



Lattice-based versus lattice-free individual-based models: impact on coexistence in competitive communities

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Abstract

Individual-based modelling is an increasingly popular framework for modelling biological systems. Many of these models represent space as a lattice, thus imposing unrealistic limitations on the movement of the modelled individuals. We adapt an existing model of three competing species by using a lattice-free approach, thereby improving the realism of the spatial dynamics. We retrieve the same qualitative dynamics as the lattice-based approach. However, by facilitating a higher spatial heterogeneity and allowing for small spatial refuges to form and persist, the maintenance of coexistence is promoted, in correspondence with experimental results. We also implement a directed movement mechanism allowing individuals of different species to pursue or flee from each other. Simulations show that the effects on coexistence depend on the level of aggregation in the community: a high level of aggregation is advantageous for maintaining coexistence, whereas a low level of aggregation is disadvantageous. This agrees with experimental results, where pursuing and escaping behaviour has been observed to be advantageous only in certain circumstances.

Keywords Cyclic competition · Coexistence · Individual-based model · Directed movement

1 Background

Spatially explicit individual-based modelling is an increasingly popular framework for simulating a wide range of phenomena in various fields of research (Grimm et al. 2010; Railsback and Grimm 2011; Railsback et al. 2006), including racial segregation (Auchincloss et al. 2011), microbial growth (Kreft et al. 1998), pandemics (Luisa et al. 2008), and multicellular self-organisation (Osborne et al. 2017).

These models can reproduce a system's complex behaviour at the macroscopic level by modelling the characteristics and interactions of its individuals, whether these are cars, people, microbes, or other entities, through simple rules at the microscopic level. The emergent macroscopic dynamics can then be analysed to gain insight into the

fundamental mechanisms underpinning the system, a key example being mechanisms that permit the coexistence of individuals of multiple types or species, even when these are engaged in competition. Determining whether this coexistence can be maintained, and under which conditions, is a major focus of modelling studies. In particular, a cyclic competition scheme has been used extensively in literature to investigate the mechanisms underlying coexistence of competing species, yielding valuable insights (May and Leonard 1975; Reichenbach et al. 2007). Such a competition scheme, where there is no strict hierarchy among the species, has been observed in natural systems of, among others, coral reefs, plant ecosystems, lizard mating strategies, and bacterial communities (Buss 1979; Kerr et al. 2002; Kirkup and Riley 2004; Taylor and Aarssen 1990).

Although their inherent flexibility allows individual-based models to be used in many different settings, this generality can lead to oversimplifications. A very common example is the use of a lattice to represent space (e.g. Kreft et al. 2001; Laird and Schamp 2009; Reichenbach et al. 2007; Vukov et al. 2013), thereby imposing an artificial restriction on the positioning of individuals, who typically occupy one lattice cell each. Although justified in

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applications where the geometry of the lattice cells has an actual meaning, such as urban planning modelling (Schelling 1969), the use of a lattice deviates significantly from reality when modelling biological systems (Ginovart 2002). Namely, the mobility of individuals in this lattice-based setting is restricted to displacement to one of their neighbouring lattice cells, uncharacteristic of the real movement of individuals (Adamson and Morozov 2012), and precluding motile behaviour (the ability to move deliberately and actively). To mitigate these disadvantages, some lattice-free approaches have been developed (Beppu et al. 2017; Gonnella et al. 2014), however, these have focused on active matter rather than on species competition and coexistence.

2 Model description

To investigate whether a lattice-free approach can enhance our understanding of coexistence mechanisms, we employ a spatially explicit individual-based model of a community of three *in silico* species engaged in cyclic competition. To do so, we adapt the two-dimensional model proposed in Reichenbach et al. (2007) to account for (1) a lattice-free representation of space, (2) a continuous migration mechanism, and (3) motility. We then assess the impact of these adaptations on the coexistence of the community by examining the respective extinction probabilities of the *in silico* species relative to those obtained using the less realistic lattice-based approach.

2.1 Benchmark lattice-based model

The model proposed in Reichenbach et al. (2007) takes into account three key demographic processes at the individual level: reproduction, competition, and migration, which occur at rates μ , σ , and ϵ , respectively, identical for all species. For simplicity, we consider equal rates of reproduction and competition, and (without loss of generality) determine the time unit by fixing $\mu = \sigma = 1$. We consider two-dimensional space divided into a regular lattice of identical square cells, occupied by at most one individual each. The system mobility M is proportional to the typical area explored by one individual per unit of time, $M = 2\epsilon N^{-1}$, where N is the number of lattice cells in the system (Reichenbach et al. 2007).

