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RESEARCH ARTICLE

From nature reserve to mosaic management: Improving matrix survival, not permeability, benefits regional populations under habitat loss and fragmentation

Yuichi Yamaura[1,2] | Robert J. Fletcher Jr[3] | Steven J. Lade[1,4] | Motoki Higa[5] | David Lindenmayer[1]

[1]Fenner School of Environment and Society, The Australian National University, Canberra, Australia

[2]Shikoku Research Center, Forestry and Forest Products Research Institute, Kochi, Japan

[3]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA

[4]Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden

[5]Faculty of Science and Technology, Kochi University, Kochi, Japan

Correspondence
Yuichi Yamaura
Email: yamaura@ffpri.affrc.go.jp

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Abstract

1. Although matrix improvement in fragmented landscapes is a promising conservation measure, matrix permeability (willingness of an organism to enter the matrix) and movement survival in the matrix are usually aggregated. Consequently, it is unknown which matrix property needs to be improved. It also remains unclear whether matrix upgrading from dispersal passage to providing reproduction opportunities has large conservation benefits and whether there are interactive effects between habitat and matrix management.
2. We examined matrix effects on regional populations across a gradient of habitat loss and fragmentation using simulation experiments that integrated demographic processes and movement modelling based on circuit theory. We separately modified the levels of matrix permeability and movement survival to evaluate their individual effects. We also altered the amount and configuration of not only habitat but also improved matrix to assess their effects on population vital rates (size, survival and density).
3. In binary landscapes comprising habitat and unimproved matrix, matrix movement survival had larger effects on population vital rates than matrix permeability. Increasing movement survival increased vital rates, yet, increasing matrix permeability decreased vital rates. Increased permeability required corresponding increased movement survival to offset potential negative population outcomes.
4. When subsets of the matrix functioning as dispersal passage only (where no reproduction opportunities existed) were improved, increasing matrix permeability but holding movement survival constant reduced all vital rates, especially with increasing habitat fragmentation. In contrast, when movement survival increased, vital rates increased given strong habitat fragmentation. The benefits of upgrading dispersal passage to provide reproduction opportunities for population survival were greatest when habitat amount was moderate. We also found synergetic effects between amounts of habitat and improved matrix, and

the benefits of matrix improvement were promoted when improvement was achieved in a spatially aggregated manner.

5. *Synthesis and applications*. Matrix improvement and connectivity modelling aimed at increasing movement survival will likely bring larger conservation benefits than those for improving permeability alone. Buffering and connecting habitat remnants with improved matrix could provide benefits as long as movement survival is increased. Simultaneous implementation of habitat management and matrix improvement would yield synergistic conservation benefits.

KEYWORDS
circuit theory, heterogeneous landscape, landscape configuration, landscape connectivity, matrix management, movement mortality, population persistence, sink population

1 | INTRODUCTION

The earth's land surface is a mosaic of land uses. More than 75% of ice-free land surface has been subject to anthropogenic alterations (Ellis & Ramankutty, 2008), and human land uses embedding natural habitats are called the 'matrix'. The matrix can affect a variety of processes in the landscape (Driscoll et al., 2013; Prevedello & Vieira, 2010) such as movement behaviour (Kuefler et al., 2010), inter-patch movement (Revilla et al., 2004), occupancy and abundance of patches (Prugh et al., 2008; Watling et al., 2011) and species–area relationships (Chase et al., 2020). Accordingly, improvement of the surrounding matrix is considered to be an important conservation measure in fragmented landscapes (Arroyo-Rodríguez et al., 2020; Kremen & Merenlender, 2018).

Vandermeer and Carvajal (2001) cautioned, however, that we should not automatically assume that increasing matrix quality will bring positive outcomes. First, although empirical studies have shown that an increase in matrix permeability can enhance emigration, colonization and inter-patch movement (Haynes & Cronin, 2003; Ricketts, 2001), Vandermeer and Carvajal (2001) showed that high permeability can lead to population extinction via population synchrony. Cronin (2007) also experimentally demonstrated that a highly permeable matrix enhanced (leaked) emigration from habitat patches, which reduced population density and led to population extinction.

