

Ecological graph theory: Simulating competition and coexistence on graphs

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Funding information
 Max-Planck-Gesellschaft

Handling Editor: Aaron Ellison

Abstract

- Since its inception, the evolutionary graph theory (EGT) has been extensively used to study the fixation probability, the rate of evolution, game-theoretical topics and related questions in a spatially structured framework. However, few attempts have been made to use this framework in ecology. We develop an ecological extension of EGT, dubbed the ecological graph theory (EcoGT), to construct a graph-based equivalent to the classic Lotka-Volterra (LV) model.
- Firstly, we apply EcoGT to simple topologies, specifically a regular dodecahedron and a King's graph, to illustrate how such extreme topologies result in deviation from the LV model. Secondly, we explore how various graph families, for example, complete graphs, random graphs, small-world graphs, affect the competitive outcome between species. Finally, we explore species competition in EcoGT on graphs with dynamic topologies.
- Our results illustrate the suitability of the EcoGT approach to investigate fundamental questions related to species competition and coexistence at community and metacommunity levels without neglecting spatial structure across these scales.

KEY WORDS

coexistence, graph theory, metacommunity models, species competition models, structured populations

1 | INTRODUCTION

Our understanding of the population dynamics of organisms in their ecological context has been informed by a myriad of modelling approaches. In broad terms, such models can be categorized as either abstract, for example, the Lotka-Volterra equations, MacArthur's consumer-resource model (MacArthur, 1970), or Chesson's lottery model (Chesson & Warner, 1981). Alternatively, they can be representational, such as various agent-based ecological models (Murphy et al., 2020; Zhang & DeAngelis, 2020). While the former

category enables rigorous mathematical analyses, extending such models to include more complex ecological scenarios can be extremely challenging, for example, to understand the coexistence of many species in a metacommunity (Lerch et al., 2023) or understanding the importance of non-genetic variation resulting from phenotypic plasticity (Kalirad & Sommer, 2024). Representational models open the door to fine-grained and complex input, but given their inherent complexity, it is both difficult to exhaustively analyse them and even report their underpinning architecture (Grimm et al., 2006).

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The evolutionary graph theory (EGT) (Lieberman et al., 2005; Nowak, 2006; Santos et al., 2006) provides a general framework to explore the effect of spatial structure on the evolutionary dynamics. In EGT, individuals are represented by nodes and edges which delineate competitive interactions between individuals (see **Supporting Information: A very short introduction to evolutionary graph theory**). EGT has been extensively used to study evolutionary questions with respect to evolutionary game theory (Szabó & Fáth, 2007), the probability of fixation of new mutations (Broom & Rychtář, 2008; Frean et al., 2013; Kuo & Carja, 2024), the effect of migration (Pattini et al., 2021, 2023), and, more recently, the influence of complex spatial structure on fixation probability amongst stem cells (Kuo et al., 2024). Even the veracity of the EGT results has been explored experimentally (Chakraborty et al., 2023). The extensive literature on EGT provides ample information on how various network topologies, including the star network (Hadjichrysanthou et al., 2011; Monk et al., 2014), megastars (Galanis et al., 2017) or the inclusion of self-loops (Sharma et al., 2023) and directed graphs (Brewster et al., 2024) can amplify or suppress selection (reviewed in Broom & Rychtář, 2024).

The application of graph theory to ecology has a long history. Notably, May's exploration of the role of complexity in the stability of communities consisting of many interacting species (May, 1972, 1973) and the subsequent works that followed, for example, Pimm and Lawton (1980), all relied on the conception of species interaction as a graph. The network representation of ecological interactions, for example, mutualistic, predatory or parasitic, has been utilized on different scales, from individual to clades (Guimarães, 2020). Specifically, a slew of recent studies have enabled empirical construction of individual-level networks for different species: Araújo et al. (2008) utilized graph theory to illustrate the effect of intraspecific competition on foraging in threespine sticklebacks (*Gasterosteus aculeatus*), Fortuna et al. (2009) analysed the social structure of the greater noctule bat (*Nyctalus lasiopterus*) using bipartite graphs, and Cantor et al. (2018) investigated the cooperative foraging between fishermen and bottlenose dolphins (*Tursiops truncatus*).

Additionally, recent empirical investigations have shown how the topology of an individual-level network can change over time in complex ways. For example, Tur et al. (2015) inferred changes in modules in networks of pollen transport as a result of seasonal changes in the foraging strategies of the pollinating insect. Similarly, Valverde et al. (2016) observed temporal change in pollination networks in *Erysimum mediohispanicum*. It has been pointed out that individual-level networks can naturally be extended to construct community networks (Dupont et al., 2011). In addition, combining multiple network representations of ecological interactions would undoubtedly provide deep insights about community stability (Brose et al., 2025). However, our understanding of the structural variations in ecological networks is, for the most part, shaped by our extensive knowledge of food webs (reviewed in Guimarães, 2020).

Surprisingly, given the extensive usage of networks in ecology across scales, there have been few attempts to explore the suitability of EGT as a framework to study ecological questions. A transformation of EGT into ecological graph theory (EcoGT) can provide an invaluable tool to explore ecological questions. Specifically, EcoGT, in which each individual is represented by a node and each edge represents ecological interaction in space, naturally includes spatial structure, whose importance in species coexistence was hinted at in the pioneering works on competition (Gause, 1932; Huffaker, 1958) and became central within the metapopulation framework (Hanski, 1981; Levin, 1976). EcoGT could also enable the exploration of change in ecological interactions over time by enabling rewiring of edges over time. In addition to the aforementioned empirical cases, the inclusion of such topological dynamics in an ecological network is crucial to reflect events such as the movements of predator and prey (Polis, 1991). Furthermore, EcoGT can be used to both investigate the ecological dynamics in a single and isolated, albeit spatially structured, community and to include the spatial arrangement of a number of such communities, that is, in a metacommunity (Leibold et al., 2004). The key aspects of the metacommunity framework, namely scale, dispersal and heterogeneity (Leibold & Chase, 2018), can be easily incorporated in EcoGT as an individual-based model with explicit spatial structure.

In this manuscript, we explore the plausibility of EGT as a starting point to construct an EcoGT. Our starting point is the classic Lotka-Volterra (LV) two-species competition model (Lotka, 1932; Volterra, 1931), which has been extensively used to study species competition and coexistence, for example, Serván et al. (2018); Lerch et al. (2023). This model provides a yardstick against which the behaviour of various versions of EcoGT will be measured. Subsequently, we construct a version of EcoGT with update rules that enable species competition and explore the dynamics on increasingly more complex topologies. Additionally, we introduce rewiring algorithms that enable temporal dynamics to the topology of interaction networks. The EcoGT would serve as a starting point for us to explore the importance of factors such as phenotypic plasticity in species coexistence in spatially structured communities and metacommunities in future studies.

