A unified mechanistic model of niche, neutrality and violation of the competitive exclusion principle

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Abstract

The origin of species richness is one of the most widely discussed questions in ecology. The absence of unified mechanistic model of competition makes difficult our deep understanding of this subject. Here we show such a two-species competition model that unifies (i) a mechanistic niche model, (ii) a mechanistic neutral (null) model and (iii) a mechanistic violation of the competitive exclusion principle. Our model is an individual-based cellular automaton. We demonstrate how two trophically identical and aggressively propagating species can stably coexist in one stable homogeneous habitat without any trade-offs in spite of their 10% difference in fitness. Competitive exclusion occurs if the fitness difference is significant (approximately more than 30%). If the species have one and the same fitness they stably coexist and have similar numbers. We conclude that this model shows diffusion-like and half-soliton-like mechanisms of interactions of colliding population waves. The revealed mechanisms eliminate the existing contradictions between ideas of niche, neutrality and cases of violation of the competitive exclusion principle.

This model is based on deterministic individual-based cellular automata model of interspecific competition that we proposed earlier[1-3]. In order to investigate the existing contradictions between niche and neutrality we must mechanistically determine the species' fitness. In general, fitness is the ability of an individual of the species to maintain its health, well being and directly competes for environmental resources. In our model fitness is revealed in direct conflicts of interest between individuals of competing species. The conflict of interest occurred when individuals try to propagate in one and the same microhabitat, i.e. they try to use one and the same resource. Fitness is mechanistically modeled as the probability of occupation of a microhabitat in direct conflict of interest (Fig. 1). The higher is the probability, the greater is the fitness.

Here we investigate only the cases of coexistence of aggressively propagating species by varying the value of species' fitness. The model assumes the absence of cooperative effects in the relationship between individuals of one and the same species, as well as the absence of any trade-offs. The species have equal parameters of fecundity, duration of the lifetime of individuals and duration of the regeneration states. Additional rules of the model are presented in Supplementary Figure 1.

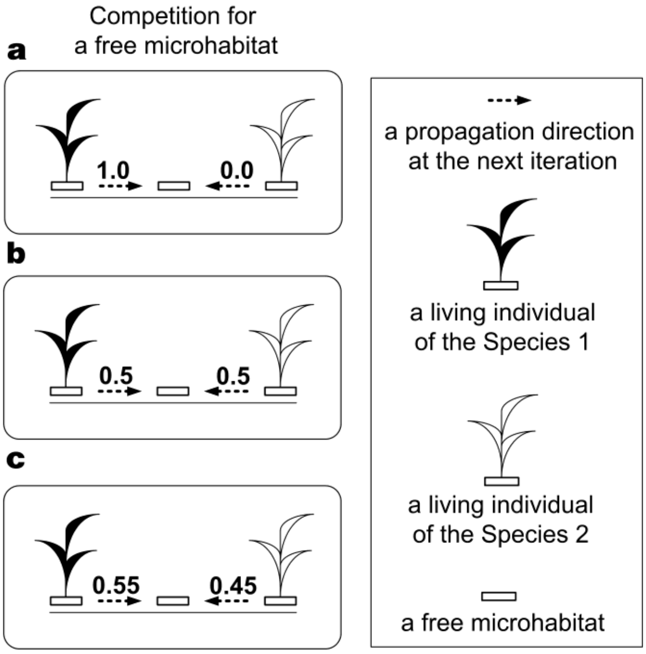


Figure 1 | Rules of interspecific competition at different values of fitness. The species compete for the same free microhabitat. If a microhabitat is in the regeneration state, then it will be the object of the competition after completion of regeneration. **a**, The species 1 has the maximum fitness compared with the species 2 (100% difference in fitness). **b**, Competing species are ecologically identical. They have the same fitness. **c**, Species have slight differences in fitness (10% difference in fitness).

The species 1 always excludes the less adapted species 2 when the difference in fitness is 100% (Figs 1a and 2; Supplementary Movie 1). The species are identical consumers who live in one and the same habitat and differ only in fitness. Different initial placement of individuals on the lattice does not affect the final result. Stability of population dynamics was tested by Monte Carlo method. Testing is consisted of random initial placements of individuals on the lattice in 200 trial experiments (Fig. 2a, b). We have used this Monte Carlo method in all experiments (Figs 2-4; Supplementary Figs 2 and 3).