This apparent contradiction in the roles of matrix permeability may be due to the fact that permeability and survival while moving through the matrix ('movement survival' hereafter) are usually aggregated (Day et al., 2020; Fletcher et al., 2019). Permeability is defined as the willingness of an organism to cross a particular environment (Adriaensen et al., 2003; Zeller et al., 2012), and often considered to be an outcome of intrinsic behavioural decisions made by an individual (Castellón & Sieving, 2006). Permeability is therefore different from movement mortality (or conversely, survival) during movement, which is often driven by extrinsic factors. Assuming that dispersers properly evaluate corresponding land cover, high permeability (low matrix resistance) likely results in high

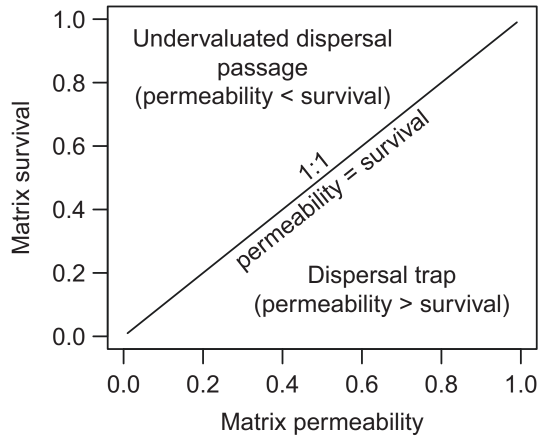

FIGURE 1 Schematic relationships between matrix permeability and movement survival of the matrix. Matrix movement mortality is the complement of movement survival. Matrix permeability represents the probability of an organism to enter the matrix. Roles of the matrix as dispersal passage depend on the relative values of its permeability and survival (after Vasudev et al., 2015)

movement survival, which in turn increases population persistence and size (Fahrig, 2001; Wiegand et al., 2005). However, mismatches can occur, such as 'dispersal traps' (e.g. high permeability but low survival: Fahrig & Rytwinski, 2009), and would have substantial impacts on population persistence (Vasudev et al., 2015). We therefore need to investigate the effects of matrix improvement by isolating permeability from movement survival (Figure 1).

Matrix improvement may convert non-habitat into sink habitat that provides breeding opportunities but where reproduction is insufficient to offset mortality (sensu Pulliam, 1988). Given this possibility, and to avoid confusion, here we use the term 'matrix' to include areas providing the potential for dispersal passage only or where sink populations occur. We use the term 'habitat' to include only patches that support source populations that are a net exporter of individuals (Pulliam, 1988). Provision of population sinks through matrix improvement has the potential for positive and negative conservation outcomes (Heinrichs et al., 2015). For example, modelling studies have shown that the existence of population sinks can increase population size via creation of refugia for floater individuals while abundant sinks can lower population size since individuals may not reach source habitats (Howe et al., 1991; Pulliam & Danielson, 1991). However, these modelling studies did not consider the roles of movement mortality. The presence of population sinks in fragmented landscapes can facilitate dispersal success by connecting source habitats (Heinrichs et al., 2015), which may offset the potential negative effects of population sinks. Consequently, understanding the effects of improving the matrix as population sinks requires considering its amount and configuration. Indeed, buffering and connecting remnant patches with an improved matrix has been suggested as a key conservation measure for decades (Franklin, 1993).

To explore these possible consequences of matrix improvement, we need a tractable framework for movement modelling in heterogeneous landscapes. When a subset of the matrix is improved, at least three cover types (habitat, improved and unimproved matrix) effectively intertwine and the resulting heterogeneous landscape quickly becomes complex. Different matrix types can have different levels of permeability and movement survival, and the isolation of remnant patches cannot be accurately represented by inter-patch Euclidian distance (Adriaensen et al., 2003). In this context, circuit theory is increasingly used to model individual movement and gene flow (Dickson et al., 2019; Fletcher et al., 2016; Hall et al., 2021).

