26th International Congress on Modelling and Simulation, Adelaide, SA, Australia, 30 Nov–4 Dec 2025
mssanz.org.au/modsim2025

A three-patch predator-prey model: migration expands the survival region

Nariyuki Nakagiri [a], Yukio Sakisaka[b] and Kei-ichi Tainaka[c]

[a] *School of Human Science and Environment, University of Hyogo, Himeji 670-0092, Japan*
[b] *Nakamura Gakuen Junior College, Fukuoka 814-0198, Japan*
[c] *Department of Systems Engineering, Shizuoka University, Hamamatsu 432-8561, Japan*
Email: nakagiri@shse.u-hyogo.ac.jp

Abstract: Habitat fragmentation poses a significant threat to biodiversity, making the understanding of metapopulation dynamics crucial for conservation strategies. We developed a lattice-linked model to investigate predator-prey dynamics in a three-patch system, focusing on how migration patterns and network connectivity affect species survival. Unlike conventional models that assume density-driven migration, our approach employs random "swapping migration" where individuals exchange positions with empty sites across patches connected by different network topologies: complete graph (Network A), edge-hub configuration (Network B), and central-hub configuration (Network C). Our agent-based simulations reveal that migration fundamentally alters population dynamics compared to isolated patches. In the absence of migration, environmental improvements in one patch lead to local predator extinction, while migration enables both predator and prey populations to persist by redistributing individuals across the network. Notably, hub patches consistently maintain the highest prey densities due to aggregation effects, with the hub serving as either a population refuge or a vulnerability point depending on whether it experiences environmental perturbation. Counter-intuitively, increasing connectivity does not always benefit conservation outcomes. While migration extends the viable parameter space for species survival, additional corridors can reduce population densities in non-hub patches by preventing predator aggregation at hubs. Our findings challenge the conventional assumption that enhanced connectivity universally improves conservation effectiveness, suggesting that corridor construction should carefully consider network topology and hub effects. This work provides new insights for designing optimal habitat networks in fragmented landscapes.

Keywords: *predator-prey dynamics, agent-based model, network topology, swapping migration, hub effect*

© MSSANZ and The Authors, CC-BY

1. INTRODUCTION

In recent years, many species have faced the risk of extinction due to environmental destruction caused by human activities. In particular, habitat fragmentation from destruction has become a critical factor undermining species survival (Haddad et al., 2015; Wilson et al. 2016), leading to a significant loss of biodiversity. As a countermeasure, habitat conservation and management are regarded as key strategies for preventing species extinction.

Habitats are often spatially heterogeneous and composed of small, discrete regions known as patches, where organisms live by migrating between them. To model population dynamics in such environments, ecologists have developed the metapopulation model, which has been widely used in many studies (Levin, 1974; Hanski and Gilpin, 1997). However, in these conventional models, patches are assumed to be homogeneous, and spatial structures and capacity limitations between patches are often not considered. In reality, habitat patches have finite spatial capacity, and individual migration is subject to excluded volume effects. To incorporate these realistic constraints, we have developed and analysed lattice-link models in which patches are represented as lattices, allowing explicit treatment of spatial limitations (Nakagiri et al., 2019; 2024).

In many traditional models, it is commonly assumed that individuals actively migrate from high-density patches to low-density ones. However, in this study, we employ a random migration model, in which individuals randomly select corridors to move between patches (Masuda et al., 2017; Nagatani et al., 2018; Yokoi et al., 2020a, 2020b). As a result, density imbalances persist, and individuals remain unevenly distributed across patches. This often leads to the formation of core patches with disproportionately high population densities (Nagatani et al., 2018).

The effects of patch connectivity on species persistence and extinction have been studied using graph-theoretic approaches. In such models, patches are treated as nodes and corridors as links to analyse landscape connectivity and conservation outcomes (Minor & Urban, 2008). However, even when a core patch is preserved, high connectivity can increase vulnerability to disturbances such as wildfires and floods, which may spread to adjacent patches. Conservation efforts can thus have unintended negative effects. For example, Nakagiri et al. (2024) showed that in a single-species system, increasing connectivity reduced population density, challenging the assumption that enhanced connectivity always improves conservation outcomes. This counterintuitive result highlights the need to reassess conventional strategies. Building on one-species system findings, this study introduces a predator-prey model with asymmetric reproductive rates and stochastic migration, advancing the lattice-link framework developed for two-patch systems (Nakagiri et al., 2019) and three-patch configurations (Nakagiri et al., 2024). Unlike earlier single-species approaches, the model incorporates interspecific interactions and reveals emergent dynamics such as rescue effects and inverse hub impacts not captured in prior studies.