During each interaction event, a focal cell is randomly selected. If the focal cell is empty, another cell is chosen randomly. If the focal cell is occupied, then one of its four von Neumann neighbours (those sharing an edge) is randomly selected. Reproduction can occur if the

neighbouring cell is empty. Competition can occur if the neighbouring cell is occupied by an individual of a different species than the focal individual, with the outcome determined by the cyclic competition scheme: species A beats species B, which beats species C, which beats species A. The defeated individual is removed and the lattice cell becomes empty. Migration can occur irrespective of the neighbouring cell's occupancy: if it is empty, the individual simply moves there, and if it is occupied then the two individuals swap positions.

Simulations advance by iterating through the following procedure at every time step: an occupied focal cell and one of its neighbouring cells are randomly selected. A random number is drawn to determine which type of interaction will occur: a reproduction event occurs with probability $\frac{\mu}{s}$, a competition event with probability $\frac{\sigma}{s}$, and a migration event with probability $\frac{\epsilon}{s}$, where $s = \mu + \sigma + \epsilon$. The interaction outcome is determined as described above, and the lattice is updated accordingly. The time step is advanced and the procedure is repeated until the end of the simulation is reached. We define one generation as the number of interactions needed so that each cell had the chance to interact on average once, namely N^2 .

2.2 Lattice-free approach

To assess the impact of continuous space on the maintenance of coexistence, we construct a model using the same framework as the benchmark model, except that individuals do not position themselves in lattice cells, but in continuous space. Each individual is represented by a circle of diameter of one unit of length, equal to the length of a lattice cell, centred at a certain point (x, y) . Two individuals i and j are considered to be neighbours if the Euclidean distance d_{ij} between their centres is less than or equal to one unit, so that they are either touching ($d_{ij} = 1$) or overlapping ($d_{ij} < 1$). We permit a certain maximal overlap between individuals, for reasons of both computational efficiency and biological realism, since the modelled individuals (e.g. bacteria) may slightly deform or cave into each other (Touhami et al. 2003). We therefore specify a threshold d_{\min} as the minimum distance permitted between the centers of two individuals, so that $d_{\min} \leq d_{ij} \leq 1$.

To minimize the overlap between individuals, thus permitting comparison with the benchmark lattice-based model (which assumes that individuals do not share space), we incorporate a distance-weighted repulsive force between overlapping individuals, modelled as soft spheres (Landau and Lifshitz 1986),

$$\mathbf{F}_{ij} = \begin{cases} \alpha(1 - d_{ij})^{\frac{5}{2}} \mathbf{r}_{ij}, & \text{if } d_{ij} < 1, \\ \mathbf{0}, & \text{otherwise,} \end{cases} \quad (1)$$

where \mathbf{F}_{ij} is the repulsive force on individual i induced by individual j , α is a weight, d_{ij} is the distance between the centres of the individuals, \mathbf{r}_{ij} is the vector defined by the centres of the two individuals, pointing outwards from the centre of individual i , and $\mathbf{0}$ is the zero vector. Hence individuals that are closer together feel a stronger repulsive force. No repulsion occurs between individuals that are touching but not overlapping, or not touching at all. The coefficient α controls the strength of this repulsive force.

When multiple individuals overlap with a given individual, vector addition of the individual forces applies. At the end of each generation, the repulsive force is computed for every individual, after which their positions are updated accordingly. Multiple iterations are executed until the minimum distance between the centres of neighbouring individuals exceeds the given threshold d_{\min} .

The distance travelled during one migration event is similar for the lattice-free and lattice-based models, since in the former case individuals can move a distance of one unit (the diameter of their body), analogous to the lattice-based displacement to a neighbouring cell (also having length one unit). Migration events may involve two neighbours exchanging their positions, again similar to the lattice-based model. Hence, we can consider the mobility $M = 2\epsilon N^{-1}$, analogous to the lattice-based model, thus allowing us to compare the two approaches.

An individual positioned at (x, y) can reproduce by splitting itself into two daughter individuals of equal size, positioned at $(x + r \cos \theta, y + r \sin \theta)$ and $(x - r \cos \theta, y - r \sin \theta)$, where r is the radius of an individual (fixed as 0.5 units) and θ is a randomly chosen angle in $[0, \pi]$. Reproduction can occur when an individual's neighbourhood is not fully populated, i.e. it has less than six neighbours, the maximum number of neighbours in a hexagonal packing of circles.