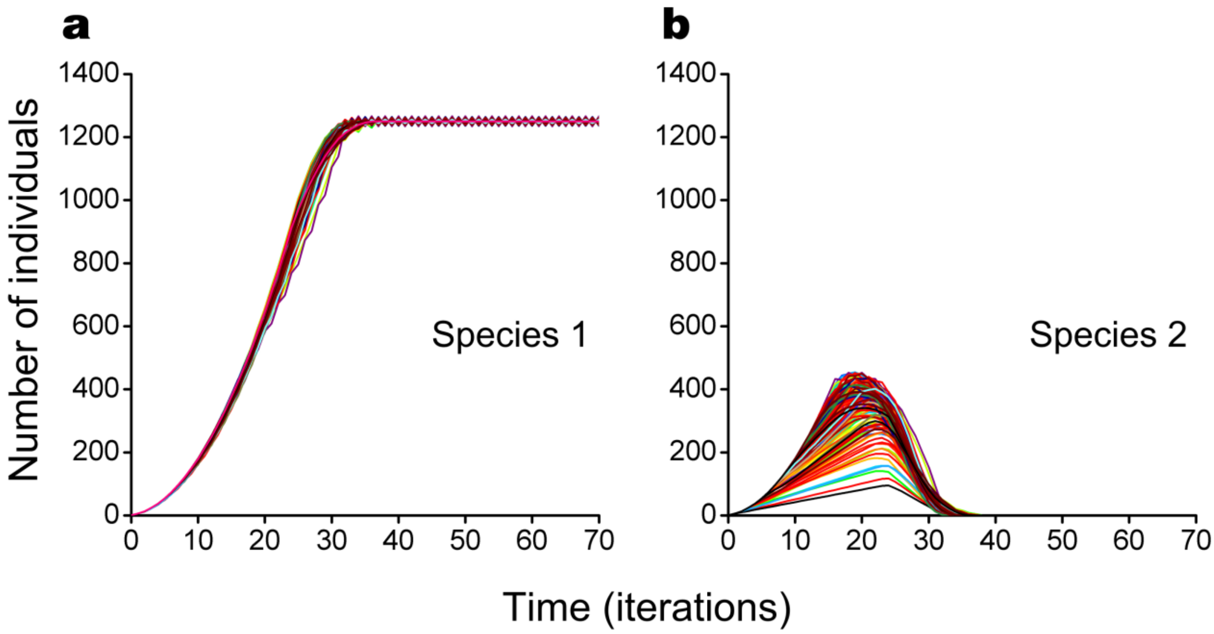


Figure 2 | A mechanistic niche model. Analysis of population dynamics by Monte Carlo method. The probability of occupation of a microhabitat in a direct conflict of interest is equal to P_1=1 for the first species and to P_2=0 for the second species. **a-b,** The results of different initial placement of individuals on the lattice for species 1 and 2, respectively (n=200).

Species 1 and species 2 stably coexist and have similar numbers of individuals (Figs 1b and 3; Supplementary Movie 2). Species 1 and species 2 are ecologically identical. If species are ecologically identical, in fact, we have a deal with one and the same species. But of course it is natural that fitness (niche) plays an important role in competition. Neutrality in our model is a special limiting case (pure null model without trade-offs), in contrast to the unified neutral theory of biodiversity and biogeography[4].