Circuit theory is based on the concept of electric current that flows across the networks of nodes connected by resistors (or circuit: McRae et al., 2008). An application of circuit theory is to inject the electric current across the circuit to view current flow as movement flow across a landscape in terms of a random walk. Different resistance can be assigned to individual resistors to reflect variations in matrix permeability. Circuit theory allows consideration of all possible (competing) movement routes in contrast to other connectivity models (e.g. least-cost path analysis). Since the theory does not simulate every behavioural decision of each individual like individual-based models (cf. Day et al., 2020), large-extent and fine-grained problems such as range-wide connectivity modelling with 30-m resolution are feasible (Gray et al., 2019). Circuit theory also allows for considering movement mortality by connecting nodes to the 'ground' (McRae et al., 2008), thereby providing a way to evaluate roles of permeability and movement survival separately.

Our objectives were to systematically examine matrix effects on regional populations using simulation experiments. We constructed a spatially explicit population model by integrating circuit theory and demographic processes to evaluate management practices on population outcomes (Moilanen, 2011). We addressed four questions. First, across the gradient of habitat loss and fragmentation, when and how do permeability and movement survival in the matrix influence population vital rates across the landscape, that is, population size, population survival and population density? Second, does the improvement of permeability and movement survival have different effects on population vital rates? Third, when does matrix improvement supporting population sinks have larger benefits than matrix improvement providing only dispersal passage? Fourth, as implied by field experiments (Baum et al., 2004; Fletcher et al., 2014), are there any interactive effects of habitat and matrix management?

2 | MATERIALS AND METHODS

2.1 | Landscape model

Our artificial landscape was 50 × 50 cells. Landscapes included three cover types—habitat, low- and high-quality matrix—similar to the approach described by Wiegand et al. (2005). In this context, habitat was areas that could support source populations that are a net exporter of individuals. Low-quality matrix was the 'background' where reproduction did not occur and only provided areas through which individuals could move (and suffer mortality). A high-quality matrix was where reproduction could occur but was insufficient for population growth (i.e. population sinks).

To create landscapes, we altered the amount and configuration of habitat and high-quality matrix. We first filled all cells with low-quality matrix, and randomly assigned habitat cells into low-quality matrix cells by different amount and fragmentation (independent of habitat amount or fragmentation per se: Fahrig, 2017) following the method of Fahrig (2001). Specifically, we randomly selected a matrix cell and generated a random number from a uniform distribution ranging 0–1 (degree of habitat fragmentation: FRAG hereafter). The selected cell became a habitat cell if the selected cell had any adjacent habitat cells based on an eight-neighbour rule or if the random number was less than FRAG. Therefore, FRAG indicates the randomness of habitat assignment in terms of spatial contiguity, with higher values indicating stronger fragmentation (see Appendix S1). We repeated this procedure until the number of habitat cells, which was specified by the habitat amount, was assigned.

We next randomly assigned high-quality matrix cells into low-quality matrix cells, which were not replaced by habitat cells, with different amount and configuration. We used another random number similar to FRAG to describe the contiguity of habitat and high-quality matrix cells. When fragmentation of high-quality matrix was weak, high-quality matrix cells were newly assigned to be adjacent to existing habitat and high-quality matrix cells (habitat and high-quality matrix cells were treated equally). This resulted in habitat remnants surrounded by, and connected to, other remnants by a high-quality matrix (Appendix S1).

2.2 | Movement model

We obtained 'expected' dispersal rates among cells with circuit theory, assuming that individuals move as biased random walker. A challenge associated with spatially explicit population modelling is dealing with movement behaviour, which is particularly important in our study where the landscape is composed of three cover types with different levels of permeability and movement survival. We overcame this issue by applying circuit theory using the program

Circuitscape (McRae et al., 2013), which is increasingly used in ecology, evolution and conservation (Dickson et al., 2019; Fletcher et al., 2016; Hall et al., 2021). Flow of the electric current across the circuit (individual movement in the landscape) is dictated by the map of movement resistance (the reciprocal of permeability or 'conductance'), which was built by the structure of simulated landscapes and specified permeability of three cover types described below.

