

Breaking Waves in Population Flows

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Abstract. We test the controversial ideas about the role of corridors in fragmented animal habitats. Using simulation studies we analyze how fragmentation affects a simple prey-predator system and how the introduction of openings that connect the habitats changes the situation. Our individual based model consists of 3 levels: renewable prey food, as well as prey and predators that both have a simple economy. We find, in line with intuition, that the fragmentation of a habitat has a strong negative effect especially on the predator population. Connecting the fragmented habitats facilitates predator (and hence prey) survival, but also leads to an important counterintuitive effect: in the presence of a high quality predator, connected fragmented systems fare better in terms of coexistence than do unfragmented systems. Using a frequency domain analysis we explain how corridors between sub-habitats serve as “wave breakers” in the population flow, thus preventing deadly density waves to occur.

Keywords: predator prey systems, animal corridors, frequency domain analysis.

1 Introduction

Wave patterns are common in biology. Spatio-temporal waves have been demonstrated in many population models. In particular, various waveforms including spiral waves can be generated in simple predator prey systems [e.g., 1]. The stability and coexistence of populations is often closely related to the existence and behavior of wave patterns. High amplitude oscillations or transients tend to destabilize systems by generating depleted resource conditions. Therefore, the understanding and active control of population waves is of high importance in a number of contexts. For example, fragmented habitats tend to produce high densities that often lead to fatal oscillations.

General spatial models in ecology, including island biogeographic models [2] as well as meta-population models [3, 4] predict that movements between patches will increase effective population size and persistence in general. Haddad & Tewksbury [5] reviewed major ecology and general biology journals from 1997 to 2003 and found only 20 studies to test the corridors’ effects on populations and diversity. They concluded that the current evidence offers only tentative support for the positive

effects of corridors, and much more work on population and community responses is needed, especially, that it is important to study the mechanisms and conditions under which we can expect corridors to impact populations. The authors also predicted an increasing importance of individual based models that can aid empirical studies by focusing on the effects of different life history parameters [5].

In this paper we present an agent based model to study the oscillatory behavior of populations in various fragmented and connected habitats, respectively. The model utilizes an approach inspired by studies of excitable media, hydrodynamics, and granular flows. Hydrodynamic analogies can often help understand wave phenomena in different domains. Wave control tools (such as wave breakers and barriers) are being extensively used in natural flow systems such as rivers, ocean shores, etc. Also, granular flows have been successfully applied to the modeling and control of the behavior of humans in mass situations such as when escaping from fire, in high traffic or in mass demonstrations [6]. We utilize a similar metaphor in the present model, where population waves are shown to be controllable by a combination of barriers and restricted passages (i.e., corridors).

2 The Model

The model (written in NetLogo 3.14) uses a simple set of assumptions:

- The system consists of predator and prey individuals, which feed on biotic resources. Prey food has an autonomous growth dynamics with saturation.
- The model is spatially explicit, consisting of $n \times n$ locations. A prey individual consumes a food token on its current location, if there is one. Similarly, the predator consumes a single prey individual if prey is found at the given location. All these behaviors are translated into a common currency, “energy”. Consumption ensures a certain amount of energy, i.e., $Gain_{PY}$ and $Gain_{PD}$ for the prey and predator, respectively. The consumed individual dies, and it is removed from the system. Death also happens if the energy level of an individual reaches zero.
- At each time step every individual is forwarded by a constant amount Fd (this speed is assumed identical for both predator and prey). Each move occurs in a uniformly selected random direction taken from the interval $\pm T$ (the degree of turning in degrees relative to the current orientations). One step costs exactly one energy token (stored “energy” thus directly converts to lifetime).
- The habitat is modeled as a rectangular area with reflecting boundaries. Each position (except the borders) can be empty or occupied by an arbitrary number of individuals (except that prey food that can only be on or off at a given location).
- Reproduction is asexual and occurs with probability R_{PY} and R_{PD} , for prey and predator. Upon reproduction, a new individual of the given type is produced, with a random spatial orientation. Energy tokens of the parent individual will be shared evenly with the offspring. Prey food regenerates in K steps.
- Prey and predator start from random initial positions as well as orientation and receive a randomized amount of startup energy (between 0 and E_{PY} or E_{PD} respectively). At every discrete time step, the following sequence of actions is performed for each individual organism in a dynamically randomized order: move, consume available resources, reproduce, and die if energy is out.