To better understand such complex interactions, this study focuses on a two-species predator-prey system (Tainaka and Fukazawa, 1992; Tainaka 1994) in which individuals move among three habitat patches. Using an agent-based model (Nakagiri et al., 2001; 2005; 2010; Nakagiri and Tainaka, 2004; Perc, 2011; Szabó and Fath, 2007; Tainaka, 1988), we simulate how increasing the reproduction rate in a specific patch, interpreted as a proxy for environmental improvement, affects predator and prey populations across all patches. In particular, we aim to clarify how migration patterns and patch connectivity structures influence the dynamics of population persistence and extinction. The metapopulation framework, originally proposed in ecology (Levin, 1974; Hanski and Gilpin, 1997), has recently been extended to a variety of fields, including epidemiology (Nagatani et al., 2019) and human behavioural modelling (Kabir and Tanimoto, 2019). In these network-based approaches, habitat patches are interpreted as nodes and the migration corridors between them as links (Seno, 1998; Nagatani et al., 2018), providing a powerful tool for analysing species dynamics and conservation strategies in complex landscapes.

To address these issues, we employ a lattice-link model in which each patch is represented as a two-dimensional lattice, capturing local interactions and spatial limitations. Moreover, individuals migrate stochastically among patches via corridors defined by a graph structure. Unlike directed or density-driven migration, this random migration scheme leads to persistent heterogeneity among patches, often forming core patches with high local density. Before analyzing multi-patch dynamics, we first describe the one-patch model which corresponds to a spatial predator-prey system without migration (Tainaka, 1994). In this model, as shown in Figure 1(a), the system consists of a single patch, where individuals are fixed on a lattice and interact locally in a stochastic manner. Consider prey and predators on a lattice. The system evolves through three types of local interactions:

(i) Predation: when a predator encounters a prey in a neighboring cell, the prey is replaced by a new predator at a rate p.

(ii) Reproduction: when a prey encounters an empty neighboring cell, it produces a new prey at a rate r.

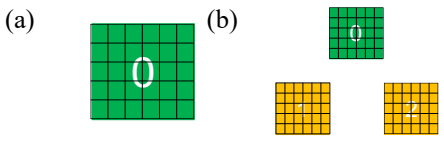

Figure 1. Schematic diagram of the patch (lattice) environment: (a) Single-patch model. (b) Three-patch model without migration. Lattices are labeled 0–2, lattice 0 having modified reproduction rate. No migration occurs between lattices. Green indicates the perturbed lattice (lattice 0), yellow represents unperturbed lattices.

© MSSANZ and The Authors, CC-BY

(iii) Death: prey and predators die spontaneously at rates d_x and d_y, respectively, leaving empty cells behind.
This model exhibits characteristic spatial structures, with prey forming clusters and predators distributed more uniformly. In a single-lattice system, Tainaka (1994) demonstrated that such clustering can lead to catastrophic transitions: small parameter changes, such as in reproduction or mortality rates, can trigger sudden prey outbreaks or predator extinctions. These phenomena arise from changes in spatial patterns and cannot be captured by mean-field approximations. This corresponds to patch 0 dynamics. As illustrated in Fig. 1(b), in the no-migration case, varying the reproduction rate of patch 0 does not affect the qualitative outcome; the same behaviour is observed.