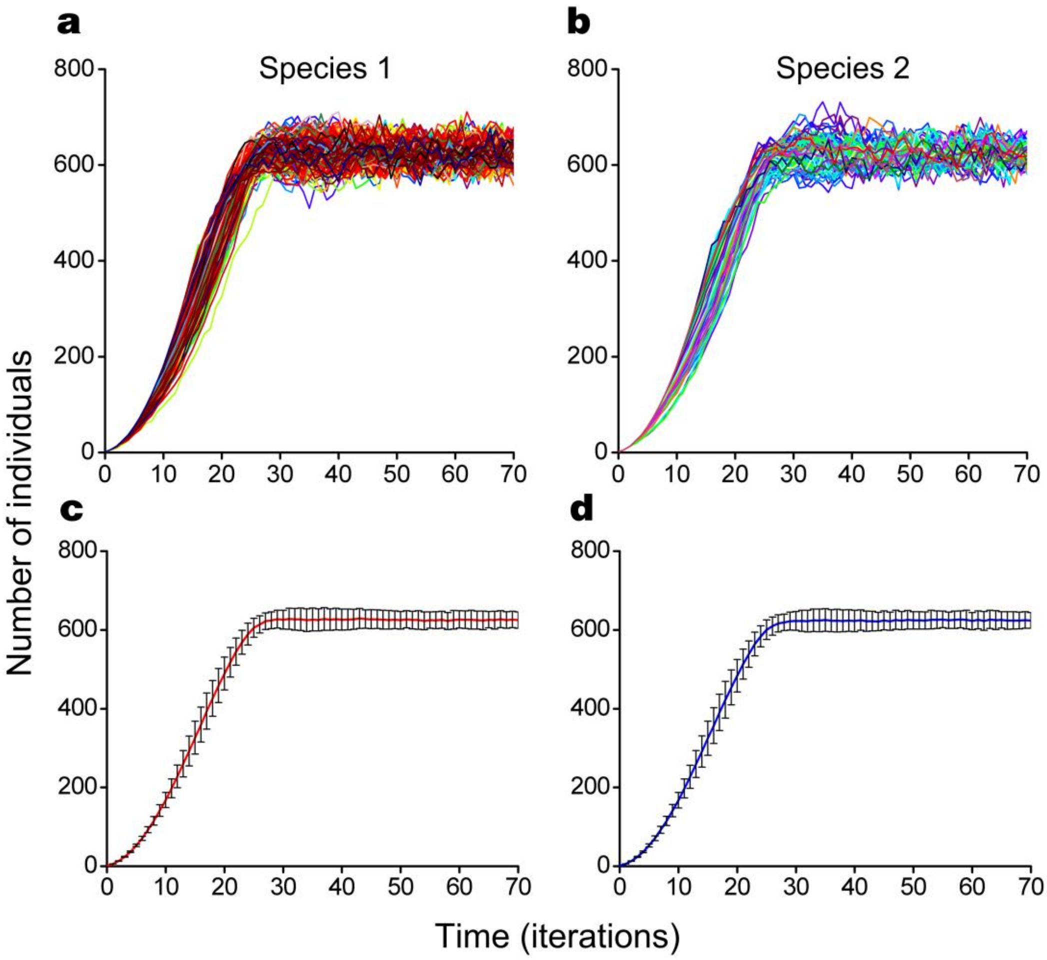


Figure 3 | A mechanistic neutral (null) model. Analysis of population dynamics by Monte Carlo method. The probability of occupation of a microhabitat in a direct conflict of interest is equal to P_1=0.5 for the first species and to P_2=0.5 for the second species. **a-b,** The results of different initial placement of individuals on the lattice for species 1 and 2. **c-d,** Arithmetic means with standard deviations for the cases (**a**) and (**b**), respectively (mean±1 SD, n=200).

An unexpected result is that trophically identical and aggressively propagating species can stably coexist in spite of their 10%, 20% and even 30% difference in fitness in one homogeneous habitat without trade-offs in constant environmental conditions (i.e. without changes in fitness) (Fig. 4; Supplementary Figs 2 and 3; Supplementary Movie 3). We have previously shown a strong violation of the competitive exclusion principle if the species have moderate fecundity, i.e. when their propagation is not agressive[2]. Here the propagation of both species is aggressive, i.e. individuals try to propagate in all adjacent microhabitats. We conclude that species coexist in spite of the competitive exclusion principle[5] (Supplementary Figs 2 and 3).

