The spatial dynamics of ecosystem engineers

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The changes on abiotic features of ecosystems have rarely been taken into account by population dynamics models, which typically focus on trophic and competitive interactions between species. However, understanding the population dynamics of organisms that must modify their habitats in order to survive, the so-called ecosystem engineers, requires the explicit incorporation of abiotic interactions in the models. Here we study a model of ecosystem engineers that is discrete both in space and time, and where the engineers and their habitats are arranged in patches fixed to the sites of regular lattices. The growth of the engineer population is modeled by Ricker equation with a density-dependent carrying capacity that is given by the number of modified habitats. A diffusive dispersal stage ensures that a fraction of the engineers move from their birth patches to neighboring patches. We find that dispersal influences the metapopulation dynamics only in the case that the local or single-patch dynamics exhibit chaotic behavior. In that case, it can suppress the chaotic behavior and avoid extinctions in the regime of large intrinsic growth rate of the population.

I. INTRODUCTION

The usefulness of the concept of ecosystem engineers as organisms that change their environment by causing physical state changes in living or non-living materials [1, 2] is somewhat controversial since all species modify their environment [3]. However, species that must modify their habitats in order to survive or that increase significantly their chances of reproduction and survival in the modified habitats certainly comprise a unique class of organisms. These benefits, in addition, are likely to alter their population dynamics, which may require the explicit incorporation of abiotic interactions [4]. For instance, beavers (Castor canadensis) are considered as model systems of ecosystem engineers [5], since the areas flooded by the beaver dams increase the distance they can travel by water, which is safer than traveling by land, and results in a net increase of their survival expectations [6].

A key feature of the population dynamics of ecosystem engineers is that the growth of the engineer population is limited by the number of usable habitats, which in turn are created by the engineers via the conversion of virgin habitats. This feedback loop results in a density-dependent carrying capacity that is behind the peculiar dynamical behavior exhibited by the mathematical models of those systems. To our knowledge, the first mathematical model of the population dynamics of ecosystem engineers that explicitly takes into account the interactions between the organisms and the habitats was put forward by Gurney and Lawton in the mid 1990s [2]. In that model, the quality of the habitats takes on three different discrete states: virgin, usable (or modified) and degraded habitats. The role of the engineers is to effect the transition from the virgin to the usable states. The modified state then transitions to the degraded state, which is unsuitable for occupation by the engineers. Finally, the degraded state recovers to the virgin state that can then be reused by the engineers. Analysis of the continuous-time population dynamics model shows the existence of fixed points characterized by the presence of all three habitat states as well as cycles in which the number of engineers and the number of virgin habitats oscillate out of phase [2].

In this contribution we consider a spatial version of Gurney and Lawton model in which the engineers and their habitats are arranged in patches fixed to the sites of regular lattices. A diffusive dispersal stage ensures that a fraction $\mu$ of the engineers move from their birth patches to neighboring patches. By patch we mean an ecosystem composed of all three types of habitats as well as of the engineer population. Hence our approach differs starkly from a previously studied patch dynamics model in which each patch represents an habitat state and only the transitions between the habitat states are considered, i.e., the dynamics of the engineer population are not accounted for [5]. To facilitate the analysis of the discrete patch model we make time discrete as well and replace the logistic growth equation of the original model by the Ricker equation [9, 10] so that the spatial model reduces to a coupled map lattice [11]. Henceforth we will refer to the system of patches as metapopulation.

We find that the diffusive dispersal stage influences the metapopulation dynamics only in the case the local or single-patch dynamics exhibits chaotic behavior. In that case, we find that for certain values of the dispersal fraction $\mu$ the chaotic behavior is suppressed and the dynamics enter a two-point cycle in which the engineer densities at each patch oscillate between high and low values, forming rich (two-dimensional) geometric patterns. Another interesting effect of the dispersal is the avoidance of extinction, which is one of the outcomes of the local dynamics when the intrinsic growth rate $r$ of the engineers is large. In fact, the unexpected possibility of extinction of the population for large $r$ is a consequence of the density-dependent carrying capacity and the study of the spatial dynamics of ecosystem engineers offers a neat example of how multiple populations coupled by diffusive dispersal can eliminate or reduce that risk.

The rest of the paper is organized as follows. In Sect.
we introduce our time discrete version of Gurney and Lawton model of ecosystem engineers and derive the recursion equations of the local or single-patch dynamics for the density of engineers as well as for the fractions of the three types of habitats. In that section we introduce also the equation that describes the diffusive dispersal stage of the engineer population. The local dynamics is then studied in great detail in Sect. [11] with emphasis on the stability analysis of the fixed points. The spatial model with the patches arranged in a chain and a square lattice is considered in Sect. [IV] where the dynamic behavior of the metapopulation is studied mainly through the analysis of bifurcation diagrams. Finally, Sect. [V] is reserved to our concluding remarks.