2. LATTICE-LINK MODEL

We consider a predator-prey system as a model ecosystem; two species live on three lattices. Each lattice is composed of discrete sites, where each site can be either empty (O), occupied by prey (X), or occupied by a predator (Y). Interactions occur that locally within each lattice are given as follows:

$$\mathrm{Y} + \mathrm{X} \xrightarrow{p} \mathrm{Y} + \mathrm{Y} \qquad \text{(rate: } p\text{)}, \qquad (1a)$$

$$\mathrm{X} + \mathrm{O} \xrightarrow{r_i} \mathrm{X} + \mathrm{X} \qquad \text{(rate: } r_i\text{)}, \qquad (1b)$$

$$\mathrm{X} \xrightarrow{d_x} \mathrm{O},\ \mathrm{Y} \xrightarrow{d_y} \mathrm{O} \qquad \text{(rate: } d_x, d_y\text{)}. \qquad (1c)$$

Reactions (1a)–(1c) denote predation, reproduction and death processes, respectively. Parameters p, r_i, d_x *and* d_y represent the predation rate, the reproduction rate of prey in lattice i, and the death rates of prey and predator, respectively. Figure 2 illustrates migration types considered here. Figure 2(a) shows a complete graph; Figures 2(b) and 2(c) depict incomplete graphs, with the perturbed lattice at the edge in Figure 2(b) and at the hub in Figure 2(c). We use the "swapping migration" method proposed by Yokoi et al. (2019), in which migration is defined as the exchange between an occupied site (X or Y) and an empty site (O):

$$k + \mathrm{O} \xrightarrow{m} \mathrm{O} + k \quad (k = X \text{ or } Y) \text{ (rate: } m\text{)}, \qquad (1d)$$

where reaction (1d) denotes the migration process. The parameter m represents the migration rate. Periodic boundary conditions were uniformly imposed on each lattice structure used in the simulations, and the simulations were performed as described below:

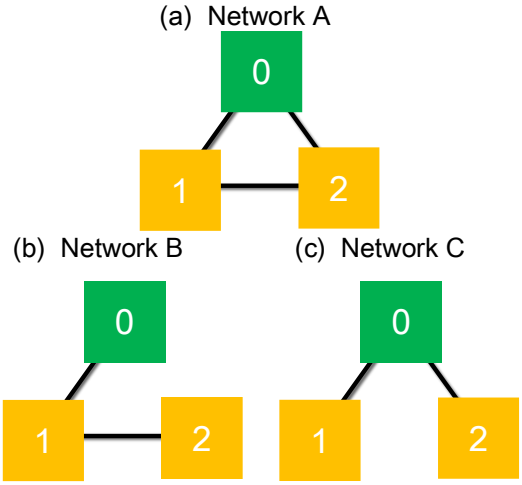

Figure 2. Schematic diagram of the migration process. (a) Network A: complete graph. (b) Network B: incomplete graph with variable edge lattices. (c) Network C: incomplete graph with variable hub lattices. Green indicates the perturbed lattice (lattice 0), yellow represents unperturbed lattices. Black lines denote possible swapping moves between lattices. If a swap requires an empty cell in lattice 2 and none are available, the agent in lattice 1 cannot move.

i) Birth process. A single site is randomly selected from the three lattices. If the selected site in lattice i is occupied by prey (X), one of its four neighbouring sites within the same lattice is randomly chosen. If this neighbouring site is empty (O), it becomes X with rate r_i.

ii) Death process. A single site is randomly selected from the three lattices. If the selected site in lattice i is occupied by prey (X) or predator (Y), it becomes empty(O) with rate d_{x_i} or d_{y_i}, respectively.

iii) Migration process. A single site (i, j) is randomly selected from one of the three lattices (lattice α). If the selected site is occupied by prey (X), then a site (g, h) is randomly selected from another patch $\beta \neq \alpha$. If the site (g, h) in patch β is empty (O), then X migrates at rate m, and the states of two sites (X and O) are exchanged.

3. RESULTS

Figure 3 shows typical population dynamics, where the densities of prey (blue) and predators (red) are plotted. Let x_0, x_1, x_2 denote the prey densities on patches 0, 1, and 2, respectively. At time t=0, the parameter r_0 is abruptly increased from 0.5 to 1.0 as an external perturbation. Before the perturbation (t<0), the system remains in an equilibrium (stationary state), defined as a state in which all densities fluctuate only slightly around constant values. In the no-migration case (m=0; Fig. 2(a)), the dynamics are similar to those in the one-patch model: in perturbed patch 0, the predator density (Y) decreases while the prey density (X) increases, and the populations in patches 1 and 2 remain unchanged (Fig. 3(a)). For $m \neq 0$, the results are shown in Figs. 3(b)–3(d). Immediately after the perturbation, the predator density in all lattices increases sharply, but later declines to a new equilibrium. In contrast, the prey density in lattice 0 increases, whereas the prey densities in lattices 1 and 2 decrease in the new equilibrium. Thus, despite the increase in r_i, the prey densities in lattices 1 and 2 decrease in the new equilibrium. This behaviour can be explained as follows: the perturbation initially increases prey density, which enhances predation and leads to the new equilibrium distribution observed in Fig. 3. A notable difference is that, regardless of migration, the increase in r_i causes the predator density y to increase; however, in the no migration (m=0), x_0

© MSSANZ and The Authors, CC-BY

decreases, whereas in the presence of migration (m=1), x_0 increases in each network type (A, B, and C).