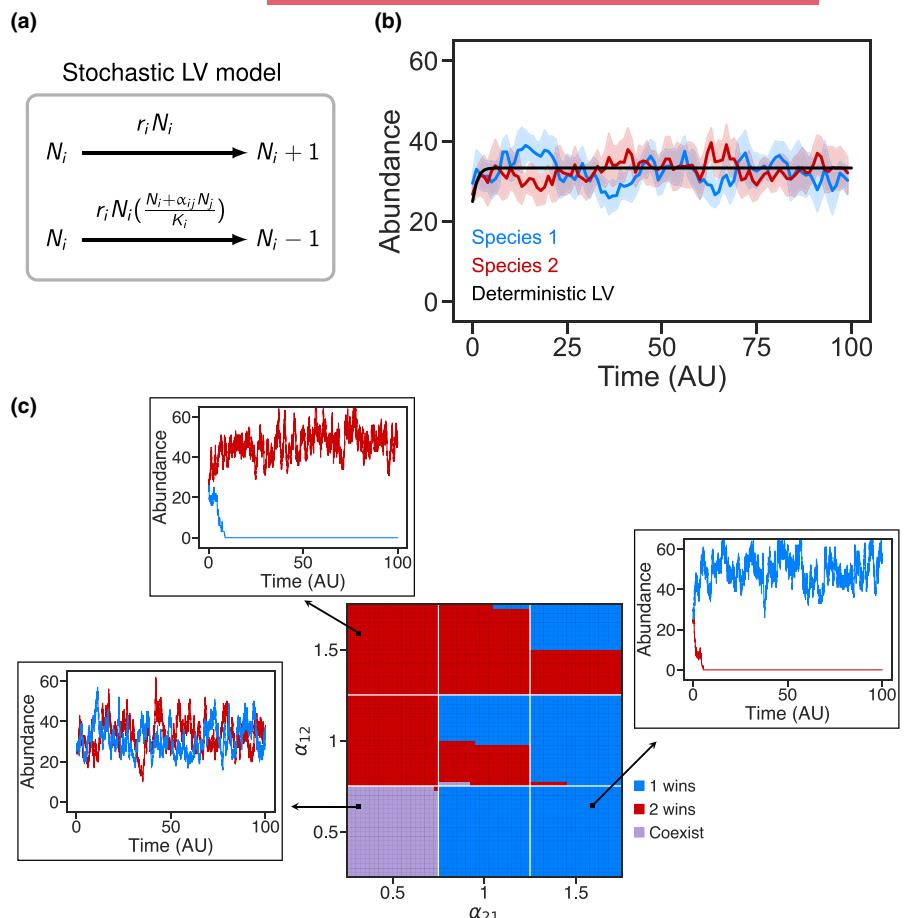
2 | MATERIALS AND METHODS

To explain EcoGT, we first introduce a stochastic version of the LV model as our point of reference. Subsequently, we use the dodecahedron graph and King's graph—both simple topologies that can be embedded in two dimensions—to better illustrate how competition in the EcoGT framework unfolds.

2.1 | Stochastic LV competition model

The classic LV competition model for two species (Lotka, 1932; Volterra, 1931) can be formulated as

FIGURE 1 (a) The stochastic version of the classic LV model, fashioned into a set of reactions. (b) The results of the stochastic LV model simulated using the Gillespie algorithm. The dotted line represents the expected deterministic result based on Equations 1. Parameters: $r_1 = r_2 = 1$, $\alpha_{12} = \alpha_{21} = 0.5$, $K = 50$. The shaded area represent 95% CI for 100 runs. (c) The competitive outcomes for the stochastic LV model with different combinations of α_{ij} . The plot is divided into 9 sections, each corresponding to a combination of α_{ij} . The colour of pixel in each region indicates the final outcome of a simulation of the stochastic LV model. The entire plot is based on a total of 3600 simulations. Simulations in which frequency of both species remained at $\geq 10\% K$ were classified as coexistence. The same visualization style is used in all the subsequent figures. Parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = 50$.



$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1}\right) \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1}{K_2}\right),\end{aligned}\quad (1)$$

where r_i is the growth rate of species i , K is the carrying capacity and α_{ij} is the effect of species j on species i . We use a stochastic version of the LV model, which, in contrast to its deterministic version, incorporates demographic stochasticity and provides a better point of reference in comparison to EcoGT where a finite number of individuals compete. The stochastic LV model is simulated using Gillespie's stochastic simulation method (Gillespie, 2007; Figure 1a,b; see Supporting Information: *Stochastic simulation of the Lotka-Volterra model*).

The competitive outcome in the classic LV model depends on α_{ij} : assuming equal carrying capacities for the competing species ($K_1 = K_2$), $\alpha_{12} < 1$ and $\alpha_{21} < 1$, results in coexistence and $\alpha_{12} = \alpha_{21} = 1$ represents the neutral case, where either of the two species can win by chance. For $\alpha_{ij} > 1$ and $\alpha_{ji} = 1$, either of the two species with larger α would exclude the competing species. If both $\alpha_{12} > 1$ and $\alpha_{21} > 1$, either of the species can competitively exclude the competing species depending on the initial conditions (Figure 1c). When comparing the EcoGT to the stochastic LV model, the number of nodes in a graph cannot be equated with the carrying capacity, since the latter can be interpreted both as reflecting resource dynamics or direct competition (Chesson, 2000a).

2.2 | Ecological competition on a graph

EGT can be considered an extension of the Moran model (Moran, 1958). In Moran model, genotype g_i has a fixed fitness w_i . In each step, an individual is chosen proportional to its fitness and its progeny replaces a randomly chosen individual, which by chance could be the parent itself. This birth-death process can be easily applied to a structured population represented by a graph. Several alternatives to this birth-death process (with selection on birth) have been introduced (see Supporting Information: *A very short introduction to evolutionary graph theory*). To construct EcoGT, we specifically modify the original EGT approach in order to better approximate a model of species competition. A comparison between EGT and EcoGT can be found in Table 1.

To recreate the random birth and the density-dependent death in the LV model on a graph, the population dynamics in EcoGT consist of two steps:

1. **Connectivity-based death:** Individual a of species i dies with probability proportional to $\frac{n_j + \alpha_{ij} n_j}{n_t}$, where n_t is the total number of nodes linked in the graph to individual a . This condition results in death events that are a function of local density. The probability of death is purely a function of the composition of the nodes connected to the focal node.
2. **Birth:** A random individual linked to a reproduces to replace the dead individual.

