

# Strong violation of the competitive exclusion principle

Lev V. Kalmykov<sup>1,3</sup> & Vyacheslav L. Kalmykov<sup>2,3\*</sup>

<sup>1</sup>*Institute of Theoretical and Experimental Biophysics, Russian Academy of Sciences, Pushchino, Moscow Region, 142290 Russia;* <sup>2</sup>*Institute of Cell Biophysics, Russian Academy of Sciences, Pushchino, Moscow Region, 142290 Russia;* <sup>3</sup>*Pushchino State University, Pushchino, Moscow Region, 142290 Russia.*

**Bacteria and plants are able to form population waves in result of their consumer behaviour and propagation. A soliton-like interpenetration of colliding population waves was assumed but not proved earlier. Here we show how and why colliding population waves of trophically identical but fitness different species can interpenetrate through each other without delay. We have hypothesized and revealed here that the last mechanism provides a stable coexistence of two, three and four species, competing for the same limiting resource in the small homogeneous habitat under constant conditions and without any fitness trade-offs. We have explained the mystery of biodiversity mechanistically because (i) our models are bottom-up mechanistic, (ii) the revealed interpenetration mechanism provides strong violation of the competitive exclusion principle and (iii) we have shown that the increase in the number of competing species increases the number of cases of coexistence. Thus the principled assumptions of fitness neutrality (equivalence), competitive trade-offs and competitive niches are redundant for fundamental explanation of species richness.**

Population waves are self-sustaining waves which use resources of a medium where they propagate. These waves are known as ‘autowaves’<sup>1</sup>. Autowaves play universal role in mechanisms of various chemical and biological processes<sup>2-5</sup>. The importance of autowaves is based on universality of their properties that are independent of a specific implementation. One such universal property is that identical autowaves annihilate each other after collision. Previously, the paradoxical phenomenon of soliton-like (quasi-soliton) behaviour of population

waves was revealed for ultra-fast chemotactic bacteria - their colliding population waves did not annihilate each other, and looked as penetrating through / reflecting from each other without significant delay<sup>1,6,7</sup>. The phenomenon of soliton-like behaviour of chemotactic bacterial waves is based on ultrafast movement and as result bacteria have no time to use all local limiting resource. Thus, a certain amount of unused resource is left behind the population waves. As a consequence the reflection of the chemotactic waves and possibly their interpenetration through each other occurs after their collision. The problem has arisen as the difficulty of understanding what is implemented with certainly - reflection, interpenetration, or both. Individuals of colliding population waves were not discerned in these experiments because they were of one and the same species and were not marked neither in vitro nor in silico experiments. A fundamental question about the possibility of soliton-like interpenetration of colliding population waves is the most intriguing for us. The mathematical modeling by partial differential equations has not helped to understand what mechanism really happens<sup>8</sup> because it phenomenologically shows what happens with population waves on a macro-level but does not show how it happens on a micro-level of individuals. Earlier Tilman noted that models of population dynamics based on differential equations are phenomenological and therefore hinder mechanistic understanding of phenomena under study<sup>9</sup>.

A similar problem of distinguishing between interpenetration and reflection arose in the studies of colliding population waves of the bacteria *Myxococcus Xanthus*<sup>10-12</sup>. Under starvation conditions these bacteria start to act cooperatively, aggregate and finally build a multicellular structure, the fruiting body. The fruiting body formation is often preceded by the pattern of periodically colliding waves called rippling patterns. In the difference from chemotactic bacteria, myxobacterial aggregation is the consequence of direct cell-to-cell contact interactions, but not of chemoreception of a food concentration gradient. When viewed from a distance, where only cell density can be perceived, the rippling waves appear to pass through one another, analogous to soliton waves in various physical systems. Nevertheless, detailed studies of the population waves' behaviour of myxobacteria showed that although they appear to interpenetrate, they actually reflect off one another when they collide, so that each wave crest oscillates back and forth with no net displacement. Without observing individual cells, the illusion that the waves pass through one another is nearly perfect. In the experimental observations some individual cells were marked by green fluorescent protein<sup>13,14</sup> and in the computational modeling the agent-based approach was implemented<sup>14,15</sup>.

**Main hypothesis.** Search of a possible mechanism of the soliton-like interpenetration of colliding population waves is of interest for us because we have supposed that it may be the base of a new mechanism of stable competitive coexistence. This assumption is based on our understanding that soliton-like interpenetration may reduce the intensity of direct competitive interactions of individuals of colliding population waves. Such mechanism would open up new prospects for understanding biodiversity and for biodiversity conservation.

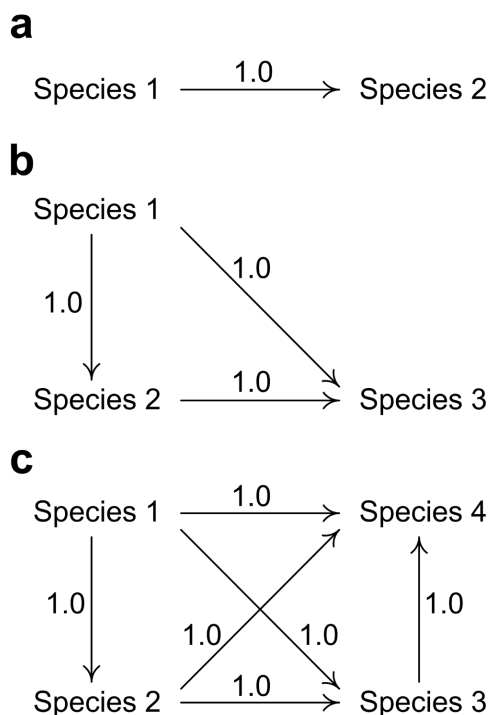
**Theoretical model.** In order to find a mechanism of possible soliton-like behaviour of colliding population waves we have developed cellular automata models of population growth<sup>16</sup> and interspecific competition. Earlier cellular automata were used for modeling a soliton-like behaviour<sup>17</sup>.

The entire cellular automaton simulates a whole ecosystem. The two-dimensional hexagonal lattice is closed to a torus by periodic boundary conditions in order to avoid boundary effects. The hexagonal lattice was used because it most naturally implements the principle of densest packing of microhabitats which we consider as circles. The lattice consists of 26x26 sites.