The spatial pattern formations are examined in Fig. 4, which shows the stationary-state distributions: (a) no migration (m=0); (b)–(d) migration (m=1) in Networks A, B, and C, respectively. In the no-migration case (Fig. 4(a)), agents aggregate and form clusters. In contrast, agents randomly disperse for m=1 (Fig. 4(b–d)). Migration enables agents to access empty sites (O) and prey (X), which are essential for the reproduction (Eq. (2b)) and predation (Eq. (2a)) processes.

Figure 5 shows the stationary-state densities in the lattice-link model as functions of the reproduction rate r_0 of lattice 0. Fig. 5 (a) corresponds to the no-migration case (m=0), whereas Figs. 5(b)–(d) show the results with migration (m=1). In the absence of migration (Fig. 5(a)), extinction occurs. In contrast, as seen in Figs. 5(b)–(d), migration prevents extinction and expands the survival region.

In Fig. 5(b)–(d), as the reproduction rate r_0 of prey (X) in patch 0 increases, the densities of both predators (Y) and prey (X) in lattice 0 increase, while the prey densities in lattices 1 and 2 decrease. Furthermore, in Fig. 5(c), the prey density is highest in lattice 1, whereas in Fig. 5(d), it is highest in lattice 0, indicating that the prey density peaks in the hub patch. In addition, under edge-side environmental changes, the predator and prey densities in patch 1 are the highest. Moreover, from the complete network graph, reducing the links between patches 1 and 2 increases the predator density in the hub (lattice 0), whereas increasing these links decreases the prey density in some patches.

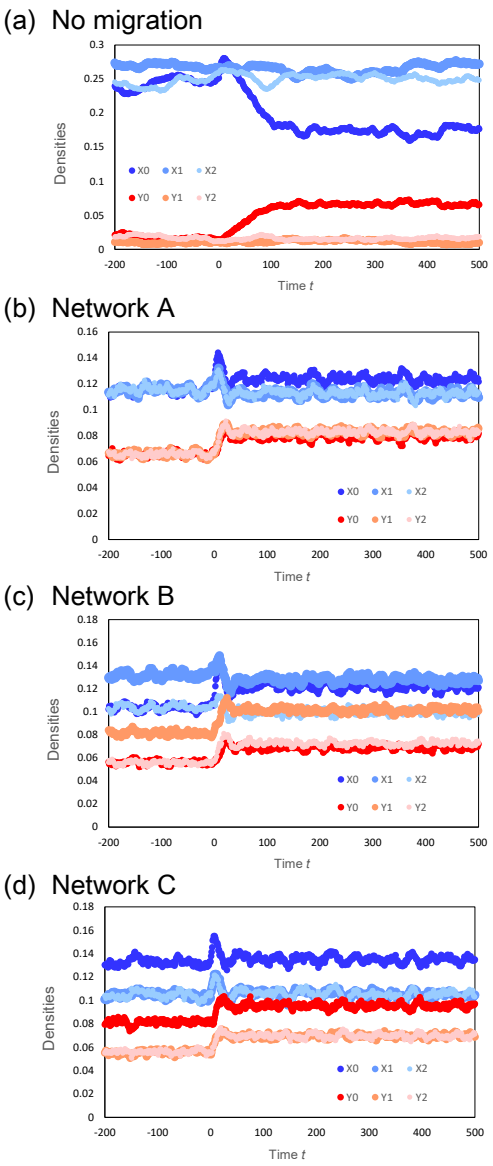

Figure 3. Population dynamics for lattice-link model with initial condition r_0= r_1= r_2=.0.5. At time t=0, r_0 is abruptly increased to 1.0. Panels (a)- (d) show no migration, network A, B, and C, respectively. All simulations use 100x100 lattice. Let x_0, x_1, x_2 denote the prey densities on patches 0, 1, and 2, respectively.