2.3 Motility

We then adapted the migration mechanism of the model described in Sect. 2.2 to make it more realistic. An individual now performs a step of random length and direction, so that it shifts from (x, y) to $(x + d_x, y + d_y)$ where d_x and d_y are randomly and independently drawn from a uniform distribution with support $[-d_{\max}, d_{\max}]$, where d_{\max} is the maximal distance an individual can move in the x - or y -direction during one time step. In contrast to both the benchmark and lattice-free models, with the continuous migration mechanism individuals may take a step of random length less than $d_{\max} = 1.5$, where in the two former cases individuals were restricted to steps of length one unit. Hence the mobility is now given by $M = \epsilon \bar{d}^2 N^{-1}$, with \bar{d} being the average distance travelled during one time step.

We also account for motility (directed movement), by allowing the different species to pursue their prey or flee from their predator, according to the cyclic competition scheme. To model pursuit, we implement a distance-weighted attraction force so that an individual is attracted in the direction of its prey according to

$$\mathbf{F}_i = \beta \sum_{j=1}^n \begin{cases} \frac{\mathbf{r}_{ij}}{d_{ij}^2}, & \text{if } i \text{ is a predator of } j, \\ \mathbf{0}, & \text{if } i \text{ is not a predator of } j, \end{cases} \tag{2}$$

where \mathbf{F}_i is the attractive force experienced by individual i due to n individuals in its neighbourhood, β is a weight analogous to α in Eq. (1), \mathbf{r}_{ij} is the vector pointing from the centre of individual i to the centre of individual j (where $j = 1, \dots, n$), and d_{ij} is the distance between the centres of individuals i and j .

Analogously, an individual escaping its predator is subject to a distance-weighted repulsive force away from the predator, given by

$$\mathbf{F}_i = \beta \sum_{j=1}^n \begin{cases} \frac{-\mathbf{r}_{ij}}{d_{ij}^2}, & \text{if } i \text{ is a prey of } j, \\ \mathbf{0}, & \text{if } i \text{ is not a prey of } j. \end{cases} \tag{3}$$

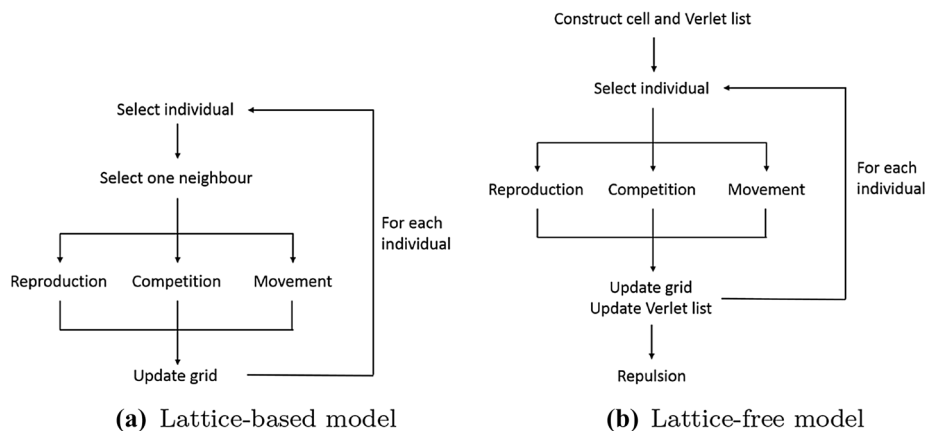
To summarize the escaping and chasing dynamics in the community, we use a shorthand three-letter notation, with the first letter representing the ability of species A to either pursue (P) their prey, to escape (E) their predator or having no directed movement (N), and the second and third letters representing corresponding abilities of species B and C, respectively. For example, a system denoted by PEN represents species A pursuing species B, species B escaping from species A, and species C without motile ability. Hence, in contrast to previous work where all species could pursue and escape each other (Avelino et al. 2018), we assign motile behaviour asymmetrically, to allow for scenarios where the three species do not necessarily have the same motile abilities.

3 In silico experiments

For the lattice-based approach, a 100×100 lattice is initialized with 10% empty lattice cells, and the remaining cells evenly and randomly distributed among the three species. Periodic boundary conditions are imposed to avoid boundary effects. Next, individual interactions are simulated as described in Sect. 2.1 for 10,000 generations.

The lattice-free approach is evolved in an analogous manner, with certain adaptations (see Fig. 1 for a comparison of the algorithms). A 100 unit \times 100 unit space is initialized with 9000 individuals evenly and randomly distributed among the three species.

Fig. 1 Flowcharts outlining the simulation procedure at each time step for both models



These parameter settings were chosen to maintain a reasonable computation time (9 h for 10,000 generations of the lattice-free model) and a sufficiently large experimental domain to minimize stochastic and finite-size effects and allow population-level patterns to emerge. We also tested larger and smaller domain sizes (and hence population sizes) to determine the efficiency of the implementation, which also confirmed the robustness of the qualitative dynamics.

