below:*

1. *Model (2.2) always have the extinction equilibrium $E_{0000}$ which is always locally asymptotically stable.*
2. *If $\frac{r_i}{2\sqrt{K_i}} \geq d_{h_i}$, Model (2.2) has the boundary equilibria with $H_j = M_i = M_j = 0$ while $H_i = N_{h_i}^*$ or $H_i = N_{h_i}^c$. The boundary equilibrium with $H_i = N_{h_i}^*$ (i.e., $E_{N_{h_1}^* 000}$ or $E_{00 N_{h_2}^* 0}$) is locally stable if one of the following two conditions hold: (i) $H_i^* > N_{h_i}^*$ or (ii) $H_i^* < N_{h_i}^*$ and $\rho_{ij} > \frac{c_i \alpha_i (N_{h_i}^* - H_i^*)(a_i + N_{h_i}^*)}{N_{h_i}^*}$; and saddle otherwise.*
3. *If $\frac{r_i}{2\sqrt{K_i}} \geq d_{h_i}$ for both $i = 1$ and 2 hold, then Model (2.2) has the boundary equilibria of $E_{N_{h_1}^* 0 N_{h_2}^* 0}$, $E_{N_{h_1}^* 0 N_{h_2}^c 0}$, and $E_{N_{h_1}^c 0 N_{h_2}^* 0}$ where $E_{N_{h_1}^* 0 N_{h_2}^* 0}$ is locally stable if one of the following conditions hold*

(a) $H_i^* > N_{h_i}^*$ for both $i = 1, 2$

(b) $H_i^* < N_{h_i}^*$, $H_j^* > N_{h_j}^*$ and

$$\frac{\rho_{ij} N_{h_i}^*}{a_i + N_{h_i}^*} + \frac{\rho_{ji} N_{h_j}^*}{a_j + N_{h_j}^*} + c_j \alpha_j (H_j^* - N_{h_j}^*) > c_i \alpha_i (N_{h_i}^* - H_i^*)$$

and

$$\frac{\rho_{ij} c_j \alpha_j N_{h_i}^* (H_j^* - N_{h_j}^*)}{a_i + N_{h_i}^*} > c_i \alpha_i c_j \alpha_j (N_{h_i}^* - H_i^*)(H_j^* - N_{h_j}^*) + \frac{\rho_{ji} c_i \alpha_i N_{h_j}^* (N_{h_i}^* - H_i^*)}{a_j + N_{h_j}^*}.$$

4. If $\frac{r_i}{2\sqrt{K_i}} \geq d_{h_i}$ and $N_{h_i}^c < \hat{H}_i^* < N_{h_i}^*$ hold, then Model (2.2) has the boundary equilibrium with $H_j = 0$, $H_i = \hat{H}_i^*$, $M_i = \hat{M}_i^*$, $M_j = \hat{M}_i^*$ which is locally stable if $\hat{H}_j^* > \sqrt{K_j}$.

5. If the boundary equilibrium $E_{N_{h_1}^* 0 N_{h_2}^c 0}$, or $E_{N_{h_1}^c 0 N_{h_2}^* 0}$, or $E_{N_{h_1}^c 000}$ or $E_{00 N_{h_2}^c 0}$ exists, it is always saddle.

**Biological Implications:** Theorem 3.3 provides sufficient conditions on the existence and stability of all possible boundary equilibria of Model (2.2). These theoretical results provide cases under which migration can promote local extinction or coexistence of honeybee in both patches when mite population is extinct in at least one patch. We note the following points regarding the migration effects on the local stability of the boundary equilibria:

1. If $\frac{r_i}{2\sqrt{K_i}} \geq d_{h_i}$ and $H_i^* < N_{h_i}^*$, then in the absence of mite migration, the population of honeybee at Patch $i$ could approach $H^*$ when $\max\left\{N_{h_i}^c, \sqrt{K_i}\right\} < H_i^* < N_{h_i}^*$ or the honeybee colony collapses when $H_i^* < \sqrt{K_i}$. However, in the presence of mite migration, the large migration rate from Patch $i$ to Patch $j$, i.e., $\rho_{ij}$, can stabilize the boundary equilibrium $H_j = M_i = M_j = 0$, $H_i = N_{h_i}^*$ (i.e., $E_{N_{h_1}^* 000}$ or $E_{00 N_{h_2}^* 0}$) of Model (2.2) such that the honeybee colony could survive locally. This implies that the large migration rate from Patch $i$ to Patch $j$ could increase the honeybee population at Patch $i$ or prevent its collapsing under certain conditions. See our bifurcation diagrams on the case of the honeybee colony collapsing in one patch (Figures 3(a)-3(c)).

2. The phenomenon mentioned above also applies to the case when $\frac{r_i}{2\sqrt{K_i}} \geq d_{h_i}$ for both $i = 1, 2$ and $H_i^* < N_{h_i}^*$, $H_j^* < N_{h_j}^*$. Figures 14 and 15 on the cases that honeybee colonies collapse in both patches without migration illustrate that the large mite migration rate could save the honeybee colony.

## 3.2. Interior equilibria and the stability

We note the following regarding Model (2.2) :

$$\frac{dH_i}{dt} = \frac{r_i H_i^2}{K_i + H_i^2} - d_{h_i} H_i - \alpha_i H_i M_i = H_i \left( \frac{r_i H_i}{K_i + H_i^2} - d_{h_i} - \alpha_i M_i \right)$$

$$\frac{dM_i}{dt} + \frac{dM_j}{dt} = c_i \alpha_i H_i M_i + c_j \alpha_j H_j M_j - d_{m_i} M_i - d_{m_j} M_j$$

with $i, j = 1, 2$, $i \neq j$. Consider $(\hat{H}_1^*, \hat{M}_1^*, \hat{H}_2^*, \hat{M}_2^*)$ an interior equilibrium of Model (2.2), then the following conditions must be satisfied:

$$\frac{r_i H_i}{K_i + H_i^2} - d_{h_i} - \alpha_i M_i = 0 \Leftrightarrow M_i = \frac{1}{\alpha_i} \left[ \frac{r_i H_i^*}{H_i^{*2} + K_i} - d_{h_i} \right] \tag{3.2}$$

$$c_i \alpha_i H_i M_i + c_j \alpha_j H_j M_j - d_{m_i} M_i - d_{m_j} M_j = 0 \tag{3.3}$$

By substituting $M_i$ and $M_j$ from (3.2) into (3.3), we obtain:

$$\frac{dM_i}{dt} + \frac{dM_j}{dt} = \underbrace{\frac{[d_{h_i}(K_i + H_i^2) - r_i H_i](d_{m_i} - c_i \alpha_i H_i)}{(K_i + H_i^2)\alpha_i}}_{\phi_i(H_i)} + \underbrace{\frac{[d_{h_j}(K_j + H_j^2) - r_j H_j](d_{m_j} - c_j \alpha_j H_j)}{(K_j + H_j^2)\alpha_j}}_{\phi_j(H_j)} = 0 \tag{3.4}$$

The complexity of Model (2.2) prevents us to obtain the explicit solutions of the interior equilibria, thus we explore the symmetric interior equilibria for Model (2.2). We say that Model (2.2) is symmetric if $c_1 = c_2 = c$, $\alpha_1 = \alpha_2 = \alpha$, $r_1 = r_2 = r$, $K_1 = K_2 = K$, $a_1 = a_2 = a$, $d_{m_1} = d_{m_2} = d_m$, $d_{h_1} = d_{h_2} = d_h$, and $\rho_{12} = \rho_{21} = \rho$. The symmetric model is hence presented as follow:

$$\frac{dH_i}{dt} = \underbrace{\frac{rH_i^2}{K + H_i^2}}_{\text{successful reproduction in colony } i} - \underbrace{d_h H_i}_{\text{natural death}} - \underbrace{\alpha H_i M_i}_{\text{parasitism effects}}$$

$$\frac{dM_i}{dt} = c\alpha H_i M_i - d_m M_i + \underbrace{\rho\left(\frac{H_j}{a + H_j}M_j - \frac{H_i}{a + H_i}M_i\right)}_{\text{dispersal effect in colony } i} \tag{3.5}$$

with $i, j = 1, 2$, $i \neq j$. We present both the analytical and numerical results of the symmetric Model (3.5). We first provide the following theorem regarding the dynamics:

**Theorem 3.4.** *[The symmetric interior equilibria and the stability] Suppose that Model (2.2) is symmetric and is reduced to Model (3.5). Let* $H^* = \frac{d_m}{c\alpha}$, *and* $M^* = \frac{1}{\alpha}\left[\frac{rH^*}{H^{*2} + K} - d_h\right]$. *Then* $E = (H^*, M^*, H^*, M^*)$ *is a symmetric interior equilibrium for Model (3.5). Moreover, E is locally asymptotically stable if* $H^* > \sqrt{K}$ *and one of the following conditions holds:*

*1.* $M^* \leq \frac{rH^*(a+H^*)[(H^*)^2 - K]}{a\alpha[(H^*)^2 + K]^2}$

*2.* $M^* > \frac{rH^*(a+H^*)[(H^*)^2 - K]}{a\alpha[(H^*)^2 + K]^2}$ *and* $\rho < \frac{c\alpha^2 M^*(a+H^*)^2[(H^*)^2 + K]^2}{2(a\alpha M^*[(H^*)^2 + K]^2 - rH^*(a+H^*)[(H^*)^2 - K])}$.

*Otherwise, E is a saddle.*



(a) $H_1$ vs $\rho$ for the effect of migrations          (b) $M_1$ vs $\rho$ for the effect of migrations
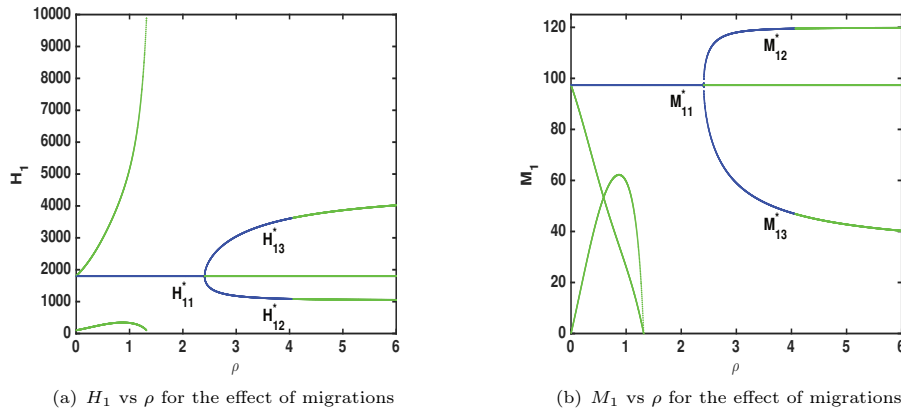
Figure 4: One parameter bifurcation diagrams of the symmetric Model (3.5) when $r = 1500, c = 0.01, d_h = 0.15, \alpha = 0.005, K = 100000, d_m = .09, a = 20000$. The interior equilibrium $(H^*, M^*) = (1800, 97.36)$ is a sink in the absence of migration for both patches. The notations $H^*_{ij}$ and $M^*_{ij}$ represent the population of honeybee and mite of the $j^{th}$ interior equilibrium at Patch $i$, respectively. The blue line represents sink and the green line a saddle.

**Biological Implications:** Theorem (3.4) implies that if $(H^*, M^*)$ is an interior equilibrium of the single patch model, (2.1), then $E = (H^*, M^*, H^*, M^*)$ is also an interior equilibrium of the symmetric model

(3.5). In addition, Theorem (3.4) indicates that the large migration rate may have destabilizing effects on population dynamics. In the absence of migration, the two uncoupled honeybee colonies in the identical environment have local stability at the honeybee-mite coexistence equilibrium $(H^*, M^*, H^*, M^*)$ if the following conditions hold

$$\frac{r}{2\sqrt{K}} > d_h, \text{ and } \max\left\{N_h^c, \sqrt{K}\right\} < H^* < N_h^*.$$

However, in the presence of migration, if $M^* > \frac{rH^*(a+H^*)[(H^*)^2 - K]}{a\alpha[(H^*)^2 + K]^2}$ holds, then the symmetric model (3.5) being locally stable at $(H^*, M^*, H^*, M^*)$ needs additional restriction on the migration rate $\rho$, i.e.,

$$\rho < \frac{c\alpha^2 M^*(a + H^*)^2[(H^*)^2 + K]^2}{2\left(a\alpha M^*[(H^*)^2 + K]^2 - rH^*(a + H^*)[(H^*)^2 - K]\right)}.$$

Otherwise, the symmetric equilibrium $E = (H^*, M^*, H^*, M^*)$ is a saddle. To further illustrate the potential effects of migration, we provide the bifurcation diagrams on the honeybee/mite population versus the migration rate $\rho$ (see Figures 4(a) and 4(b)) by letting

$$r_1 = r_2 = r = 1500, \ c_1 = c_2 = c = 0.01, \ d_{h_1} = d_{h_2} = d_h = 0.15,$$

$$\alpha_1 = \alpha_2 = \alpha = 0.005, \ K_1 = K_2 = K = 1000000.$$

Under this set of parameter values, we have $M^* > \frac{rH^*(a+H^*)[(H^*)^2 - K]}{a\alpha[(H^*)^2 + K]^2}$. We provide a brief summary on the dynamical effects of migration as follows:

1. Large migration rate could destabilize the interior equilibria such that the honeybee colony collapses. This has been illustrated in the bifurcation diagram of Figure 4.
2. Intermediate value of migration rate could generate multiple locally stable honeybee-mite coexistence equilibria.