4. DISCUSSION

Conventional theory emphasizes corridor-based migration toward low-density patches (Hanski and Gilpin, 1997). In contrast, we adopt a lattice-centric model in which individuals move randomly. Extending previous lattice-link frameworks, our three-patch predator–prey system incorporates interspecific interactions and spatial perturbations, revealing complex spatiotemporal dynamics beyond earlier single-species models. Unlike our previous prey-only migration models (Nakagiri et al., 2019; 2024), this extension enables examination of interspecific responses to stochastic movement and spatial heterogeneity. Individuals randomly select corridors to determine destinations (Masuda et al., 2017; Nagatani et al., 2018; Yokoi et al., 2020a; Tainaka et al., 2021). Using this mechanism, we simulated sudden environmental improvements and spatially uneven perturbations to examine interspecific responses under stochastic movement, where random transitions are considered advantageous.

If migration does not occur, prey tend to form spatial clusters (Figure 4(a)). However, because predators remain in lattice 0, predation pressure gradually reduces the prey density x_0 over time. In contrast, when migration is allowed, predators migrate from lattice 0—where prey density has increased—to other lattices. As a result, predator density y_0 in lattice 0 increases. However, since predation pressure is not excessively high, predation remains limited, and the prey density actually increases. In this way, both predator and prey densities in lattice 0 increase. On the other hand, predators that migrate to other lattices can prey more efficiently, leading to reductions in the prey densities x_1 and x_2. Moreover, migration inhibits the formation of spatial prey clusters (Figures 4(b)–(d)), which likely lowers local density and thereby reduces the protective effect against predation.

We discuss the effect of the hub in three-patch networks. In Fig. 5(c), prey density of lattice 1 is highest; in Fig. 5(d), prey density of lattice 0 is highest. This indicates that the density of the lattice with the hub structure is the highest. This can be considered as follows: due to the hub effect, individuals tend to gather at hubs (Nakagiri et al., 2024). Therefore, the hub lattice has higher prey density than other patches. In Fig. 5(c), patch 1 is the hub,

© MSSANZ and The Authors, CC-BY

whereas in Fig. 5(d), patch 0 is the hub containing both prey and predators. This aggregation often makes the hub a focal point influencing population dynamics and spatial distribution. When the hub is not the target of perturbation (Network B), it can serve as a refuge that buffers against environmental stress, resulting in increased local densities in the hub lattice. Conversely, if the hub experiences perturbation, its central role can cause rapid population declines. Therefore, the high prey density in the hub lattice (Fig. 5(c) and 5(d)) reflects this network-driven aggregation and its ecological implications. The issue of corridor construction in conservation biology has been discussed by Nakagiri et al. (2024), who demonstrated that in a single-species system, Network C is optimal for the survival of a single species under favourable environmental conditions. However, if Network C is converted into Network A by constructing an additional corridor, the effectiveness of conservation measures is reduced. In our two-species model, it is difficult to determine a universally optimal network for the survival of each species.