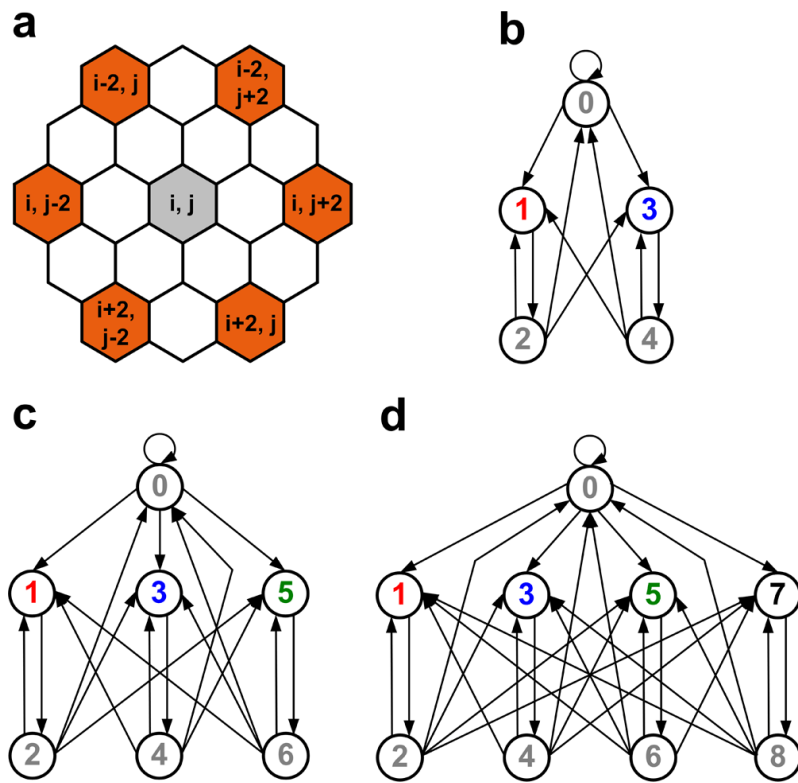
Each site of the lattice models a microhabitat, which in the free state contains resource for existence of one individual of any species and can be occupied by one individual only. A life cycle of an individual lasts a one iteration of the automaton. All states of all sites are of the same duration. Every individual of all species consumes identical quantity of identical resources by identical way i.e. they are identical per capita consumers. Individuals of the plant species are immobile in lattice sites and populations waves spread only due to propagation of individuals (Supplementary Fig. 2). The closest biological analogue of the models is vegetative propagation of plants (Supplementary Movies 1-4).

Trophically identical, but fitness different competing species were modelled. The dominance we define as the primary ability of an individual of a species with greater fitness to occupy a free microhabitat in a direct conflict of interest with an individual of a less adapted species (Supplementary Fig. 1). The rules of competitive interactions between the species are represented by diagrams of competitive interactions between species in the general form (Fig. 1). The competing species have no any adaptive trade-offs what is important for strict search of the expected mechanisms of competitive coexistence.

In search of mechanism of a soliton-like behaviour of population waves, we have found a hexagonal rosette-like cellular automaton's neighbourhood (Fig. 2a), which allowed us to model the incomplete consumption of nearest environmental resources as the consequence of the moderate vegetative propagation of plants. Every individual can use for propagation no more than one third of resources of its nearest environment (Fig. 2a). The incomplete use of resources underlies of behaviour of chemotactic bacterial population waves in studies which have assumed the possibility of the soliton-like interpenetration<sup>1,6,7</sup>.



**Figure 1 | The rules of competitive interactions between the species.** Arrows point from the dominant species to the recessive species. The probability of occupation of a microhabitat by an offspring of a species with greater fitness in a direct conflict of interest is equal to 1.0, i.e. the dominant species wins in direct conflicts in 100% of cases. **a**, The diagram of the model with the two competing species. The species 1 wins the species 2. **b**, The diagram of the model with the three competing species. The species 1 wins the species 2 and 3, while the species 2 wins the species 3. **c**, The diagram of the model with the four competing species. The species 1 wins the species 2, 3, 4, while the species 2 wins the species 3 and 4, and the species 3 wins the species 4.

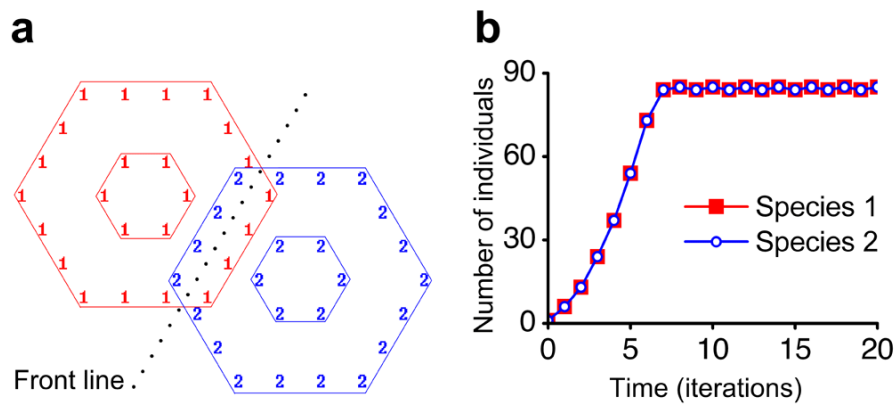


**Figure 2 | The rules of the cellular-automata models.** **a**, The hexagonal rosette-like neighbourhood where  $i$  and  $j$  are integer numbers. The site with parental individual has coordinates  $(i, j)$  and marked by the grey colour. The sites with possible offsprings have coordinates  $(i, j-2)$ ,  $(i-2, j)$ ,  $(i-2, j+2)$ ,  $(i, j+2)$ ,  $(i+2, j)$ ,  $(i+2, j-2)$  and marked by the orange colour. **b-d**, Directed graphs of transitions between states of a lattice site: in the two-species competition model (**b**), in the three-species competition model (**c**), in the four-species competition model (**d**). States of a lattice site are denoted as: '0' – a free site. '1', '3', '5', '7' – the states of a site occupied by individuals of the first, second, third, fourth species, respectively. In movies these states are represented as the symbols '1', '2', '3', '4'. The regeneration states of a site after death of an individual of the first, second, third, fourth species denoted as '2', '4', '6', '8' and in Supplementary Movies these regeneration states are represented by the symbols '.', '\*', '@', '#', respectively, to distinguish them from living individuals.

Rosettes of rhizomes of asexually propagating turf grasses *Poa pratensis* L. and *Festuca rubra* L. ssp. *rubra* were the biological prototypes of the specific form of this neighbourhood. The cellular automata models are individual-based and their rules consist of deterministic logical 'if-then' statements only. Thus, the models are fully mechanistic. The models take into account a regeneration state of a microhabitat after an individual's death. In ecology regenerative processes of a microhabitat are considered in the regeneration niche concept<sup>18,19</sup>. According to this concept