## 4. Effects of migration rates on population dynamics of honeybees and mites

To further explore the role of mite migration on the population of varroa mites and bees due to the honeybee foraging behavior, we perform one and two parameter bifurcation analysis of Model (2.2) by choosing the typical parameter values from Table (1).

$$r_1 = r_2 = 1500, \ c_1 = c_2 = 0.01, \ d_{h_1} = 0.15, \ d_{h_2} = 0.13, \ \alpha_1 = \alpha_2 = 0.005, \ a_1 = 22000, \ a_2 = 23000.$$

Colonies infested by varroa mites are typically faced with infection by viruses such as Deformed Wing Virus or Israeli Acute Paralysis Virus ([13]) and the level of infection drive the strength of the colonies. Similarly nutrition is another factor that contribute to the strength of a colony. These two factors are however not taken into account in our model so we consider multiple scenarios in order to implicitly model the variation that occur in colonies due to disease dynamics or nutritional factors. Specifically, we investigate the following two scenarios of patch dynamics in the absence of migration:

**Case one:** Honeybees and mites can coexist in both patches (non-symmetric case).
**Case two:** Honeybees and mites can coexist in one patch while the honeybee colony collapses in the other patch that has a highly mite infested colony or a potential colony collapsing event.

### 4.1. Case one

Let $d_{m_1} = 0.095$, $d_{m_2} = 0.0906$ and $K_1 = K_2 = 1000000$. In the absence of migration, the uncoupled two colonies of Model (2.1) are locally asymptotically stable at $(H_1^*, M_1^*) = (1900, 93.6)$ and $(H_2^*, M_2^*) = (1812, 101.9)$, respectively.

In the presence of migration, we first perform two dimensional bifurcation diagrams to explore how migration rates affect the number of interior equilibria (see Figure 5(a)) and their stability (see Figure 5(b)). These two dimensional bifurcation diagrams suggest that: (1) Intermediate values of migration

rates of $\rho_{12}$ and $\rho_{21}$ could generate multiple attractors: two stable interior equilibria and two boundary attractors $E_{N^*_{h_1}000}, E_{00N^*_{h_2}0}$ (see the purple regions in Figure 5(a)). (2) Large values of migration rates of $\rho_{12}$ and $\rho_{21}$ could destabilize the dynamics leading to the extinction of honeybee and mite in at least one patch (see the overlapping regions of black in Figure5(a) and yellow in Figure 5(a)). Additional simulations show that small values of migration can generate one interior attractor where $E_{N^*_{h_1}000}$ and/or $E_{00N^*_{h_2}0}$ are either saddle or locally stable depending on the migration rate (e.g., $\rho_{12} < 1.29$ leads to $E_{N^*_{h_1}000}$ being saddle while $\rho_{21} < 1.45$ lead to $E_{00N^*_{h_2}0}$ being saddle); and the two-patch model (2.2) has only two boundary attractors $E_{N^*_{h_1}000}, E_{00N^*_{h_2}0}$ when it has only one stable interior equilibrium (see the cyan regions of Figure 5(a)).



(a) $\rho_{21}$ vs $\rho_{12}$ for the number of interior equilibria.

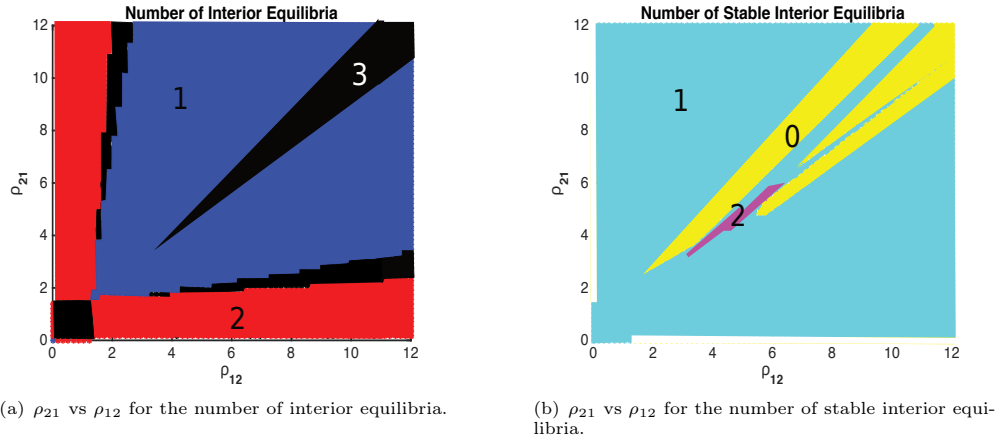(b) $\rho_{21}$ vs $\rho_{12}$ for the number of stable interior equilibria.

Figure 5: Two parameter bifurcation diagrams of Model (2.2) when $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.095$, $d_{m_2} = 0.0906$, $K_1 = K_2 = 1000000$. The interior equilibria $(H^*_1, M^*_1) = (1900, 93.6)$ and $(H^*_2, M^*_2) = (1812, 101.9)$ are sink in the absence of migration for both patches. Figure 5(a) describes the number of interior equilibria where black region have three interior equilibria; red regions have two interior equilibria; the blue regions have one interior equilibrium; and the white regions have no interior equilibria. Figure 5(b) illustrates the number of stable interior equilibria where the cyan region have one stable interior equilibria; the magenta region have two stable interior equilibria; the yellow region have no stable interior equilibria; and the white regions have no interior equilibria.

To explore how migration rates affect the dynamical patterns, we perform one dimensional bifurcation diagrams for the following two subcases, where the migration rates, not having data on which to base them, are given hypothetical, perhaps even biologically unrealistic, toy values, to provide some guidelines on their dynamical effects:

1. **Same migration rates between two patches:** $\rho_{12} = \rho_{21} = \rho$. One dimensional bifurcation diagrams (see Figures 6(a), 6(b), 6(c), and 6(d)) show that: (1) small values of migration rate could generate three interior equilibria where two are saddle and one is locally stable; (2) intermediate values of migration could generate multiple stable interior equilibria that lead to the bistability between interior attractors; and (3) large values of migration could destabilize the system such that dynamics converging to the boundary attractors $E_{N^*_{h_1}000}$ or $E_{00N^*_{h_2}0}$ depending on initial conditions. This phenomenon can lead to the collapsing of at least one honeybee colony. We also note from Figures 6(a) - 6(d) that depending on the initial conditions, when migration is in the intermediate value range, an increase in the mite migration rate yields a growth of the varroa population which in return have a negative feedback on honeybee population in both patches. This result is supported by the field work of [13,40].
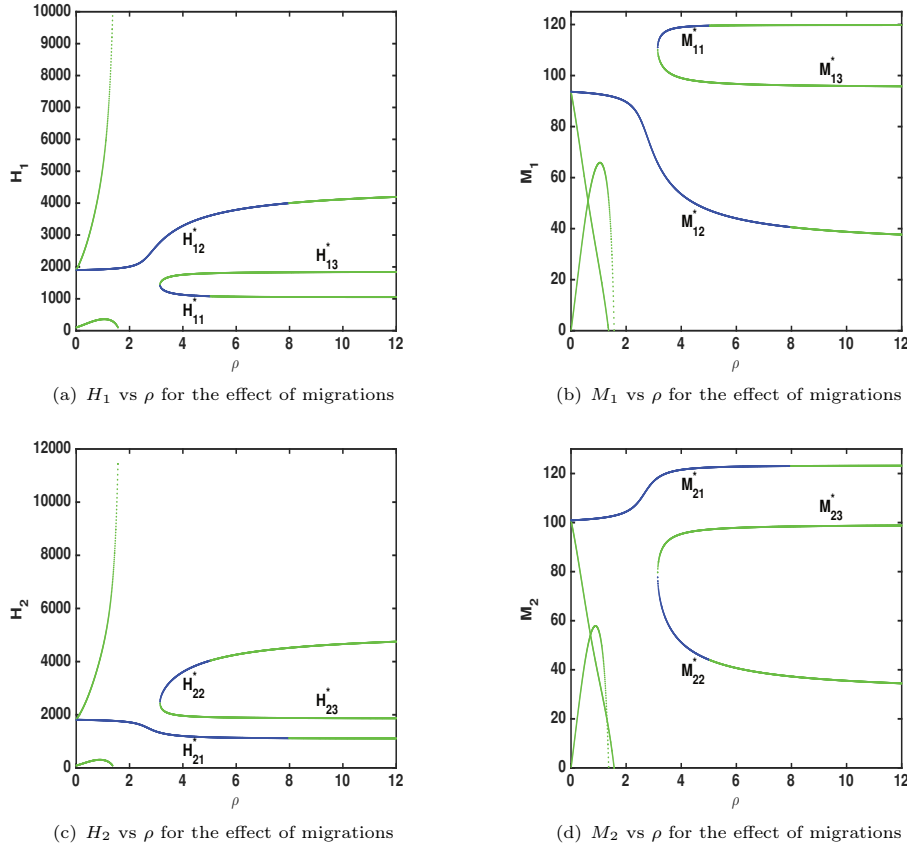
(a) $H_1$ vs $\rho$ for the effect of migrations



(b) $M_1$ vs $\rho$ for the effect of migrations



(c) $H_2$ vs $\rho$ for the effect of migrations



(d) $M_2$ vs $\rho$ for the effect of migrations

Figure 6: One parameter bifurcation diagrams of Model (2.2) when $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.095$, $d_{m_2} = 0.0906$, $K_1 = K_2 = 1000000$. The interior equilibria $(H_1^*, M_1^*) = (1900, 93.6)$ and $(H_2^*, M_2^*) = (1812, 101.9)$ are stable in the absence of migration for both patches. The notations $H_{ij}^*$ and $M_{ij}^*$ represent the population of honeybee and mite of the $j^{th}$ interior equilibrium at Patch $i$, respectively. The blue line represents sink and the green line a saddle.

2. **Different migration rates:** $\rho_{12} \neq \rho_{21}$. We perform one dimensional bifurcation diagrams on $\rho_{12} \in [0, 12]$ by fixing $\rho_{21} = 5$. Note that when $\rho_{12} = 0$, Model (2.2) is stabilized at the equilibrium $(H_1, M_1, H_2, M_2) = (1900, 93.64, 11451.1, 0)$ which corresponds to the case when foraging of honeybee is occurring in one way. Our bifurcation diagrams (Figures 7(a)-7(d)) suggest that the intermediate values of migration rates in mites (i.e., the value of the ratio $\frac{\rho_{21}}{\rho_{12}}$ is close to 1) could generate multiple interior/boundary attractors; and the large values of migration rates tend to make Model (2.2) have one stable interior equilibrium. In addition, we note that when the values of migration rates are small (i.e., the value of the ratio $\frac{\rho_{21}}{\rho_{12}} < 1$), an increase in the mite migration rate yields a rapid growth of the varroa population which in return have a negative feedback on honeybee population in both patches. This result is supported by the field work of [13,40].

### 4.2. Case two

Let $d_{m_1} = 0.317$, $d_{m_2} = 0.095$, $K_1 = 1000000$ and $K_2 = 4000000$. In the absence of migration, Model (2.1) is locally asymptotically stable at $(H_1^*, M_1^*) = (6340, 16.17)$ at Patch 1, and has its interior equilibrium being a source at $(H_2^*, M_2^*) = (1900, 48.9)$ in Patch 2 that has a highly mite infested colony such that both honeybees and mites go extinct (i.e., Patch 2 is the collapsing colony).

In the presence of migration, we first perform two dimensional bifurcation diagrams to explore how migration rates affect the number of interior equilibria (see Figure 8(a)) and their stability (see Figure 8(b)). These two dimensional bifurcation diagrams (Figure 8) suggest that the large ratio of $\frac{\rho_{21}}{\rho_{12}}$ (i.e.,

the migration rate from the collapsing colony at Patch 2 to the healthy colony at Patch 1 is larger than the other direction) can save the collapsing colony such that both honeybees and mites could coexist at both patches (see the cyan regions in Figure 8(b)). On the other hand, when the values of the ratio of $\frac{\rho_{21}}{\rho_{12}}$ are less than 1, Model (2.2) has no stable interior equilibrium with dynamics converging to the two boundary attractors $E_{N_{h_1}^* 000}, E_{00N_{h_2}^* 0}$ depending on initial conditions (see yellow regions in Figure 8(b)). This is the case suggesting that migrations could indeed lead to the extinction of mites.