	EGT	EcoGT
Node	An individual with a given genotype or transmissible behaviour (cultural evolution)	An individual belonging to a species or a strain
Edge	It specifies the static arrangement of individuals in space	It specifies the arrangement of individuals in an ecological community, can change over time due to movement or environmental change. A metacommunity can be specified by treating each community as a subgraph
Update method	Depending on the method of choice, individuals are chosen for reproduction (or death) proportional (or inversely proportional) to their fitness given their genotypes or transmissible behaviours	Death probability of a node is dependent on the composition of nodes that are directly connected to it and the species competition parameter α_{ij}
Goal	Understanding the role of topology as suppressor or amplifier of selection and its effect on the fixation probability of beneficial mutations. Additionally, it can be used to explore evolutionary stable strategies	Exploring the effect of topology—both static and dynamic—on species coexistence. As an individual-based model, EcoGT can explore the importance of intraspecific trait variation—in particular, phenotypic plasticity—and various sources of variability—including demographic stochasticity and environmental variability—in shaping community and metacommunity composition

TABLE 1 A summary of major differences and similarities between EGT and EcoGT.

If in a given graph, a node that is not linked to any other node is randomly picked in step 1, we assume that its own offspring replace the dead parent in that node. To illustrate the competitive outcome arising from this death-birth process, we explore two topologies that, while unrealistic in biological terms, provide visual clarity. The first, is the dodecahedron graph (Figure 2a,b). Given its small size, the competitive outcome on the dodecahedron deviates from that of the LV model in the coexistence regime ($\alpha_{12} < 1$ and $\alpha_{21} < 1$). However, the outcome of the competition on the dodecahedron graph for the rest of parameter combinations is indistinguishable from the LV model (Figure 2c). All the nodes in dodecahedron have the same degree, that is, each node is connected to three nodes and given its small size, this topology favours ecological drift when $\alpha_{12} = \alpha_{21}$.

However, different topologies can result in outcomes that divert considerably from the LV model. To illustrate this point, we explore the competition between two species on a King's graph. King's graph represents all the legal moves of a king in Chess over an $m \times m$ lattice (Figure 3a). Individual simulation on a king's graph under the coexistence regime, sensu LV, similarly results in coexistence (Figure 3b). While individual runs on this topology under the neutral regime ($\alpha_{12} = \alpha_{21} = 1$) can result in competitive exclusion (Figure 3c), king's graph deviates from the LV model and promotes coexistence whenever $\alpha_{12} = \alpha_{21}$ (Figure 3d). Although, both the dodecahedron graph case and king's graph present extreme topologies (Figure S6), these

topologies provide a pedagogical tool to illustrate a clear link between space and its influence on ecological competition (Figure S7).

3 | RESULTS

3.1 | Competition on different families of graphs with static topologies

Relatively realistic topologies can be generated by various methods. The most trivial is a complete graph, where every node is linked to every other node. While trivial on the surface, a complete graph is intriguing since it should, in theory, resemble a well-mixed community—in the sense of all-to-all interactions (Herreras-Azcue et al., 2018)—and provides the closest case to the LV model in the context of EcoGT. In a complete graph, like the LV model, the death rate of a given individual (a node) is affected by the rest of individuals in the population. In fact, the simulation of competition on a complete graph is indistinguishable from the classic LV model (Figure 4a). From this starting point, we explore the effect of spatial structure in EcoGT by specifying the topology of the graph using the Erdős-Rényi (ER) model. In this model, random graphs are generated by introducing a link between any pair of nodes with probability p , resulting in a random graph with a binomial degree distribution