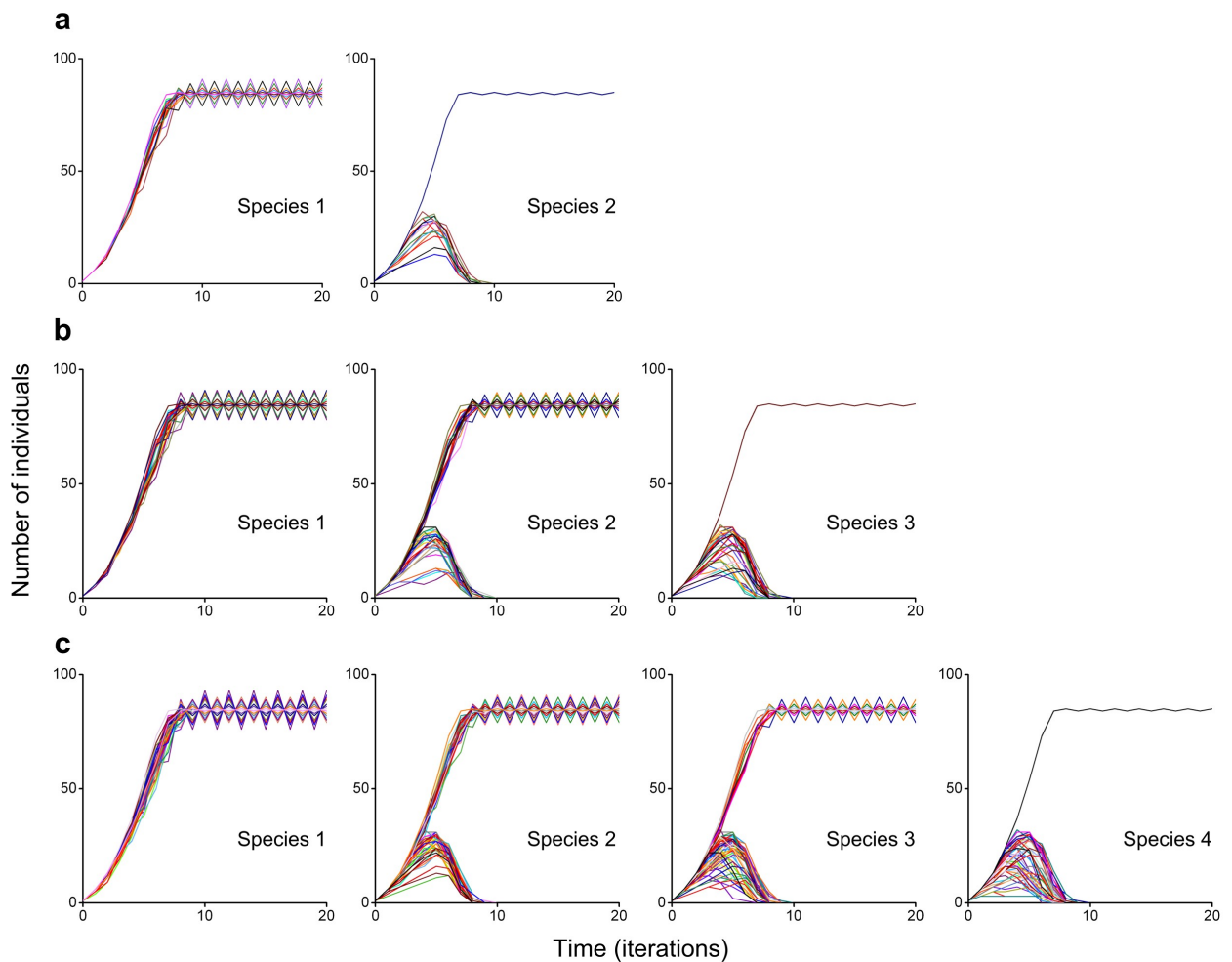
for subsequent successful occupation of a microhabitat after an individual's death a set of conditions must be restored. For example, obstacles in the form of dead roots, dead tillers and of soil toxins must be eliminated.

The necessary mineral components, including the optimum moisture content must also be restored. Inclusion of the regeneration state allowed us to implement the accordance of our model with the axiomatic formalism of Wiener and Rosenblueth which was used for simulation of excitation propagation in an active medium<sup>20</sup>. The three successive states - rest, excitation and refractoriness of each site of the cellular automaton lattice are the main features of that formalism. In our models the 'rest' corresponds to the 'free' state of a microhabitat, the 'excitation' corresponds to the life activity of an individual in a microhabitat and the 'refractoriness' corresponds to the regeneration of microhabitat's resources including recycling of a dead individual. Here the occupation of a microhabitat by an offspring of one of the competitors is the analogue of excitation of active medium. A populated microhabitat goes into the regeneration state after an individual's death (Fig. 2). A populated microhabitat and a microhabitat in the regeneration state cannot be occupied. A microhabitat can only be occupied if it is in the free state or after finishing the regeneration state (Fig. 2b-d and Supplementary Fig. 3). Thus we have modelled a birth-death-regeneration process. The regeneration niche is often not taken into account in existing cellular automata models of plant communities and that is the imperfection of these models. In addition, the regeneration state of a microhabitat allows us to avoid a predator-prey analogy in models of competition, when one individual directly replaces another one. This analogy seems unnatural in competition models of plant species. Directed graphs of transitions between states of a lattice site in the models with the two, three and four competing species are presented in Fig. 2b-d. Incomplete consumption of resources of the nearest environment of individuals is based on the rosette-like neighbourhood that leads to formation of gaps in population waves. These gaps may be occupied by individuals of another species at collision of the population waves. Individuals of the both colliding population waves freely interpenetrate through the waves owing to the arising gaps (Fig. 3a; Supplementary Movie 1). As result, both competing species have the same numbers of individuals (Fig. 3b). So, the mechanism of interpenetration of colliding population waves occurs as interpenetration of individuals through the gaps in the waves (Fig. 3a; Supplementary Movies 1 and 3). Earlier the phenomenon of interpenetration of chemical autowaves through the gaps in polymer membranes was demonstrated in experiments and in computer simulations<sup>21</sup>. The existence of gaps in fronts of segmented chemical autowaves was experimentally demonstrated as dash waves, based on Belousov-Zhabotinsky reaction in a water-in-oil reverse microemulsions<sup>22,23</sup>.



**Figure 3 | Two-species competition.** **a**, Outline of the interpenetration of colliding fronts of hexagonal population waves at the third iteration of the cellular automaton. ‘1’ - an individual of the first (dominant) species. ‘2’ - an individual of the second (recessive) species. The dotted front line represents the collision front line of the colliding population waves. **b**, Population dynamics of the two species.

**Testing stability of the species coexistence.** Realization of the interpenetration mechanism which leads to the species coexistence depends on starting positions of initial individuals on the lattice. We used Monte Carlo simulations to check the stability of coexistence of competing species in the models with two, three and four species (Fig. 4). The Monte Carlo simulations were based on random initial positioning of single individuals of each competing species on the lattice before an each trial experiment. Supplementary Movie 2 shows how the dominant species 1 excludes the recessive species 2. We show how one species can exclude the other if competitors do not avoid direct conflicts of interest (Supplementary Movie 2). Nevertheless competitive exclusion does not always happen in result of competition of trophically identical but fitness different species in one closed homogeneous ecosystem, although in this case the exclusion is required in accordance with the competitive exclusion principle (Supplementary Movies 1, 3 and 4). Plots of the Monte Carlo simulations for competition of two, three and four species are shown in Fig. 4.



**Figure 4 | Tests of stability of the coexistence of the competing species by Monte Carlo method.** Random initial placements of individuals on the lattice were used in each trial experiment. 200 trial experiments were in each series. 100 series of the experiments were performed for each model. Results of one series of trials are graphically presented here. Further here the numerical values are given as the averaged results of all 100 series of the trial experiments for the each model. **a**, The two-species competition model. The number of coexistence cases was  $150.06 \pm 6.26$  (mean  $\pm 1$  SD;  $n=100$ ) of 200 trial experiments (i.e. coexistence was approximately in 75% of cases) in each of the 100 test series. **b**, The three-species competition model. The numbers of coexistence cases were:  $76.8 \pm 6.65$  for the three species and  $188.17 \pm 3.67$  for any two species. **c**, The four-species competition model. The numbers of coexistence cases were:  $18.44 \pm 4.52$  for the four species,  $132.06 \pm 7.79$  for any three species and  $197.28 \pm 1.69$  for any two species (i.e. coexistence of two species was approximately in 99% of cases).