To explore how migration rates affect the dynamical patterns, we perform one dimensional bifurcation diagrams 9 by letting $\rho_{12} = \rho_{21} = \rho \in [0, 6]$ based on two dimensional bifurcation diagrams 8. Figures 9(a), 9(b), 9(c), and 9(d) suggest that for small migration rates, Model (2.2) converges to one of the boundary attractors (i.e., $E_{\hat{H}_1^* \hat{M}_1^* 0 \hat{M}_2^*}$ or $E_{0 \bar{M}_1^* \bar{H}_2^* \bar{M}_2^*}$) where honeybee population goes extinct in one patch. In addition, it seems that intermediate and large values of migration rates (when $\rho_{12} = \rho_{21}$) could stabilize the dynamics such that both honeybees and mites are able to coexist in both patches.
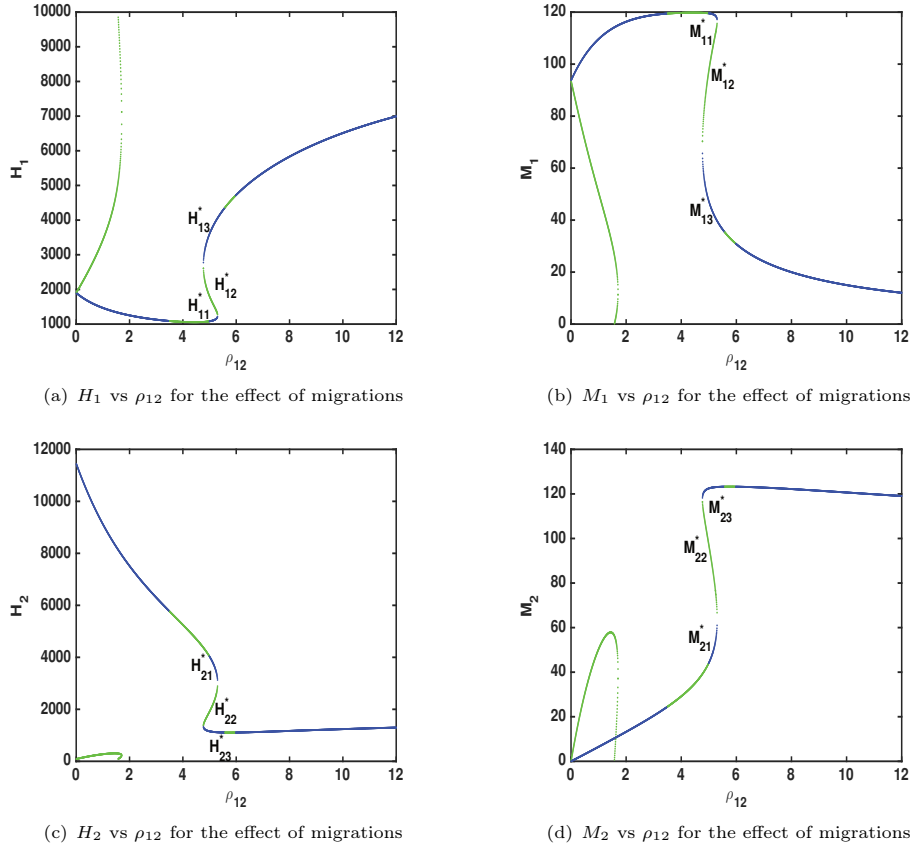


(a) $H_1$ vs $\rho_{12}$ for the effect of migrations

(b) $M_1$ vs $\rho_{12}$ for the effect of migrations

(c) $H_2$ vs $\rho_{12}$ for the effect of migrations

(d) $M_2$ vs $\rho_{12}$ for the effect of migrations

Figure 7: One parameter bifurcation diagrams of Model (2.2) when $\rho_{21} = 5$, $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.095$, $d_{m_2} = 0.0906$, $K_1 = K_2 = 1000000$. The interior equilibria $(H_1^*, M_1^*) = (1900, 93.6)$ and $(H_2^*, M_2^*) = (1812, 101.9)$ are stable in the absence of migration for both patches. The notations $H_{ij}^*$ and $M_{ij}^*$ represent the population of honeybee and mite of the $j^{th}$ interior equilibrium at Patch $i$, respectively. The blue line represents sink and the green line a saddle.
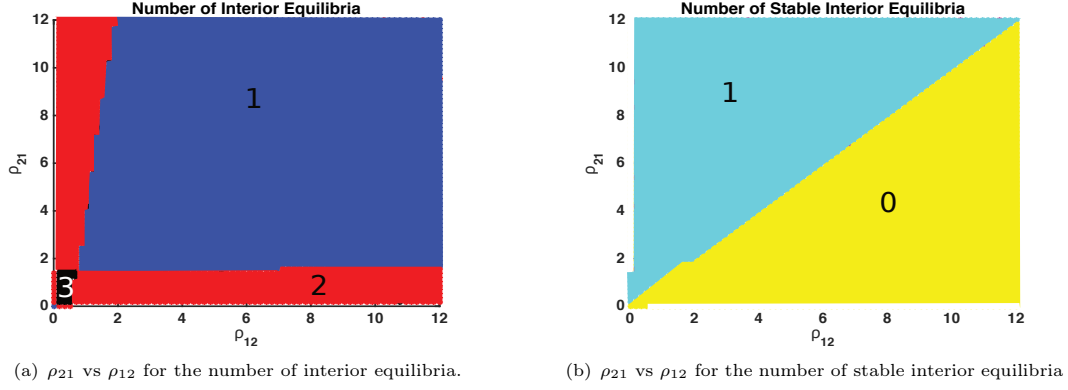
(a) $\rho_{21}$ vs $\rho_{12}$ for the number of interior equilibria.

(b) $\rho_{21}$ vs $\rho_{12}$ for the number of stable interior equilibria

Figure 8: Two parameter bifurcation diagrams of Model (2.2) when $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.317$, $d_{m_2} = 0.095$, $K_1 = 1000000$, $K_2 = 4000000$. The interior equilibrium $(H_1^*, M_1^*) = (6340, 16.17)$ of patch 1 is a sink and the interior equilibrium $(H_2^*, M_2^*) = (1900, 48.9)$ is a source in the absence of migration. Figure 8(a) describes the number of interior equilibria where black region have three interior equilibria; red regions have two interior equilibria; the blue regions have one interior equilibrium; and the white regions have no interior equilibria. Figure 8(b) illustrates the number of stable interior equilibria where the cyan region have one stable interior equilibria; the yellow region have no stable interior equilibria; and the white regions have no interior equilibria.
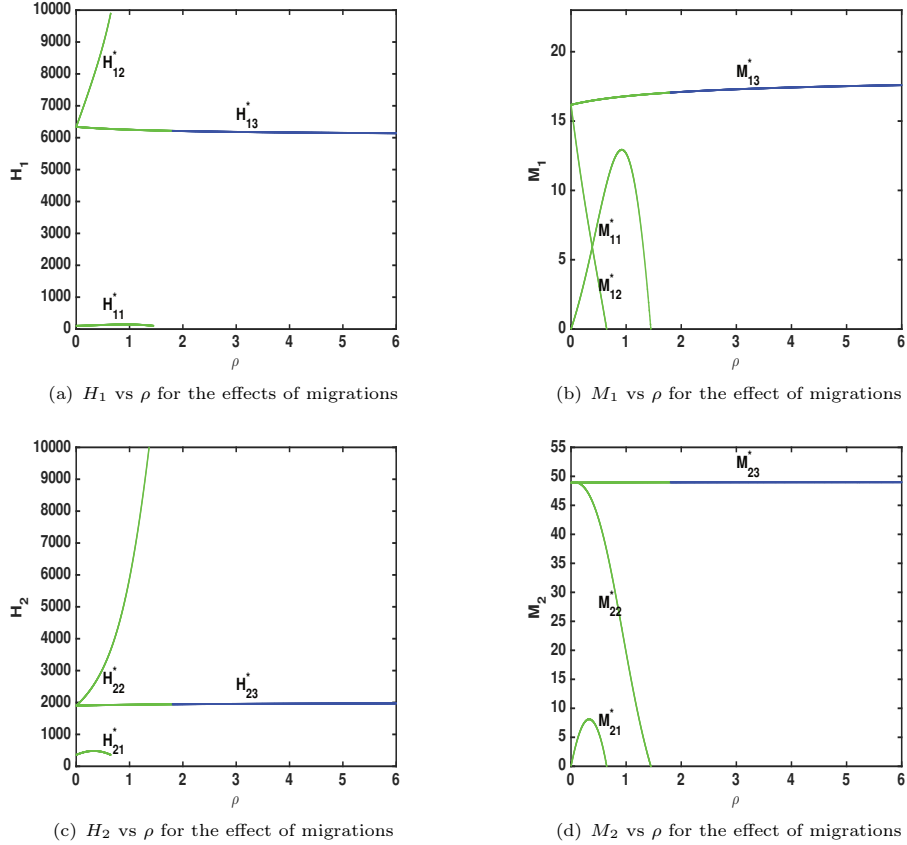


(a) $H_1$ vs $\rho$ for the effects of migrations

(b) $M_1$ vs $\rho$ for the effect of migrations

(c) $H_2$ vs $\rho$ for the effect of migrations

(d) $M_2$ vs $\rho$ for the effect of migrations

Figure 9: One parameter bifurcation diagrams of Model (2.2) when $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.317$, $d_{m_2} = 0.095$, $K_1 = 1000000$, $K_2 = 4000000$. The interior equilibrium $(H_1^*, M_1^*) = (6340, 16.17)$ of Patch 1 is a sink and the interior equilibrium $(H_2^*, M_2^*) = (1900, 48.9)$ is a source in the absence of migration. The notations $H_{ij}^*$ and $M_{ij}^*$ represent the population of honeybee and mite of the $j^{th}$ interior equilibrium at Patch $i$, respectively. Green line represents saddle.

To further explore the effects of migration rates in mites on population dynamics, let $K_1 = 1000000$, $K_2 = 4000000$, $d_{m_1} = 0.095$ and $d_{m_2} = 0.0906$ such that, in the absence of migrations, Model (2.2) has local stability at $(H_1^*, M_1^*) = (1900, 93.6)$ for Patch 1 (i.e., the healthy patch) while $(H_2^*, M_2^*) = (1812, 48.6)$ is a source at Patch 2 (i.e., the collapsing patch). We perform one dimensional bifurcation diagrams (Figure 10(a), 10(b), 10(c), and 10(d)) by fixing $\rho_{21} = 12$ and letting $\rho_{12} \in [0, 12]$ which is less than $\rho_{21}$. Our bifurcation diagrams 10 show that not large values of migration rates from the healthy patch to the collapsing patch, e.g., $\rho_{12} < 9$, could stabilize the system such that both honeybees and mites could coexist. While the larger values of $\rho_{12}$ could not have coexistence of both honeybees and mites, and the dynamics of Model (2.2) converge to one of the two boundary attractors $E_{N_{h_1}^* 000}$ or $E_{00 N_{h_2}^* 0}$ depending on initial conditions. This implies that the proper values of the mite migration rate could save the honeybee colony from collapsing.
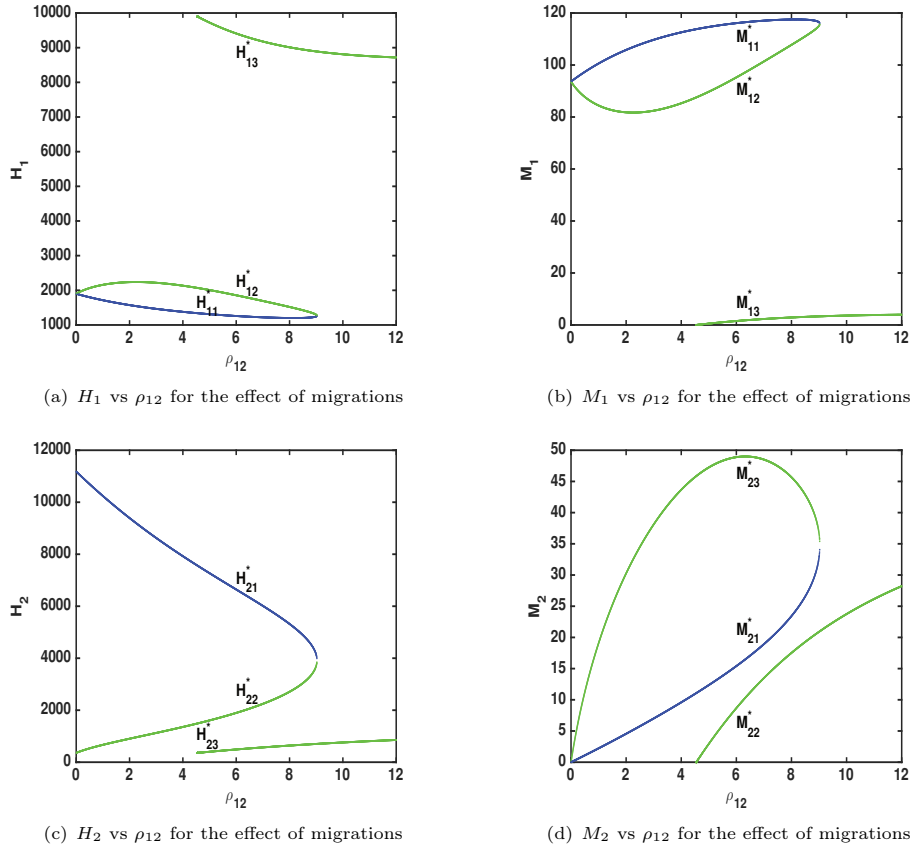