At the start of each generation, a cell list (Mattson and Rice 1999) and Verlet list (Verlet 1967) are constructed to efficiently keep track of each individual's neighbours, as defined in Sect. 2.2. These two specialised data structures were initially developed for molecular dynamics simulations, and permit the practical simulation of large numbers of interacting individuals (particles). The cell list subdivides the continuous *in silico* domain into blocks and sorts the individuals into these blocks, so that interactions are computed between individuals in the same or neighbouring blocks. The Verlet list overcomes the need to determine an individual's neighbours at each interaction: by determining them only once, saving this information and updating it when needed, the computational demand scales linearly with population size, in contrast to an exponential increase in a naive implementation.

After an interaction event, the Verlet list and the *in silico* domain are updated accordingly. At the end of a generation, the repulsion mechanism described in Sect. 2.2 is executed, with $\alpha = 5$ and a threshold of $d_{\min} = 0.95$ for the minimum distance between the centres of individuals, so that the repulsion mechanism converges rapidly (provided the system carrying capacity is not reached).

At each time step, the identity and location of each individual are tracked. The probability of extinction P_{ext} is calculated at the end of the simulations as the fraction of

simulations with at least one extinction event. Patchiness, a measure of spatial aggregation, is calculated as the average fraction of neighbours of the same species (Lloyd 1967). Similarly, the probability of interspecific encounter (PIE) is calculated as the average fraction of an individual's neighbours that are predator species (Hurlbert 1978). A pressure distribution, visualizing the number of individuals within a certain distance, and thus spatial heterogeneity, is calculated from the position of the individuals, using the method described in Bernard and Krauth (2011).

In a first experiment, the lattice-based approach is compared with the lattice-free approach to assess the impact of the latter on the probability of extinction. We simulate each model for different values of mobility M between 2×10^{-4} and 1.6×10^{-2} , by varying the migration rate ϵ from 0 to 80 with a step size of 10. Fifty replicate simulations are run for each parameter setting.

In a second experiment, we investigate the impact of motility on coexistence. Motile abilities were assigned to the species in different combinations. Scenarios with species having multiple abilities were not investigated to avoid confounding effects. This yields a total of eight unique scenarios: PNN, PNE, PPN, PPE, PEN, PEE, ENN, and EEN. The NNN scenario (no motile behaviour for any species) is included as a benchmark. The mobility M is set at 1.5×10^{-3} , since exploratory simulations showed that $P_{ext} \approx 0.5$ for this mobility value. The scenarios can thus be classified as promoting (lower P_{ext}), jeopardizing (higher P_{ext}), or having no effect (similar P_{ext}) on coexistence relative to this benchmark.

The models are implemented in Mathematica (version 11.0, Wolfram Research, Champaign, IL, USA). Simulations are carried out using the High Performance Computing infrastructure at Ghent University.

4 Results and discussion

4.1 Comparison of lattice-based and lattice-free models

Figure 2 shows an example of the spatial dynamics arising from the lattice-based and lattice-free models. Both models result in the same qualitative behaviour, with the individuals arranging themselves in stable spatial structures, thereby facilitating coexistence of all species. Moreover, these emerging spatial structures are of equal size for the same mobility, irrespective of the approach, thus resembling the results obtained with a similar lattice-free model (Avelino et al. 2017). However, the latter model considers a system where the total density of individuals is conserved, which is not always realistic.

Figure 3 shows the extinction probability P_{ext} as a function of mobility M for both approaches. In both cases, we can observe a qualitative behaviour similar to the findings of Reichenbach et al. (2007), namely a higher probability of extinction P_{ext} for higher mobility M . However, the lattice-based P_{ext} is consistently higher than the lattice-free P_{ext} for the same mobility M . For the former, the transition from stable coexistence ($P_{ext} = 0$) to extinction ($P_{ext} = 1$) sharpens at the critical mobility $M_c = (5 \pm 1) \times 10^{-3}$. In contrast, this happens at the critical mobility $M_c = (1.3 \pm 0.1) \times 10^{-2}$ for the lattice-free approach. Hence, when using the latter approach, coexistence is maintained for a wider parameter range than its lattice-based counterpart, and coexistence may be considered more robust.