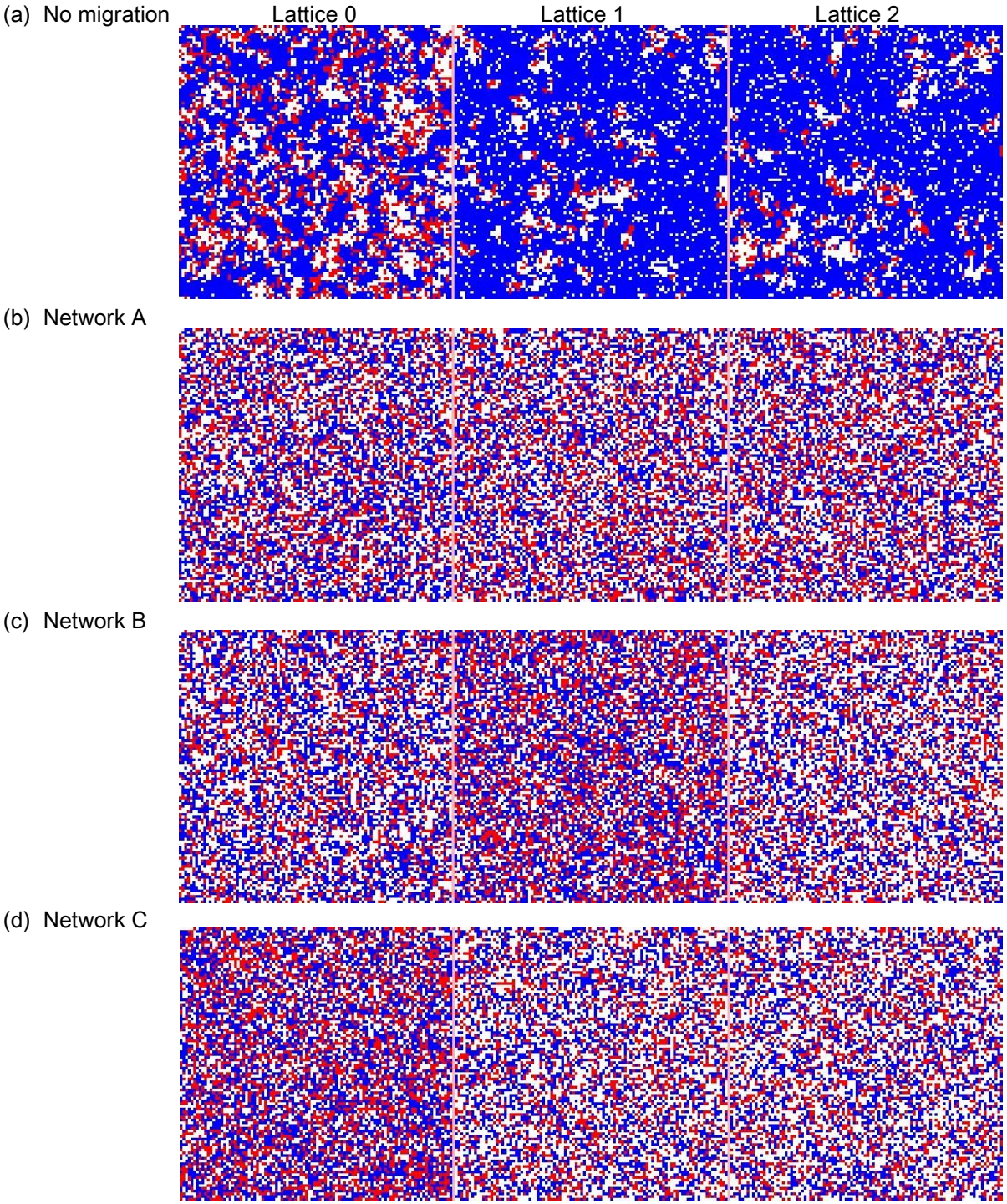

Figure 4. Typical stationary-state spatial patterns for the three network types at t=1000. Prey (X), predators (Y), and empty sites (O) are indicated in blue, red, and white. (a) No migration (m=0); (b) Network A (m=1); (c) Network B (m=1); (d) Network C (m=1).