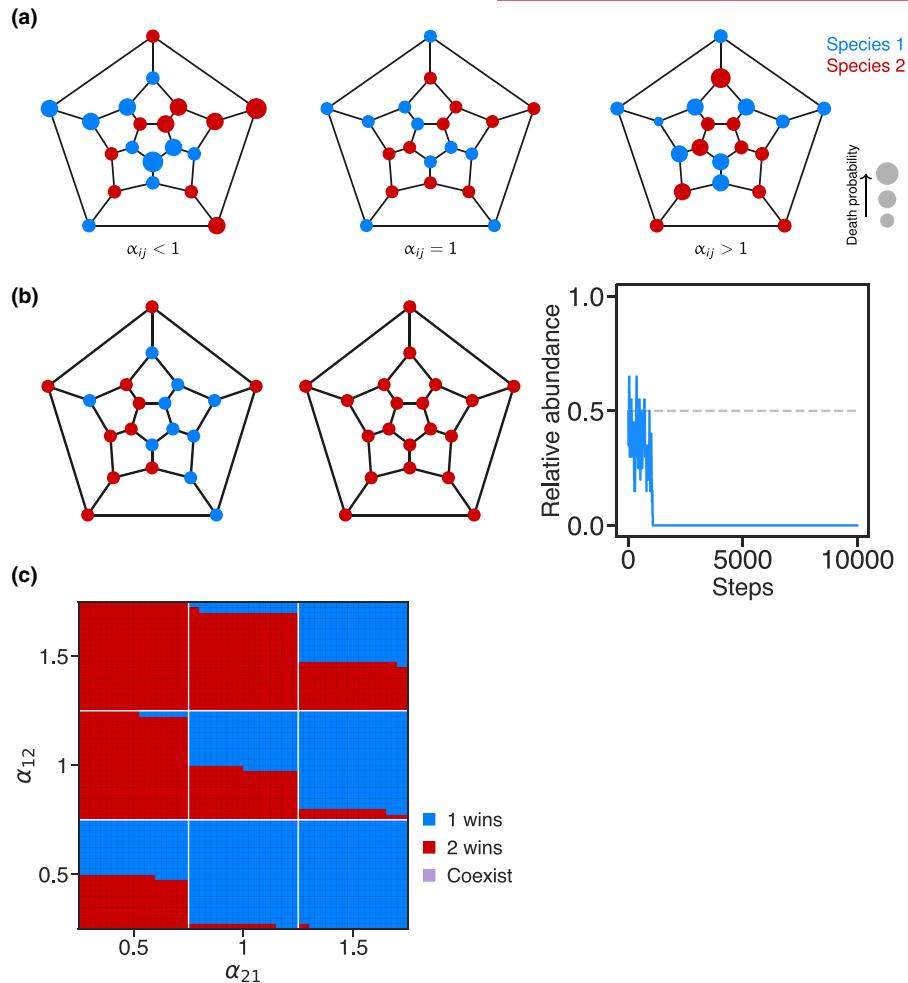


FIGURE 2 (a) The effect of value of α_{ij} on connectivity-based death probability in the dodecahedron graph. In $\alpha_{12} = \alpha_{21} < 1$, the presence of conspecific individuals negatively affects the death rate of a given individual, in contrast to $\alpha_{12} = \alpha_{21} > 1$, where an individual's death rate is reduced when surrounded by conspecific individuals. In $\alpha_{12} = \alpha_{21} = 1$, the death rate is independent of the composition of individuals in localities across the graph. (b) The initial and final on a dodecahedron graph with $\alpha_{12} = \alpha_{21} = 1$ and the abundance of species 1 during the simulation. (c) The competitive outcome of competition on the dodecahedron graph with varying α_{ij} values base. Each pixel indicates the final outcome of a EcoGT simulation on a dodecahedron, for a given combination of α_{12} and α_{21} for 10,000 steps. Simulations in which frequencies of both species remained at $\geq 10\% N$ were classified as coexistence. For this and subsequent figures, simulations start with equal number of each species, distributed at random on the graph. In comparison to the classic LV model (Figure 1c), the topology of simple dodecahedron favours all-or-nothing competitive outcomes.

(Erdős & Rényi, 1959; Gilbert, 1959). In the ER model, the competitive outcome diverges from the LV model only at low p and exclusively in $\alpha_{12} = \alpha_{21} < 1$ (Figure 4b), whereas, expectedly increasing p , results in competitive outcomes similar to the complete graph case (Figure 4c,d). More extreme topologies can greatly affect the competitive outcome. For instance, in a ring topology, the $\alpha_{12} = \alpha_{21} = 1$ regime, which in the LV model is described as the neutral cases, results in coexistence, as well as the $\alpha_{12} = \alpha_{21} > 1$ (Figure 4e). In addition, a small-world network, constructed using the Newman-Watts-Strogatz model, in which a fixed number of links are rearranged to create the small-world property—that is, networks in which any pair of nodes are rarely connected by a single edge but can nevertheless be reach by traversing only a handful of edges—in a graph (Newman & Watts, 1999), deviates from the LV model in the neutral $\alpha_{12} = \alpha_{21} = 1$ regime (Figure 4f,g).

3.2 | The effect of random rewiring of a graph on competition

When considering ecological competition in the wild, many instances would entail the movement of individuals during the competition, as undirected or directed movements in response to biotic or abiotic factors in the environment. Thus far, we have only considered competition over topologies that are fixed at the start of competition, reflecting random placement of individuals of competing species in space. We can include the movement of organisms during competition by allowing for the rewiring of edges during the simulation (partly inspired active link formation in social networks, for example, (Pacheco et al., 2006; Wu et al., 2010)).

Given the variety of locomotion in biology, for example, passive, active, etc., one can conceive a multitude of ways of implementing

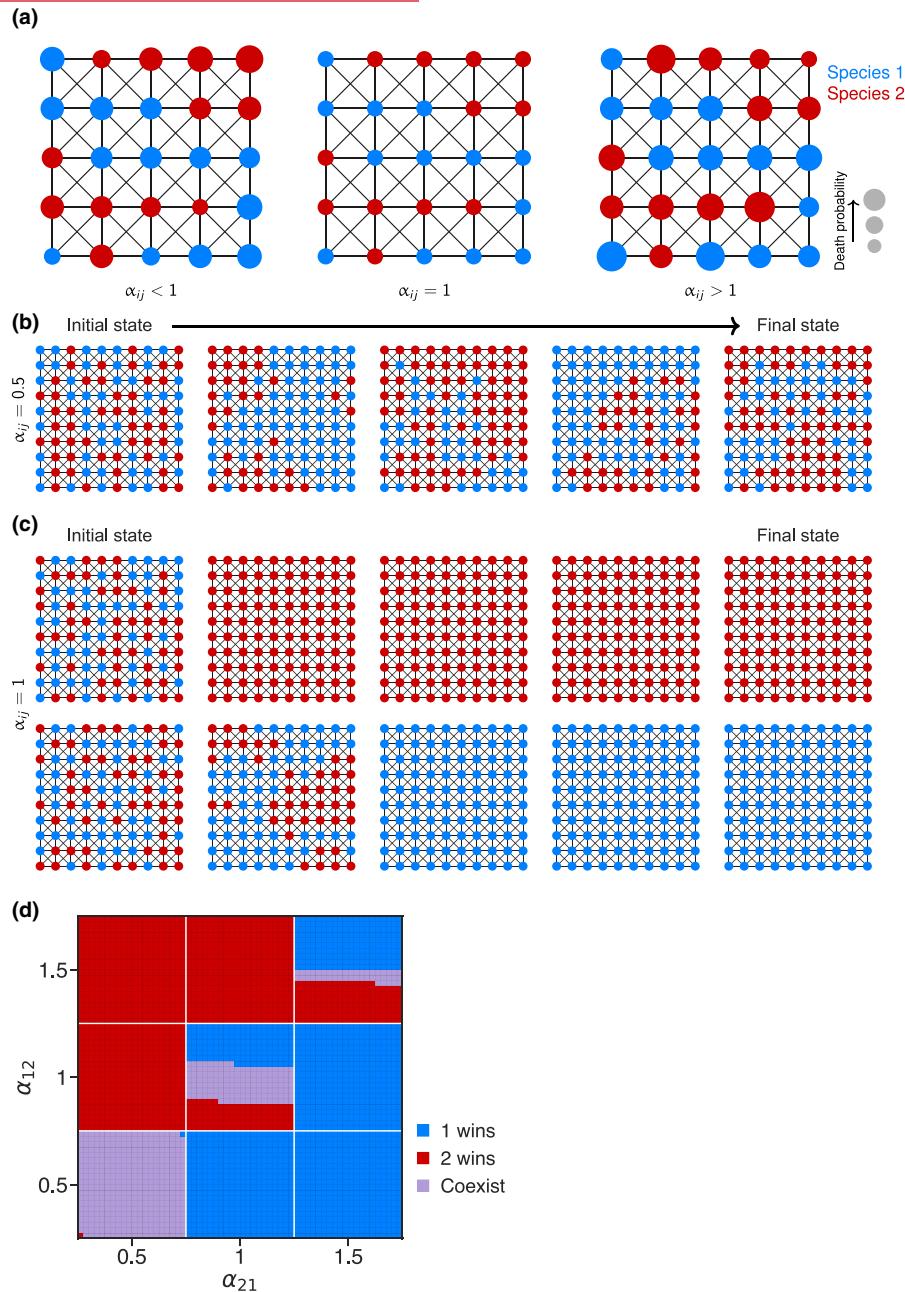
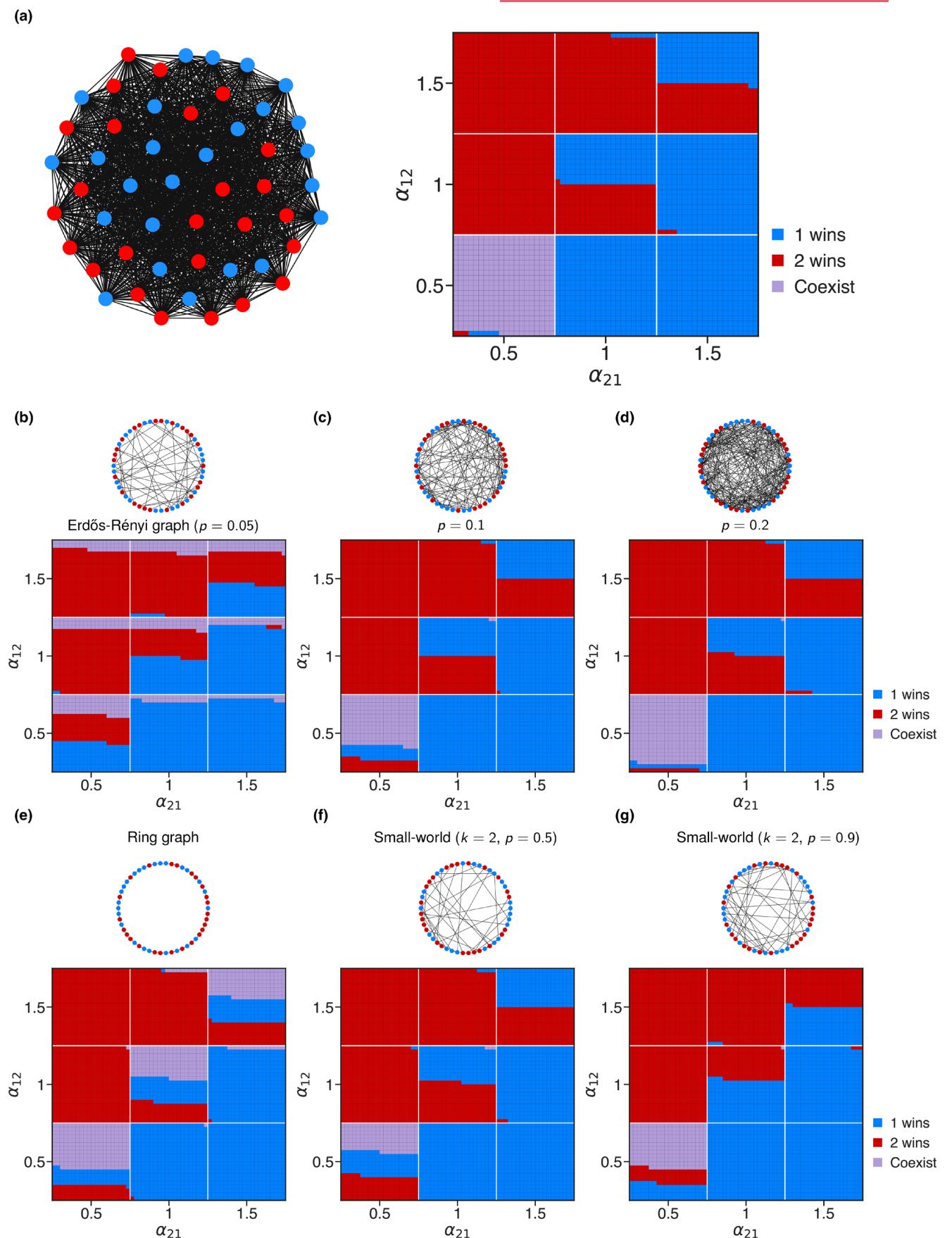