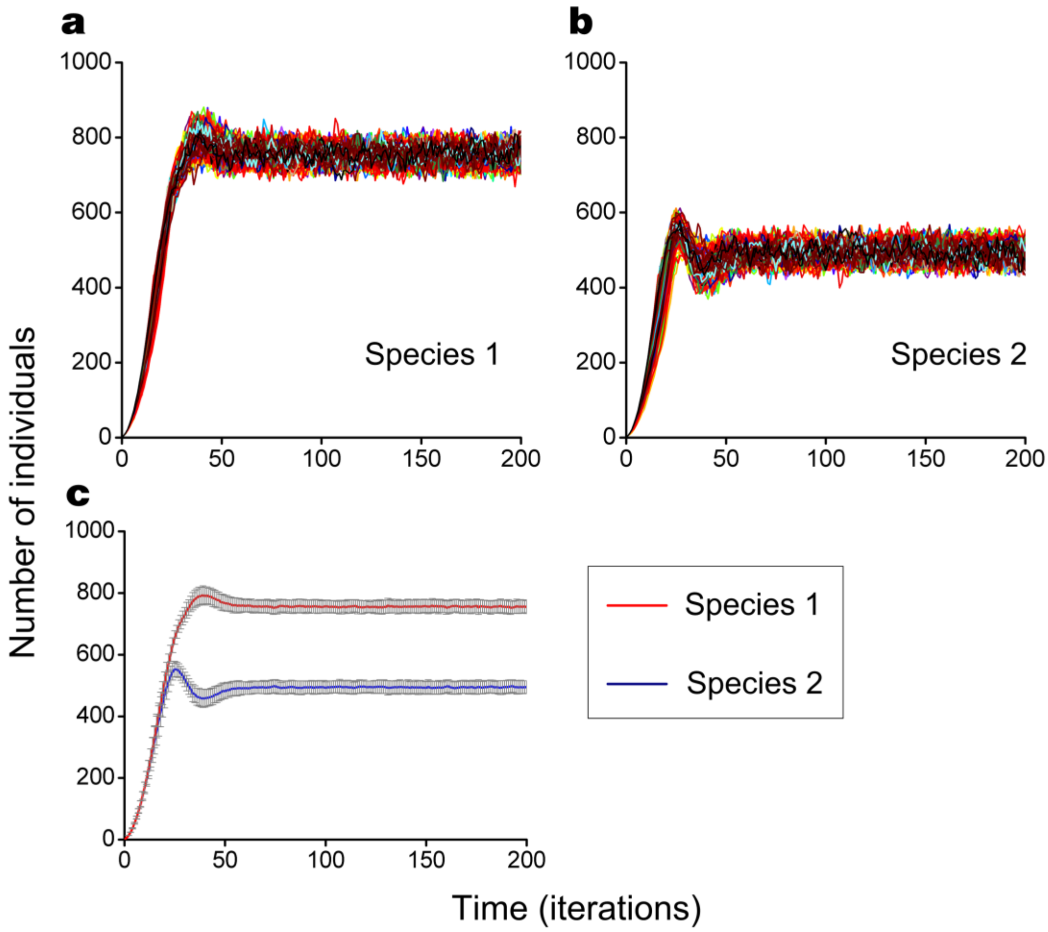


Figure 4 | A mechanistic violation of the competitive exclusion principle. Analysis of population dynamics by Monte Carlo method. The probability of occupation of a microhabitat in a direct conflict of interest is equal to P_1=0.55 for the first species and to P_2=0.45 for the second species. 10% difference in fitness. **a-b,** The results of different initial placement of individuals on the lattice for species 1 and 2. **c,** Arithmetic means with standard deviations for the cases (**a**) and (**b**), respectively (mean±1 SD, n=200).

We consider the limiting case of interspecific competition without trade-offs. One of the advantages of mechanicalness of our model is that trade-offs can be strictly avoided. Our model consists of both a mechanistic neutral (null) model (Supplementary Movie 2) on the one hand and a mechanistic niche model on the other hand (Supplementary Movie 1). And between these extremes are the cases of violation of the competitive exclusion principle (Fig. 4; Supplementary Figs 2 and 3; Supplementary Movie 3).