(a) $H_1$ vs $\rho_{12}$ for the effect of migrations

(b) $M_1$ vs $\rho_{12}$ for the effect of migrations

(c) $H_2$ vs $\rho_{12}$ for the effect of migrations

(d) $M_2$ vs $\rho_{12}$ for the effect of migrations

Figure 10: One parameter bifurcation diagrams of Model (2.2) when $\rho_{21} = 12$, $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.095$, $d_{m_2} = 0.0906$, $K_1 = 1000000$, $K_2 = 4000000$. The interior equilibrium $(H_1^*, M_1^*) = (1900, 93.6)$ of patch 1 is a sink and the interior equilibrium $(H_2^*, M_2^*) = (1812, 48.6)$ of patch 2 is a source in the absence of migration. The notations $H_{ij}^*$ and $M_{ij}^*$ represent the population of honeybee and mite of the $j^{th}$ interior equilibrium at Patch $i$, respectively. The blue line represents sink and the green line a saddle.

One interesting observation is that when the migration rates from the healthy patch (i.e patch 1) to the collapsing patch (patch 2), $\rho_{12}$ is less than 9, **an increasing migration rate could result in the growth of mite population and the decline of honeybee population** (see the blue lines in Figures 10(a)-10(d)). This fits in the field work of [13,40]. On the other hand, if we decrease the migration rates from the healthy patch to the collapsing patch $\rho_{12}$, we could also observe the similar patterns. As an example, we provide time series of honeybee and mite population at two patches by letting $c_1 = c_2 = .01$, $K_1 = 1000000$, $K_2 = 4000000$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = .005$, $a_1 = 22000$, $a_2 = 230000$,

$d_{m_1} = 0.095$, $d_{m_2} = .0906$. Under this set of parameter values, Model (2.2) has $(H_1^*, M_1^*)$ being a sink at Patch 1 and $(H_2^*, M_2^*)$ being a source at Patch 2 when $\rho_{12} = \rho_{21} = 0$. However, if we take $\rho_{12} = 3$ or 7 (see the blue lines for $\rho_{12} = 3$ and black lines for $\rho_{12} = 7$ in Figures 11(b) and 11(a)) while keeps $\rho_{21} = 12$, we could observe that increasing the value of $\rho_{12}$ results in the rapid growth of mite population and the decline of honeybee population.
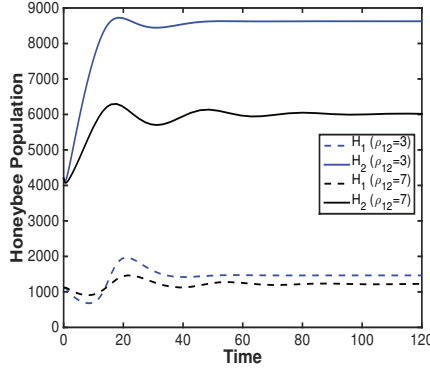


(a) Migrations effect on honeybee populations in patch 1 and patch 2 when $H_1(0) = 1100$, $M_1(0) = 100$, $H_2(0) = 4200$, $M_2(0) = 56$.
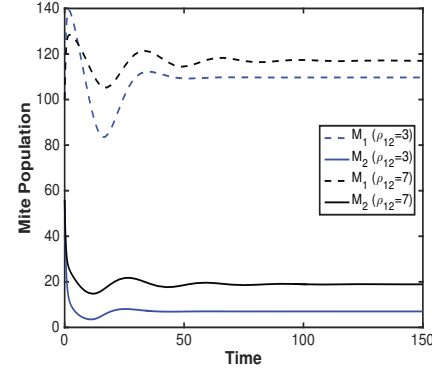
(b) Migrations effect on mite populations in patch 1 and patch 2 when, $H_1(0) = 1100$, $M_1(0) = 100$, $H_2(0) = 4200$, $M_2(0) = 56$.
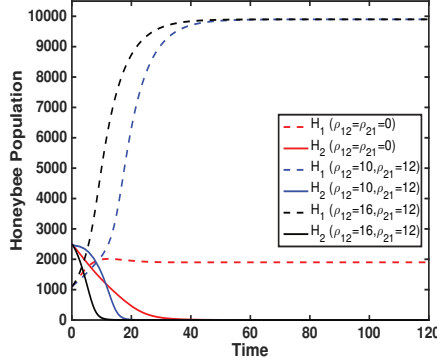
Figure 11: Time series of Model (2.2) when $\rho_{21} = 12$, $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.095$, $d_{m_2} = 0.0906$, $K_1 = 1000000$, $K_2 = 4000000$. The interior equilibrium $(H_1^*, M_1^*) = (1900, 93.6)$ of patch 1 is a sink and the interior equilibrium $(H_2^*, M_2^*) = (1812, 48.6)$ of patch 2 is a source in the absence of migration. Figure 11(a) and 11(b) represent respectively the population of honeybees and mites in both patches when $\rho_{12} = 3$ (see the blue lines) or $\rho_{12} = 7$ (see the black lines) while $\rho_{21} = 12$. For $\rho_{12} = 3$, the population converge to $(H_1, M_1, H_2.M_2) = (1464.8, 109.7, 8625.4, 7)$ and for $\rho_{12} = 7$ the population stabilize at $(H_1, M_1, H_2.M_2) = (1220.9, 117, 6013, 18.9)$.

## 4.3. Migration effects on colony extinction time

In this subsection, we use time series simulations to illustrate how migration in mites may affect the extinction time of collapsing event for two cases. As mentioned in the simulations with no migrations, the half saturation constant $a_1$ and $a_2$ are here given two hypothetical values that differ by one order of magnitude, because there are no data on which to base these estimates. The latter might perhaps be biologically unrealistic, but are meant to be understood as toy values, to help assessing their effect on the dynamical behavior of the ecosystem. Perhaps a possible justification for this huge difference could be given by observing that some colonies may have disease dynamics due to parasitism behavior, that are not taken into account in our model. Furthermore, there may be a large variations in these parameters due to nutrition, disease dynamics, and other factors. In order to incorporate these factors, we allow large variations in these coefficients. In addition, this variation reflects the fact that there are usually many colonies in the natural habitat, facing different ecological situations; the ability of mites to attach to the bees differs from colony to colony.

1. Let $c_1 = c_2 = .01$, $K_1 = 1000000$, $K_2 = 4000000$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = .005$, $a_1 = 22000$, $a_2 = 230000$, $d_{m_1} = 0.095$, $d_{m_2} = .0906$. Under this set of parameter values, in the absence of migration, Model (2.2) has $(H_1^*, M_1^*)$ being a sink at Patch 1 and $(H_2^*, M_2^*)$ being a source at Patch 2, i.e., Patch 1 is a healthy colony while Patch 2 colony dies at time 59.61 when its honeybee population drops below 1.

   (a) Fix $\rho_{21} = 12$ and let $\rho_{12} = 10$ or 16 (see Figure 12): Figure 12 shows that increasing migration rate from the healthy colony to the collapsing colony (i.e., $\rho_{12}$) decreases the extinction time in Patch 2 with only honeybee surviving in Patch 1 (i.e., no mites survive at neither patch). In addition, the population of honeybee at Patch 1 increases as $\rho_{12}$ increases. This implies that large mite migration of $\rho_{12}$ may lead to the earlier colony death event in Patch 2, however, it may increase honeybee population at Patch 1 and drive the extinction of mites in both patches.

(b) Fix $\rho_{12} = 12$ and let $\rho_{21} = 10$ or $16$ (see Figure 13): Figure 13 shows similar patterns as Figure 12, the difference is that increasing mite migration rate from the collapsing colony to the healthy colony (i.e., $\rho_{21}$) leads to the later death event in Patch 2 but still earlier than the case when no migration at all (i.e., $\rho_{21} = \rho_{12} = 0$).
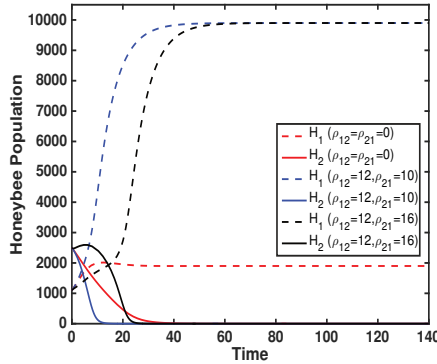


(a) Migrations effect on honeybee population when $H_1(0) = 1100$, $M_1(0) = 100$, $H_2(0) = 2500$, $M_2(0) = 56$.
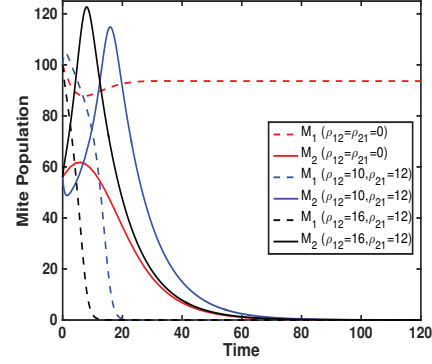
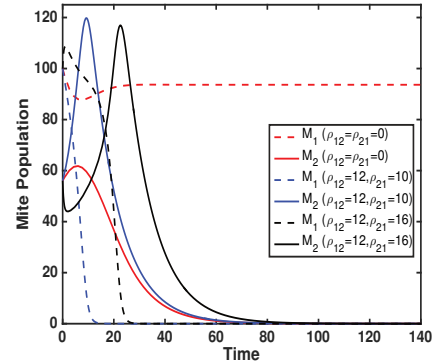(b) Migration effects on honeybee population when $H_1(0) = 1100$, $M_1(0) = 100$, $H_2(0) = 2500$, $M_2(0) = 56$.

Figure 12: Time series of Model (2.2) when $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.095$, $d_{m_2} = 0.0906$, $K_1 = 1000000$, $K_2 = 4000000$. The interior equilibrium $(H_1^*, M_1^*) = (1900, 93.6)$ of patch 1 is a sink and the interior equilibrioum $(H_2^*, M_2^*) = (1812, 48.6)$ of patch 2 is a source in the absence of migration. Dash lines represent population of honeybees and mites in patch 1 and solid lines represent population of honeybees and mites in patch 2. Red lines indicate the population of mites and honeybees when $\rho_{12} = \rho_{21} = 0$; blue lines indicate the population of honeybees and mites when $\rho_{12} = 10$, $\rho_{21} = 12$; and black lines indicates the population of honeybees and mites when $\rho_{12} = 16$, $\rho_{21} = 12$.



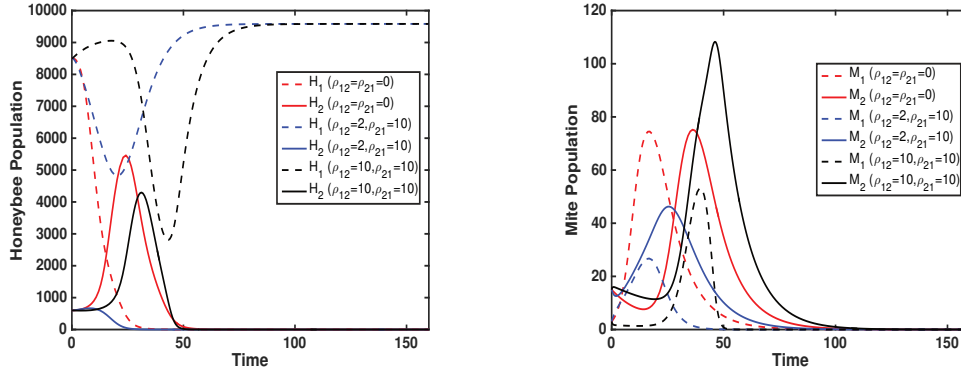(a) Migrations effect on honeybee population when $H_1(0) = 1100$, $M_1(0) = 100$, $H_2(0) = 2500$, $M_2(0) = 56$.