FIGURE 3 (a) The topology of King's graph and the connectivity-based death probabilities for nodes as a function of α_{ij} . (b) The changing composition of a population consisting of two species on a King's graph with $\alpha_{12} = \alpha_{21} < 1$. The final state represents the composition of the population after 10,000 steps, and intermediate composition where sampled at fixed intervals during the simulation. In this regime, in concert with the classic LV competition model, species coexist. (c) Two simulations on a King's graph in the neutral scenario ($\alpha_{12} = \alpha_{21} = 1$), resulting in the extinction of one of the competing species due to ecological drift. (d) The competitive outcome of competition on a King's graph with varying α_{ij} values. Each pixel indicates the final outcome of a EcoGT simulation on a King's graph, for a given combination of α_{12} and α_{21} for 10,000 steps. In comparison to the classic LV model (Figure 1c), the topology of the King's graph promotes coexistence whenever $\alpha_{12} = \alpha_{21}$.

FIGURE 4 (a) The simulation of competition between two species on a complete graph. Each pixel indicates the final outcome of a EcoGT simulation on a complete graph with $N = 50$ nodes, with a given for a given combination of α_{12} and α_{21} for 10,000 steps. Simulations in which frequency of both species remained at $\geq 10\% N$ were classified as coexistence. The results are consistent with the classic LV model (Figure 1c). (b-d) The competitive outcome of EcoGT on an Erdős-Rényi graph ($N = 50$) with different combination of α_{12} and α_{21} . (e) The competitive outcome of EcoGT on a ring graph ($N = 50$). (f and g) The competitive outcome of EcoGT on a small-world Newman-Watts-Strogatz graph ($N = 50$).



edge rewiring in the EcoGT framework. We explore five different versions of such rewiring methods:

1. *Uniform rewiring*: In this method, m edges are randomly rewired at each step (Figure 5a,b). This method approximates passive locomotion and random walk.
2. *Rich-gets-richer (RR) rewiring*: In this method, inspired by the preferential attachment, specifically the Barabási–Albert model (Albert & Barabási, 2002), a new edge is formed between the randomly chosen node a and node b proportional to $\frac{k_b}{\sum k_j}$, where k_b is the degree of node b and $\sum k_j$ is the sum of degrees of all the nodes that are not linked to node a . In this method, a node with more links is more likely to receive new links during rewiring (Figure 5c,d). This form of rewiring resembles the formation of biological clusters such as microbial biofilm (Sauer et al., 2022).
3. *Poor-gets-rich (PR) rewiring*: A contrast to the RR method, in the PR method, a node with fewer links is more likely to receive new links during rewiring. Specifically, a new edge is formed between the randomly chosen node a and node b proportional to $\frac{\Delta_b}{\sum \Delta_j}$, where $\Delta_b = \max(k_j) - k_b$ (Figure 5e,f). This method approximates scenarios in which species in community are evenly arranged in space. For example, *Pseudomonas aeruginosa* cells—in order to better compete—evenly disperse in space to engulf *Agrobacterium tumefaciens* (An et al., 2006).
4. *Aggregator rewiring*: In this method, rewiring is done such that an individual of species i is more likely to be linked to a conspecific individual during rewiring, $P_i \rightarrow i > P_i \rightarrow j$ (Figure 5g,h). This method reflects many cases of conspecific aggregations, for example, in insect (Wertheim et al., 2005).
5. *Repulsive rewiring*: In this method, rewiring is done such that an individual of species i is more likely to be linked to an individual of species j during rewiring, $P_i \rightarrow j > P_i \rightarrow i$ (Figure 5i,j). This method could be used to simulate reciprocal interactions in which both

species prefer to interact with an allospecific individual, for example symmetrical intraguild predation, where both species prey on each other (Polis et al., 1989).