II. MODEL

Here we build on the model of Gurney and Lawton [2] to study the dynamics of a population of organisms that must modify their own habitat in order to survive. Let us first rewrite the original, continuous-time model as a discrete-time model. We assume that the population of engineers at generation $t$ is composed of $E_t$ individuals and that each individual requires a unit of usable habitat to survive. In addition, we denote the number of units of usable habitats available at generation $t$ by $H_t$. Since $H_t$ plays the role of a time-dependent carrying capacity for the population of engineers, we can use Ricker model to write the expected number of engineers at generation $t + 1$ as

$$E_{t+1} = E_t \exp \left[ r \left( 1 - \frac{E_t}{H_t} \right) \right],$$  
(1)

where $r$ is the intrinsic growth rate of the population of engineers [9] [10].

What makes the model interesting is the requirement that usable habitats be created by engineers working on virgin habitats. More pointedly, if $V_t$ denotes the units of virgin habitats at generation $t$, then a portion $C(E_t)V_t$ of them will be transformed in usable habitats at the next generation, $t + 1$. Here $C(E_t)$ is any function that satisfies $0 \leq C(E_t) \leq 1$ for all $E_t$ and $C(0) = 0$. However, usable habitats do not last forever and eventually decay to degraded habitats which are useless to the engineers. Denoting by $\delta H_t$ the portion of usable habitats that decay to degraded habitats in one generation, we can immediately write an equation for the expected number of units of usable habitats at generation $t + 1$

$$H_{t+1} = (1 - \delta) H_t + C(E_t)V_t,$$  
(2)

where $\delta \in [0, 1]$ is the decay fraction. Degraded habitats will eventually recover and become virgin habitats again. If we denote by $\rho D_t$ the portion of degraded habitats that recover to virgin habitats we have

$$D_{t+1} = (1 - \rho) D_t + \delta H_t,$$  
(3)

where $\rho \in [0, 1]$ is the recovery fraction. Finally, the recursion equation for the expected number of units of virgin habitats is simply

$$V_{t+1} = [1 - C(E_t)]V_t + \rho D_t.$$  
(4)

We note that $V_{t+1} + H_{t+1} + D_{t+1} = V_t + H_t + D_t = T$ so that the total supply of habitats $T$ is fixed. This remark motivates the introduction of the habitat fractions $v_t \equiv V_t/T$, $h_t \equiv H_t/T$ and $d_t \equiv D_t/T$ that satisfy $v_t + h_t + d_t = 1$ for all $t$. In addition, we introduce the density of engineers $e_t \equiv E_t/T$ which, differently from the habitat fractions, may take on values greater than 1. In terms of these quantities, the recursion equations are rewritten as

$$e_{t+1} = e_t \exp \left[ r \left( 1 - e_t / h_t \right) \right]$$  
(5)

$$h_{t+1} = (1 - \delta) h_t + c(e_t) v_t$$  
(6)

$$v_{t+1} = \rho (1 - v_t - h_t) + [1 - c(e_t)] v_t,$$  
(7)

where we have used $d_t = 1 - v_t - h_t$ and $c(e_t) \equiv C(Te_t)$. Here we will consider the function

$$c(e_t) = 1 - \exp (-\alpha e_t),$$  
(8)

where $\alpha > 0$ is the productivity parameter, which measures the efficiency of conversion of virgin to usable habitats by the engineers. This function indicates that the engineers do not work independently on the construction of usable habitats, otherwise one should have $c(e_t) \propto e_t$. This is actually the situation for small population sizes, where $c(e_t) \approx \alpha e_t$ but as the population of engineers increases they begin to interact antagonistically (i.e. the production of two engineers is actually less than the sum of their productions taken independently of each other) since $c(e_1)/\alpha e_1 < 1$ for all densities $e_t$.

In fact, the abstract function $c(e_t)$ incorporates, perhaps, the most interesting features of the system of engineers as, for instance, the cooperation strategies and the communication networks that allowed this class of organisms to build complex collective structures (e.g. termite mounds and anthills), which may be viewed as the engineers’ solutions to the problems that endanger their existence [12] [14]. For humans, this function must incorporate the beneficial effects of the technological advancements [15] [16] and this opens the interesting possibility of studying the interplay between technology evolution and population dynamics, similarly to what has been done for genetics and culture [17]. It is also interesting to note that if one chooses the function $c(e_t)$ such that it vanishes with the square of the density of engineers for small population sizes, then one would observe an Allee effect, in which the population quickly goes extinct below a critical population size or density [15]. This choice would correspond to the situation where the engineers are obligate cooperators.

Although the decay of usable to degraded habitats is probably density dependent, particularly if the degradation results from the overexploitation of resources, here we have modelled it by a constant probability $\delta$. There
are examples, however, that conform to this assumption such as the case of bark beetles that cannot breed in old dead wood so that the usable habitats, namely, recently killed trees, degrade at a rate that does not depend on the presence of those insects [19].