Borders with reflecting walls implement fragmentation in the habitat. Borders (similar to real roads, canals, or fences) do not decrease the overall habitat size significantly, and behave in the same way, as does the outer boundary. Corridors are implemented as openings in the walls where the organisms can pass through freely. Corridors have zero length (beyond the wall thickness) and are wide enough to permit several organisms to cross at the same time.

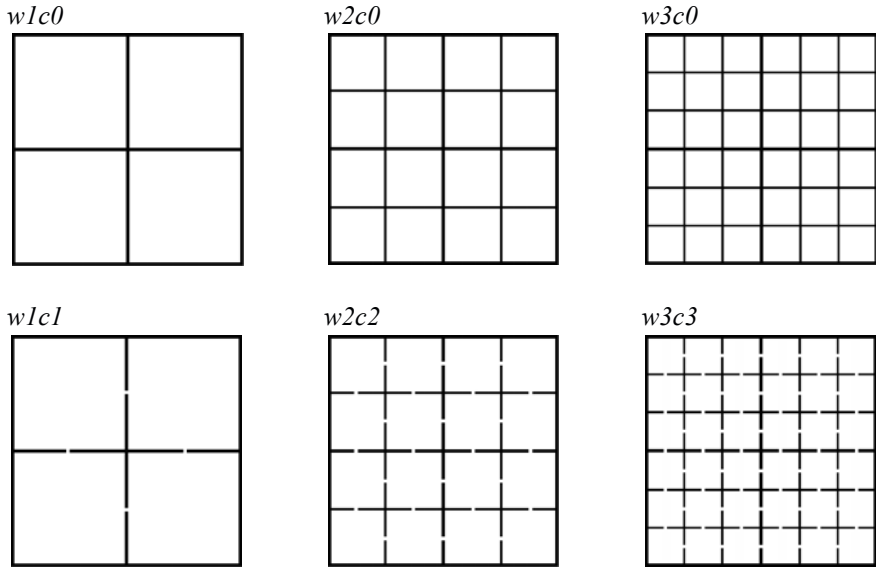


Fig. 1. Fragmentation schemes studied in the paper: $wXcY$ is an X walls and Y corridors system

The main numerical control parameter of the model is $Gain_{PD}$, i.e., the amount of energy gained by the predator when a prey individual is consumed (this can be thought of as representing a “quality” parameter for the predator: thus, the parameter is used as an umbrella descriptor for many direct and indirect relationships between several individual predator traits). In the model, high levels of predator gain and the resulting higher energy reserves of the predators imply a higher expected predator lifetime, which corresponds to an efficient natural predator that can control a large area.

An additional, and most important, control parameter is the number of boundaries and openings in the system. We studied several different combinations (see Fig. 1.) Baseline settings define an initial area large enough to support a high population size (about 10,000 individuals) of prey and predator (Table 1.). Under the baseline conditions, in the unfragmented area ($w0c0$) the prey population always persists indefinitely without the predators, while prey and predator tend to coexist together.

In the experiments, the value of $Gain_{PD}$ and the number of boundaries and corridors were varied, while all other parameters were kept unchanged. Many of these parameters have various effects on dynamic properties that we cannot study in this paper. Treatments consisted of an exhaustive combination of the values $Gain_{PD} = 10$

(baseline), 30, 50 and 70, with a complete set of boundary-corridor systems as presented on Fig.1. (For each treatment, we started simulation runs with a delay $t=50$ in initial prey food re-growth, to avoid extreme initial prey densities and follow-up extinctions.) A high number (≥ 50) of simulation runs with different random seeds and $t = 4,596$ time steps were carried out for each treatment. Data were analyzed and plotted using the R statistical package.