© MSSANZ and The Authors, CC-BY

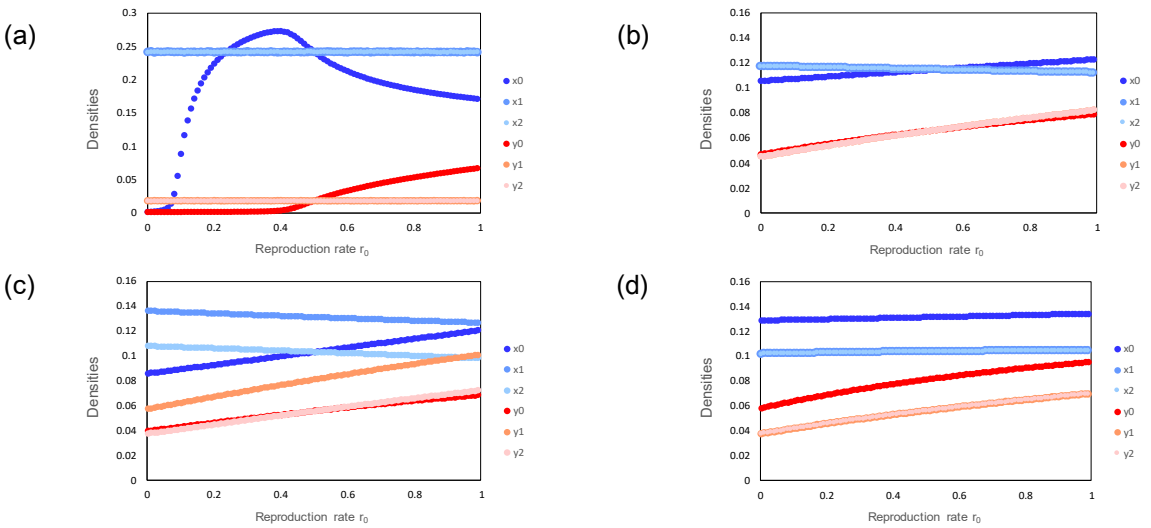

Figure 5. The steady-state densities of prey of lattice 0 (x_0), 1 (x_1) and 2 (x_2) and predator of lattice 0 (y_0), 1 (y_1) and 2(y_2) are plotted against r_0. When reproduction rate of lattice 0 (r_0) increases, the survival parameter region is extended. (a) m=0, (b) m=1.0, network A, (c) m=1.0, network B, (d) m=1.0, network C. Let x_0, x_1, x_2 denote the prey densities on patches 0, 1, and 2, respectively. Each data point shows mean steady state density, from 100 simulations per reproduction rate r_0 and network type, averaged over final 1000 time steps.

Nevertheless, our results show that adding corridors (links) to increase connectivity raises prey density on hub patches but reduces it on non-hub patches. This counterintuitive outcome arises because additional corridors prevent predators from aggregating at the hub, thereby diminishing the hub effect. Thus, corridor construction does not necessarily lead to beneficial outcomes, and connectivity should be increased with caution, taking into account the role of hub patches in the network.

5. CONCLUSION

Migration has been widely observed in nature (Alerstam et al., 2003; Shaw, 2016). In this study, we used a lattice-link model to analyse the effects of spatial structure on a predator-prey system. We employed the "swapping migration" method, in which migration is defined as the exchange between an occupied cell (X or Y) and an empty cell (O). Such swapping movements are also observed in other transport phenomena (Nakagiri et al., 2019). For example, vehicle movement in traffic flow (Gupta et al., 2013) can be described similarly, where vehicles move by exchanging positions with empty cells. Similarly, random walks of individuals in ecosystems follow this pattern (Berg, 1993; Sato et al., 2015), with individuals moving randomly but only into empty sites.

Our analysis revealed that, under both non-migratory (m=0) and migratory (m=1) conditions, increasing the reproduction rate in lattice 0 decreased the prey populations in lattices 1 and 2. This suggests that environmental improvements in one patch may negatively affect other patches. Conversely, predator and prey populations in lattice 0 tended to increase. Furthermore, extinction was observed in the absence of migration, but not in its presence. Therefore, migration appears to extend the viable parameter space for species survival. However, how these findings translate to real ecosystems remains to be fully elucidated.

This study extends previous single-species models into predator-prey systems and embeds them in a spatially structured lattice-link framework. This approach includes interspecific interactions, patch-specific reproduction, and stochastic migration, revealing novel dynamics such as rescue effects and hub impacts. These findings underscore the importance of considering species interactions and spatial heterogeneity in conservation planning.

ACKNOWLEDGEMENTS

This work was supported by JSPS KAKENHI Grant Number JP23K11264.

REFERENCES

Alerstam T, Hedenström A and Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103, 247–260

Berg HC (1993) Random Walks in Biology. Princeton University Press, New Jersey

Gupta AK and Redhu P (2013) Analyses of driver's anticipation effect in sensing relative flux in a new lattice model for two-lane traffic system. *Physica* A 392, 5622–5632

© MSSANZ and The Authors, CC-BY

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song D-X and Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1(2), e1500052

Hanski I and Gilpin ME (1997) Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego

Kabir KMA and Tanimoto J (2019) Evolutionary vaccination game approach in metapopulation migration model with information spreading on different graphs. *Chaos, Solitons and Fractals* 120, 41–55

Masuda N, Porter MA and Lambiotte R (2017) Random walks and diffusion on networks. *Physics Reports* 716–717, 1–58

Minor ES and Urban DL (2008) A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conservation Biology* 22, 297–307