We refer to the system of recursion equations (5)-(7) as the local or single-patch population dynamics. By patch we mean a ecosystem, say an isle, with the three types of habitats and, possibly, a thriving population of engineers. Let us consider now a system of $N$ patches, say an archipelago, and assume that the engineers can diffuse to neighboring patches. More pointedly, we assume that a fraction $\mu$ of the population of engineers of patch $i$ moves to the neighboring patches, so that after the dispersal stage the population at patch $i$ is

$$E'_{i,t} = (1-\mu)E_{i,t} + \mu \sum_j E_{j,t}/K_i,$$

where the sum is over the $K_i$ nearest neighbors of patch $i$. Assuming that the total supply of habitats $T$ is the same for all patches and dividing both sides of this equation by $T$ we get

$$e'_{i,t} = (1-\mu)e_{i,t} + \mu \sum_j e_{j,t}/K_i,$$

which describes the effect of dispersal on the density of engineers in patch $i$. We note that in the case the patches have different sizes, which are gauged by the total supply of habitats $T_i$, we can still get an equation similar to eq. (10) relating the engineer densities in neighboring patches. The only complication is the appearance of the ratios $T_j/T_i$ multiplying the densities $e_j$ in the sum over the neighbors of patch $i$. The density after dispersal then follows the local dynamics equations within each patch. We postpone to Section IV the presentation of the complete set of equations, where the habitat fractions exhibit the patch indices as well.

In summary, for each generation the dynamics consist of two phases: a dispersal phase and a growing phase. In the dispersal phase, a fraction $\mu$ of engineers in each patch moves to neighboring patches according to eq. (10), whereas in the growing phase the engineers reproduce and modify the habitat composition of their patches according to the local dynamics equations (5)-(7).

III. LOCAL POPULATION DYNAMICS

In this section we study the system of recursion equations (5)-(7) and, as usual, we begin with the analysis of the fixed-point solutions, obtained by setting $e_{t+1} = e_t = e^*$, $h_{t+1} = h_t = h^*$ and $v_{t+1} = v_t = v^*$. Then we consider the oscillatory solutions, which are explored in a somewhat more qualitative way through the analysis of the bifurcation diagrams. By oscillatory solutions we mean both periodic and chaotic solutions.

A. Zero-engineers fixed point

Setting $e^* = 0$ we obtain $h^* = 0$ and $v^* = 1$. This means that in the absence of the engineers, all usable habitats will degrade, then recover to virgin habitats, and stay forever in that condition. The study of the local stability of this fixed point, however, is somewhat complicated because the ratio $x_t = e_t/h_t$ is indeterminate. To circumvent this difficulty we rewrite the recursion equations (5)-(7) in terms of the variables $x_t$, $e_t$ and $v_t$.

$$e_{t+1} = e_t \exp[r(1-x_t)],$$

$$x_{t+1} = x_t \exp[r(1-x_t)]/(1-\delta)+x_tv_c(e(t)),$$

$$v_{t+1} = \rho(1-v_t-e_t/x_t)+(1+c(e_t))v_t,$$

with the notation $\hat{c}(e_t) = c(e_t)/e_t$, such that $\hat{c}(0) = \alpha$. At the fixed point $x_{t+1} = x_t = x^*$ we have

$$1 - \delta + \alpha x^* = \exp[r(1-x^*)].$$

For $\delta = \alpha$ the solution is $x^* = 1$ and we can easily show that $x^*>1$ for $\delta > \alpha$ and $x^*<1$ for $\delta < \alpha$. The local stability of the zero-engineers fixed point is determined by requiring that the three eigenvalues of the Jacobian matrix

$$J_0 = \begin{bmatrix}
(\alpha x^*)^2/2\xi^* & 1-x^*(r+\alpha/\xi^*) & 0 \\
0 & -\alpha - \rho/x^* & -\alpha x^*/\xi^*
\end{bmatrix}$$

have absolute values less than 1. Here we used the notation $\xi^* = \exp[r(1-x^*)]$. The eigenvalues are $\lambda_1 = \xi^*$, $\lambda_2 = 1-x^*(r+\alpha/\xi^*)$ and $\lambda_3 = 1-\rho$. The condition $|\lambda_1| < 1$ is satisfied provided that $x^*>1$, which is guaranteed for $\delta > \alpha$, whereas the condition $|\lambda_3| < 1$ is always satisfied since $\rho < 1$. However, the condition $|\lambda_2| < 1$ is violated for $r > r_c$, where $r_c$ is determined by setting $\lambda_2 = -1$. Figure 1 shows $r_c$, as function of $\delta > \alpha$ for fixed values of $\alpha$. In particular, for $\alpha = 0$ we find $r_c = 2 + \ln (1-\delta)$ so that for $\delta > 1 - \exp(-2) \approx 0.865$ the zero-engineers fixed point is unstable regardless of the value of $\delta$. We note that the recovery fraction $\rho$ has no effect whatsoever on the stability of the zero-engineers fixed point.