Table 1. Model parameters and initial values used in the simulations

| | |
|---|---------------------------|
| Initial prey $N_{PY} = 1,000$; predator $N_{PD} = 100$ | n area size = 200 |
| Fertility $R_{PY} = R_{PD} = 15\%$ | Corridor width = 3 |
| Motion speed $Fd = 0.9$; | Max. turning $T = 50$ |
| $Gain_{PY} = 4$, $Gain_{PD} = \text{varied} (10, 30, 50, 70)$ | Regeneration time $K = 5$ |
| Initial energy maximum $E_{PY} = 2 * Gain_{PY}$, $E_{PD} = 2 * Gain_{PD}$ | |

3 Results and Discussion

The various effects of fragmentation and corridors exerted on the quantitative behavior of coexistence dynamics has been explored in (Karsai and Kampis 2011, submitted). The basic – and seemingly counterintuitive – finding is that, although fragmentation decreases the chance of survival for the predator (as expected), yet a combined effect of fragmentation and corridors produces a situation favoring the coexistence and stable dynamics of prey and predator above the chance of coexistence found in the unfragmented system. In the present paper we study the oscillatory behavior and the effect of boundaries and corridors on the emerging spatio-temporal waves understood as population oscillations. Accordingly, the main results reported here are based on a frequency domain analysis.

3.1 Qualitative Behavior

In an unfragmented habitat (Fig. 2.a), massive waves (typical for high density populations) together with a high risk of extinction are experienced at high values of predator gain. In isolated fragmented habitats (Fig. 2.b), under the same conditions a system of short-lived dynamic transients dominates the system in each isolated fragment, leading to the extinction of the predator or the prey (and then both of them) in almost every trial and any degree of fragmentation applied. Wave phenomena are not strongly expressed in these cases, because of the lack of a stationary domain of existence and also due to the strongly limited size of the isolated fragments.

In a connected-fragmented system, however, an entirely new phenomenon is found. “Broken” waves appear that can percolate through boundaries via the openings and tend to form a new seed for newer waves (Fig. 2c.). The typical mechanism is that some prey individuals get into (“escape” into) new territories, followed by the predator somewhat later. The new territories often lack predators as a result from earlier overexploitation. Hence, a new territory can be freely repopulated by the prey, harvested by the predator later; and so on. Unlike in isolated fragments, in connected

fragments the local extinction dynamics does not lead to a fatal population level consequence. New growth and new oscillations can start in neighboring fragments and spread all over in a recursive fashion. In the following, we analyze these behaviors using Fourier analysis to quantify the nature of the summarized effects.

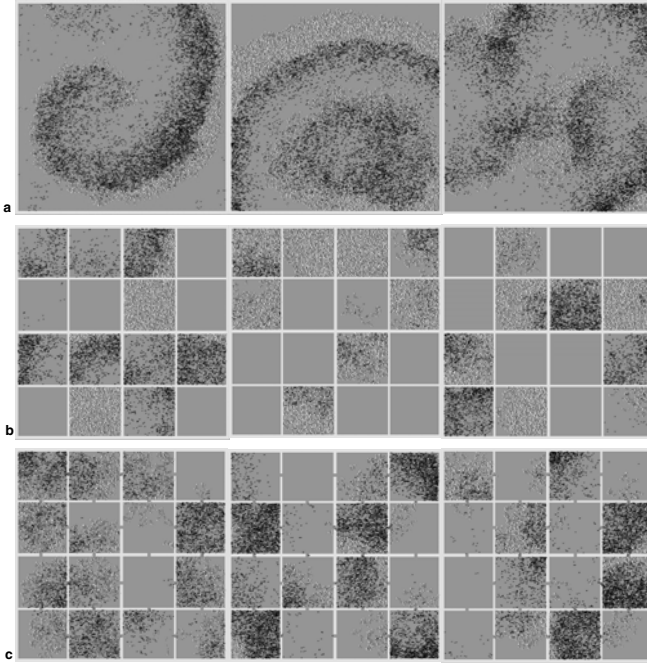


Fig. 2. Population distributions in unfragmented: a, fragmented: b; fragmented and connected: c habitats. Prey food (grey), prey (white) and predator (black).

3.2 Frequency Domain Analysis

Prey behavior is clearly derived from predatory effects. It will, therefore, be instructive to focus on the behavior of the population of predators.