(b) Migration effects on honeybee population when $H_1(0) = 1100$, $M_1(0) = 100$, $H_2(0) = 2500$, $M_2(0) = 56$.

Figure 13: Time series of Model (2.2) when $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.095$, $d_{m_2} = 0.0906$, $K_1 = 1000000$, $K_2 = 4000000$. The interior equilibrium $(H_1^*, M_1^*) = (1900, 93.6)$ of patch 1 is a sink and the interior equilibrioum $(H_2^*, M_2^*) = (1812, 48.6)$ of patch 2 is a source in the absence of migration. The dash lines represent population of honeybees and mites in patch 1 and the solid lines represent population of honeybees and mites in patch 2. The red lines indicate the population of mites and honeybees when $\rho_{12} = \rho_{21} = 0$; the blue lines indicate the population of honeybees and mites when $\rho_{21} = 10$, $\rho_{12} = 12$; and the black lines indicates the population of honeybees and mites when $\rho_{21} = 16$, $\rho_{12} = 12$.

2. Let $c_1 = c_2 = .01$, $K_1 = K_2 = 4000000$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = .005$, $a_1 = 22000$, $a_2 = 230000$, $d_{m_1} = 0.095$, $d_{m_2} = .0906$. Under this set of parameter values, in the absence of migration, Model (2.2) has the interior equilibrium $(H_1^*, M_1^*)$ at Patch 1 and $(H_2^*, M_2^*)$ at Patch 2,

being source. More specifically, both Patch 1 and 2 colony die (i.e., the population of honeybee drops below 1) at times 19.85, 58.52, respectively.

(a) Fix $\rho_{21} = 10$ and let $\rho_{12} = 2$ or $10$ (see Figure 14): Figure 14 shows that: (1) mite migrations can save Patch 1 from collapsing such that its honeybee colony survives; (2) mite migration may not be able to save mites from extinction; and (3) increasing migration rate from Patch 1 to Patch 2 (i.e., $\rho_{12}$) can increase the extinction time to the collapse of Patch 2.



(a) Migrations effects on honeybee populations when $H_1(0) = 8500$, $M_1(0) = 3$, $H_2(0) = 600$, $M_2(0) = 15$.

(b) Migrations effects on honeybees populations when $H_1(0) = 8500$, $M_1(0) = 3$, $H_2(0) = 600$, $M_2(0) = 15$.

Figure 14: Time series of Model (2.2) when when $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.095$, $d_{m_2} = 0.0906$, $K_1 = K_2 = 4000000$. The interior equilibria $(H_1^*, M_1^*)$ and $(H_2^*, M_2^*)$ are both source in the absence of migration. The dash lines represent population of honeybees and mites in patch 1 and the solid lines represent population of honeybees and mites in patch 2. The red lines indicate the population of mites and honeybees when $\rho_{12} = \rho_{21} = 0$; the blue lines indicate the population of honeybees and mites when $\rho_{12} = 2$, $\rho_{21} = 10$; and the black lines indicates the population of honeybees and mites when $\rho_{12} = 10$, $\rho_{21} = 10$

(b) Fix $\rho_{12} = 10$ and Let $\rho_{21} = 2$ or $10$ (see Figure 15): Figure 15 shows the similar patterns as Figure 15 with difference in increasing migration rate from Patch 2 to Patch 1 (i.e., $\rho_{21}$) can decrease the extinction time to collapsing event in Patch 2.
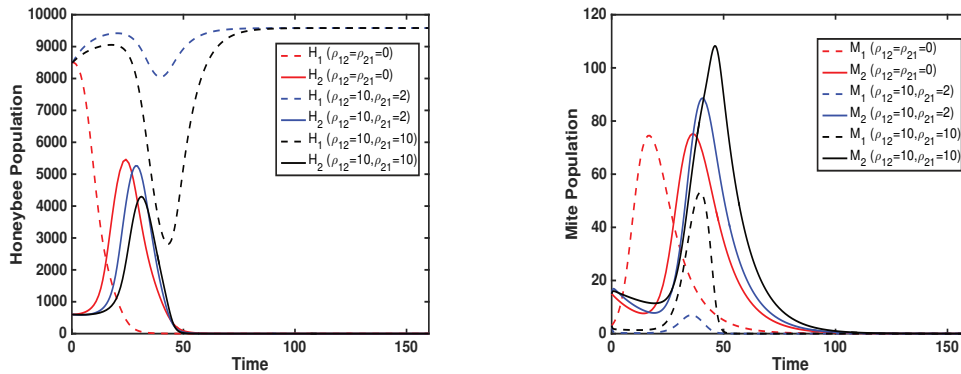


(a) Migrations effects on honeybee populations when $H_1(0) = 8500$, $M_1(0) = 3$, $H_2(0) = 600$, $M_2(0) = 15$.

(b) Migrations effects on honeybee populations when $H_1(0) = 8500$, $M_1(0) = 3$, $H_2(0) = 600$, $M_2(0) = 15$.

Figure 15: Time series of Model (2.2) when when $r_1 = r_2 = 1500$, $c_1 = c_2 = 0.01$, $d_{h_1} = 0.15$, $d_{h_2} = 0.13$, $\alpha_1 = \alpha_2 = 0.005$, $a_1 = 22000$, $a_2 = 23000$, $d_{m_1} = 0.095$, $d_{m_2} = 0.0906$, $K_1 = K_2 = 4000000$. The interior equilibria $(H_1^*, M_1^*)$ and $(H_2^*, M_2^*)$ are both source in the absence of migration. The dash lines represent population of honeybees and mites in patch 1 and the solid lines represent population of honeybees and mites in patch 2. The red lines indicate the population of mites and honeybees when $\rho_{12} = \rho_{21} = 0$; the blue lines indicate the population of honeybees and mites when $\rho_{21} = 2$, $\rho_{12} = 10$; and the black lines indicates the population of honeybees and mites when $\rho_{21} = 10$, $\rho_{12} = 10$

## 5. Conclusion

Migrations in general have huge impacts on population dynamics [1,2,5,10,26,36,37]. In susceptible-infective-susceptible disease transmission models, [11] found that dispersal may promote bistability dynamics leading to an increases in life history diversity, thus reducing the likelihood of extinction (also see [50] for multiple attractors generated by dispersal in metapopulation study). The recent field work of [13] shows that the migration of mites through their attachments to forager bees has an impact on the rapid population growth of mites, and thus contribute to the decline of honeybee populations. Motivated by this, we proposed a nonlinear system of ordinary differential equations that describes the interactions between honeybees and mites in a two-patch framework where migration of mites occurs via attaching to the honeybee foragers. In fact, honeybee foragers may provide different levels of coexistence for the same migration rates but different initial conditions (see the bifurcation diagrams in Figures 4(a) and 4(b)). The theoretical results combined with numerical simulations including one and two dimensional bifurcation diagrams provide us useful insights on how migration in mites affects dynamical outcome of honeybee and mite populations. More specifically, our theoretical work suggests what follows:

1. As we would expect, if the mite population in each patch goes extinct in the absence of mite migration, extinction cannot be prevented by migration. However, if honeybees go extinct in one patch and survive in the other patch, then migration could potentially make mites survive in both patches (i.e., honeybees and mites coexist at both patches). On the other hand, migration could also drive the extinction of mites in both patches. In the case that honeybee colonies go extinct in both patches in the absence of migrations, the large migration rate in mites could save the colony in one patch from collapsing (see Theorem (3.1)).
2. If honeybee colonies collapse in one or both patches in the absence of migration, depending on situations (see the conditions in Theorem (3.2)), large migration rates may drive mite populations to extinction (also see Figures 2(a)-2(c)); intermediate or large migration rates could also save honeybee colonies from collapsing (also see Figures 3(a)-3(c), respectively).
3. Theorem (3.3) provides theoretical results that the large migration rate from Patch $i$ to Patch $j$ could possibly increase the honeybee population at Patch $i$ or prevent its collapsing in one patch or both patches under certain conditions (see Figures 3(a)-3(c); 6(a)-6(d)).
4. The large migration rate could also destabilize the interior equilibria such that the honeybee colony collapses under proper conditions, while the intermediate value of migration rate could generate multiple locally stable honeybee-mite coexistence equilibria (see Theorem (3.4); also Figures 4(a) and 4(b)).

To further explore the role of mite migration on the population of mites and bees, we perform one and two parameter bifurcation analysis of Model (2.2) by considering the following two cases in the absence of migration: (1) honeybees and mites can coexistence in both patches; and (2) honeybees and mites can coexistence in one patch while the colony collapses in the other. Our bifurcation analysis illustrate the complex dynamics of Model (2.2) driven by mite migration rates.

1. Migration in mites could generate multiple attractors in Model (2.2) as shown in Figures 7(a)-7(d) that Model (2.2) could have one or two stable interior equilibria.
2. When Model (2.2) have three interior equilibria among which two are saddles and one is sink, its typical dynamics involve bistability between boundary attractor(s) and interior coexistence equilibrium.
3. When Model (2.2) has three interior equilibria among which one is saddle and two are sinks, its typical dynamics involve four attractors: two boundary attractors and two interior attractors (see Figures 6(a)-6(d) or Figures 7(a)-7(d)).
4. When Model (2.2) has three interior equilibria being saddle, it has only boundary attractors that may lead to the collapsing event in one of the two patches with only honeybee surviving in the other patch (i.e., $E_{N_{h_1}^* 000}$ or $E_{00 N_{h_2}^* 0}$ in Figures 6(a)-6(d)) or the coexistence of both honeybee and mite in one patch with only mite surviving in the other patch (i.e., $E_{H_1,M_1,0,M_2}$ or $E_{0,M_1,H_2,M_2}$ in Figures 9(a)-9(d)) where Model (2.2) convergence depends on the initial conditions.
5. Depending on local environments, large values of mite migration rates may have stabilizing or destabilizing effects on the interior equilibrium.

6. One interesting observation that is supported by the field work of [13,40] is that, increasing mite migration rate could lead to the rapid population growth in mites and the declined population in honeybees (see Figures 10(a)-10(d)).

7. **Migration effects on the time to colony death**: If at least one patch exhibits colony death in the absence of migration, the mite migration may save at least one patch from collapsing such that honeybees can survive at least in one patch while mites go extinct in both patches. In addition, increasing the mite migration from the healthy patch to the collapsing patch can decrease the extinction time in the collapsing patch (see Figures 12) while increasing the mite migration from the collapsing patch to the healthy patch can increase the extinction time in the collapsing patch (see Figures 13).

Our findings illustrate how population dynamics of honeybees and mites are affected by the foraging behavior of bees when healthy colonies are surrounded by infested ones. While our proposed model neglects other causes of colony death such as pathogens, poor nutrition, or exposure to pesticides, the model provides a better understanding of the interrelationships of colony and Varroa population dynamics in a framework that includes mite migration and predicts that migration can result in colony death. It will be interesting to investigate the effect of migration in honeybee colonies in the presence of honeybee diseases transmitted by varroa mites. This will be subject of future study by the authors.

## 6. Proofs

### Proof of Theorem 3.1

*Proof.* Observe that $\frac{dH_i}{dt}\big|_{H_i=0} = 0$ and $\frac{dM_i}{dt}\big|_{M_i=0} = \rho_{ij}\frac{H_i}{a_i+H_i}M_j \geq 0$ if $M_j \geq 0$ for $i = 1,2$, $j = 1,2$, and $i \neq j$, thus we can conclude that model (2.2) is positive invariant in $\mathbb{R}_+^4$ by Theorem A.4 (p.423) in [47]. We now proceed with the boundedness as follows:

$$\frac{dH_i}{dt} = \frac{r_i H_i^2}{K_i + H_i^2} - d_{h_i}H_i - \alpha_i H_i M_i \leq \frac{r_i H_i^2}{K_i + H_i^2} - d_{h_i}H_i$$

for $i = 1,2$. This implies that $\limsup_{t\to\infty} H_i(t) \leq \frac{\left(\frac{r_i}{d_{h_i}}\right)+\sqrt{\left(\frac{r_i}{d_{h_i}}\right)^2-4K_i}}{2} = N_{h_i}^*$. Thus if $\frac{r_i}{2\sqrt{K_i}} < d_{h_i}$ or

$H_i(0) < \frac{\left(\frac{r_i}{d_{h_i}}\right)-\sqrt{\left(\frac{r_i}{d_{h_i}}\right)^2-4K_i}}{2} = N_{h_i}^c$ then $\limsup_{t\to\infty} H_i(t) = 0$. This proves Item 2 and 4 of the theorem.