In our application of circuit theory, we added 'grounds' into the circuit to consider movement mortality (McRae et al., 2008), analogous to an 'absorbing' state in Markov chain theory (Fletcher et al., 2019). The use of grounds greatly expands the utility of circuit theory to model landscape-level connectivity, yet in practice, this functionality of considering movement mortality has rarely been utilized (Fletcher et al., 2019). For individual matrix cells, we therefore assigned the resistance dictating the amount of current exiting the circuit as movement mortality (we call exiting resistance) based on the specified movement mortality and movement resistance in the surrounding cells (Appendix S2).

After executing Circuitscape, we retrieved cell-to-cell dispersal success rates (proportion of the current reaching every recipient habitat cell from a certain habitat cell) from the current map. This process was repeated for all habitat cells to create a mathematical transition matrix—that we call **D** (spatially explicit dispersal) analogous to Fletcher et al. (2019)—and it comprised elements as expected dispersal success rates among habitat cells in the landscape (see Appendix S2 for the details). Here we can derive dispersal success rates for individual habitat cells (proportion of the current reaching any other habitat cells) and their mean value across all habitat cells may be used as a measure of landscape connectivity.

2.3 | Demography and movement simulation

To simplify the model, we simulated asexual populations; that is, we omitted males and dealt only with females as in other spatially explicit population models (e.g. Fahrig, 2001). Our first focus was to assess the roles of the matrix as a dispersal passage, that is, intervening areas which individuals had to cross to colonize new breeding habitats. We therefore changed matrix quality by altering permeability and movement survival. In these cases, reproduction occurred only in habitat patches. However, we also considered cases where an improved high-quality matrix acted as a population sink, that is, individuals could breed but productivity was insufficient to offset annual mortality. Specifically, according to the structure of our demographic model (described in Appendix S3), the intrinsic population growth rate (λ) of breeding habitat can be formulated as $\lambda = (1 + \beta) \times P$ where β is productivity (expected number of offspring per individual per breeding attempt) and P is annual survival rate (complement of annual mortality). Within this structure, sink populations have $\lambda < 1$. Since our objective was to assess the roles of landscape structure and matrix quality, we held demographic parameters of habitat (e.g. β, P) constant (Appendix S3). Our demographic model was based on Howe et al. (1991) and Fahrig (2001).

At the onset of simulations (the beginning of the first year), we filled all habitat cells with individuals (10 individuals: ceiling value of a habitat cell). When a high-quality matrix supporting sink populations occurred, 10 individuals were also assigned (the ceiling was the same). Individuals then attempted reproduction with 0.1 average productivity. This value was set to 0.05 for sink populations. The actual number of offspring (recruitment) was generated by a Poisson distribution. Then, 0.05 annual (natural) mortality rate was incurred by a binomial distribution (0.1 for sink population, i.e. $\lambda_{\text{source}} = 1.045$, $\lambda_{\text{sink}} = 0.945$). Among survivors, surplus individuals beyond the ceiling of each cell were forced to disperse. A portion of the remaining individuals also joined the fraction of dispersers based on an intrinsic dispersal (emigration) rate of 0.1 (0.5 for sink populations), a binomial distribution was used to generate actual numbers. We chose these values of demographic parameters following Fahrig (2001).

We made emigrants disperse following **D** that indicates the expected dispersal rates quantified with circuit theory. Specifically, we randomly assigned the number of emigrants from every habitat cell into possible recipient habitat cells using multinomial distributions with the number of emigrants as the number of trials and expected dispersal success rate as the event probability. After adding colonists to local populations, over-abundance mortality occurred at the end of the year (abundance of each cell was reduced to the ceiling). An annual census was conducted immediately before reproduction. This annual step was repeated for 2,000 years, and total population size was recorded at the final year. We divided population size by the number of habitat cells to give population density, and the reduced binary variable of the population size (larger than 0 or not) was treated as population survival. We did not calculate population density when a high-quality matrix resulted in population sinks.