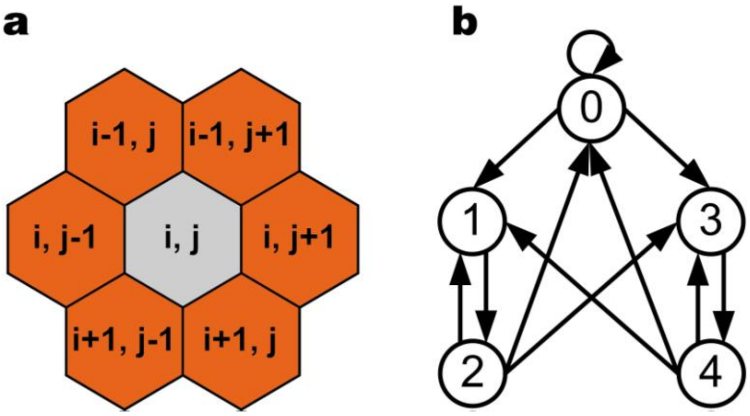
Physically speaking, this model shows diffusion-like (Supplementary Movies 2 and 3) and half-soliton-like (Supplementary Movie 1) mechanisms of interactions of colliding population autowaves propagating in an active medium.

Conclusion

We have shown the model of interspecific competition, which unify the next three our models:

- A mechanistic niche model (Supplementary Movie 1);
- A mechanistic neutral model (Supplementary Movie 2);
- A mechanistic violation of the competitive exclusion principle (Supplementary Movie 3).

SUPPLEMENTARY INFORMATION



Supplementary Figure 1 | The rules of the cellular automata model.

a, The hexagonal 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-1), (i-1, j), (i-1, j+1), (i, j+1), (i+1, j), (i+1, j-1) and marked by the orange colour. **b**, Graph of transitions between the states of a microhabitat (lattice site) in the two-species competition model. Transitions between states are defined in probabilistic "if-then" rules (Fig.1). States of a lattice site are denoted as: ‘0’ – a free site. ‘1’, ‘3’ – the states of a site occupied by an individual of the first and the second species, respectively. In the movies these two last states are represented as the symbols ‘1’ and ‘2’. The regeneration states of a site after death of an individual of the first or the second species are denoted here as ‘2’, ‘4’ and in Supplementary Movies these states are represented by the symbols ‘.’ and ‘*’, respectively, to distinguish them from living individuals.

Basic provisions of the model

- The entire cellular automaton simulates a whole ecosystem;
- The lattice of the cellular automaton simulates a habitat;
- A single lattice site simulates a one microhabitat;
- A neighbourhood simulates a minihabitat;
- A one microhabitat may contain resources for life of a one individual of any species.

States of a microhabitat

Each microhabitat (i.e. each lattice site) may be in one of the five states (Supplementary Fig 1b):

- Free (may be occupied);
- Occupied by a one immobile individual of the first or the second species;
- Regeneration (restoring conditions and resources of a microhabitat after an individuals's death and recycling of a dead individual of the first or the second species).

Characteristics of the model

- The hexagonal lattice consists of NxN sites and is closed to a torus (N=50).
- The set of states of a lattice site is {0, 1, 2, 3, 4}.
- The graph of the transitions between the states of a site (Supplementary Fig. 1b).
- Rules of interspecific competition (Fig. 1).
- Cellular automata neighbourhood (Supplementary Fig. 1a).