Define $V = c_1 H_1 + M_1 + c_2 H_2 + M_2$, then we have

$$\begin{aligned}\frac{dV}{dt} &= c_1\frac{dH_1}{dt} + \frac{dM_1}{dt} + c_2\frac{dH_2}{dt} + \frac{dM_2}{dt}\\ &= \frac{c_1 r_1 H_1^2}{K_1+H_1^2} - c_1 d_{h_1}H_1 - d_{m_1}M_1 + \frac{c_2 r_2 H_2^2}{K_2+H_2^2} - c_2 d_{h_2}H_2 - d_{m_2}M_2\\ &\leq T - \min\{d_{h_1},d_{m_1},d_{h_2},d_{m_2}\}(c_1 H_1 + M_1 + c_2 H_2 + M_2) = T - d_{\min}V\end{aligned}$$

where

$$T = \max_{N_{h_1}^c \leq H_1 \leq N_{h_1}^*}\left\{\frac{c_1 r_1 H_1^2}{K_1+H_1^2}\right\} + \max_{N_{h_2}^c \leq H_2 \leq N_{h_2}^*}\left\{\frac{c_2 r_2 H_2^2}{K_2+H_2^2}\right\}.$$

Therefore, we have

$$\limsup_{t\to\infty} V(t) = \limsup_{t\to\infty}(c_1 H_1(t) + M_1(t) + c_2 H_2(t) + M_2(t)) \leq \frac{T}{d_{\min}}$$

which implies that Model (2.2) is bounded in $\mathbb{R}_+^4$.

$E_{0000}$ always exist and is always locally stable, however we will return to the existence and local stability of $E_{0000}$ when we prove Item 1 of Theorem 3.3. In addition, if $\frac{r_i}{2\sqrt{K_i}} < d_{h_i}$, $i = 1$ and 2, then the extinction equilibrium $E_{0000}$ is the only locally stable equilibrium from the upper bound argument of the honeybee population presented above. we can conclude that $E_{0000}$ is globally stable.

Recall that $\frac{dH_i}{dt}\big|_{H_i=0} = 0$ and $\frac{dM_i}{dt}\big|_{M_i=0} = \rho_{ij}\frac{H_i}{a_i+H_i}M_j \geq 0$ if $M_j \geq 0$ for $i = 1, 2$, $j = 1, 2$, and $i \neq j$ thus the set $\{(H_1, M_1, H_2, M_2) \in \mathbb{R}_+^4 : H_i = 0\}$ is invariant for both $i = 1, 2$. This indicates that if $H_i(0) = 0$, then $H_i(t) = 0$ for all $t > 0$. Thus, the population $M_i$ converges to 0 since $\lim_{t\to\infty} M_j = \lim_{t\to\infty} M_i = 0$ when $H_i = 0$. This prove item 1 of the theorem.

Now the proof of Item 5 is as follow. Define $M = M_1 + M_2$ and from Model (2.2), we have

$$\frac{dM}{dt} = (c_1\alpha_1 H_1 - d_{m_1})M_1 + (c_2\alpha_2 H_2 - d_{m_2})M_2$$

$$= c_1\alpha_1\left(H_1 - \frac{d_{m_1}}{c_1\alpha_1}\right)M_1 + c_2\alpha_2\left(H_2 - \frac{d_{m_2}}{c_2\alpha_2}\right)M_2$$

$$\leq \max_{\substack{N_{h_1}^c \leq H_1 \leq N_{h_1}^* \\ N_{h_2}^c \leq H_2 \leq N_{h_2}^*}}\left\{c_1\alpha_1\left(H_1 - \frac{d_{m_1}}{c_1\alpha_1}\right), c_2\alpha_2\left(H_2 - \frac{d_{m_2}}{c_2\alpha_2}\right)\right\}(M_1 + M_2)$$

For $N_{h_i}^* < H_i^* = \frac{d_{m_i}}{c_i\alpha_i}$, $i = 1$ and 2,

$$\frac{dM}{dt} \leq \max_{\substack{N_{h_1}^c \leq H_1 \leq N_{h_1}^* \\ N_{h_2}^c \leq H_2 \leq N_{h_2}^*}}\left\{c_1\alpha_1\left(H_1 - \frac{d_{m_1}}{c_1\alpha_1}\right), c_2\alpha_2\left(H_2 - \frac{d_{m_2}}{c_2\alpha_2}\right)\right\}(M_1 + M_2) \leq 0 \Rightarrow \limsup_{t\to\infty} M(t) = 0.$$

Consequently the populations $M_1$ and $M_2$ go extinct when $N_{h_i}^* < H_i^* = \frac{d_{m_i}}{c_i\alpha_i}$, $i = 1$ and 2. This concludes the proof of Theorem 3.1. $\qquad\square$

## Proof of Theorem 3.2

*Proof.* We note that Model (2.2) is reduced to Model (3.1) when $H_i = 0, i = 1$ or 2 which always have the extinction equilibrium $E_{000}$. From the results of Theorem (3.3), we know that Model (2.2) has the boundary equilibria $E_{N_{h_1}^c 0 N_{h_2}^c 0}$ and $E_{N_{h_1}^* 0 N_{h_2}^* 0}$ when $\frac{r_i}{2\sqrt{K_i}} \geq d_{h_i}$, $i = 1, 2$ thus when $H_i = 0$, $i = 1$ or 2, Model (3.1) has the boundary equilibria $E_{0N_{h_2}^c 0}$ and $E_{0N_{h_2}^* 0}$ for $i = 1$ or $E_{N_{h_1}^c 00}$ and $E_{N_{h_1}^* 00}$ for $i = 2$. Now we prove the existence of the interior equilibria of Model (3.1). Recall that Model (2.2) is reduced to the following when $H_i = 0$

$$\frac{dM_i}{dt} = -d_{m_i}M_i + \rho_{ji}\frac{H_j}{a_j + H_j}M_j$$

$$\frac{dH_j}{dt} = \frac{r_j H_j^2}{K_j + H_j^2} - d_{h_j}H_j - \alpha_j H_j M_j$$

$$\frac{dM_j}{dt} = c_j\alpha_j H_j M_j - d_{m_j}M_j - \rho_{ji}\frac{H_j}{a_j + H_j}M_j$$

for $i, j = 1, 2$, $i \neq j$. Solving for $M_i$ in $\frac{dM_i}{dt} = 0$ and $M_j$ in $\frac{dH_j}{dt} = 0$ yields respectively

$$M_i = \frac{\rho_{ji}H_j M_j}{d_{m_i}(a_j + H_j)} \qquad \text{and} \qquad M_j = \frac{1}{\alpha_j}\left[\frac{r_j H_j}{H_j^2 + K_j} - d_{h_j}\right]$$

Now we note that $H_i^* = \frac{d_{m_i}}{c_i\alpha_i}$, $i = 1, 2$ and solving for $H_j$ in $\frac{dM_j}{dt} = 0$ yields the following unique positive solution

$$\hat{H}_j^* = \frac{\left(H_j^* - a_j + \frac{\rho_{ji}}{c_j\alpha_j}\right) + \sqrt{4a_j H_j^* + \left(H_j^* - a_j + \frac{\rho_{ji}}{c_j\alpha_j}\right)^2}}{2} > 0.$$

Also, $\limsup_{t\to\infty} H_j(t) \leq \frac{\left(\frac{r_j}{d_{h_j}}\right) + \sqrt{\left(\frac{r_j}{d_{h_j}}\right)^2 - 4K_j}}{2} = N_{h_j}^*$ and if $\frac{r_j}{2\sqrt{K_j}} < d_{h_j}$ or $H_j(0) < \frac{\left(\frac{r_j}{d_{h_j}}\right) - \sqrt{\left(\frac{r_j}{d_{h_j}}\right)^2 - 4K_j}}{2} = N_{h_i}^c$ then $\limsup_{t\to\infty} H_j(t) = 0$ as noted in Theorem 3.1. By the arguments above, Model (3.1) has the unique interior equilibrium $E_{\hat{M}_1^* \hat{H}_2^* \hat{M}_2^*}$ when $H_1 = 0$ or $E_{\hat{H}_1^* \hat{M}_1^* \hat{M}_2^*}$ when $H_2 = 0$ with

$$\hat{H}_j^* = \frac{\left(H_j^* - a_j + \frac{\rho_{ji}}{c_j\alpha_j}\right) + \sqrt{4a_j H_j^* + \left(H_j^* - a_j + \frac{\rho_{ji}}{c_j\alpha_j}\right)^2}}{2}, \quad \hat{M}_j^* = \frac{1}{\alpha_j}\left[\frac{r_j \hat{H}_j^*}{(\hat{H}_j^*)^2 + K_j} - d_{h_j}\right], \quad \text{and} \quad \hat{M}_i^* = \frac{\rho_{ji}\hat{H}_j^* \hat{M}_j^*}{d_{m_i}(a_j + \hat{H}_j^*)}$$

for $i, j = 1, 2$, $i \neq j$ under the condition $N^c_{h_j} < \hat{H}^*_j < N^*_{h_j}$.

We continue our proof with the local stability of the equilibria $E_{000}$, $E_{0N^*_{h_j}0}$, $E_{0N^c_{h_j}0}$, and $E_{\hat{H}^*_1 \hat{M}^*_1 \hat{M}^*_2}$ which can be determined by the eigenvalues $\lambda_i$, $i = 1, 2, 3$ of the Jacobian matrix (6.1) evaluated at the equilibria

$$
J_{(\hat{M}^*_i, \hat{H}^*_j, \hat{M}^*_j)} =
$$

$$
\begin{bmatrix}
-d_{m_i} & \frac{a_j \hat{M}^*_j \rho_{ji}}{(a_j + \hat{H}^*_j)^2} & \frac{\hat{H}^*_j \rho_{ji}}{a_j + \hat{H}^*_j} \\
0 & -d_{h_j} + \frac{2 r_j \hat{H}^*_j K_j}{((\hat{H}^*_j)^2 + K_j)^2} - \alpha_j \hat{M}^*_j & -\alpha_j \hat{H}^*_j \\
0 & \hat{M}^*_j \left( c_j \alpha_j - \frac{a_j \rho_{ji}}{(a_j + \hat{H}^*_j)^2} \right) & -d_{m_j} + c_j \hat{H}_j \alpha_j - \frac{\hat{H}^*_j \rho_{ji}}{a_j + \hat{H}^*_j}
\end{bmatrix}
=
\begin{bmatrix}
-d_{m_i} & \frac{a_j \hat{M}^*_j \rho_{ji}}{(a_j + \hat{H}^*_j)^2} & c_j \alpha_j \hat{H}^*_j - d_{m_j} \\
0 & -d_{h_j} + \frac{2 r_j \hat{H}^*_j K_j}{((\hat{H}^*_j)^2 + K_j)^2} - \alpha_j \hat{M}^*_j & -\alpha_j \hat{H}^*_j \\
0 & \hat{M}^*_j \left( c_j \alpha_j - \frac{a_j \rho_{ji}}{(a_j + \hat{H}^*_j)^2} \right) & 0
\end{bmatrix}
\tag{6.1}
$$

since

$$
\frac{dM_j}{dt} = 0 \Rightarrow -d_{m_j} + c_j H_j \alpha_j - \frac{H_j \rho_{ji}}{a_j + H_j} = 0 \text{ or } c_j \alpha_j H_j - d_{m_j} = \frac{H_j \rho_{ji}}{a_j + H_j}
$$

1. After substitution of the equilibrium $E_{000}$ into the Jacobian matrix (6.1), we obtain the eigenvalues:

$$
\lambda_1 = -d_{h_j} < 0, \quad \lambda_2 = -d_{m_i} < 0, \quad \lambda_3 = -d_{m_j} < 0
$$

thus we can conclude that $E_{000}$ is always locally asymptotically stable.