We stress that the violation of the condition $|\lambda_2| < 1$ results in the oscillatory behavior of the ratio $x_t$ (hence the instability of the fixed point solution) and that the numerical iteration of the recursion equations (10) and (11) indicates that $e_t \to 0$ and $v_t \to 1$ in the asymptotic limit $t \to \infty$, despite the oscillatory behavior of $x_t$.

Hence we conclude that for $\delta > \alpha$ there is always a zero-engineers attractor (not necessarily a fixed point) characterized by $\lim_{t \to \infty} e_t = 0$, regardless of the values of the parameters $\rho$ and $r$. Somewhat surprisingly, we will see in Section IV that the zero-engineers oscillating attractor plays a role in the dynamics even for $\delta < \alpha$. 

B. Finite-engineers fixed point

Since $e^* > 0$ we have $h^* = e^*$ (i.e., $x^* = 1$) and $v^* = 1 - e^*(1 + \delta/\rho)$ with $e^*$ given by the solution of the transcendental equation

$$\delta e^* = [1 - \exp(-ae^*)][1 - e^*(1 + \delta/\rho)]. \quad (16)$$

For $e^* \ll 1$ we find

$$e^* \approx \frac{1 - \delta/\alpha}{1 + \delta/\rho} \quad (17)$$

and $v^* = \delta/\alpha$, indicating that this fixed point is physical for $\delta < \alpha$ only. We find that the density of engineers at equilibrium increases monotonically from $e^* = 0$ at $\alpha = \delta$ to $e^* = 1/(1 + \delta + \delta/\rho)$ as $\alpha \to \infty$. Moreover, as $\delta$ increases from 0 to $\alpha$, $e^*$ decreases monotonically from 1 to 0. Finally, for small $\rho$ we find $e^* \approx \rho(1/\delta - 1/\alpha)$ and $v^* \approx \delta/\alpha$. As $\rho$ increases, both $e^*$ and $v^*$ increase monotonically until some maximum values that depend on the parameters $\delta$ and $\alpha$, as illustrated in Fig. 2. Interestingly, although $\rho$ is the recovery fraction of degraded habitats that turn into virgin habitats, its increase results only in a slight increment in the number of virgin habitats. This is so because of the efficiency of the engineers in transforming virgin into usable habitats, which increases to 1 exponentially fast with the density of engineers, regardless of the value of the parameter $\alpha > \delta$.

The analysis of the local stability of the finite-engineers fixed point is facilitated if we use the variable $x_t = e_t/h_t$ as before. The Jacobian matrix associated to the recursion equations \((11), (12), (13)\) is

$$J_e = \begin{bmatrix} 1 - \delta/c(e^*) & -r e^* & 0 \\ -\rho - \alpha (v^* - \delta e^*) & 1 - \delta/c(e^*) & \delta (e^*) \\ \rho e^* & 1 - \rho - \delta (e^*) \end{bmatrix} \quad (18)$$

with the notation $\delta (e^*) = \delta \hat{c}(e)/de|_{e=e^*}$, such that $\hat{c}'(0) = -\delta^2/2$. This matrix reduces to $J_0$, given by eq. \((15)\), provided that $e^* = 0$ is the solution of the fixed point equation \((16)\), viz. for $\alpha = \delta$, since only in this case the zero-engineers fixed point has $x^* = 1$.

Analysis of the eigenvalues of the Jacobian matrix $J_e$ in the region $\alpha > \delta$ where $e^* > 0$ (see eq. \((17)\)) shows that $\lambda_k < 1$ for $k = 1, 2, 3$ (the labeling of the eigenvalues is the same as for the stability analysis of the zero-engineers fixed point). However, for large $r$ we find $\lambda_2 < -1$ thus violating the condition of local stability of the finite-engineers fixed point. Since $e^*$ and $v^*$ do not depend on $r$ it is easy to obtain numerically the value $r = r_c$ above which the fixed point is unstable. Figure 2 shows the dependence of $r_c$ on the model parameters. Regardless of the parameters we find that $r_c \in [2 - \delta, 2]$. The lower bound $r_c = 2 - \delta$ is reached for $\alpha = \delta$ at which $e^* \to 0$. The upper bound $r_c = 2$ is reached in the limit $\alpha \to \infty$. In fact, since in this limit we have $v^*/e^* = \delta$, we can readily obtain $\lambda_2 = 1 - r$. Then setting $\lambda_2 = -1$ yields $r_c = 2$. Actually, since $c(e_t) = 1$ in the limit $\alpha \to \infty$, the fraction of usable habitats $h_t$ become independent of the engineer density $e_t > 0$ (see eqs. \((6)\) and \((7)\)) and so the equation for the engineer density (see eq. \((6)\)) reduces to the classic Ricker equation for which the carrying capacity is density independent.