The unexpected result here was that the more species competed, the more cases of coexistence occurred contrary to the competitive exclusion principle (Fig. 4 and Supplementary Fig. 9). We consider this fact as an explanation of the mystery of biodiversity. Unusually large numbers of cases of existence of individual species were found in the models of competition between two, three and four species (Supplementary Fig. 6). In addition, we have shown that the species can coexist with each other in all possible combinations in violation of the competitive exclusion principle (Supplementary Figs 7 and 8).

Cases of coexistence also depend on the lattice size and were implemented if the lattice consisted of  $N \times N$  lattice sites, where  $N$  is an even number (Fig. 4; Supplementary Figs 4 and 5). If  $N$  is an odd number the mechanism could not be implemented and species did not coexist (Supplementary Figs 4 and 5).

**Violation of the principle of competitive exclusion.** Verification of this principle is undertaken to demonstrate that the discovered mechanism of competitive coexistence supports our main hypothesis. The principle of competitive exclusion (the Gause's principle) postulates that species, competing for the same limiting resource in one homogeneous habitat, cannot coexist<sup>24</sup>. This principle contradicts observed natural species richness. This contradiction is known as the biodiversity paradox and this paradox is one of the central ecological problems<sup>25</sup>. The Gause's principle<sup>24,26</sup> belongs to the one side of this paradox, while the paradox of the plankton<sup>25</sup> together with at least 120 different hypotheses<sup>27</sup> of natural species richness are on the other side<sup>28-31</sup>. Many separate explanations of the biodiversity paradox were supposed, however a clear solution has not been offered<sup>28,32</sup>. Different competitive trade-offs do not violate the competitive exclusion principle because the principle of competitive exclusion in the formulation of Gause suggests that "one of species has any advantage over the other", i.e. one and the same species always keeps a definite uncompensated benefit<sup>26</sup>. One of the most known examples of coexistence based on competitive trade-offs with fitness compensations is the cyclic, non-hierarchical dominance represented in rock–paper–scissors games<sup>33</sup>.

Earlier, Hardin underlined that any empirical studies cannot prove and hardly falsify the competitive exclusion principle<sup>24</sup>. We believe that only a strict and fully mechanistic modeling may allow to prove or to falsify the competitive exclusion principle. The computer models in this paper permit to do such rigorous test as they are based on fully deterministic individual-based

approach. A rigorous proof of the violation of the competitive exclusion principle was obtained as our model provides a number of positive answers to the next question:

“Is it possible a stable coexistence of two trophically identical but fitness different species, which compete for one limiting resource in one uniform habitat under the definite complex of the following specially formulated preconditions (all are natural)?” Six points of these strict preconditions are:

1. There are no any fitness trade-offs between competing species;
2. Competing species are genetically stable and their propagation occurs only vegetatively;
3. Individuals of one and the same species always win individuals of competing species at direct conflicts of interest (one competing species is stably dominant, the other one is stably recessive);
4. Habitat is limited, homogeneous, stable (its configuration and sizes, and also the climate and weather are constant), closed for immigration and emigration and, additionally, predation, herbivory and parasitism are absent;
5. Only one individual of competing species may occupy a one free microhabitat and cannot leave its limits.
6. Competing species do not have any co-operative interactions and are per capita identical and constant in ontogeny, in fecundity rates, in regeneration features of their microhabitats and in environmental requirements (they are identical consumers).

To get a positive answer to the formulated rigorous question it was sufficient to find at least one case of stable competitive coexistence which is implemented within our stringent conditions. Our model with the two species satisfies to all these requirements and gives the positive answer on our rigorous question (Figs 3 and 4a; Supplementary Movie 1).

We continued the testing with three (the rules graphs are in figures 1b and 2c) and four (the rules graphs are in figures 1c and 2d) trophically identical but fitness different species, which compete for one limited resource in one homogeneous environment. In these experiments the competitors also may coexist (Fig. 4b-c; Supplementary Movie 3).

All these cases of the stable coexistence of the two, three and four trophically identical but fitness different species in one homogeneous habitat under constant conditions strongly violate the competitive exclusion principle in our formulation. The equality of the numbers of individuals of coexisting competing species in each moment of time is a highly unexpected result especially taking into account that environmental conditions are stable and any fitness trade-offs are absent (Fig. 3b, Supplementary Movies 1, 3 and 4).

We found the coexistence mechanism of competing species which are identical consumers. This mechanism provides strong violation of the principle of competitive exclusion and helps to explain the observed natural species richness. The mechanism implements the optimal allocation of a limiting resource among competitors, enabling them to eliminate interspecific competitive conflicts and to maintain equal numbers of the populations. As the revealed mechanism provides strong violation of the competitive exclusion principle and as we have shown that the increase in number of competing species increases number of cases of coexistence of competitors in one and the same habitat, we mechanistically explained the mystery of biodiversity. Thus principled assumptions of fitness neutrality (equivalence)<sup>34</sup>, competitive niches and competitive trade-offs are redundant for fundamental explanation of species richness.

**Future prospects.** The proposed cellular automata models allow a mechanistic understanding of interspecific competition. The discovered mechanism of soliton-like interpenetration of colliding population waves gives new insights in physics of autowaves, in theoretical ecology and in conservation biology. The universality of our models of competition follows from the universal properties of autowaves. We consider the prospect of further development of the cellular-automata approach as very challenging because it allows an individual-based modeling of dynamics of complex spatio-temporal systems and permits unlimited extension by use of additional nested and adjoint lattices, additional states of sites, various types of neighbourhoods and individuals' behaviour rules with combination of the approach with the known modelling methods.

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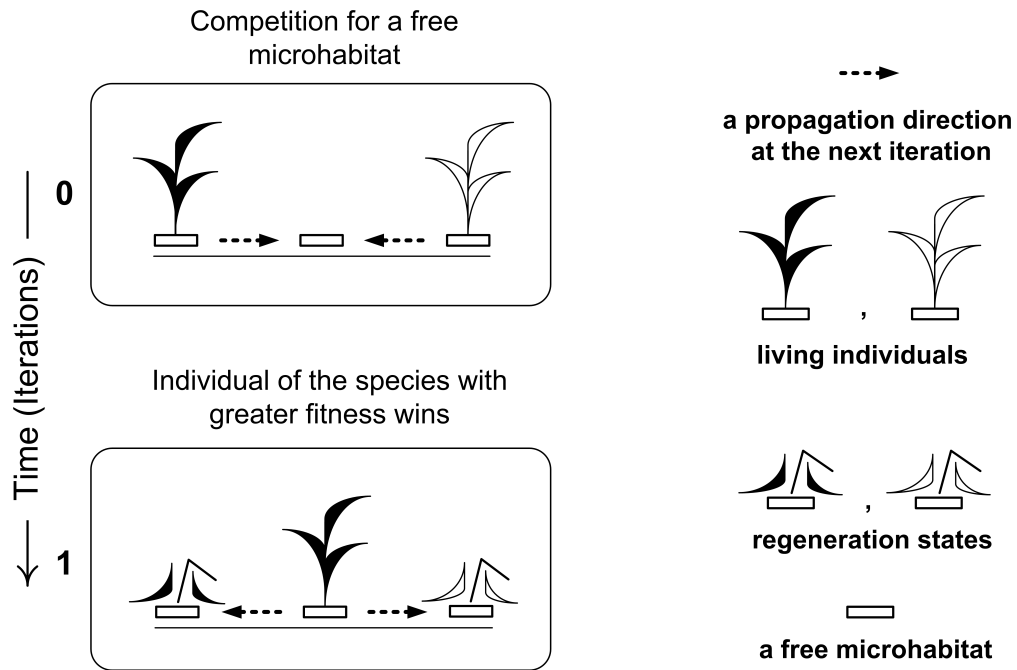
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**Author Contributions** V.L.K. designed the research. L.V.K. created the programs, investigated the models and made the figures and the movies of the experiments. Both authors discussed the results, interpreted them and wrote the manuscript.