2. The proof for the local stability of the boundary equilibria $E_{0N^c_{h_j}0}$ and $E_{0N^*_{h_j}0}$ are as follows. Recall that $\frac{r_j}{2\sqrt{K_j}} \geq d_{h_j}$ is the necessary condition for $E_{0N^*_{h_j}0}$ and $E_{0N^c_{h_j}0}$ to exist. Substitution of the equilibrium $E_{0N^*_{h_j}0}$ into the the Jacobian Matrix (6.1) yield the following eigenvalues :

$$
\lambda_1 = -d_{h_i} < 0, \quad \lambda_2 = \frac{r_j \hat{H}^*_j [K_j - (N^*_{h_j})^2]}{[K_j + (N^*_{h_j})^2]^2}, \quad \lambda_3 = c_j \alpha_j (N^*_{h_j} - H^*_j) - \frac{\rho_{ij} N^*_{h_j}}{a_j + N^*_{h_j}}.
$$

Then we have:

$$
\lambda_2 = \frac{r_j \hat{H}^*_j [K_j - (N^*_{h_j})^2]}{[K_j + (N_{h_j})^2]^2} < 0 \quad \text{since} \quad N^*_{h_j} = \frac{\left(\frac{r_j}{d_{h_j}}\right) + \sqrt{\left(\frac{r_j}{d_{h_j}}\right)^2 - 4 K_j}}{2} > \sqrt{K_j} \Leftrightarrow \frac{r_j}{2\sqrt{K_j}} > d_{h_j}
$$

and

$$
\lambda_3 = c_1 \alpha_1 (N^*_{h_1} - H^*_1) - \frac{\rho_{12} N^*_{h_1}}{a_1 + N^*_{h_1}} = N^*_{h_j} \left( 1 - \frac{\rho_{ji}}{c_j \alpha_j (\alpha_j + N^*_{h_j})} \right) < \frac{d_{m_j}}{c_j \alpha_j} = H^*_j < 0
$$

$$
\Rightarrow H^*_j > N^*_{h_j} \text{ or } H^*_j < N^*_{h_j} \text{ and } \rho_{ij} > \frac{c_j \alpha_j (N^*_{h_j} - H^*_j)(a_j + N^*_{h_j})}{N^*_{h_j}}.
$$

Thus $E_{0N^*_{h_j}0}$ is sink if one of the following conditions is satisfied:

(i) $H^*_j > N^*_{h_j}$ or (ii)$\rho_{ji} > \frac{c_j \alpha_j (N^*_{h_j} - H^*_j)(a_j + N^*_{h_j})}{N^*_{h_j}} > 0$, otherwise, $(0, N^*_{h_j}, 0)$ is a saddle.

Now substitution of the boundary equilibrium $E_{0N^c_{h_j}0}$ into the the Jacobian Matrix (6.1) gives the following eigenvalues :

$$
\lambda_1 = -d_{h_i} < 0, \quad \lambda_2 = \frac{r_j \hat{H}^*_j [K_j - (N^c_{h_j})^2]}{[K_j + (N^c_{h_j})^2]^2}, \quad \lambda_3 = c_j \alpha_j (N^c_{h_j} - H^*_j) - \frac{\rho_{ij} N^c_{h_j}}{a_j + N^c_{h_j}}.
$$

Note that $\lambda_2 > 0$ consider $N^c_{h_j} = \frac{\left(\frac{r_j}{d_{h_j}}\right) - \sqrt{\left(\frac{r_j}{d_{h_j}}\right)^2 - 4 K_j}}{2} < \sqrt{K_j} \Leftrightarrow \frac{r_j}{2\sqrt{K_j}} > d_{h_j}$

therefore $E_{0N^c_{h_j}0}$ is saddle.

3. A substitution of the interior equilibrium $E_{\hat{M}_i^* \hat{H}_j^* \hat{M}_j^*}$ into the Jacobian matrix (6.1) yield the following characteristic polynomial

$$\lambda^3 - \left[\sum_{k=1}^{3} \lambda_k\right]\lambda^2 + \left[\sum_{k,s=1,k\neq s}^{3} \lambda_k \lambda_s\right]\lambda - \prod_{k=1}^{3}\lambda_k$$

where the eigenvalues $\lambda_k(\hat{M}_i^*, \hat{H}_j^*, \hat{M}_j^*)$, $k = 1, 2, 3$ are the roots of the above characteristic equation. We then have:

$$\sum_{k=1}^{3}\lambda_k = -d_{m_i} + \frac{r_j \hat{H}_j^*[K_j - (\hat{H}_j^*)^2]}{[K_j + (\hat{H}_j^*)^2]^2} < 0 \quad \text{if} \quad \hat{H}_j^* > \sqrt{K_j}$$

$$\sum_{k,s=1,k\neq s}^{3}\lambda_k \lambda_s = -d_{m_i}\frac{r_j \hat{H}_j^*[K_j - (\hat{H}_j^*)^2]}{[K_j + (\hat{H}_j^*)^2]^2} + \alpha_j \hat{M}_j^* \hat{H}_j^*\left(c_j \alpha_j - \frac{a_j \rho_{ji}}{(a_j + \hat{H}_j^*)^2}\right) > 0 \quad \text{if} \quad \hat{H}_j^* > \sqrt{K_j}$$

$$\prod_{k=1}^{3}\lambda_k = -d_{m_i}\alpha_j \hat{M}_j^* \hat{H}_j^*\left(c_j \alpha_j - \frac{a_j \rho_{ji}}{(a_j + \hat{H}_j^*)^2}\right) < 0 \quad \text{if} \quad 0 < \rho_{ji} < \frac{c_j \alpha_j (a_j + \hat{H}_j^*)^2}{a_j}$$

consider

$$c_j \alpha_j - \frac{a_j \rho_{ji}}{(a_j + \hat{H}_j^*)^2} = \frac{c_j \alpha_j\left[\left(\hat{H}_j^*\right)^2 + a_j H_j^* + a_j\sqrt{4a_j H_j^* + \left(H_j^* - a_j + \frac{\rho_{ji}}{c_j \alpha_j}\right)^2}\right]}{(a_j + \hat{H}_j^*)^2} > 0.$$

Thus $E_{\hat{M}_i^* \hat{H}_j^* \hat{M}_j^*}$ is locally stable when $\hat{H}_j^* > \sqrt{K_j}$ and saddle otherwise.

This concludes the proof of Theorem (3.2).

□

**Proof of Theorem 3.3**

*Proof.* Observe that the single Colony Model (2.1) always has the extinction equilibrium $(0, 0)$. Therefore Model (2.2) always has the extinction equilibrium $E_{0000}$ as well. In addition the boundary $(N_{h_i}^c, 0)$ and $(N_{h_i}^*, 0)$ exists for Model (2.1) when $\frac{r_i}{2\sqrt{K_i}} \geq d_{h_i}$, $i = 1, 2$ and these conditions guarantee the existence of the equilibria $E_{N_{h_1}^c 000}$, $E_{N_{h_1}^* 000}$, $E_{00N_{h_2}^c 0}$, $E_{00N_{h_2}^* 0}$, $E_{N_{h_1}^* 0N_{h_2}^* 0}$, $E_{N_{h_1}^* 0N_{h_2}^c 0}$, $E_{N_{h_1}^c 0N_{h_2}^* 0}$, $E_{N_{h_1}^* 0N_{h_2}^* 0}$. Now we look at the local stability of the boundary equilibria which can be determined by the eigenvalues $\lambda_i$, $i = 1, 2, 3, 4$ of the Jacobian matrix (6.2) evaluated at the equilibrium

$$J_{(\bar{H}_1^*, \bar{M}_1^*, \bar{H}_2^*, \bar{M}_2^*)} =$$

$$\begin{bmatrix} -d_{\bar{H}_1^*} - \alpha_1 \bar{M}_1^* + \frac{2r_1 K_1 \bar{H}_1^*}{[K_1 + (\bar{H}_1^*)^2]^2} & -\alpha_1 \bar{H}_1^* & 0 & 0 \\ c_1 \alpha_1 \bar{M}_1^* - \frac{\rho_{12} a_1 \bar{M}_1^*}{(a_1 + \bar{H}_1^*)^2} & -d_{\bar{M}_1^*} + c_1 \alpha_1 \bar{H}_1^* - \frac{\rho_{12}\bar{H}_1^*}{a_1 + \bar{H}_1^*} & \frac{\rho_{21} a_2 \bar{M}_2^*}{(a_2 + \bar{H}_2^*)^2} & \frac{\rho_{21}\bar{H}_2^*}{a_2 + \bar{H}_2^*} \\ 0 & 0 & -d_{\bar{H}_2^*} - \alpha_2 \bar{M}_2^* + \frac{2r_2 K_2 \bar{H}_2^*}{[K_2 + (\bar{H}_2^*)^2]^2} & -\alpha_2 \bar{H}_2^* \\ \frac{\rho_{12} a_1 \bar{M}_1^*}{(a_1 + \bar{H}_1^*)^2} & \frac{\rho_{12}\bar{H}_1^*}{a_1 + \bar{H}_1^*} & c_2 \alpha_2 \bar{M}_2^* - \frac{\rho_{21} a_2 \bar{M}_2^*}{(a_2 + \bar{H}_2^*)^2} & -d_{\bar{M}_2^*} + c_2 \alpha_2 \bar{H}_2^* - \frac{\rho_{21}\bar{H}_2^*}{a_2 + \bar{H}_2^*} \end{bmatrix} \quad (6.2)$$

1. After substitution of the equilibrium $E_{0000}$ into the Jacobian Matrix (6.2), we obtain the eigenvalues:

$$\lambda_1 = -d_{h_1} < 0, \quad \lambda_2 = -d_{m_1} < 0, \quad \lambda_3 = -d_{h_2} < 0, \quad \lambda_4 = -d_{m_2} < 0$$

thus we can conclude that $E_{0000}$ is always locally asymptotically stable.
2. Now we look at the stability of the boundary equilibria $E_{N_{h_1}^* 000}$, $E_{N_{h_1}^c 000}$, $E_{00N_{h_2}^* 0}$, and $E_{00N_{h_2}^c 0}$. Substitution of the equilibrium $E_{N_{h_1}^* 000}$ into the the Jacobian Matrix (6.2) yields the following eigenvalues :

$$\lambda_1 = -d_{h_2} < 0, \quad \lambda_2 = -d_{m_2} < 0, \quad \lambda_3 = -\left(\frac{d_{h_1}^2}{r_1}\right)\sqrt{\left(\frac{r_i}{d_{h_i}}\right)^2 - 4K_i} < 0, \quad \lambda_4 = c_1 \alpha_1 (N_{h_1}^* - H_1^*) - \frac{\rho_{12} N_{h_1}^*}{a_1 + N_{h_1}^*}$$

We note that

$$\lambda_4 = c_1\alpha_1(N_{h_1}^* - H_1^*) - \frac{\rho_{12}N_{h_1}^*}{a_1 + N_{h_1}^*} < 0 \Rightarrow H_1^* > N_{h_1}^* \text{ or } H_1^* < N_{h_1}^* \text{ and } \rho_{12} > \frac{c_1\alpha_1(N_{h_1}^* - H_1^*)(a_1 + N_{h_1}^*)}{N_{h_1}^*}$$

Consequently the equilibrium $E_{N_{h_1}^* 000}$ is locally asymptotically stable if

(i) $H_1^* > N_{h_1}^*$ or

(ii) $H_1^* < N_{h_1}^*$ and $\rho_{12} > \frac{c_1\alpha_1(N_{h_1}^* - H_1^*)(a_1 + N_{h_1}^*)}{N_{h_1}^*}$

and a saddle otherwise. We continue with the local stability of $E_{N_{h_1}^c 000}$. Substitution of the equilibrium $E_{N_{h_1}^c 000}$ into the the Jacobian Matrix (6.2) yield the following eigenvalues :

$$\lambda_1 = -d_{h_2} < 0, \quad \lambda_2 = -d_{m_2} < 0, \quad \lambda_3 = \left(\frac{d_{h_1}^2}{r_1}\right)\sqrt{\left(\frac{r_1}{d_{h_1}}\right)^2 - 4K_1} > 0, \quad \lambda_4 = c_1\alpha_1(N_{h_1}^c - H_1^*) - \frac{\rho_{12}N_{h_1}^c}{a_1 + N_{h_1}^c}$$

Thus $E_{N_{h_1}^c 000}$ is always saddle. Similarly we can obtain the stability condition of the equilibria $E_{00N_{h_2}^* 0}$ and $E_{00N_{h_2}^c 0}$ therefore the proof is omitted.