Overall we conclude that increase of $\alpha$ and $\rho$ as well as decrease of $\delta$ favor the stability of the finite-engineers fixed point, but the determinant parameter is the intrinsic growth rate $r$. For instance, the finite-engineers fixed point $e^* > 0$ is always unstable for $r > 2$ and always stable for $r < 1$.
FIG. 3. (Color online) Intrinsic growth rate $r_c$ above which the engineer population exhibits oscillatory behavior as function of the parameter $\alpha > \delta$ for (top to bottom) $\delta = 0.2, 0.4, 0.6, 0.8$. For $\alpha \approx \delta$ we have $r_c \approx 2 - \delta$ and for $\alpha \to \infty$ we have $r_c \to 2$ regardless of the values of the parameters $\delta$ and $\rho$.

C. Bifurcation diagrams

The analysis of the oscillatory regime for $r > r_c$ must be done by iterating numerically the equations of the local population dynamics (5)-(7). The oscillatory regime comprehends periodic oscillations and chaos. A traditional way to present the results is through the so-called bifurcation diagrams [20] which exhibit a long-exposure photography of the attractors, as shown in Fig. 3. The bifurcation diagrams for the habitat fractions $v$ and $h$ show similar patterns. Since the source of nonlinearity of the population dynamics is Ricker’s formula for the growth of the engineer population [9], the observed period-doubling bifurcation cascade is expected. We note that the transitions from fixed-points to two-point cycles occur at $r = r_c$ (see Fig. 3).

There are, however, some interesting peculiarities about the dynamics (5)-(7) in the case the decay fraction $\delta$ is large, as shown in the bifurcation diagram of Fig. 3. The interesting point here is that for large $r$ (more pointedly, $r > 3.4$ for the parameters of the figure) as well as for several small windows of the interval of variation of $r$, the attractor has $e = h = 0$ and $x = e/h$ oscillating, i.e., it is the same attractor that we came across in our study of the stability of the zero-engineers fixed point. We recall that since $\delta < \alpha$, the fixed point with $e^* = h^* = 0$ is unstable. It is interesting that the domain of the zero-engineers oscillating attractor is practically unaffected by the increase of the recovery fraction $\rho$. In fact, setting $\rho = 1$ does not alter qualitatively the bifurcation diagram of Fig. 3.

The presence of this attractor for large $r$ cannot be explained by the violent oscillations and low minimum population densities that may eventually lead

FIG. 4. (Color online) Bifurcation diagram for the local population dynamics (5)-(7) with parameters $\alpha = 1$, $\delta = 0.1$ and $\rho = 0.01$. The points on the y-axis show the values of the engineer density visited asymptotically from all initial conditions with $e_0 > 0$.

FIG. 5. (Color online) Same as for Fig. 4 but for the parameters $\alpha = 1$, $\delta = 0.5$ and $\rho = 0.01$. For $r > 3.4$ the attractor has $e = h = 0$ with $x = e/h$ oscillating.
to the extinction of the population and so justify the rarity of chaotic behavior in nature [21, 22]. In fact, for large \( r \) the density \( c \) does not experience large fluctuations and simply oscillates with decreasing amplitude towards the zero-engineers attractor. We note that for \( \delta > \alpha \) the only attractors are the fixed point \( e^* = h^* = 0 \) for \( r < r_c \) and the attractor with \( e = h = 0 \) and \( x = e/h \) oscillating for \( r > r_c \), where \( r_c \) is shown in Fig. 4.

IV. SPATIAL POPULATION DYNAMICS

As described in Section [1] we allow that a fraction \( \mu \) of the engineer population in a given patch, say patch \( i \), moves to the \( K_i \) nearest neighbors of patch \( i \). The density of engineers after the dispersal stage in each patch \( i = 1, \ldots, N \) is given by eq. (10). In this section we consider a chain with reflective boundary conditions (i.e., \( K_1 = K_N = 1 \) and \( K_i = 2, \forall i \neq 1, N \)) and a square lattice with the Moore neighborhood and reflective boundary conditions (i.e., \( K_i = 8 \) for internal patches, \( K_i = 5 \) for patches on the edges and \( K_i = 3 \) for patches on the corners of the lattice). We recall that for internal patches (or cells) on a two-dimensional square lattice, the Moore neighborhood is composed of a central patch and the eight patches that surround it. After dispersal of the engineers, the local population dynamics takes place within each patch:

\[
e_{i,t+1} = e'_{i,t} \exp \left[ r \left( 1 - e'_{i,t}/h_{i,t} \right) \right] \\
h_{i,t+1} = (1 - \delta) h_{i,t} + c(e'_{i,t}) v_{i,t} \\
v_{i,t+1} = \rho (1 - v_{i,t} - h_{i,t}) + [1 - c(e'_{i,t})] v_{i,t},
\]

for \( i = 1, \ldots, N \). These equations together with eq. (10) can be seen as a coupled map lattice (see, e.g., [1]) that describe the dynamics of the system of patches or metapopulation.

In the following, we consider a colonization or invasion scenario where at generation \( t = 0 \) only the central patch \( i_c \) of the lattice is populated, whereas the other patches are composed entirely of virgin habitats [8].