2.4 | Simulation experiment 1: Matrix effects across habitat loss and fragmentation

We first conducted a simulation experiment to examine effects of permeability and movement survival in the matrix when habitat loss and fragmentation were varied systematically. To do so, we considered a binary landscape composed only of habitat and a low-quality matrix. We expected that this simple simulation would provide insights into when and how the matrix matters across a gradient of habitat amount and configuration. We changed the proportion of habitat in the landscape (habitat proportion) by 11 levels from 0.01 to 0.9 (0.01, 0.05, 0.1, 0.2, ..., 0.8, 0.9), FRAG by seven levels (0.0001, 0.0005, 0.002, 0.01, 05, 0.21, 0.99), as well as permeability and movement survival of low-quality matrix by seven levels (0.01, 0.05, 0.25, 0.5, 0.75, 0.95, 0.99). We made the permeability of habitat constant (1.0) in this study (throughout three experiments), meaning that when low-quality matrix had 0.5 permeability, individuals moved to adjacent habitat cells at a two times higher rate than the adjacent low-quality matrix. The number of parameter combinations was 3,773 (= 11 × 7 × 7 × 7). For each parameter combination, we repeated landscape generation, demographic and movement simulations 100 times in this study. Therefore, the total replication of simulations was 377,300.

2.5 | Simulation experiment 2: Systematic assessment of matrix improvement

We then examined the role of matrix improvement on population outcomes using two scenarios. First, we considered the scenario where a portion of the low-quality matrix was improved as a dispersal passage. We were specifically interested in population outcomes through increased permeability and/or survival (as matrix improvement) subject to different amount and configuration of habitat and improved matrix. We therefore changed the following factors: proportion of habitat (0.05, 0.1, 0.2) and high-quality matrix (0, 0.1, 0.4, 0.7), fragmentation of habitat and high-quality matrix (FRAG: 0.0001, 0.01, 0.99), and permeability and survival of low-quality and high-quality matrix (0.05, 0.5, 0.95). We confined habitat proportion to smaller values (≤0.2) for which population survival can be low. We changed the amount of high-quality matrix by four levels to consider cases with no high-quality matrix (its proportion = 0.0). No high-quality matrix cases were a reference set whose population vital rates were compared to those with matrix improvement (>0 high-quality matrix proportion). To focus on matrix improvement, we considered only cases where permeability and movement survival of high-quality matrix was equal to, or higher than, that of low-quality matrix (i.e. parts of low-quality matrix were improved in terms of at least one matrix property). The total number of parameter combinations was 2,268.

Second, we considered the scenario where the matrix was improved to provide the potential for sink populations (i.e. some breeding could occur). In this case, matrix permeability (= 0.95) and movement survival (= 1.0) in a high-quality matrix had high constant values. We changed six factors (amount and configuration of habitat as well as those of high-quality matrix, and permeability and survival of low-quality matrix) by the three levels described above. The total number of parameter combinations was 729 (= 3 × 3 × 3 × 3 × 3 × 3).

2.6 | Simulation experiment 3: Interaction between habitat and matrix management

Baum et al. (2004) and Fletcher et al. (2014) experimentally demonstrated that the effects of habitat amount and configuration depend on matrix quality, which in turn suggests that consequences of matrix improvement can depend on habitat amount and configuration. To fully elucidate such interactions, we considered the specific situation where the magnitude of matrix improvement providing dispersal passage was high: low movement survival of low-quality matrix (0.05), high permeability of low-quality matrix (0.95) and high values for movement survival and permeability of high-quality matrix (0.95). We modified the amount and configuration of habitat and high-quality matrix by 10 levels, each with equal intervals: habitat amount (0.05–0.2), amount of high-quality matrix (0–0.7), fragmentation of habitat and high-quality matrix (0.0001–0.99). The total number of parameter combinations was 10,000 (= 10 × 10 × 10 × 10).

