Inter-Tunneling Mechanism of Colliding Population Waves

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Abstract

Here we show a new interaction mechanism of colliding population waves. It provides a stable coexistence of two similar, but different species competing for the same limiting resource during their asexual propagation in a limited homogeneous environment under constant conditions. The revealed mechanism opens new opportunities in conservation biology.

Population waves are autowaves, i.e. they are self-sustaining waves, which use resources of media in which they propagate. The importance of autowaves based on the fact that they have universal properties that are independent of specific implementation (*1*). One such property is that these waves annihilate each other after collision. This annihilation occurs, for example, in result of collision of two fronts of the fire, which spread in a field with dry grass. Previously a paradoxical phenomenon of behavior of population waves was revealed - the colliding waves were not annihilated, but they looked as if they are penetrating through / reflecting from each other (*2*). The problem of interpretation of this phenomenon has been in the difficulty of understanding what specific mechanism is implemented - reflection, inter-penetration, or both. It is so because in both experiments in vitro and in silico individuals of different species were not discerned because they were not marked. The mathematical modeling by partial differential equations also has not helped to understand what mechanism really happens (*3*) because it shows what happens with population waves but do not show how and why. In this paper, for the first time, we directly model the mechanistic mechanism of inter-tunneling of colliding population waves of two similar but different competing species, which are identical consumers (Fig 1; Movie S1). The species differ in their fitness - individuals of the first species are dominant, i.e. have the primary ability to use resources of an environment for propagation in situation of direct competition for a free microhabitat. The model reproduces propagation of two species of loose-bunch turf grasses in a small homogeneous ecosystem. Our cellular automaton model of interspecific competition is individual-based and its rules are based on deterministic logical "if-then" statements, which define direct processes of competition. It makes the model mechanistic. Earlier the phenomenon of tunneling of chemical autowaves through gaps in polymer membranes was demonstrated in experiment and in computer simulation (*4*). The existence of gaps in fronts of autowaves was experimentally demonstrated as dash waves based on Belousov-Zhabotinsky reaction (*5*). We simulate here gaps in population waves. An important feature of our model is that all individuals have moderate propagation. This is reflected in the fact that every individual can use for propagation no more than one third of resources of its nearest environment. It leads to formation of gaps with possibility of their occupation by individuals of another species. Individuals of colliding population waves freely penetrate the perimeters of hexagonal fronts due to arising gaps (Fig. 1A and Movie S1). As result, both species have the same numbers of individuals on all iterations

(Fig. 1B). The discovered in silico new mechanism of inter-tunneling of colliding population waves is the direct mechanistic answer to the old question of ecology. It shows how two similar but different species can coexist in homogeneous ecosystem under constant environmental conditions in spite of that fact that they need the same limiting resource. The revealed mechanism opens new opportunities in conservation biology and is the step towards a solution of the mystery of biodiversity.

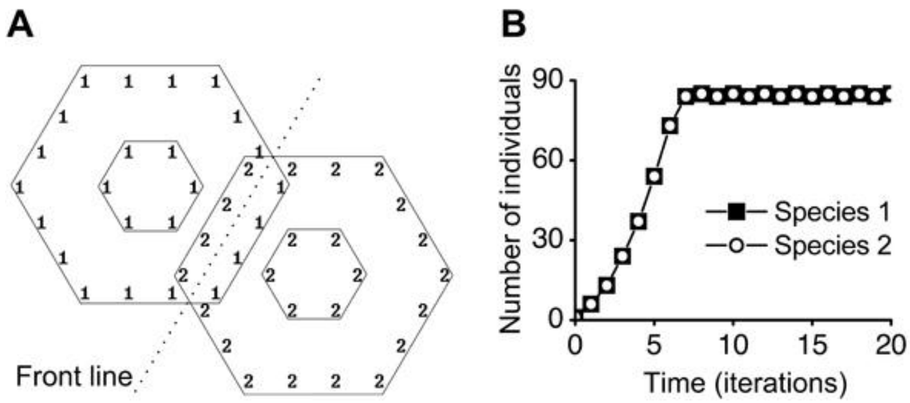

Fig. 1. The inter-tunneling of colliding population waves during interspecific competition. (**A**) Outline of the inter-tunneling of colliding fronts of hexagonal population waves on the third iteration of the cellular automaton. ‘1’ - an individual of the first (dominant) species; ‘2’ - an individual of the second (recessive) species. Hexagons indicate the positions of the fronts. The dotted front line represents the collision line of the fronts of population waves. (**B**) The graph with the number of individuals of both species.