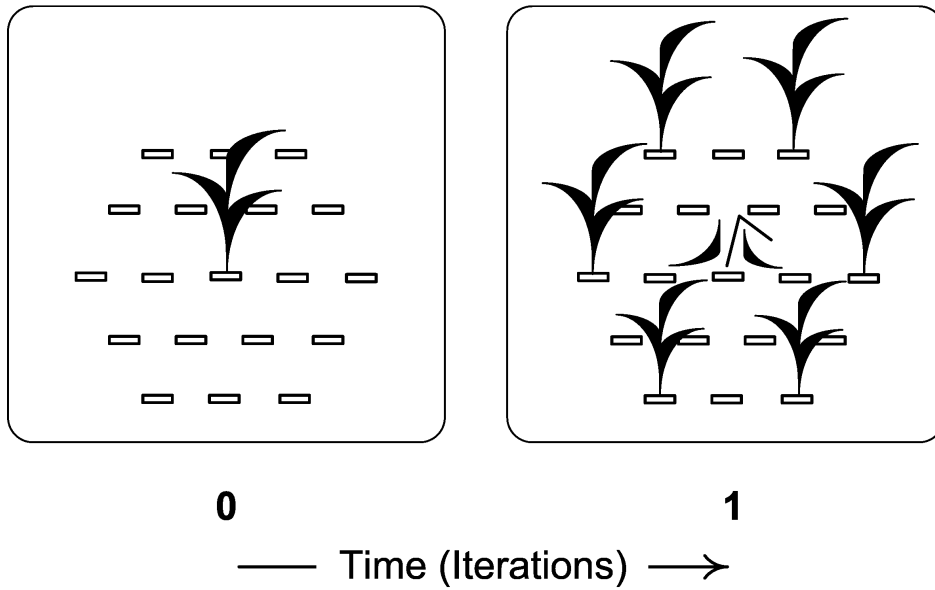
**Author Information** Correspondence and requests for materials should be addressed to V.L.K (vyacheslav.l.kalmykov@gmail.com).

# SUPPLEMENTARY INFORMATION

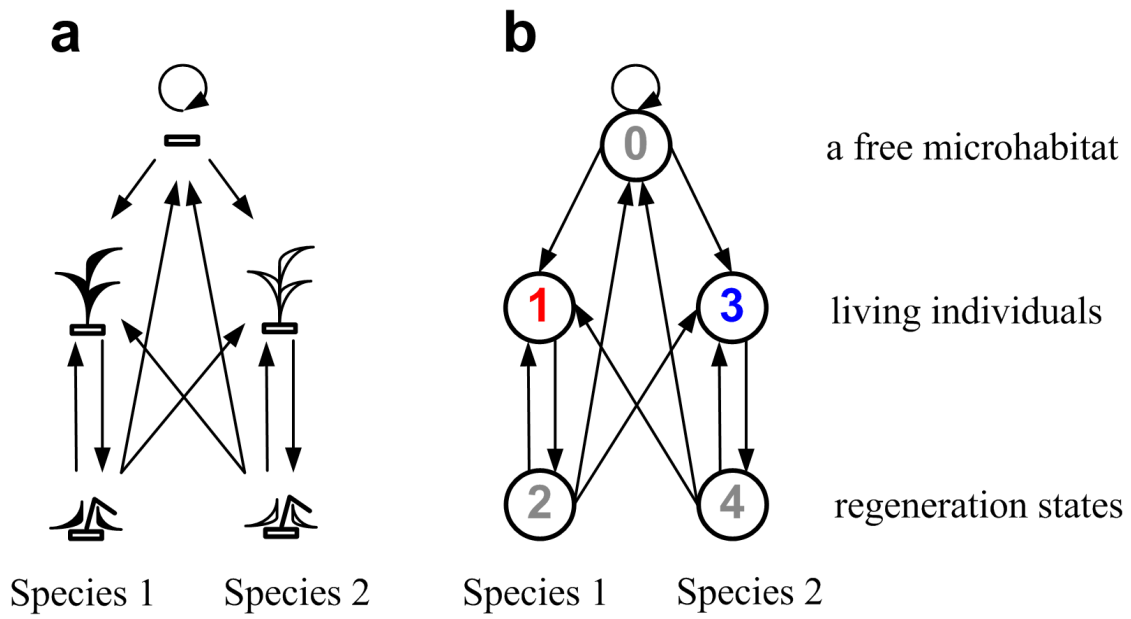


**Supplementary Figure 1 | Mechanistic definition of competition between individuals of two trophically identical but fitness different species.**