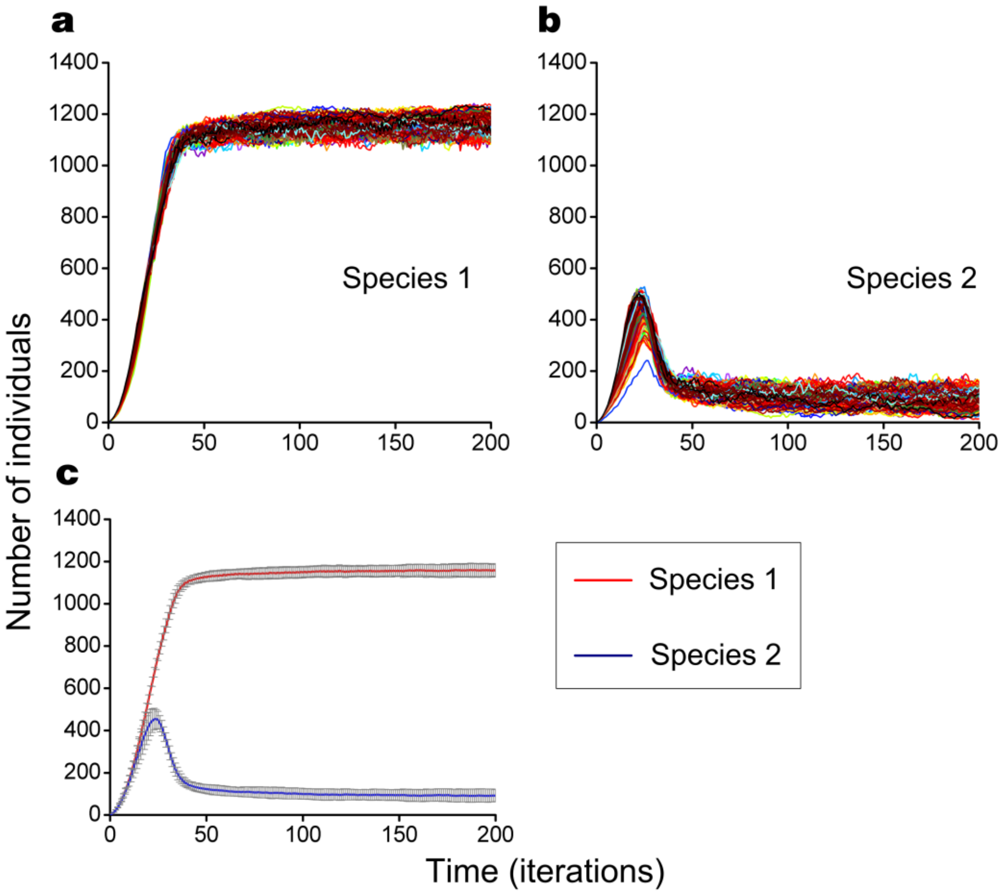
Properties of states of a microhabitat

- A free microhabitat may be occupied only by one individual;
- Populated microhabitat and microhabitat in the regeneration state can not be occupied;
- Occupied microhabitat goes into the regeneration state after an individual's death;
- Microhabitat in the regeneration state becomes free or may be occupied immediately after finishing of the regeneration state.