Nagatani T, Ichinose G and Tainaka K (2018) Heterogeneous network promotes species coexistence: metapopulation model for rock-paper-scissors game. *Scientific Reports* 8, 7094

Nagatani T, Ichinose G and Tainaka K (2019) Epidemic spreading of random walkers in metapopulation model on an alternating graph. *Physica* A 520, 350–360

Nakagiri N and Tainaka K (2004) Indirect effects of habitat destruction in model ecosystems. *Ecological Modelling* 174, 103–114

Nakagiri N, Tainaka K and Tao T (2001) Indirect relation between extinction and habitat destruction. *Ecological Modelling* 137, 109–118

Nakagiri N, Tainaka K and Yoshimura J (2005) Bond and site percolation and habitat destruction in model ecosystems. *Journal of the Physical Society of Japan* 74, 3163–3166

Nakagiri N, Sakisaka Y, Togashi T, Morita S and Tainaka K (2010) Effects of habitat destruction in model ecosystems: parity law depending on species richness. *Ecological Informatics* 5, 241–247

Nakagiri N, Sato K, Yokoi H and Tainaka K (2019) Two-patch model for contact process: migration extends the survival region of species. In: Elsawah S (ed.) MODSIM2019, 23rd International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, 407–413

Nakagiri N, Yokoi H, Morishita A and Tainaka K (2024) Three-lattice metapopulation model: connecting corridor between patches may be harmful due to "hub effect". *Ecological Complexity* 59, 101090

Nisbet RM and Gurney WSC (1976) A simple mechanism for population cycles. *Nature* 263, 319–320

Perc M (2011) Does strong heterogeneity promote cooperation by group interactions? *New Journal of Physics* 13, 123027

Sato K, Hasegawa T, Morita S, Yoshimura J and Tainaka K (2015) Advantage or disadvantage of migration in a prey-predator system. *Far East Journal of Applied Mathematics* 93, 109–121

Seno H (1998) Effect of a singular patch on population persistence in a multi-patch system. *Ecological Modelling* 43, 271–286

Shaw AK (2016) Drivers of animal migration and implications in changing environments. *Evolutionary Ecology* 30, 991–1007

Szabó G and Fath G (2007) Evolutionary games on graphs. *Physics Reports* 446, 97–216

Szolnoki A and Perc M (2017) Second-order free-riding on antisocial punishment restores the effectiveness of prosocial punishment (spatial public goods game). *Physical Review* X 7, 041027

Tainaka K (1988) Lattice model for the Lotka-Volterra system. *Journal of the Physical Society of Japan* 57, 2588–2590

Tainaka K and Fukazawa S (1992) Spatial pattern in a chemical reaction system: prey and predator in the position-fixed limit. *Journal of the Physical Society of Japan* 61, 1891–1894

Tainaka K (1994) Intrinsic uncertainty in ecological catastrophe. *Journal of Theoretical Biology* 166, 91–99

Tainaka K, Nakagiri N, Yokoi H and Sato K (2021) Multi-layered model for rock-paper-scissors game: a swarm intelligence sustains biodiversity. *Ecological Informatics* 66, 101477

Wilson, M. C., Chen, X. Y., Corlett, R. T., Didham, R. K., Ding, P., Holt, R. D., Holyoak, M., Hu, G., Hughes, A. C., Jiang, L., Laurance, W. F., Liu, J., Pimm, S. L., Robinson, S. K., Russo, S. E., Si, X., Wilcove, D. S., Wu, J., and Yu, M. (2016). Habitat fragmentation and biodiversity conservation: Key findings and future challenges. *Landscape Ecology, 31*, 219–227.

Yokoi H, Tainaka K and Sato K (2019) Metapopulation model for a prey-predator system: nonlinear migration due to the finite capacities of patches. *Journal of Theoretical Biology* 477, 24–35

Yokoi H, Sato K and Tainaka K (2020a) Parity laws in a cyclic ecosystem: metapopulation migration model with different patch capacities. *Journal of the Physical Society of Japan* 89, 033801

Yokoi H, Tainaka K, Nakagiri N and Sato K (2020b) Self-organized habitat segregation in an ambush-predator system: nonlinear migration of prey between two patches with finite capacities. *Ecological Informatics* 55, 101022

© MSSANZ and The Authors, CC-BY