## Propagation

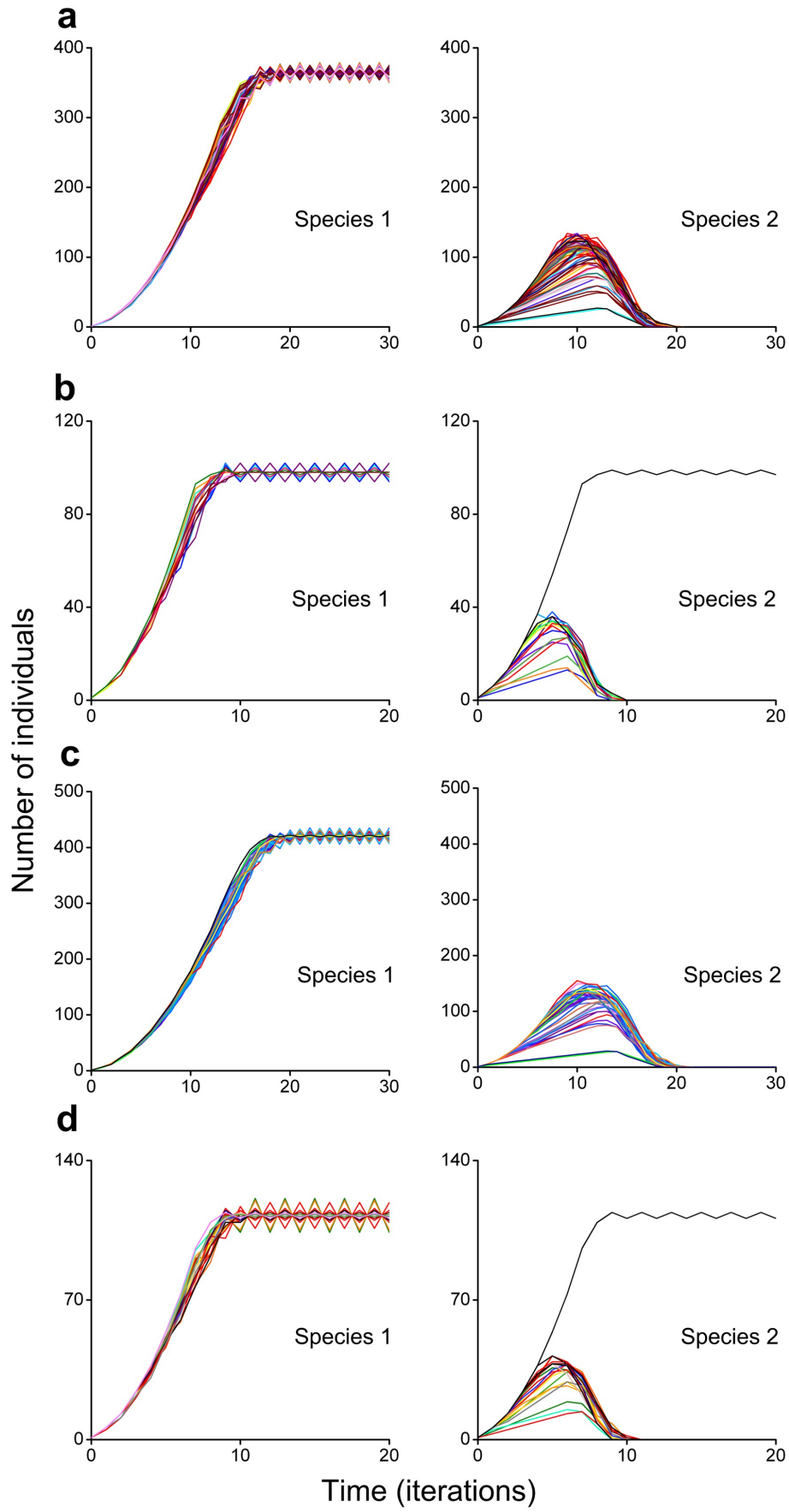


**Supplementary Figure 2 | Modelling of vegetative propagation of plants into the hexagonal rosette-like neighbourhood (Figure 2a).**

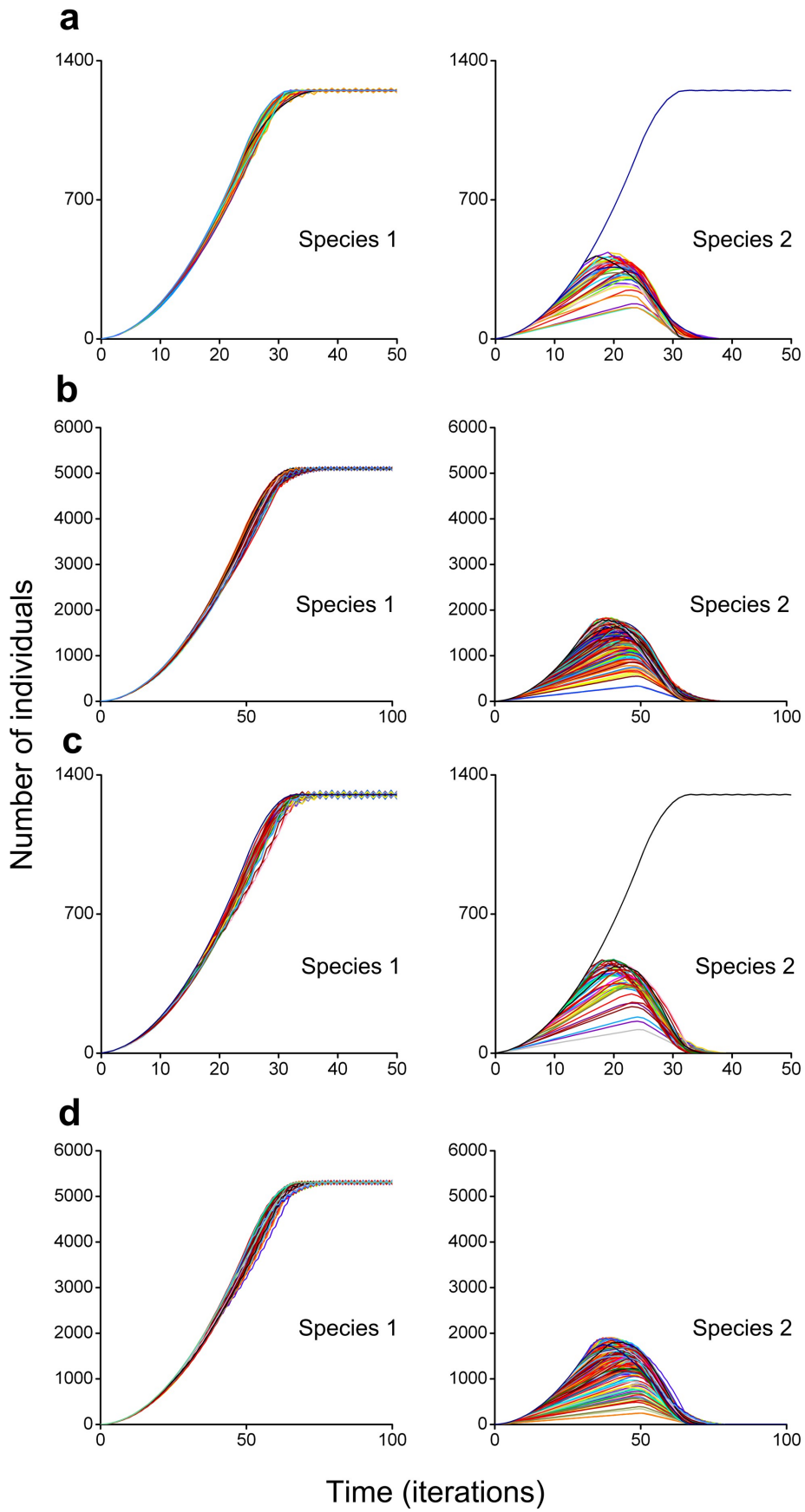


**Supplementary Figure 3 | Graph of transitions between the states of a microhabitat (lattice site) in the two-species competition model. a**, Microhabitat states are represented in pictorial form. **b**, Microhabitat states are represented in numeric form of program implementation.