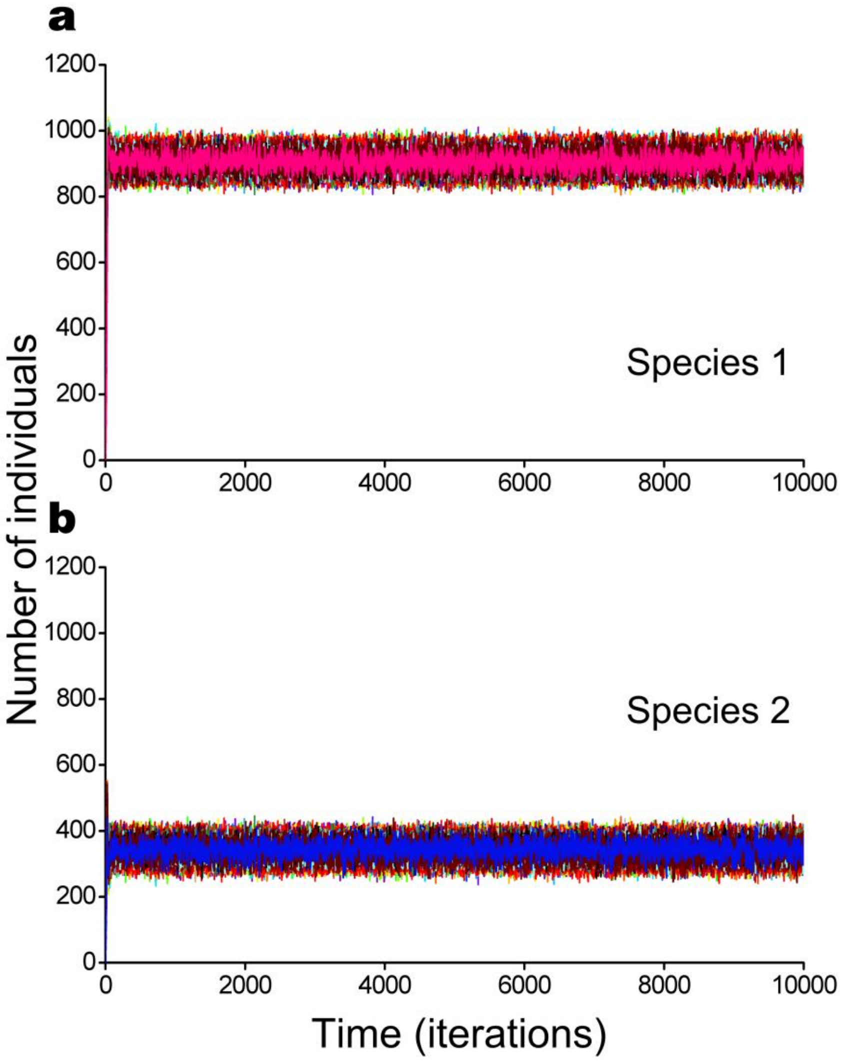
Neighbourhood

- A neighbourhood consists of a site and its intrinsically defined neighbour sites.
- All sites have the same rules for updating.
- A neighbourhood simulates an individual's minihabitat.
- A neighbourhood also determines the number of possible offsprings (fecundity).

The closest analogy of an individual’s propagation determining by a neigbourhood is asexual (vegetative) propagation of turf grasses by rhizomes.



Supplementary Figure 2 | A mechanistic violation of the competitive exclusion principle. Analysis of population dynamics by Monte Carlo method. The probability of occupation of a microhabitat in a direct conflict of interest is equal to P_1=0.65 for the first species and to P_2=0.35 for the second species. 30% difference in fitness. **a-b,** The results of different initial placement of individuals on the lattice for species 1 and 2. **c,** Arithmetic means with standard deviations for the cases (**a**) and (**b**), respectively (mean±1 SD, n=200).



Supplementary Figure 3 | Analysis of stability of coexistence of the species during 10 000 iterations by Monte Carlo method (n=200). Here is the case of a mechanistic violation of the competitive exclusion principle. The probability of occupation of a microhabitat in a direct conflict of interest is equal to P_1=0.6 for the first species and to P_2=0.4 for the second species. 20% difference in fitness. **a-b,** The results of different initial placement of individuals on the lattice for species 1 and 2. **c,** Arithmetic means with standard deviations for the cases (**a**) and (**b**), respectively.

Supplementary Movies

The symbols of the five states of a site (microhabitat) which are used in all three movies:

'0' - a free microhabitat that can be occupied by an offspring of any species;

'1' – a microhabitat occupied by a living individual of the species 1;

'.' – a regeneration state of a microhabitat after the death of an individual of the species 1;

'2' – a microhabitat occupied by a living individual of the species 2;

'*' – a regeneration state of a microhabitat after the death of an individual of the species 2.

Supplementary Movie 1 | A mechanistic niche model. The case of the competitive exclusion. Individual based cellular automata model of two-species competition. The hexagonal lattice consists of 50x50 sites. The cellular automata neighbourhood is hexagonal. The rules of competitive interactions between the species are presented in Fig. 1a.

http://youtu.be/bHaG2sq8SiA?hd=1

Supplementary Movie 2 | A mechanistic neutral (null) model. The case of neutrality. Individual based cellular automata model of two-species competition. The hexagonal lattice consists of 50x50 sites. The cellular automata neighbourhood is hexagonal. The rules of competitive interactions between the species are presented in Fig. 1b.

http://youtu.be/zMgoZpDjPVI?hd=1

Supplementary Movie 3 | A mechanistic violation of the competitive exclusion principle. Individual based cellular automata model of two-species competition. The hexagonal lattice consists of 50x50 sites. The cellular automata neighbourhood is hexagonal. The rules of competitive interactions between the species are presented in Fig. 1c.

http://youtu.be/U9ZDHjobqmA?hd=1

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Author Contributions L.V.K. designed the research, 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.

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