A. One-dimensional lattice

Here we consider a chain with \( N \geq 3 \) patches in order to study the colonization scenario. Accordingly, we set the initial density of the central patch \( e_{i_c,0} \) to a random value drawn from a uniform distribution in the unit interval. In addition, we set \( h_{i_c,0} = e_{i_c,0} \) and \( v_{i_c,0} = 1 - h_{i_c,0} \). All the other patches have \( e_{i,0} = h_{i,0} = 0 \) and \( v_{i,0} = 1 \) for \( i \neq i_c \). (Note that \( i_c = 2 \) for \( N = 3 \)).

We find that the diffusive dispersal has no impact on the behavior of the individual patches in the case the attractor of the local or single-patch dynamics is a fixed-point or an \( n \)-point cycle. In particular, we find that the metapopulation is spatially homogeneous and oscillates with the same period of a single patch. However, when

![Figure 6](image-url)

FIG. 6. (Color online) Bifurcation diagram for the engineer population in the central patch in the case of \( N = 3 \) patches with parameters \( r = 3.6, \alpha = 1, \delta = 0.5 \) and \( \rho = 0.01 \).

The local dynamics is chaotic the introduction of diffusive dispersal produces remarkable results as discussed next.

![Figure 7](image-url)

FIG. 7. (Color online) Bifurcation diagram for the engineer population in the central patch in the case of \( N = 3 \) patches with parameters \( r = 3.6, \alpha = 1, \delta = 0.5 \) and \( \rho = 0.01 \).

The main effect of the diffusive dispersal is already visible in the case of \( N = 3 \) patches as illustrated in Fig. 6 which shows the bifurcation diagram for the engineer population in the central patch of the chain as function of the dispersal fraction \( \mu \). The bifurcation diagrams are qualitatively similar for the other two patches. This figure reveals that the chaotic behavior is suppressed and the metapopulation enters a two-point cycle regime or a fixed-point regime for some values of \( \mu \). For instance, in the region around \( \mu = 0.1 \) the three patches alternate between high \((e \approx 0.3)\) and very low \((e \sim 10^{-3})\) population densities, such that neighboring patches (i.e., patches 1 and 2 or patches 2 and 3) always have different densities.
In the region around \( \mu = 0.9 \) the dynamics is attracted to a fixed point in which the two unconnected patches have the same density. We note that the reason the bifurcation diagram is not symmetric about \( \mu = 0.5 \) is that the habitats do not move to neighboring patches, only the engineers do and when they arrive in a new patch they encounter a different environment.

Another unexpected effect of the engineer dispersal is a partial avoidance of extinction. Consider the case illustrated in Fig. 5 where large values of the intrinsic growth rate (more pointedly, \( r > 3.4 \)) lead to the extinction of the engineers in the single-patch situation. The bifurcation diagram of Fig. 7 shows the effect of dispersal for \( r = 3.6 \) and the same parameters used in Fig. 5. As in the single-patch case, the only attractor is the zero-engineers attractor for a large range of values of the dispersal fraction, \( \alpha \), for \( \mu \in [0.2, 8] \), but Fig. 7 shows that there are regions for small and large values of \( \mu \) where the population of engineers can actually thrive due to the possibility of migration to more hospitable patches.

The bifurcation diagram for a large number of patches, say \( N = 101 \), exhibits a pattern similar to that for \( N = 3 \) with a window of two-point cycles around \( \mu = 0.1 \). However, a large window of \( n \)-point cycles appears around \( \mu = 0.5 \) and the periodic window for large \( \mu \) is suppressed. The spatial patterns observed within the periodic windows are essentially an juxtaposition of high and low population densities. The next section will explore the more interesting spatial patterns that emerge in a two-dimensional lattice.

### B. Two-dimensional lattice

As expected, the conclusion that diffusive dispersal impacts the metapopulation only when the single-patch dynamics is chaotic applies to the square lattice as well. Its effect is the appearance of windows in the bifurcation diagrams in which chaos reverts to periodic motion.

Since the numerical errors accumulate very fast when we implement the local dynamics of thousands of interconnected patches in the chaotic regime, in spite of the use of quadruple precision, it is useful to have a marker to signal when the numerical results are unreliable. Since we start the dynamics with a single populated patch located at the center of the lattice, the spreading of the engineers must preserve the symmetries of the square lattice. Hence, in the colonization scenario our marker of the unreliability of the numerical results is the breaking of the symmetries of the square lattice. We refer the reader to Ref. [23] for a detailed discussion of the symmetry breaking caused by the chaotic amplification of numerical noise.

Figure 8 shows two snapshots of the lattice at short times, when the spreading colony is still far from the borders. The figure reveals two interesting features, \( \text{viz.} \), the high density of engineers in the patches located at the wavefront and the square symmetry of the colony due to the choice of the Moore neighborhood. For low values of the dispersal fraction (e.g., \( \mu = 0.1 \)) the dynamics converge to a two-point cycle steady state, and Fig. 9 shows snapshots at two consecutive times in this state. The rich tapestry of these patterns is the result of the propagation of arrow-shaped groups of migrants out of the lattice center that form before the wavefront reaches the lattice borders, as shown in Fig. 8. We find essentially the same spatial patterns for different values of \( \delta \) and \( \rho \) provided the dynamics enters the two-point cycle stationary regime.