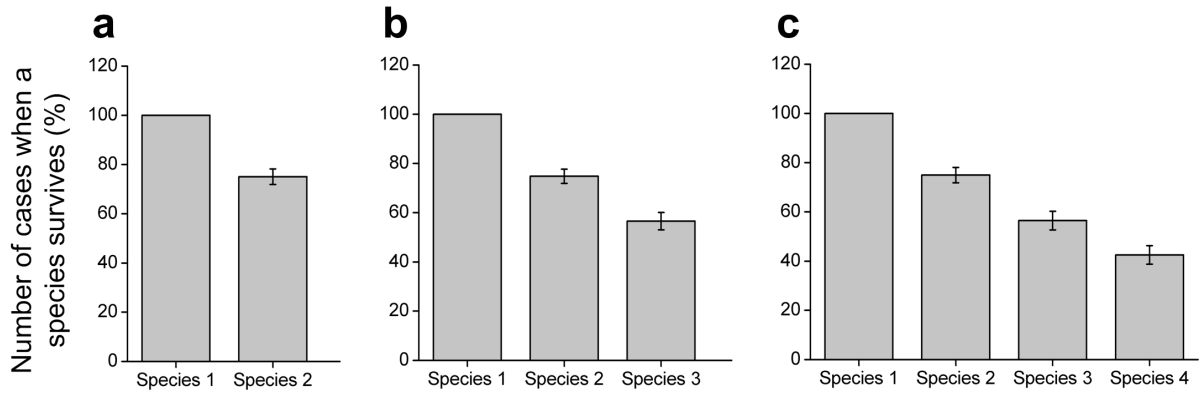




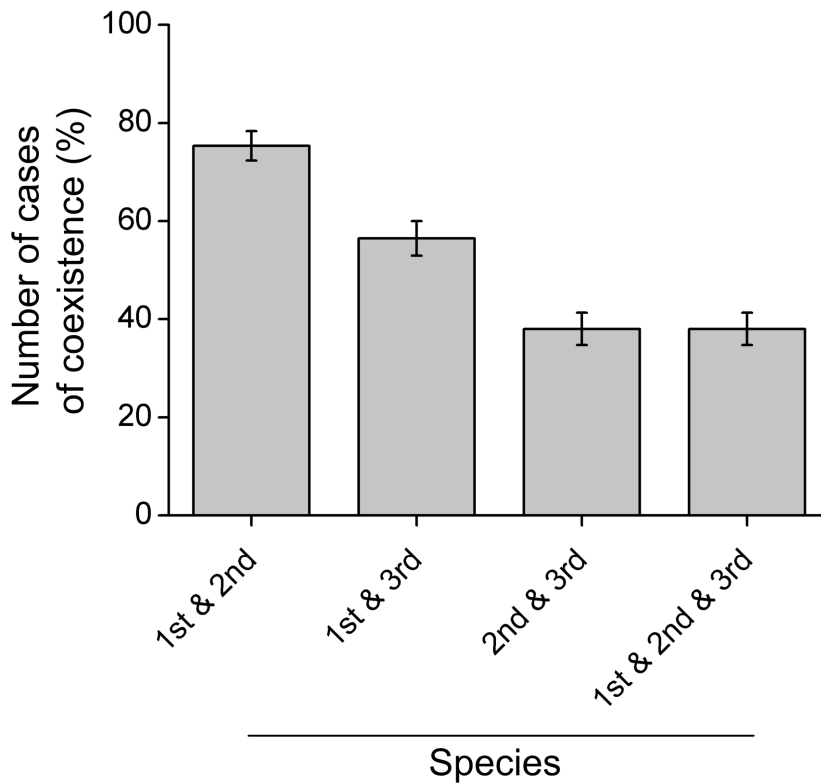
**Supplementary Figure 4 | Tests of stability of the coexistence of two competing species at different lattice sizes by Monte Carlo method.** Random initial placements of individuals on the lattice were used in each trial experiment. 200 trial experiments were in each series. 100 series of the experiments were performed for each model. Results of one series of trials are graphically presented here. Further here the numerical values are given as the averaged results of all 100 series of the trial experiments for the each model. **a**, The lattice consists of 27x27 sites. Species 1 excludes species 2 in direct conflicts of interest. **b**, The lattice consists of 28x28 sites. The number of coexistence cases was  $150.84 \pm 6.31$  (mean  $\pm$  1 SD; n=100) of 200 trial experiments in each of the 100 test series (i.e. coexistence was approximately in 75% of cases). **c**, The lattice consists of 29x29 sites. Species 1 excludes species 2 in direct conflicts of interest. **d**, The lattice consists of 30x30 sites. The number of coexistence cases was  $151 \pm 6.52$  (mean  $\pm$  1 SD; n=100) of 200 trial experiments in each of the 100 test series (i.e. coexistence was approximately in 76% of cases).



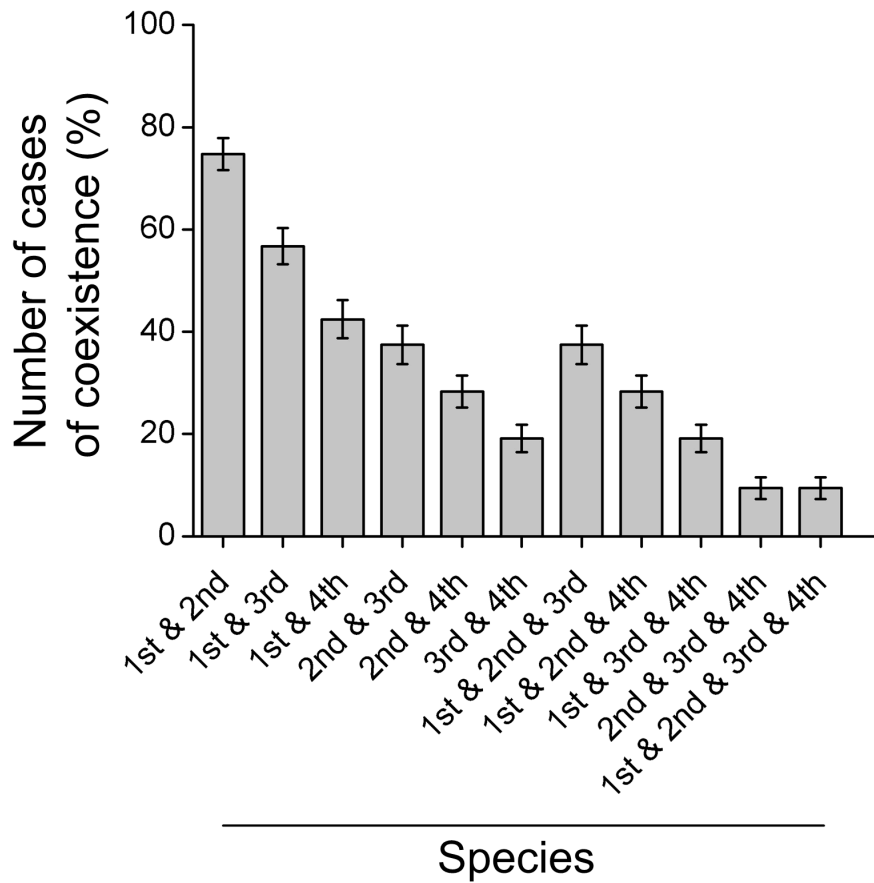
**Supplementary Figure 5 | Tests of stability of the coexistence of two competing species at different lattice sizes by Monte Carlo method.** Random initial placements of individuals on the lattice were used in each trial experiment. 200 trial experiments were in each series. 100 series of the experiments were performed for each model. Results of one series of trials are graphically presented here. Further here the numerical values are given as the averaged results of all 100 series of the trial experiments for the each model. **a**, The lattice consists of 100x100 sites. The number of coexistence cases was  $150.61 \pm 5.94$  (mean  $\pm$  1 SD; n=100) of 200 trial experiments in each of the 100 test series (i.e. coexistence was approximately in 75% of cases). **b**, The lattice consists of 101x101 sites. Species 1 excludes species 2 in direct conflicts of interest. **c**, The lattice consists of 102x102 sites. The number of coexistence cases was  $149.65 \pm 6.4$  (mean  $\pm$  1 SD; n=100) of 200 trial experiments in each of the 100 test series (i.e. coexistence was approximately in 75% of cases). **d**, The lattice consists of 103x103 sites. Species 1 excludes species 2 in direct conflicts of interest.