Recurrence plots for $N=1024$ steps are shown on Fig. 3. To appreciate these recurrent plots, note that a perfectly regular plot (for instance, the recurrence plot of a sinus wave) shows a regular, reticular pattern. Transients are visible as stripes and smudges. Disregarding transient irregularities, Fig. 3. shows a clear overall pattern. The upper row shows the unfragmented situation. The baseline case $Gain_{PD} = 10$ yields a quite perfect regular recurrence pattern, showing the dominance of a single frequency and its higher harmonics. Increasing $Gain_{PD}$ (going right) leads to slower and less sharp recurrences, visualized as a decay of the original regular reticular pattern. Below the upper row, we show similar plots for a feasible fragmented connected habitat ($w2c2$). Here, even at higher values of $Gain_{PD}$, the recurrence structure is maintained in an undamaged and sharp condition.

We also performed a (Fast) Fourier Transformation on the predator records for the various habitat types as shown in Fig. 1, using $N=4096$ steps, and discarding the initial transients ($t < 500$). Plots vary in vertical resolution but are identical in the horizontal axis, showing the actual frequencies (i.e., modes). At the base level of predator gain ($Gain_{PD}=10$), an invariant, single frequency peak characterizes the dynamics, which is independent from the number of fragments and corridors (Fig. 4, upper row). This invariant frequency arises from the interaction between the population and the spatial environment, parameterized here as a special case.

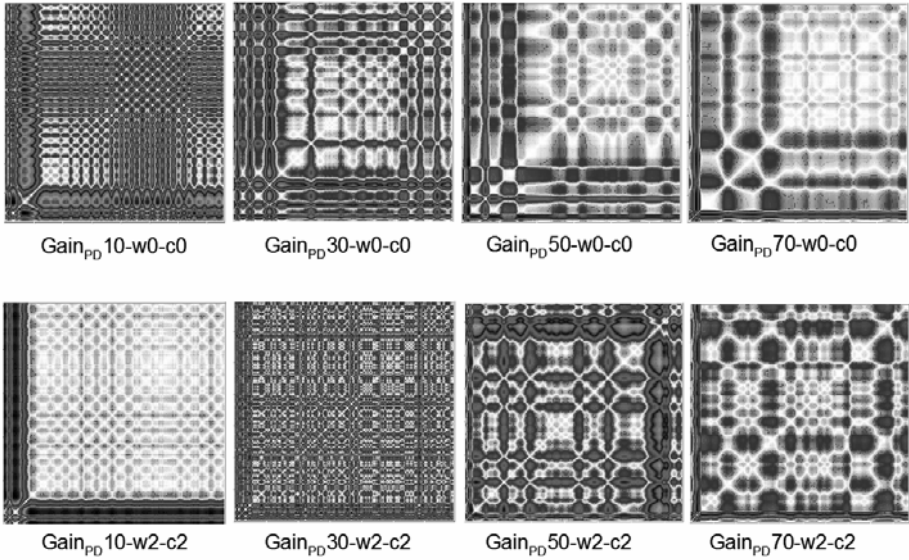


Fig. 3. Recurrence plots of various unfragmented viz. connected fragmented systems. For high quality predators (large $Gain_{PD}$), connected fragmented systems show sustained oscillations.

Fragmented isolated habitats show obligate extinction transients in the high predator gain region (i.e., $Gain_{PD} \geq 50$). Because of the universality of the extinction transients, a systematic frequency analysis of these systems would not be informative. In the unfragmented case, however, we see a different situation. We can observe that the increase of $Gain_{PD}$ leads to a characteristic slowdown (Fig. 4., lower row) and a heavy, low-frequency tail, appearing due to various transients that arise from irregular oscillations with spatial inhomogeneity (as seen in Fig. 2.a), topped by a zero frequency component that corresponds to the extinctions (Fig.4., lower row, right); this combined tail finally suppresses the periodic signal ($Gain_{PD} = 70$, $w3c3$).