References and Notes

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6. Author Contributions: Vyacheslav L. Kalmykov designed the research. Lev V. Kalmykov created the program, investigated the model and made the figures and the movie of the experiments. Both authors discussed the results, interpreted them and wrote the manuscript.
7. This paper is a format-modified version of a manuscript which was submitted to Science on June 01, 2011 (it was rejected without in-depth review).

Supporting Material for

Inter-Tunneling Mechanism of Population Waves

This Supporting Material includes:

Materials and Methods
Fig. S1
Legend for Supporting Online Movie S1 -
http://www.youtube.com/watch?v=gZa2QIAdRBA

Materials and Methods

Deterministic cellular automaton was used for modeling the spatio-temporal dynamics of simultaneous colonization of a free small ecosystem by two similar but different competing species. An integral ecosystem (macrohabitat) is modeled by the whole cellular automaton. The lattice is closed to a torus by periodic conditions for avoiding boundary effects. The hexagonal lattice was used, because it most naturally corresponds to the principle of densest packing of round projections of microhabitats. Resources of ecosystem are homogeneously distributed over all microhabitats. Each site models a microhabitat, which in the free state contains resource for existence of any one individual. A life cycle of an individual lasts one iteration of the automaton. All states of microhabitats have the same duration. All microhabitats are identical, i.e. every individual of both species consumes identical quantity of identical resources. The lattice consists of 26x26 sites. The initiate individuals of the two competing species are placed in the coordinates (10, 10) for the first and (15, 15) for the second species. One of the species is dominant and the other one is recessive. The dominance is defined as the primary ability of an individual to occupy a free microhabitat in a direct conflict of interests with an individual of the other species. Propagation of individuals is defined by the neighborhood of the cellular automaton (Fig. S1A). Each site (microhabitat) can be in one of the five states. Specification of states and possible transitions between the states of a site are represented in Fig. S1B.

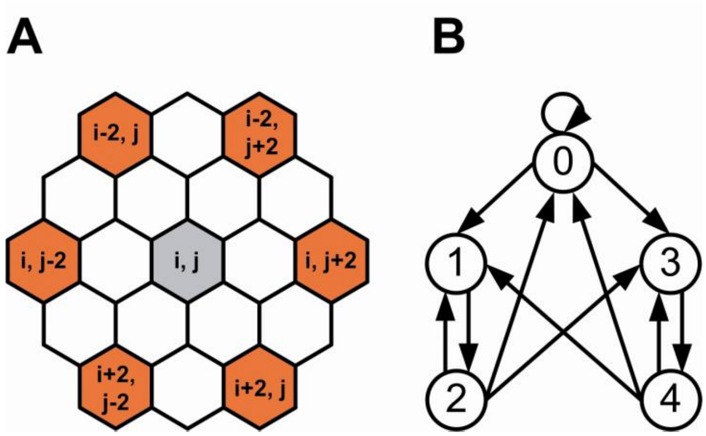

Figure S1. Characteristics of the model. (**A**) Cellular automaton's neighborhood (**i**, **j** are integer). A parental individual has coordinates (i, j) and marked by the grey color. Possible offsprings have coordinates (i, j-2), (i-2, j), (i-2, j+2), (i, j+2), (i+2, j), (i+2, j-2) on the next iteration and marked by orange color. (**B**) Directed graph of transitions between states of a lattice site (microhabitat).

'0' – a free microhabitat that can be occupied by offspring of any species.

'1' – a living individual of the first (dominant) species occupies a microhabitat.

'2' – the regeneration state of a microhabitat after living of an individual of the first species. In Movie S1 this state is represented as symbol '.'

'3' – a living individual of the second (recessive) species occupies a microhabitat. In Movie S1 this state is represented as symbol '2'.

'4' - the regeneration state of a microhabitat after living of an individual of the second species. In Movie S1 this state is represented as symbol '*'.

Movie S1 is available on YouTube -
http://www.youtube.com/watch?v=gZa2QIAdRBA

Movie S1. Inter-tunneling mechanism of colliding population waves**.** This video consist of three dynamical parts of the one model: cellular automaton's lattice with all processes on it up to the 20th iteration; the graph of the number of both species; statistics with the number of individuals and the number of iteration. After collision of population waves' fronts on the 3rd iteration, the mechanistic demonstration of their *free inter-penetration through each other* is appeared. States of a lattice site (microhabitat):

'**0**' – a free site that can be occupied by offspring of any species;

'**1**' – a site is occupied by a living individual of the first (dominant) species;

'.' – the regeneration state of a microhabitat after living of an individual of the first species;

'**2**' – a site is occupied by a living individual of the second (recessive) species;

'*' - the regeneration state of a microhabitat after living of an individual of the second species.