2.7 | Data analysis

To assess the effects of experimental factors (i.e. altered landscape properties), we calculated proportions of sums of squares of population vital rates (population size, survival and population density) explained by experimental factors using analysis of variance (ANOVA: Fahrig, 2001). We graphically showed the results by producing boxplots and contour plots using 'GGPLOT2' R package ver. 3.3.2 (Wickham, 2016). For experiment 2, to isolate the effects of matrix improvement, our response variable was the differences in mean values (rather than raw values in the other experiments) of population vital rates across 100 replications between binary (composed of habitat and low-quality matrix) and triplet (composed of habitat, low-quality and high-quality matrix) landscapes. For the scenario with population sinks, to elicit the advantage of matrix upgrading, we graphically compared the improvement relative to those of providing for similar high-quality matrix that did not act as population sinks (i.e. no breeding occurred: permeability and movement survival = 0.95). For experiments 1 and 3, we fitted logistic regression models with binary population survival as a response variable and experimental factors as covariates. We conducted statistical analysis using R ver. 4.0.2 (R Core Team, 2020) and executed simulation experiments in high performance cluster computing system using R ver. 3.3.2 that called Circuitscape v5 (Appendix S2).

3 | RESULTS

3.1 | Simulation experiment 1: Matrix effects across habitat loss and fragmentation

Matrix survival had larger effects than matrix permeability on all three population vital rates in the binary landscape (Table 1a). Decreased permeability and increased survival promoted all three population vital rates (Figure 2; Figure S4-1). When permeability increased, a corresponding increase in movement survival was required to prevent negative population outcomes. With increased habitat loss and fragmentation, the importance of matrix permeability decreased, and matrix survival primarily determined vital rates (Figure 2). Negative effects of habitat fragmentation were lessened but still occurred under high matrix survival.

TABLE 1 Variation (proportions of sums of squares in ANOVA) in population vital rates in three experiments

		Population vital rate		
Experimental factor	*df*	Size	Survival	Density
(a) Experiment 1: Binary landscape				
Habitat proportion	10	0.96	0.33	0.43
Habitat fragmentation (FRAG)	6	0.01	0.08	0.14
Low-quality matrix permeability	6	0.00	0.01	0.01
Low-quality matrix survival	6	0.01	0.03	0.18
Residuals	377,271	0.02	0.55	0.24
(b) Experiment 2: Triplet landscape with high-quality matrix as dispersal passage[a]				
Habitat proportion	2	0.07	0.01	0.01
Habitat fragmentation	2	0.01	0.06	0.03
Low-quality matrix permeability	2	0.02	0.01	0.03
Low-quality matrix survival	2	0.02	0.01	0.05
High-quality matrix proportion	2	0.06	0.01	0.06
High-quality matrix fragmentation	2	0.00	0.00	0.01
High-quality matrix permeability	2	0.04	0.03	0.06
High-quality matrix survival	2	0.16	0.07	0.23
Residuals	2,170	0.62	0.80	0.52
(c) Experiment 2: Triplet landscape with high-quality matrix providing for population sink[a]				
Habitat proportion	2	0.19	0.01	NA[b]
Habitat fragmentation	2	0.03	0.18	NA[b]
Low-quality matrix permeability	2	0.00	0.01	NA[b]
Low-quality matrix survival	2	0.03	0.04	NA[b]
High-quality matrix proportion	2	0.20	0.05	NA[b]
High-quality matrix fragmentation	2	0.01	0.00	NA[b]
Residuals	716	0.54	0.72	NA[b]
(d) Experiment 3: Interaction between habitat and matrix improvement[c]				
Habitat proportion	9	0.28	0.05	0.03
Habitat fragmentation	9	0.53	0.52	0.81
High-quality matrix proportion	9	0.06	0.04	0.08
High-quality matrix fragmentation	9	0.00	0.00	0.01
Residuals	999,963	0.13	0.39	0.07

Note. No interaction terms among factors were considered.

[a]Effects of matrix improvement were assessed by comparing to cases of binary landscapes with the same habitat amount and configuration and properties of low-quality matrix.

[b]Density was not calculated.