By not constraining the individuals to lattice cells, the lattice-free model permits individuals more freedom to position themselves. This influences the formation of spatial structures. In Fig. 4 we show an example of the pressure distribution, representing the number of individuals within a certain distance, therefore visualizing the spatial heterogeneity of the system. Comparing this plot with the

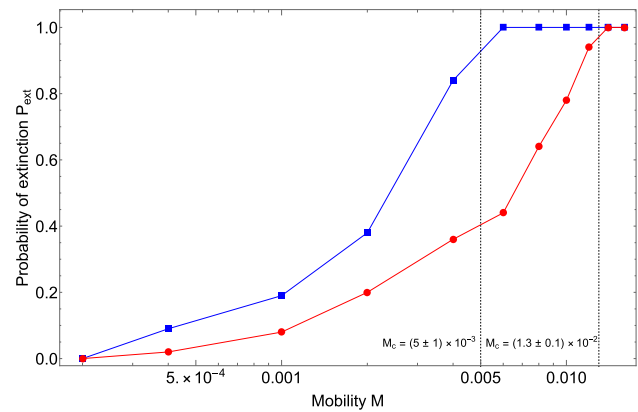


Fig. 3 Extinction probability P_{ext} (50 simulations, 10 000 generations) versus mobility M for the lattice-based model (blue, square) and the lattice-free model (red, circle). (Color figure online)

spatial species distribution reveals that pressure is highest inside the spatial structures, and lowest along the borders between clusters of species, where interactions are manifold. This heterogeneity is in contrast to the lattice-based model, where the pressure is spatially homogeneous, and explains the more robust coexistence, since spatial heterogeneity is known to promote coexistence (Neuhauser 2001).

It is known that threatened species, when reduced to a few individuals, often retreat into small spatial structures called refuges (Laird and Schamp 2008). Figure 5 shows an example of an in silico spatial refuge obtained with both approaches. When spatial refuges become surrounded by their predator, they are quickly destroyed (Laird and Schamp 2008). However, inspection of the simulation results reveals that refuges tend to be more resilient in the lattice-free approach. Individuals can arrange themselves more compactly, since the highest density arrangement of circles in a continuous space (a hexagonal tessellation) leads to an area occupancy of $\pi/\sqrt{12}$, which is greater than the highest area occupancy that can be achieved with a square lattice arrangement, namely $\pi/4$ (Chang and Wang

Fig. 2 Example of the spatial dynamics obtained for $M = 2 \times 10^{-4}$ with the lattice-based model (left) and the lattice-free model (right)

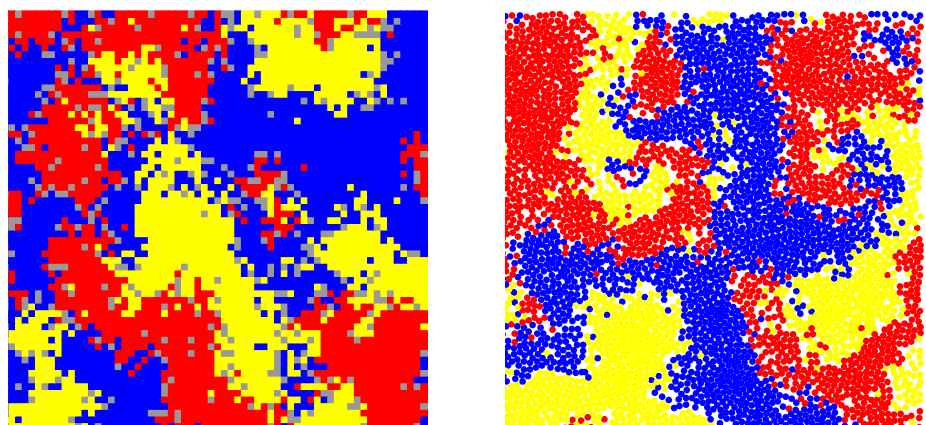


Fig. 4 Example of the spatial dynamics (left) obtained with the lattice-free model for $M = 2 \times 10^{-4}$, and corresponding pressure distribution (right), representing the number of individuals within a certain distance (darker colour indicates higher density of individuals). (Color figure online)