A more interesting scenario appears in the spatio-temporal chaotic regime of the metapopulation that occurs for values of the dispersal fraction outside the periodic windows. Figure 10 shows snapshots of the lattice at different times for \( \mu = 0.5 \). The new feature revealed by
FIG. 9. (Color online) Local density of engineers for $101^2$ patches arranged in a square lattice in the two-point cycle steady state for $\alpha = 0.11$ (upper row), $\alpha = 0.5$ (middle row) and $\alpha = 1.0$ (lower row) The panels in a same row show the lattice at consecutive times. In the initial condition, all patches are empty virgin habitats, except the central patch that has $e = h = v = 0.5$. The other parameters are $\mu = 0.1$, $r = 3.6$, $\delta = 0.1$ and $\rho = 0.01$. These patterns is the existence of isolated isles of engineers surrounded by patches of virgin habitats. This patchi-
FIG. 10. (Color online) Local density of engineers for $101^2$ patches arranged in a square lattice in the spatio-temporal chaotic regime. The panels show the lattice at different times as indicated. In the initial condition, all patches are empty virgin habitats, except the central patch that has $e = h = v = 0.5$. The model parameters are $\mu = 0.5$, $r = 3.6$, $\alpha = 1$, $\delta = 0.1$ and $\rho = 0.01$.

ness, where regions of high and low population densities alternate, is characteristic of biological patterns [24, 25].
It is interesting that although the patterns shown in Figs. 9 and 10 differ in their dispersal fraction only, the mean density of engineers in the metapopulation \( \langle e_t \rangle = \sum_{i=1}^{N} e_{i,t}/N \) at the stationary regime decreases with increasing \( \mu \) as shown in Fig. 11. The initial increase of \( \langle e_t \rangle \) reflects the expansion phase of the engineers that halts when they reach the lattice borders. The end of the availability of unexplored virgin habitats leads to a sharp drop on the density of engineers, which then enters the stationary regime with oscillations of limited amplitude. This phenomenon was also observed in the study of the one-dimensional lattice. In fact, the patches at the borders of the colonization wavefront exhibit a very high density of engineers \( e \approx 3.0 \) (see panels for \( t = 50 \) and \( t = 150 \) in Fig. 10) that are sustained by the unexplored patches ahead of the wavefront. When the supply of unexplored virgin habitats is exhausted, the values of the highest densities undergo an almost tenfold drop and plunge to \( e \approx 0.4 \). We note that Fig. 11 offers a crude way to estimate the mean speed of the colonization wavefronts as the ratio between the shortest distance from the center to the borders of the lattice and the time to reach those borders.

![Graph](image)

**FIG. 11.** (Color online) Time evolution of the mean engineer density \( \langle e \rangle \) in a square lattice with \( 10^5 \) patches for the dispersal fractions \( \mu = 0.1 \) and \( \mu = 0.5 \) as indicated. The other model parameters are \( r = 3.6, \alpha = 1, \delta = 0.1 \) and \( \rho = 0.01 \).

Finally, we should mention that we do not find any significant variations in the spatial patterns for different lattice sizes. In fact, as pointed out before the patterns close to the center of the lattice are formed well before the engineers reach the lattice boundaries. Hence the particular geometric patterns observed in the square lattice are essentially a consequence of the choice of the Moore neighborhood for the engineers dispersal as well as of the symmetry of the initial distribution of the engineers in the patches.

V. DISCUSSION

There are hardly any ecosystems on earth that have not been engineered by past or present organisms, as attested by the highly unstable, life-regulated composition of the atmosphere of our planet \[27\]. However, the importance of ecosystem engineering \[1] or, more generally, of niche construction \[28\] has been somewhat overlooked by the ecological and evolutionary literatures. (We refer the reader to the ongoing debate \[29, 30\] within the evolutionary biology community whether niche construction is a new concept on evolution or is simply the well-known feedback between organisms and the environment, whose study was pioneered by Darwin himself \[31\]. See also \[32\] for support of the view that theories in evolutionary biology are based on concepts rather than laws.)

We note that within the theoretical ecology perspective, the population dynamics of predator-prey systems has been studied for almost a century \[33, 34\], whereas a first attempt to model mathematically the dynamics of ecosystem engineers took place in the mid 1990s only \[2\]. The interesting feature of the ecosystem engineers model proposed by Gurney and Lawton is that both the density of organisms – the engineers – and the quality of their habitats vary in time, as their survival depends on the existence of engineered habitats \[2\]. This contrasts with less transparent models of ecosystem engineers where the habitat changes are not explicitly taken into account \[4\].