3. We now provide the stability of the boundary equilibria $E_{N_{h_1}^* 0 N_{h_2}^* 0}$, $E_{N_{h_1}^* 0 N_{h_2}^c 0}$, $E_{N_{h_1}^c 0 N_{h_2}^* 0}$, and $E_{N_{h_1}^c 0 N_{h_2}^c 0}$ which are obtain by the eigenvalues of the Jacobian matrix (6.2) evaluated at the equilibria. At first, the detail on the stability of $E_{N_{h_1}^* 0 N_{h_2}^* 0}$ is given below through the eigenvalues of $J_{E_{N_{h_1}^* 0 N_{h_2}^* 0}}$:

$$\lambda_1\lambda_2 = \left[-\left(\frac{d_{h_1}^2}{r_1}\right)\sqrt{\left(\frac{r_1}{d_{h_1}}\right)^2 - 4K_1}\right]\left[-\left(\frac{d_{h_2}^2}{r_2}\right)\sqrt{\left(\frac{r_2}{d_{h_2}}\right)^2 - 4K_2}\right] > 0$$

$$\lambda_1 + \lambda_2 = -\left[\left(\frac{d_{h_1}^2}{r_1}\right)\sqrt{\left(\frac{r_1}{d_{h_1}}\right)^2 - 4K_1} + \left(\frac{d_{h_2}^2}{r_2}\right)\sqrt{\left(\frac{r_2}{d_{h_2}}\right)^2 - 4K_2}\right] < 0$$

$$\lambda_3\lambda_4 = \frac{c_2\alpha_2(a_2 + N_{h_2}^*)(H_2^* - N_{h_2}^*)[c_1\alpha_1(a_1 + N_{h_1}^*)(H_1^* - N_{h_1}^*) + \rho_{12}N_{h_1}^*] + \rho_{21}c_1\alpha_1(a_1 + N_{h_1}^*)(H_1^* - N_{h_1}^*)N_{h_2}^*}{(a_1 + N_{h_1}^*)(a_2 + N_{h_2}^*)}$$

$$\lambda_3 + \lambda_4 = -\frac{(a_2 + N_{h_2}^*)[(a_1 + N_{h_1}^*)(c_1\alpha_1(H_1^* - N_{h_1}^*) + c_2\alpha_2(H_2^* - N_{h_2}^*)) + \rho_{12}N_{h_1}^*] + \rho_{21}(a_1 + N_{h_1}^*)N_{h_2}^*}{(a_1 + N_{h_1}^*)(a_2 + N_{h_2}^*)}$$

Observe that for $H_i^* > N_{h_i}^*$, $i = 1$ and 2, $\lambda_3\lambda_4 > 0$ and $\lambda_3 + \lambda_4 < 0$. In addition,

$$\lambda_3\lambda_4 = \frac{c_2\alpha_2(a_2 + N_{h_2}^*)(H_2^* - N_{h_2}^*)[c_1\alpha_1(a_1 + N_{h_1}^*)(H_1^* - N_{h_1}^*) + \rho_{12}N_{h_1}^*] + \rho_{21}c_1\alpha_1(a_1 + N_{h_1}^*)(H_1^* - N_{h_1}^*)N_{h_2}^*}{(a_1 + N_{h_1}^*)(a_2 + N_{h_2}^*)}$$

$$= \frac{\rho_{12}c_2\alpha_2 N_{h_1}^*(H_2^* - N_{h_2}^*)}{a_1 + N_{h_1}^*} + c_1\alpha_1 c_2\alpha_2(H_1^* - N_{h_1}^*)(H_2^* - N_{h_2}^*) + \frac{\rho_{21}c_1\alpha_1 N_{h_2}^*(H_1^* - N_{h_1}^*)}{a_2 + N_{h_2}^*}$$

and

$$\lambda_3 + \lambda_4 = -\frac{(a_2 + N_{h_2}^*)[(a_1 + N_{h_1}^*)(c_1\alpha_1(H_1^* - N_{h_1}^*) + c_2\alpha_2(H_2^* - N_{h_2}^*)) + \rho_{12}N_{h_1}^*] + \rho_{21}(a_1 + N_{h_1}^*)N_{h_2}^*}{(a_1 + N_{h_1}^*)(a_2 + N_{h_2}^*)}$$

$$= -\frac{\rho_{12}N_{h_1}^*}{a_1 + N_{h_1}^*} - \frac{\rho_{21}N_{h_2}^*}{a_2 + N_{h_2}^*} - c_1\alpha_1(H_1^* - N_{h_1}^*) - c_2\alpha_2(H_2^* - N_{h_2}^*)$$

If $H_1^* < N_{h_1}^*$ and $H_2 > N_{h_2}^*$ then from the equations above

$$\lambda_3\lambda_4 > 0 \quad \Rightarrow \quad \frac{\rho_{12}c_2\alpha_2 N_{h_1}^*(H_2^* - N_{h_2}^*)}{a_1 + N_{h_1}^*} > c_1\alpha_1 c_2\alpha_2(N_{h_1}^* - H_1^*)(H_2^* - N_{h_2}^*) + \frac{\rho_{21}c_1\alpha_1 N_{h_2}^*(N_{h_1}^* - H_1^*)}{a_2 + N_{h_2}^*}$$

$$\lambda_3 + \lambda_4 < 0 \quad \Rightarrow \quad \frac{\rho_{12}N_{h_1}^*}{a_1 + N_{h_1}^*} + \frac{\rho_{21}N_{h_2}^*}{a_2 + N_{h_2}^*} + c_2\alpha_2(H_2^* - N_{h_2}^*) > c_1\alpha_1(N_{h_1}^* - H_1^*)$$

Therefore $E_{N_{h_1}^* 0 N_{h_2}^* 0}$ is locally asymptotically stable if one of the following two conditions is satisfied:

(i) $H_i^* > N_{h_i}^*$ for both $i = 1, 2$

(ii) $H_i^* < N_{h_i}^*$, $H_j^* > N_{h_j}^*$ for $i, j = 1, 2, i \neq j$ and

$$\frac{\rho_{ij} N_{h_i}^*}{a_i + N_{h_i}^*} + \frac{\rho_{ji} N_{h_j}^*}{a_j + N_{h_j}^*} + c_j \alpha_j (H_j^* - N_{h_j}^*) > c_i \alpha_i (N_{h_i}^* - H_i^*)$$

and

$$\frac{\rho_{ij} c_j \alpha_j N_{h_i}^* (H_j^* - N_{h_j}^*)}{a_i + N_{h_i}^*} > c_i \alpha_i c_j \alpha_j (N_{h_i}^* - H_i^*)(H_j^* - N_{h_j}^*) + \frac{\rho_{ji} c_i \alpha_i N_{h_j}^* (N_{h_i}^* - H_i^*)}{a_j + N_{h_j}^*}.$$

$E_{N_{h_1}^* 0 N_{h_2}^* 0}$ is saddle when $H_i^* > N_{h_i}^*$, $i = 1$ and $2$. We now proceed with the local stability of the boundary equilibrium $E_{N_{h_1}^c 0 N_{h_2}^c 0}$. The following eigenvalues of $J_{E_{N_{h_1}^c 0 N_{h_2}^c 0}}$ are obtain from the Jacobian matrix (6.2):

$$\lambda_1 \lambda_2 = \left[ \left( \frac{d_{h_1}^2}{r_1} \right) \sqrt{\left( \frac{r_i}{d_{h_i}} \right)^2 - 4K_i} \right] \left[ \left( \frac{d_{h_2}^2}{r_2} \right) \sqrt{\left( \frac{r_2}{d_{h_2}} \right)^2 - 4K_2} \right] > 0$$

$$\lambda_1 + \lambda_2 = - \left[ \left( \frac{d_{h_1}^2}{r_1} \right) \sqrt{\left( \frac{r_i}{d_{h_i}} \right)^2 - 4K_i} + \left( \frac{d_{h_2}^2}{r_2} \right) \sqrt{\left( \frac{r_2}{d_{h_2}} \right)^2 - 4K_2} \right] < 0$$

$$\lambda_3 \lambda_4 = \frac{c_2 \alpha_2 (a_2 + N_{h_2}^c)(H_2^* - N_{h_2}^c)[c_1 \alpha_1 (a_1 + N_{h_1}^c)(H_1^* - N_{h_1}^c) + \rho_{12} N_{h_1}^c] + \rho_{21} c_1 \alpha_1 (a_1 + N_{h_1}^c)(H_1^* - N_{h_1}^c) N_{h_2}^c}{(a_1 + N_{h_1}^c)(a_2 + N_{h_2}^c)}$$

$$\lambda_3 + \lambda_4 = - \frac{(a_2 + N_{h_2}^c)[(a_1 + N_{h_1}^c)(c_1 \alpha_1 (H_1^* - N_{h_1}^c) + c_2 \alpha_2 (H_2^* - N_{h_2}^c)) + \rho_{12} N_{h_1}^c] + \rho_{21} (a_1 + N_{h_1}^c) N_{h_2}^c}{(a_1 + N_{h_1}^c)(a_2 + N_{h_2}^c)}$$

Again notice that $\lambda_3 \lambda_4 > 0$ and $\lambda_3 + \lambda_4 < 0$ when $H_i^* > N_{h_i}^c$, $i = 1$ and $2$. Therefore $E_{N_{h_1}^c 0 N_{h_2}^c 0}$ is a saddle if $H_i^* > N_{h_i}^c$ and a source if $H_i^* < N_{h_i}^c$, $i = 1$ and $2$. Similar argument follow for the stability of the equilibria $E_{N_{h_1}^* 0 N_{h_2}^c 0}$ and $E_{N_{h_1}^c 0 N_{h_2}^* 0}$ thus the proof is omitted.

Based on the discussions above, we can conclude that Theorem (3.3) holds.

$\square$

## Proof of Theorem 3.4

*Proof.* First we show the existence of the symmetric interior equilibrium $E = (H^*, M^*, H^*, M^*)$ of Model (3.5). We denote

$$H^* = \frac{d_m}{c\alpha} \quad \text{and} \quad M^* = \frac{1}{\alpha} \left[ \frac{rH^*}{H^{*2} + K} - d_h \right]$$

And notice that

$$H_1 = \left[ H^* + \frac{(H^* M_2 - H_2 M_2)}{M_1} \right] = F_1(H_2) \quad \text{and} \quad H_2 = \left[ H^* + \frac{(H^* M_1 - H_1 M_1)}{M_2} \right] = F_2(H_1)$$

are nullclines of Model (3.5) and we have the following properties:

$$F_1(M^*) = F_2(M^*) = M^*$$

This conclude that $H = H^* = \frac{d_m}{c\alpha}$ is a positive solution of the nullclines $F_1(H_2)$ and $F_2(H_1)$. We can hence say that $E = (H^*, M^*, H^*, M^*)$ is an interior equilibrium of Model (3.5).

The local stability of $E = (H^*, M^*, H^*, M^*)$ is obtained by the eigenvalues of the Jacobian matrix (6.2) evaluated at this equilibrium as follow:

$$\lambda_1 + \lambda_2 = \frac{rH^*(K - H^{*2})}{(K + H^*)^2} < 0 \ \text{ if } \ H^* > \sqrt{K}$$

$$\lambda_1 \lambda_2 = c\alpha^2 H^* M^* > 0$$

$$\lambda_3 + \lambda_4 = \frac{H^*(K - H^{*2})}{(K + H^*)^2} - \frac{2H^*\rho}{H^* + a} < 0 \ \text{ if } \ H^* > \sqrt{K}$$

$$\lambda_3 \lambda_4 = 2H^* \left[ \frac{a\alpha M^*}{(a + H^*)^2} - \frac{rH^*(H^* - K)}{[K + (H^*)^2](a + H^*)} \right] \rho + c\alpha^2 H^* M^*$$

First note that the eigenvalues $\lambda_1$ and $\lambda_2$ being negative is equivalent to the case where the unique interior equilibrium $(H_1^*, M_1^*)$ is locally asymptotically stable for the single patch Model (2.1) under the condition $H^* > \sqrt{K}$. We now explore the sufficient condition for $\lambda_3$ and $\lambda_4$ being negative through the following two cases when $H^* > \sqrt{K}$:

1. $\lambda_3 + \lambda_4 < 0$ when $H^* > \sqrt{K}$ and if

$$M^* \leq \frac{rH^*(a + H^*)[(H^*)^2 - K]}{a\alpha[(H^*)^2 + K]^2}$$

then the first term in the right hand side of the second equality of $\lambda_3 \lambda_4$ is positive and therefore $\lambda_3 \lambda_4 > 0$. Since $\lambda_3 + \lambda_4 < 0$ and $\lambda_3 \lambda_4 > 0$ then both $\lambda_3$ and $\lambda_4$ are negative.

2. For

$$M^* > \frac{rH^*(a + H^*)[(H^*)^2 - K]}{a\alpha[(H^*)^2 + K]^2} \ \text{ and } \ \rho < \frac{c\alpha^2 M^*(a + H^*)^2[(H^*)^2 + K]^2}{2\left(a\alpha M^*[(H^*)^2 + K]^2 - rH^*(a + H^*)[(H^*)^2 - K]\right)}$$

$\lambda_3 \lambda_4 > 0$ then both $\lambda_3$ and $\lambda_4$ are negative since $\lambda_3 + \lambda_4 < 0$.

Summarizing the discussions above, we can conclude that the symmetric interior equilibrium $E = (H^*, M^*, H^*, M^*)$ of Model (3.5) is locally asymptotically stable if $H^* > \sqrt{K}$ and one of the following conditions holds:

(a) $M^* \leq \frac{rH^*(a+H^*)[(H^*)^2 - K]}{a\alpha[(H^*)^2 + K]^2}$

(b) $M^* > \frac{rH^*(a+H^*)[(H^*)^2 - K]}{a\alpha[(H^*)^2 + K]^2}$ and $\rho < \frac{c\alpha^2 M^*(a+H^*)^2[(H^*)^2 + K]^2}{2(a\alpha M^*[(H^*)^2 + K]^2 - rH^*(a+H^*)[(H^*)^2 - K])}$

And $E = (H^*, M^*, H^*, M^*)$ is a saddle if $H^* < \sqrt{K}$.

Based on the discussion above, we can conclude that the statement of Theorem 3.4 holds.

$\square$

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