[c]High-quality matrix provided for dispersal passage (rather than population sink).

3.2 | Simulation experiment 2: Systematic assessment of matrix improvement

We first examined the effects of improving a portion of the matrix to provide for dispersal passage only (i.e. no breeding occurred). Movement survival through a high-quality matrix explained the largest variation in effects for all population vital rates (Table 1b). Permeability and amount of high-quality matrix were also important. Improved permeability without survival improvement led to decreased population vital rates in many cases (Figure 3, Figure S4-2). These negative effects were much stronger with increasing habitat fragmentation and larger amounts of high-quality matrix. Improving matrix survival had positive outcomes, and the effects were greatest with higher habitat fragmentation and larger amounts of high-quality matrix. The same patterns also were found for the effects of habitat amount (abundant habitat yielded contrasted outcomes depending on the improvement of movement survival: Figure S4-2). Although a marked improvement of permeability in large areas (via abundant high-quality matrix) decreased population vital rates in many cases, there were some cases with large positive outcomes (Figure 3), which occurred when matrix survival also was greatly improved (Yamaura et al., 2022).

When the matrix was improved to create population sinks, the amount of high-quality matrix explained population size to a similar degree as habitat amount (Table 1c; Figure S4-3). Population survival was greatly influenced by habitat fragmentation, and populations were persistent when habitat was contiguous in most cases (FRAG = 0.0001 and 0.01). When habitat fragmentation was pronounced (FRAG = 0.99), as a comparison, matrix improvement supporting dispersal passage only (where no reproduction occurred) decreased population survival subject to low habitat amount (habitat proportion = 0.05: Figure 4). Upgrading a high-quality matrix to population sinks negated these negative outcomes and led to neutral effects. When habitat was relatively abundant (0.2), sink populations and dispersal passage cases did not yield differences. When the habitat amount was intermediate (0.1), positive outcomes of population sink cases surpassed those of dispersal passage.

3.3 | Simulation experiment 3: Interaction between habitat and matrix management

In this final experiment of matrix improvement providing for dispersal passage, we found varied interactive effects, or context dependency, among experimental factors (Figure 5, Figure S4-4). For example, the effects of the amount of high-quality matrix increased with habitat fragmentation (Figure 5b). We also identified a synergistic effect between amounts of habitat and high-quality matrix (Figure 5d). Effects of high levels of fragmentation of high-quality matrix were evident (Figure 5e), indicating that benefits of increasing the amount of high-quality matrix can be further promoted by aggregating high-quality matrix (avoiding fragmented high-quality matrix: Figure 5f).