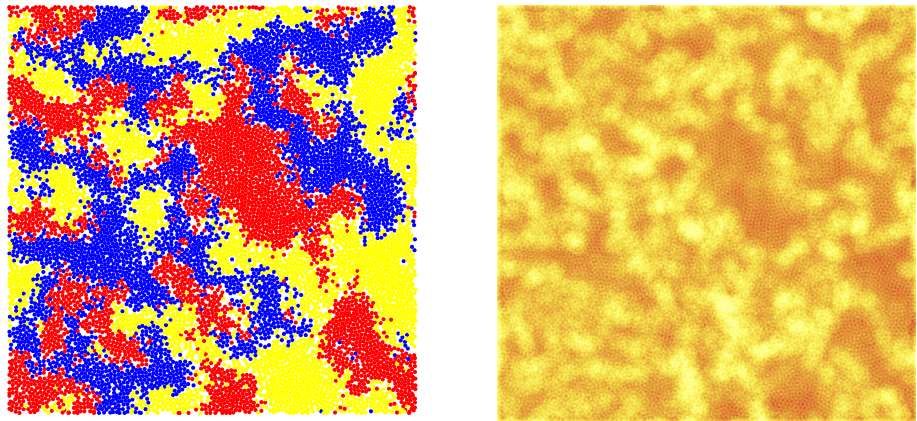
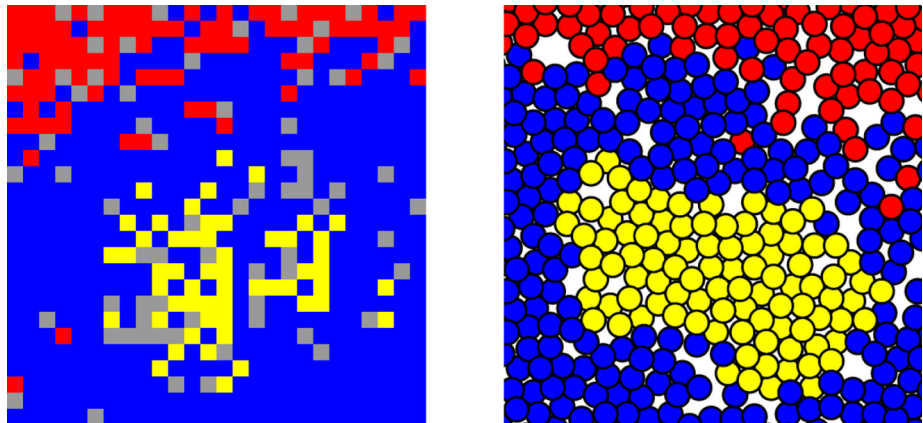


Fig. 5 Examples of spatial refuges retrieved with the lattice-based model (left) and the lattice-free (right) model



2010). Furthermore, individuals have more degrees of freedom in their movement, allowing them to rearrange themselves at refuge borders when gaps appear due to their neighbours being killed. For example, if an individual at the edge of a fully packed neighbourhood is killed, the remaining individuals can rearrange themselves from a hexagonal packing to a pentagonal packing by slightly increasing the distance between each other. This reduces the gap left by the killed individual, minimizing the space vulnerable to predator infiltration. This response is not possible in the lattice-based case, where the movement of individuals is constrained by the lattice and gaps can only be reduced by the births of new individuals. This effect can be seen in Fig. 4, where species aggregations have clearly defined borders with few gaps and therefore permit fewer hostile intrusions. This increases their robustness in terms of maintaining coexistence, implying a lower extinction probability P_{ext} at the same mobility rate.

This effect could also be achieved using a hexagonal lattice, where individuals can be packed similarly tightly. However there are still important differences when compared to the lattice-free approach. For example, hexagonal lattices and square lattices shared the same issue of being restricted by their packing configuration (discussed above),

so that gaps at refuge borders cannot be filled by movement but rather by births of new individuals. This problem is less severe in the hexagonal case, since if an individual is removed a hexagonal packing presents smaller gaps compared to a square packing.

Hence the hexagonal lattice approach could be considered as a midpoint between the computationally simple but unrealistic square lattice setting, and the more complex, realistic lattice-free setting. In comparison to square lattices, hexagonal lattices are infrequently used in ecological modelling (Birch et al. 2006), mainly for reasons of computational complexity: there is no hexagonal coordinate system that is both symmetric and orthogonal, whereas square lattices do have such a coordinate system (the Cartesian system). If one wishes to move away from the use of a square lattice, it remains a choice whether to adopt a more realistic hexagonal lattice, or to entirely avoid the restrictions of a lattice, as in our case. In the simple ecological models presented in this paper, the differences in behaviour between a hexagonal lattice setting and the lattice-free setting are already notable, but when extending to more complex behaviours (including for example diffusion of environmental substrates or other environmental

heterogeneity), the differences will likely become more significant (Baetens et al. 2013).

Our results correspond with experimental findings, where spatial refuges have been found to be important for maintaining diversity in predator–prey systems of, among others, crab-molluscs (Arsenault and Himmelman 1996) and spider-bugs (Finke and Denno 2006). Furthermore, it reflects in vivo ecosystems, which are typically composed of a few dominant species and many rare species (Ashby et al. 2007; Wilsey 2004). We can thus conclude that, by constraining individuals to a lattice, the lattice-based approach tends to underestimate the ability to maintain coexistence, compared to the more realistic lattice-free approach.