In contrast, fragmented connected habitats show the most interesting behavior. We observe that predators respond to increasing fragmentation and to growing $Gain_{PD}$ differently. The opening of corridors introduces a left shift and a wider base in the frequency distribution; this means that many new frequencies emerge with small amplitude but also that the waves are slowing down (Fig. 5, throughout). The overall system dynamics also depends on the degree of fragmentation via the appearance of

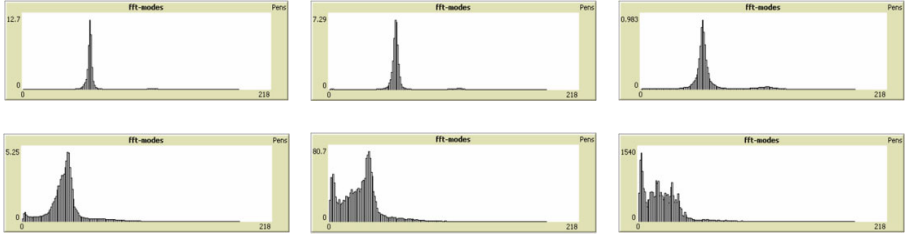


Fig. 4. Connected fragmented habitats I. Upper row: Sharp oscillations in the baseline case ($Gain_{PD}=10$). Left to right: $w0c0$, $w1c1$, and $w3c3$. Lower row: unfragmented ($w0c0$) case with increasing predator gain ($Gain_{PD}=30, 50$ and 70), showing low viz. zero frequency tail.

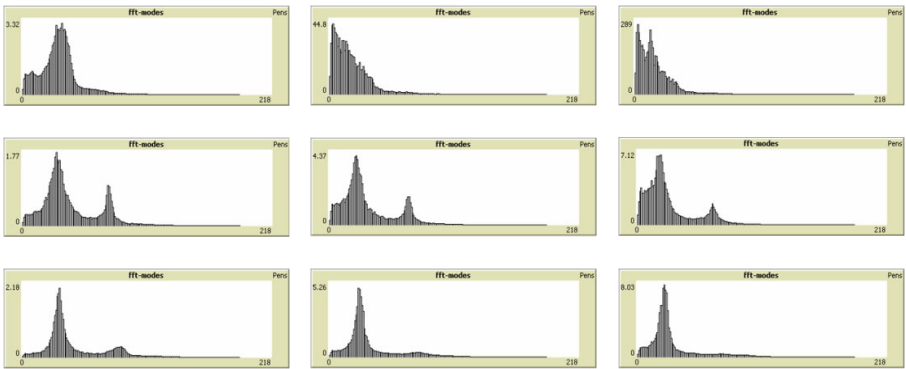


Fig. 5. Connected fragmented habitats II. Left to right: increasing predator gain ($Gain_{PD}=30, 50$ and 70). Top to bottom: increasing fragmentation: $w1c1$, $w2c2$ and $w3c3$.

global harmonics that survive despite local extinctions (Fig. 5, middle and lower rows) (A notable contingency is the occurrence of higher harmonics when fragment size supports multiple oscillations, see Fig. 5, middle row). The quality of the predator ($Gain_{PD}$) also has a profound effect here. As in the unfragmented case, increasing predator quality leads to a left shift (i.e., slowdown) on the frequency plot, and the same low-frequency tail appears. This tail is again associated with the transients and extinctions in the same way as in the unfragmented case. However, this time we deal with an asynchronous process, which is the result of the independent dynamics of the several fragments, and accordingly, we see that the local transients do not destroy the main population harmonics. Indeed, in the connected-fragmented case, increasing fragmentation (Fig. 5, top to bottom) increasingly *restores* the original harmonics.

Thus, we observe that two interwoven effects arise from fragmentation and predator quality. A worst combination case is seen on Fig. 5, upper row (viz. $w1c1$), where fragmentation biases the system towards extinctions in the individual fragments (shown by the notorious low-frequency tail), but at the same time, the positive effect arising from corridors (Fig. 5, middle and lower rows) is not strong enough yet to support the survival of the lead frequency in the combined system of fragments.

4 Conclusions and Interpretation

There is a natural analogy with wave-breakers here. Wave-breakers are obstacles that disrupt otherwise fatal sea or river waves, dispersing the effects of energy. Here, similarly, fragmentation barriers can break population waves – however, of course, here the end effect is the opposite on the system; exactly by breaking the otherwise fatal waves can the population escape and via the “leaking” of corridors a sufficient amount of organisms can survive, to build up new waves, to be broken up again, etc.

This mechanism explains our otherwise highly counterintuitive main finding that more fragmentation can be better than little or – what is the least expected – no fragmentation at all. The key is connectedness in fragmentation: the higher the fragmentation, the more effective the wave breakers, and via the connections, the more efficient the regeneration process of subpopulations.

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