Although there are a few unquestionable examples of ecosystem engineers, such as beavers that carry out extensive changes on their ecosystems through clearcutting and damming \[35\] and caterpillars that create shelters from leaves that may also be occupied by other organisms \[36\], the field studies of these model systems are not comprehensive enough to parameterize the theoretical models \[2\]. We note that, in addition to the usual demographic variables, those models require information about the transition rates between the different habitat types. Perhaps, the study of the ultimate ecosystem engineers, humans \[37\], may offer the desired data: primitive societies that rely on slash-and-burn and shifting cultivation agricultural systems as their means of subsistence \[38\] may be seen as model systems of spatial ecosystem engineers, since they must leave their burnt fields and return back after they recover in a cyclic scheme similar to that introduced in our spatial model.

A word is in order about the existence of a natural spatial scale in our model of ecosystem engineers. We envision two scenarios to which the spatial model could be applied: the colonization of an archipelago and the colonization of a galaxy. Regarding the latter scenario, we remind the reader of the concept of terraforming as a planetary engineering process. In both cases, the engineers are humans, which can be viewed as the ultimate ecosystem engineers as pointed out before, but the spatial scales are completely distinct. The common feature is that the typical size of the patches (isles or planets) is much smaller than the typical distance between patches.
In fact, an implicit assumption of the model of Gurney and Lawton [2] is that the engineers move between habitats within a same patch with virtually infinite speed, otherwise the virgin habitats would remain virgin forever. Hence the relevant condition for the applicability of the model is that the diffusion rate within a patch be much greater than the diffusion rate among patches. This condition may arise from differences in the spatial scales, as already mentioned, or from the lack of an efficient technology to travel between patches.

As expected, we find that the local or single-patch dynamics converges to zero-engineers attractors whenever the number of usable habitats decreases more rapidly than they are produced by a vanishingly small population of engineers working on virgin habitats, i.e., whenever the decay fraction \( \delta \) is greater than the per capita productivity \( \alpha \). A curious feature of the local dynamics, which is due to the density-dependent carrying capacity in Ricker equation, is the existence of an oscillating zero-engineers attractor for which both the density of engineers \( e_t \) and the fraction of usable habitats \( h_t \) tend to zero in the time-asymptotic limit, but the ratio \( x_t = e_t/h_t \) oscillates with finite amplitude. Interestingly, the appearance of this attractor for large values of the engineers’ intrinsic growth rate \( r \) leads to the extinction of the population even in an apparently thriving scenario where \( \alpha > \delta \). Otherwise, the local dynamics exhibits the period-doubling route to chaos, which is expected since the population growth is governed by Ricker’s model [3].

The engineers’ intrinsic growth rate \( r \) is the parameter responsible for the main differences between the time-discrete and the time-continuous single-patch dynamics. In fact, in the continuous version, \( r \) simply sets the natural time-scale and so it plays no role at all in the dynamics [2]. Similarly, the value of \( r \) is inconsequential for the calculation of the finite-engineers fixed point of the time-discrete model, but it is crucial for establishing its local stability (see Section III B). In addition, only large values of \( r \) can sustain the chaotic dynamical behavior, which is the most distinctive feature of the time-discrete formulation of the population dynamics of ecosystem engineers.

We find that the spatial organization of patches and the dispersal of a fraction \( \mu \) of engineers to neighboring patches have no influence on the metapopulation dynamics, provided that the attractors of the local dynamics are periodic. In fact, our simulations show that the finite-engineers fixed point and the \( n \)-cycle attractors and the \( n \)-point cycles are always stable with respect to spatially inhomogeneous perturbations. However, in the case the local dynamics is chaotic the diffusive dispersal produces nontrivial effects, as shown in Figs. 3, 9 and 10. In particular, for certain values of the dispersal fraction \( \mu \) the chaotic behavior is suppressed and the dynamics enters a two-point cycle or a fixed-point attractor (see Fig. 6). Perhaps more telling is the finding that diffusive dispersal can prevent the extinction of the metapopulation in a case where a single population would die off in the absence of dispersal (see Fig. 7). This finding is in agreement with the notion that extinctions resulting from large fluctuations of the chaotic dynamics can be eluded if the population is composed of patches weakly coupled by migration [30].

Our more interesting findings regarding the spatial aspects of the model of ecosystem engineers are the patchy, biological-like patterns illustrated in Fig. 10 which appear only in the regime of spatio-temporal chaos of the metapopulation dynamics. Since the chaotic behavior is often viewed as a mathematical artifact rather than a genuine property of ecological systems [22, 30], it may be argued that our results suggest the absence of patchy patterns in natural engineer ecosystems. However, since the chaotic dynamics emerge when positive feedback growth processes are reinforced and regulatory (negative feedback) processes are delayed, and since these processes may be purposely altered by the engineers actions [22], the emergence of the chaotic dynamics, and consequently of the nontrivial spatial organization, may be commonplace in engineered ecosystems.

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