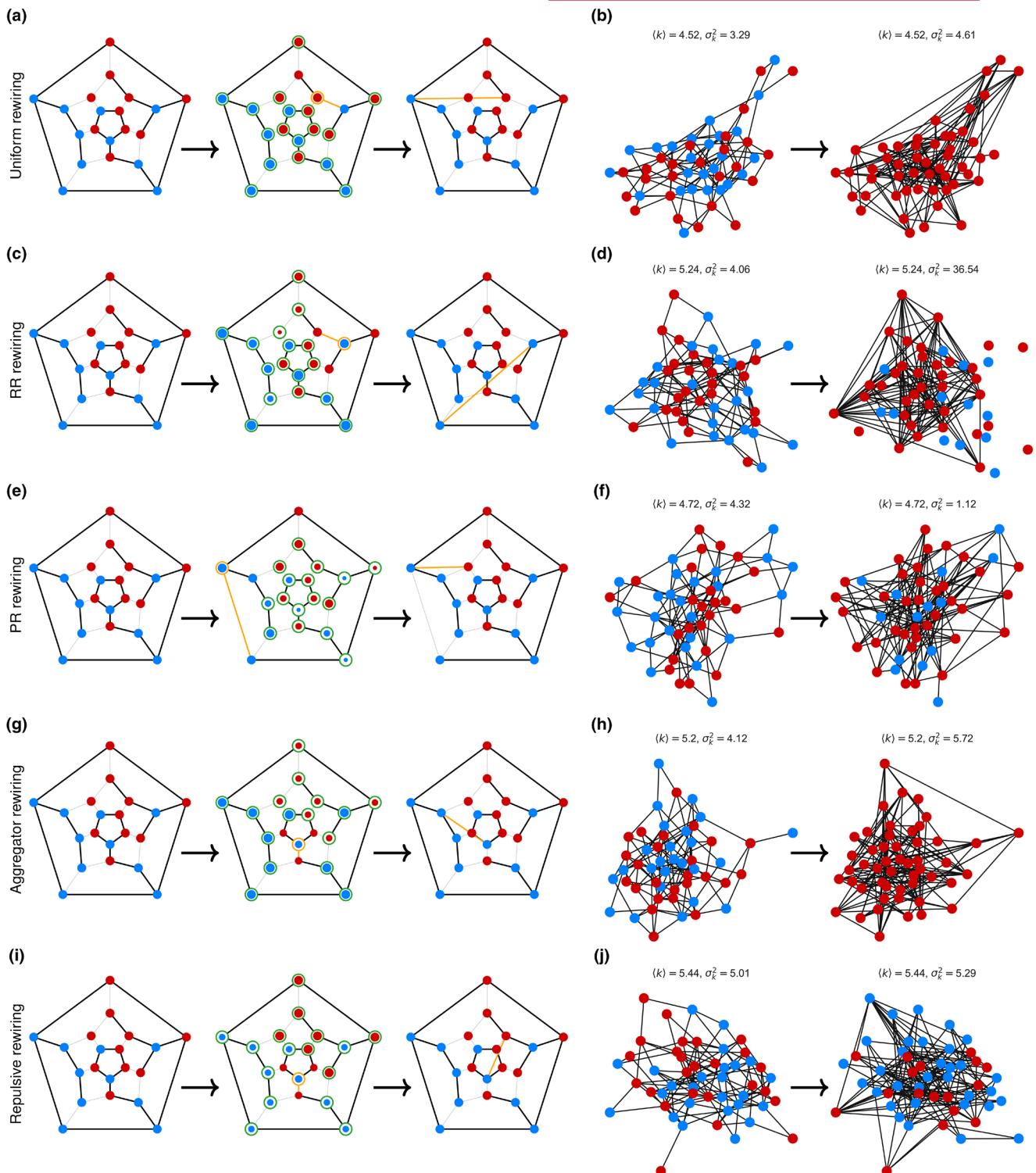
To simulate the effects of each of the aforementioned rewiring methods on the competitive outcome, we start a simulation with a topology generated by the Erdős–Rényi model, and at each step during the simulation rewire m using a rewiring method.

The lowest intensity of uniform rewiring ($m = 1$) does not diverge from the static ER graphs with respect to its competitive outcomes (Figure 4b vs. Figure 6a). However, higher intensity of uniform rewiring ($m = 20$), results in markedly different competitive outcomes under the coexistence regime (Figure 6b), which resemble more those of a complete graph (Figure 4a) and the classic LV model (Figure 1c).

Interestingly, the RR rewiring promotes coexistence under all the parameter combinations (Figure 6c). At a topological level, the RR rewiring does not change the mean degree distribution, but greatly increases the variance in the degree distribution (Figure S7). The PR algorithm does not affect the average degree but reduces the variance in degree distribution compared to the uniform rewiring (Figure S8D). This change in the topology results in competitive outcomes that resemble the LV expectation (Figure 5d).