4.2 Impact of motility

The model described in Sect. 2.3 involves two components. First, a continuous mobility mechanism, whereby individuals no longer move in steps of length strictly equal to one unit, but instead may take steps of a random length smaller than the specified maximum. Second, a motility (or directed movement) mechanism that involves an attractive force towards a species’ prey and a repulsive force away from a species’ predator.

We first investigated the effect of the continuous mobility mechanism on coexistence without the motility component. We found that it does not lead to significantly different results than those obtained with the implementation described in Sect. 2.2. Notably, the spatial dynamics and the relationship between the system’s mobility and its probability of extinction are qualitatively very similar (results not shown).

We now turn to the effect of directed movement induced by proximity to predator or prey species. Table 1 lists the probability of extinction P_{ext} and the probability of a

monoculture of species A, B, or C for the scenarios described in Sect. 3 at mobility $M = 1.5 \times 10^{-3}$. For the benchmark scenario NNN, P_{ext} equals 0.52. We can then classify the eight scenarios according to whether they result in a higher P_{ext} (PNE, PPE, PEE, and ENN), or a lower P_{ext} (PNN, PPN, and EEN) than the benchmark. In one scenario, PEN, we find little change in P_{ext} compared to the benchmark scenario.

To illustrate the spatial and population dynamics that can emerge from this experiment, we show in Fig. 6 a representative evolution of the PNN scenario, where species A (blue) pursues species B (yellow). We track the changes in the community’s patchiness (a measure of its aggregation), shown in Fig. 6 as the dashed line. We find three distinct phases in the community’s evolution: a first phase defined by a logarithmic increase, corresponding to the formation of spatial structures; a second phase with a linear increase, corresponding to decreasing community evenness; and a third chaotic phase where extinctions occur and the system collapses. The probability of interspecific encounter (PIE) follows the same evolution, but with a decreasing trend.

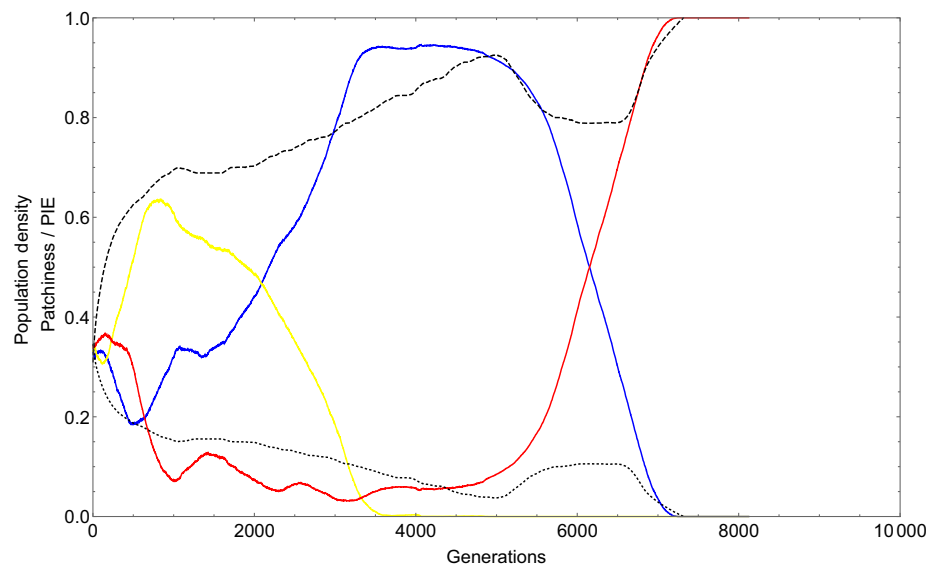
The population dynamics are also strongly affected by the species’ motile abilities. During the first phase, the pursuing behaviour of species A increases its mobility relative to that of B and C. This also increases its probability of encountering its own predator, and thus also its probability of extinction. Pursuing behaviour is therefore an initial disadvantage to species A, demonstrated by the decrease in its density. This benefits species B by allowing it to expand its territory at the expense of species C. During the second phase where spatial structures have emerged, the pursuing behaviour of species A becomes an advantage, since it can quickly invade the territory of species B without encountering its own predator species C. This substantial advantage allows species A to drive species B extinct. However, this fatally unbalances the cyclic competition scheme: now species A is alone with its predator, and so it quickly collapses to extinction. These dynamics are clearly detrimental to a stable community, and indeed we find that with $P_{ext} = 0.82$, the system maintains coexistence less frequently than in the benchmark scenario.