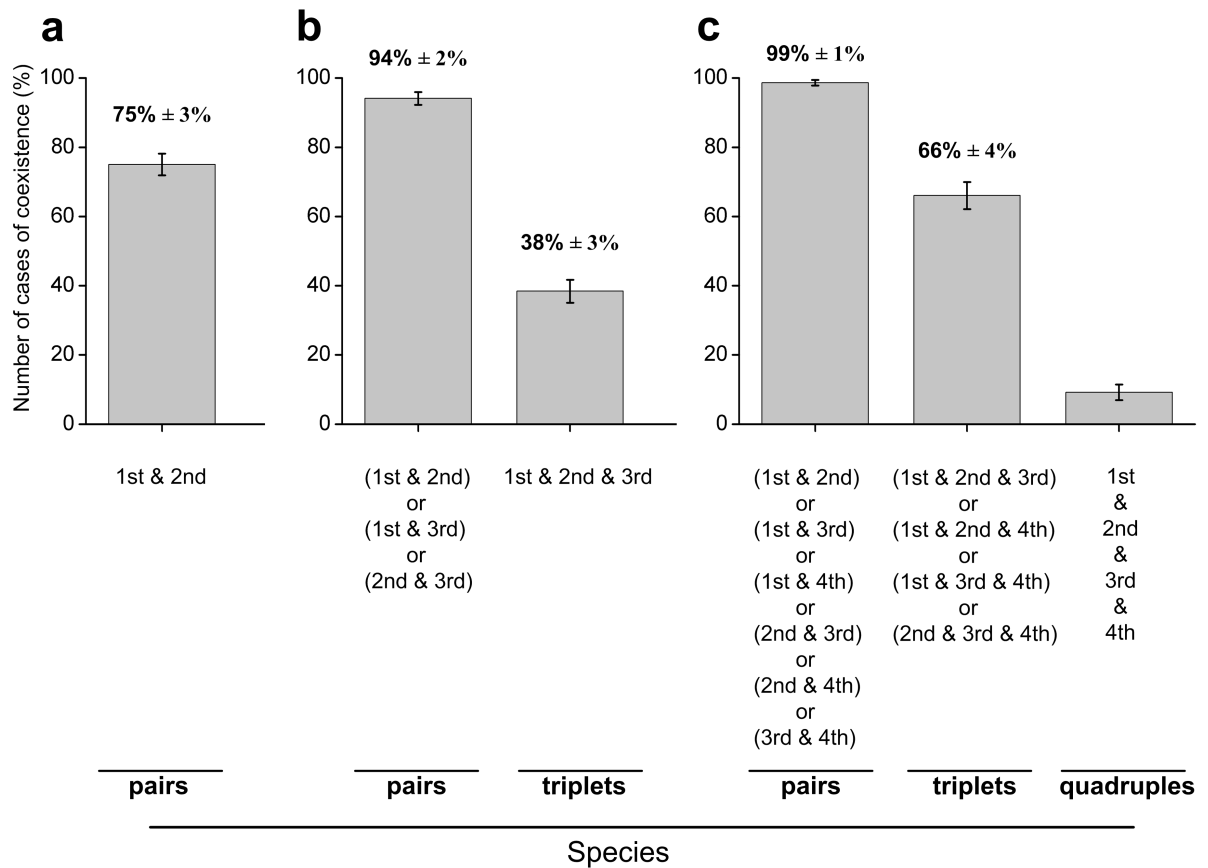
**Supplementary Figure 6 | Testing stability of survival of individual competing species by Monte Carlo method.** Random initial placements of individuals on the lattice were used in each trial experiment. 200 trial experiments were in each series. 100 series of the experiments were performed for each model. Cellular automata lattice is of 26x26 sites. Number of cases when a species survives are shown as mean  $\pm 1$  SD (n=100). **a**, The two-species competition model. **b**, The three-species competition model. **c**, The four-species competition model.



**Supplementary Figure 7 | Testing stability of coexistence of the species in the three-species competition model by Monte Carlo method.** Random initial placements of individuals on the lattice were used in each trial experiment. 200 trial experiments were in each series. 100 series of the experiments were performed. Cellular automata lattice is of 26x26 sites. Number of cases of species coexistence are shown as mean  $\pm$  1 SD (n=100).



**Supplementary Figure 8 | Testing stability of coexistence of the species in the four-species competition model by Monte Carlo method.** Random initial placements of individuals on the lattice were used in each trial experiment. 200 trial experiments were in each series. 100 series of the experiments were performed. Cellular automata lattice is of 26x26 sites. Number of cases of species coexistence are shown as mean  $\pm$  1 SD (n=100).



**Supplementary Figure 9 | Testing stability of coexistence of the species by Monte Carlo method.** Random initial placements of individuals on the lattice were used in each trial experiment. 200 trial experiments were in each series. 100 series of the experiments were performed for each model. Cellular automata lattice is of 26x26 sites. Number of cases of species coexistence are shown as mean  $\pm$  1 SD (n=100). **a**, The two-species competition model. **b**, The three-species competition model. **c**, The four-species competition model.



## Supplementary Movies

### **Supplementary Movie 1 | Strong violation of the competitive exclusion principle.**

Deterministic individual based cellular automata model of two-species competition.

[http://www.youtube.com/watch?feature=player\\_profilepage&v=3kTjeJphTZ0](http://www.youtube.com/watch?feature=player_profilepage&v=3kTjeJphTZ0)

### **Supplementary Movie 2 | The case of the competitive exclusion.**

Deterministic individual based cellular automata model of two-species competition.

[http://www.youtube.com/watch?feature=player\\_profilepage&v=ofAhxrtm7e0](http://www.youtube.com/watch?feature=player_profilepage&v=ofAhxrtm7e0)

### **Supplementary Movie 3 | Strong violation of the competitive exclusion principle.**

Deterministic individual based cellular automata model of three-species competition.

[http://www.youtube.com/watch?feature=player\\_profilepage&v=wBfBfBza2A0](http://www.youtube.com/watch?feature=player_profilepage&v=wBfBfBza2A0)

### **Supplementary Movie 4 | Strong violation of the competitive exclusion principle.**

Deterministic individual based cellular automata model of four-species competition.

[http://www.youtube.com/watch?feature=player\\_profilepage&v=ci2aqyMUasQ](http://www.youtube.com/watch?feature=player_profilepage&v=ci2aqyMUasQ)