The aggregator rewiring, in which it is more likely for a member of species i to be linked to a conspecific during the rewiring step, results in all-or-nothing outcomes, where no coexistence is possible. This result is not entirely surprising since such rewiring would limit the potential effect of a species on the death rate of the other species, the condition that would promote coexistence in the LV framework (Figure 6e). Surprisingly, the repulsive rewiring, which favours the formation of edges between individuals belonging to different species during rewiring, promotes coexistence in all cases where $\alpha_{12} = \alpha_{21}$ (Figure 6f). Both of these rewiring algorithms affect neither

FIGURE 5 The illustration of five rewiring methods on the dodecahedron graph. To introduce variance in degree distribution, 10 edges were randomly removed out of the 30 possible edges in a dodecahedron. (a) In uniform rewiring, a random edge is chosen (the orange line) and one of the node involved in that edge (indicated by an orange circle) that can be linked at random to any potential node (indicated by green circles). (b) A comparison between the initial state of a population and the final state of a population after 10,000 steps with $m = 10$ uniform rewirings at each step. In this and the subsequent examples, the initial topology was generated by the ER model with $p = 0.1$ with 50 nodes. Uniform rewiring does not affect the average degree, $\langle k \rangle$, nor its variance, σ_k^2 . (c) In rich-gets-richer (RR) rewiring, the probability of the new edge being attached to any of the potential nodes (indicated by green circles) is proportional to the degree of each node (indicated by the diameter of each potential node). (d) A comparison between the initial state of a population and the final state of a population after 10,000 steps with $m = 10$ RR rewirings at each step. The RR rewiring does not affect the average degree, $\langle k \rangle$, but increases the variance in degree amongst nodes, σ_k^2 , resulting in isolated nodes. (e) In poor-gets-rich (PR) rewiring, nodes with fewer links have higher probability of being involved in the new edge than nodes with more links. (f) A comparison between the initial state of a population and the final state of a population after 10,000 steps with $m = 10$ PR rewirings at each step. The PR rewiring does not affect the average degree, $\langle k \rangle$, but decreases the variance in degree amongst nodes, σ_k^2 . (g) In aggregator rewiring, a node is more likely to be linked to a conspecific node during rewiring. In this example the randomly chosen node (indicated by an orange circle) has a higher probability of being linked to any of the blue nodes amongst the potential nodes than any red node (indicated by the larger diameter of blue potential node). (h) A comparison between the initial state of a population and the final state of a population after 10,000 steps with $m = 10$ aggregator rewirings at each step. The aggregator rewiring does not affect the average degree, $\langle k \rangle$, nor its variance, σ_k^2 . (i) In repulsive rewiring, a node is more likely to be linked to a node belonging to a different species during rewiring. In this example the randomly chosen node (indicated by an orange circle) has a higher probability of being linked to any of the red nodes amongst the potential nodes. (j) A comparison between the initial state of a population and the final state of a population after 10,000 steps with $m = 10$ repulsive rewirings at each step. The repulsive rewiring does not affect the average degree, $\langle k \rangle$, nor its variance, σ_k^2 . In (i) $P_{i \rightarrow i} = 4P_{i \rightarrow j}$ and in (j) $P_{i \rightarrow j} = 4P_{i \rightarrow i}$.



the average degree nor the variance in degree (Figure S8), despite directly affecting the proportion of edges that connect conspecific nodes (Figure S9).

4 | DISCUSSION

Evolutionary graph theory remains attractive as a tool to study evolution in structured populations to address a wide range of questions,

including the spread of infectious agents (Grenfell et al., 2001; May & Lloyd, 2001), the formation of tumours (Noble et al., 2022; Waclaw et al., 2015), not to mention its extensive application in evolutionary game theory (Broom & Rychtář, 2024). Surprisingly, the potential of the EGT approach to address foundational ecological questions—with few exceptions (Pattni et al., 2021, 2023; Svoboda et al., 2023)—remains untapped.

The importance of spatial structure in shaping ecological dynamics has long been understood (Andrewartha & Birch, 1954;