At the other end of the range of experimentally observed P_{ext} values, we find the PEE scenario with comparatively stable coexistence ($P_{ext} = 0.16$). In this community, all species exhibit motile behaviour and therefore none has an advantage during the first disaggregated phase without spatial structures. Once spatial structures emerge and aggregation increase, the spatial and population dynamics become dominated by the motile behaviour. Species B is able to escape from species A’s pursuit, thereby maintaining its density. However, the escaping behaviour of

Table 1 Probability of extinction P_{ext} and probability of monoculture (P_A , P_B , and P_C) dominated by the respective species at mobility $M = 1.5 \times 10^{-3}$

Scenario	P_{ext}	P_A	P_B	P_C
NNN	0.52	0.14	0.18	0.20
PNN	0.82	0.00	0.04	0.78
PNE	0.04	0.00	0.00	0.04
PPN	1.00	0.00	0.00	1.00
PPE	0.14	0.08	0.00	0.06
PEN	0.56	0.22	0.20	0.14
PEE	0.16	0.02	0.02	0.12
ENN	0.38	0.08	0.24	0.06
EEN	0.82	0.14	0.50	0.18

Fig. 6 Population density for species A (blue), species B (yellow), and species C (red), patchiness (dashed), and probability of interspecific encounter (PIE, dotted) plotted through time for a representative evolution of the PNN scenario at mobility $M = 1.5 \times 10^{-3}$. (Color figure online)



species C creates space for species B, giving its predator an advantage and hence disadvantaging itself. Hence, in this community no species has a clear advantage. This allows the system to maintain coexistence more frequently than in the benchmark scenario.

The other scenarios show similar dynamics: when species are disaggregated and no spatial structures are present, motile behaviour is a disadvantage by increasing the mobility of the species and hence the probability of encountering a predator. However, when spatial structures are present, pursuing behaviour is an advantage. Escaping behaviour can also be an advantage in cases where a species is being pursued, since this counters its predator's motile advantage. However, escaping behaviour is not advantageous when not being pursued, since this opens up space for its predator to expand into. This corresponds with experimental findings, where herding and escaping behaviour are only advantageous under certain circumstances (Schreiber et al. 2006).

Our approach to pursuit and escape is comparable to the well-known Boids model (Reynolds 1987), which simulates the flocking behaviour of birds by modelling three forces: separation (avoiding collisions with nearby individuals), alignment (aligning direction of velocity with nearby individuals) and cohesion (not moving too far from the flock's centre of mass). Whereas in the Boids model all individuals are attempting the same balancing act of avoiding collisions while still staying close to and aligned with their neighbours, in our model individuals have different goals depending on their species and the particular pursuit scenario. Thus some individuals will be focused only on chasing their prey or escaping their predator, while others will be attempting to balance both of these behaviours. Hence it is no surprise to see chaotic movement

patterns emerge from our model, in contrast to the ordered flocking behaviour that the Boids model can produce. These differences can be summarized by noting that in the Boids model the collective goal is to preserve the cohesion of the flock, whereas in our model individuals act to ensure their own survival. In both models, these local processes at the level of individuals' directed movement lead to the emergence of population-level patterns.

Similar attraction and repulsion dynamics have also been studied using Particle Swarm Optimization (Kennedy and Eberhart 1995), a computational technique developed for collective movement (such as bird flocking, fish schooling, or swarming). In this approach, an individual's direction and velocity are updated according to the suitability of its current position relative to a global "best" location (possibly a food source, a desirable roost location, etc.). To guide this search, individuals can both "remember" their previous best location and learn the best position found by other individuals. So at each time step, an individual compares the suitability of its current location with the remembered best location, and then adjusts its velocity by a random amount in the direction of the best location. In this way, Particle Swarm Optimization also focuses on individual survival as our model does. However, in our model the "best location" for an individual is entirely dependent on the positions of other individuals (its predator and/or its prey) rather than an environmental feature.

5 Conclusions

We have compared a lattice-based individual-based model with a three-species cyclic competition scheme to a more realistic lattice-free model. By permitting more spatial

heterogeneity and enhancing the formation and persistence of spatial refuges, the lattice-free model tends to be more robust in terms of maintaining coexistence. We then extended the model by allowing species to either pursue their prey or escape their predator in different scenarios. The effects on coexistence depend on the degree of species aggregation, in correspondence with experimental results.

We have focused on the simplest possible lattice-free model so that we are able to make the most direct comparison with the lattice-based benchmark. Avoiding the restrictions and simplifications that are intrinsic to a lattice-based approach is of great importance for any future work seeking to understand the complex and inherently lattice-free phenomena found in real-world biological systems, such as directed movement of various kinds, the effect of variable body sizes, or biased movement. Overall, a lattice-free approach improves the realism of the individual-based model, and allows us to study more realistic scenarios related to the conditions under which coexistence is maintained in biological systems.

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