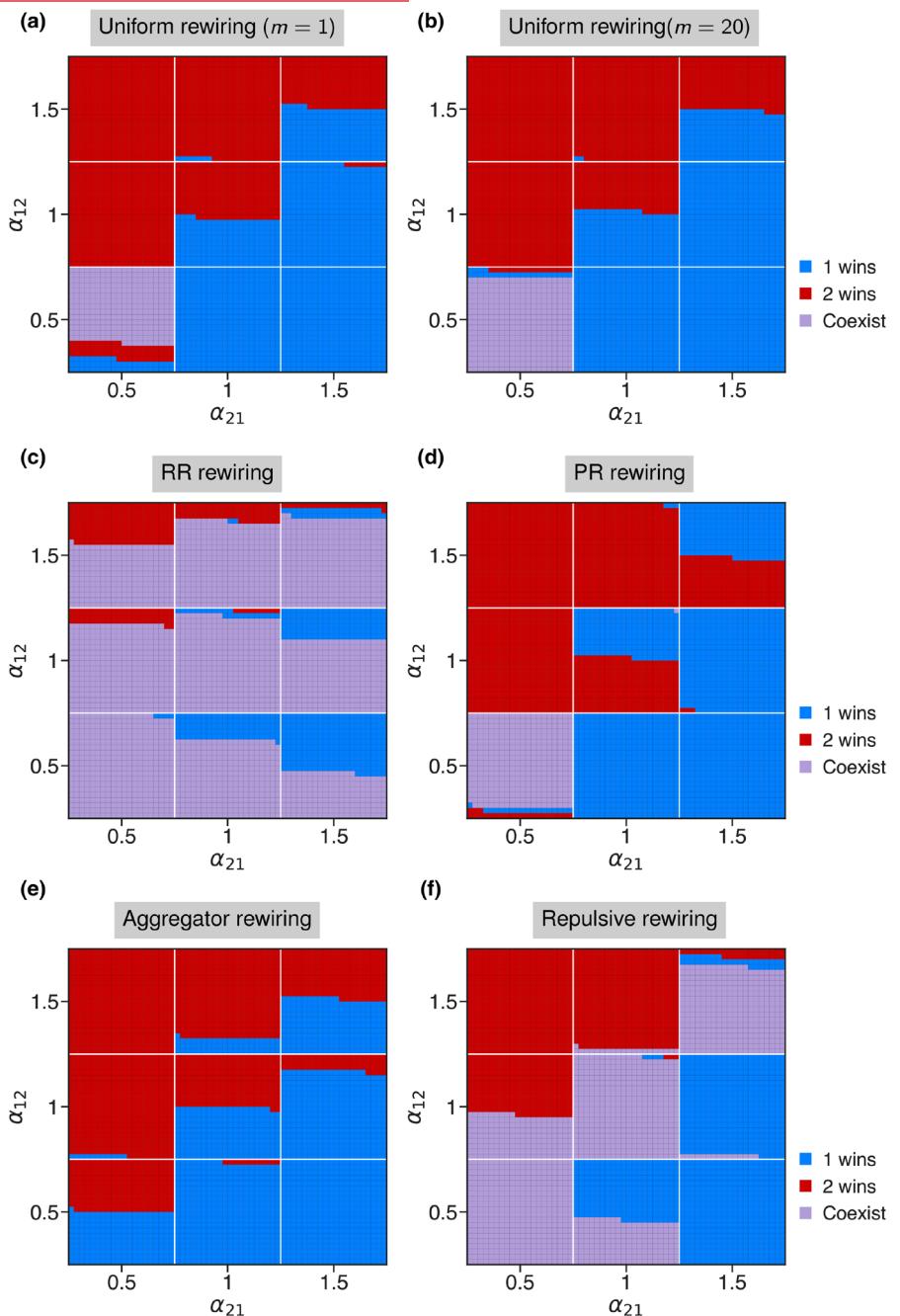


FIGURE 6 (a) The competitive outcome of EcoGT with the weakest uniform rewiring ($m = 1$). (b) The competitive outcome of EcoGT with high uniform rewiring ($m = 20$). (c) The competitive outcome of EcoGT with RR rewiring. Comparison between (a and b) indicates how the temporal rewiring could affect the possibility of coexistence in $\alpha_{12} = \alpha_{21} = 0.5$ case. (d) The competitive outcome of EcoGT with PR rewiring. (e) The competitive outcome of EcoGT with aggregator rewiring. (f) The competitive outcome of EcoGT with repulsive rewiring. All the simulations started from an ER graph ($p = 0.1$). In (c-f), $m = 10$. The results for each combination of α_{12} and α_{21} are based on 200 simulations for 10,000 steps. The initial topology of the population in each simulation was generated by the ER model with $p = 0.1$ with $N = 50$ nodes. In (e) $P_{i \rightarrow i} = 4P_{i \rightarrow j}$ and in (F) $P_{i \rightarrow j} = 4P_{j \rightarrow i}$.

Hanski & Gilpin, 1991; Levin, 1992). However, treating populations as well-mixed solutions remains the norm rather than the exception (Battey et al., 2020). Notably, the LV model and its extensions, which have been extensively used to explore competition between species and the possibility of their coexistence, have limited capacities

in representing space. Although a dispersal term can be added to the LV model to mimic a patchy environment, each patch remains a well-mixed population (Zhang et al., 2021). The same limitation is observed in metapopulation models (Hanski & Gilpin, 1991; Levin, 1976; Levins & Culver, 1971; Tilman & Kareiva, 1997; Wilson, 1992).

EcoGT can reflect spatial arrangement at the level of community, since the interaction between individuals is determined by a network, as well as the level of metacommunity, since a patch can be treated as a subgraph embedded in a graph, itself representing the arrangement of patches in space. Nature is rarely static and a network representation of the spatial arrangement of organisms should reflect this fact. Such a protean state of affairs can be included in EcoGT using various rewiring methods. In this regard, EcoGT can be used to shed light on the potential interplay between space and animal movement in relation to species coexistence, thus linking movement ecology (Shaw, 2020) with coexistence theories. In addition, spatial variability in the environment—which has been hypothesized to greatly influence competition and coexistence (Chesson, 2000b)—can be explored by including the effect of the environment on the species competition parameter or other attributes on a subset of nodes in a graph. In this regard, EcoGT complements the classical models of species competition by enabling a fine-grained inclusion of space and movement, adding to the growing number of spatially explicit ecological models (DeAngelis & Yurek, 2017).

Additionally, as an individual-based approach, EcoGT enables the inclusion of intraspecific trait variation. There has been an intensifying focus on the importance of intraspecific variation in influencing ecological interactions and shaping community composition (Bolnick et al., 2011; Schoener, 2011; Jung et al., 2010; Viole et al., 2012; Des Roches et al., 2018; Westerband et al., 2021). In particular, further investigation on the importance of phenotypic plasticity—a major source of intraspecific variation—in ecological interactions remains necessary. Astonishingly, phenotypic plasticity is often absent from most ecological models, in spite of its prevalence in nature (Sommer, 2020) and a growing body of literature on its importance in competition and coexistence (Hess et al., 2022; Kalirad & Sommer, 2024; Turcotte & Levine, 2016). Furthermore, the often-discussed shortcomings of classical models of ecological systems—namely, their reliance on mean trait value and a deterministic framework that excludes various sources of stochasticity (Schreiber et al., 2023)—are not applicable to EcoGT.

The EcoGT model introduced in this study serves as a first step in utilizing this approach to further explore the importance of various ecological factors that can affect community and metacommunity dynamics and complements the emerging usage of temporal multilayer networks in capturing the complexity of ecological systems (Hutchinson et al., 2019; Pilosof et al., 2017). Given its capacity to reflect both static and dynamic spatial arrangements of individuals in space and time, EcoGT can be used to construct models to explore the effect of the spatial distribution of individuals on coexistence as a supplement to other spatial models, for example, patch occupancy models (Hanski, 1998; Semper-Pascual et al., 2023; Sutherland et al., 2014), to facilitate decision-making in conservation efforts. Finally, the capacity of EcoGT to seamlessly incorporate factors such as scale, dispersal and heterogeneity makes it a fascinating theoretical tool in the pursuit of ‘über’ models in metacommunity (Leibold & Chase, 2018).

AUTHOR CONTRIBUTIONS

Ralf J. Sommer and Ata Kalirad conceived the ideas and designed methodology; Ata Kalirad wrote the software and visualized the results of the simulations; Ralf J. Sommer and Ata Kalirad led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

The authors thank R. B. R. Azevedo and A. Zare for helpful discussions. We used the Sabine cluster from the Hewlett Packard Enterprise Data Science Institute at the University of Houston. We thank the advanced support from the Research Computing Data Core at the University of Houston. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.70121>.

DATA AVAILABILITY STATEMENT

The software is available at <https://github.com/Kalirad/EcoGT> and archived at <https://doi.org/10.5281/zenodo.1602833>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. A single simulation of the stochastic version of the LV model using Gillespie's first-reaction method.

Figure S2. Simulation of EGT on a complete graph with $n=100$ nodes, using two different update methods.

Figure S3. Comparison between the temperature of nodes in a complete graph versus a random graph.

Figure S4. The effect of topology on the temperature of nodes and the death probabilities.

Figure S5. Comparison between the classic WS model and the NWS model when used to generate small-world graphs with the same parameters.

Figure S6. The temperature of dodecahedron and King's graph.

Figure S7. The initial and the final distribution of individuals on a King's graph after 10,000 steps of competition with $\alpha_{12}=\alpha_{21}=1$.

Figure S8. The effect of each rewiring method on mean degree, $\langle k \rangle$, and its variance, σ_k^2 .

Figure S9. The effects of uniform rewiring on the proportion of edges that connect conspecific nodes during a simulation (A), versus the aggregator (B) and the repulsive rewiring (C) algorithms.

How to cite this article: Kalirad, A., & Sommer, R. J. (2025).

Ecological graph theory: Simulating competition and coexistence on graphs. *Methods in Ecology and Evolution*, 16, 2667–2680. <https://doi.org/10.1111/2041-210X.70121>