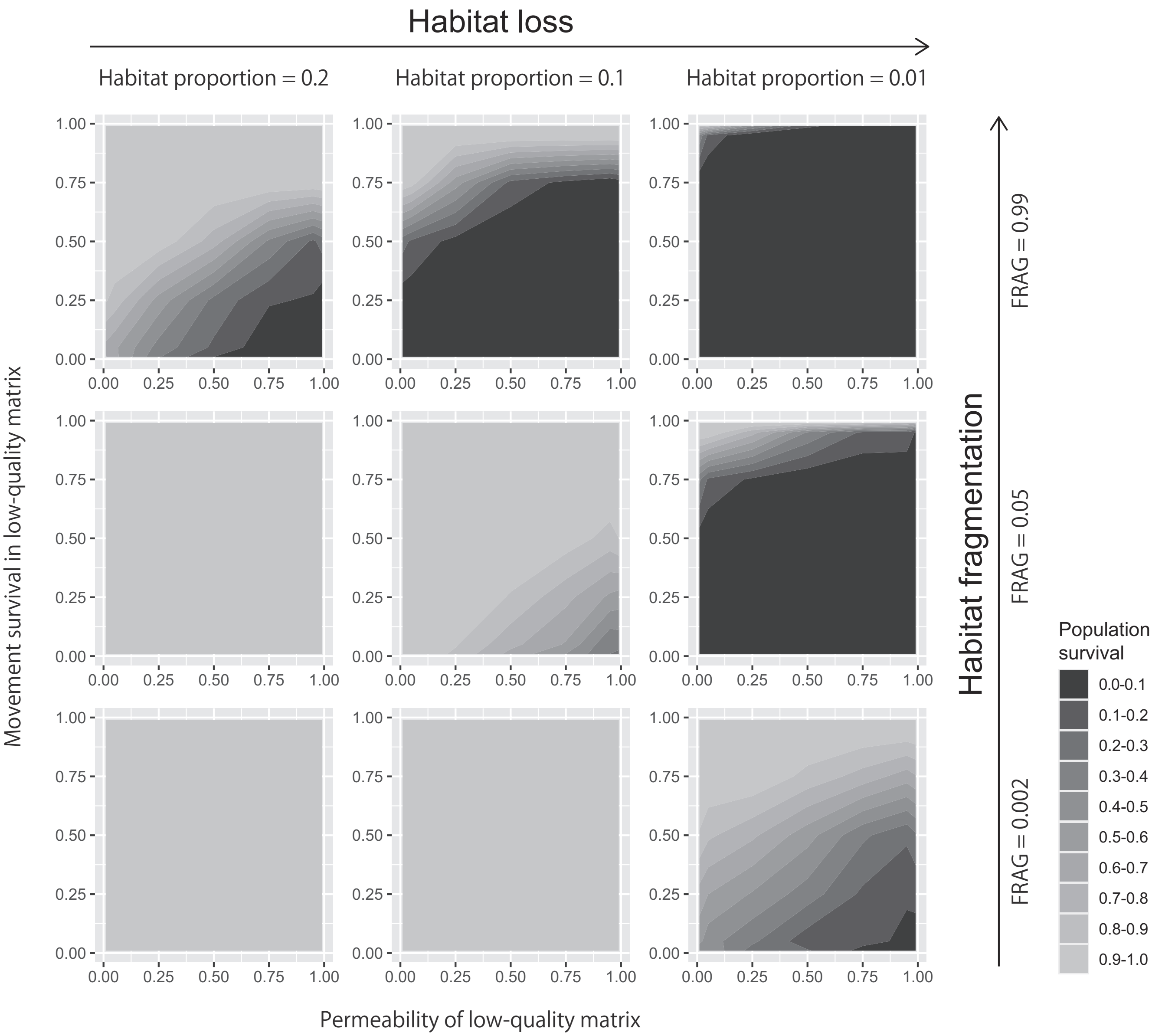

FIGURE 2 Effects of matrix permeability and movement survival as a function of habitat amount and fragmentation on population survival in binary landscape (experiment 1). To elicit matrix effects, only subset combinations of habitat amount and fragmentation are presented. In the experiment, habitat proportion was changed by 11 levels (0.01–0.9) and fragmentation (FRAG) was changed by seven levels (0.0001–0.99). See Appendix S4 for full results of population survival, population size and density

4 | DISCUSSION

4.1 | Matrix permeability and movement survival in fragmented landscape

Our first experiment emphasizes that effects of movement survival in the matrix far outweigh those of matrix permeability across a gradient of habitat loss and fragmentation. Increased matrix permeability decreased all three population vital rates, which is consistent with other modelling studies finding negative effects of emigration rates on population persistence (Bevers & Flather, 1999; Fahrig, 2001). Although some previous empirical studies found positive effects of matrix permeability on inter-patch movement (Haynes & Cronin, 2003; Ricketts, 2001), a permeable matrix in these studies implicitly indicates high movement survival and that dispersers would have made adaptive movement decisions to enter the matrix, which resulted in high dispersal success.

Our results also suggest that when matrix permeability is increased, increased movement survival is needed to offset potential negative consequences. Indeed, empirical studies suggested that high emigration rates deplete local populations (Cronin, 2007; Kuussaari et al., 1996). As population survival was greatly increased by simultaneously increased permeability and movement survival, a permeable matrix does not necessarily bring negative population outcomes. Instead, these results emphasize that permeability and movement survival are different matrix properties. We also found

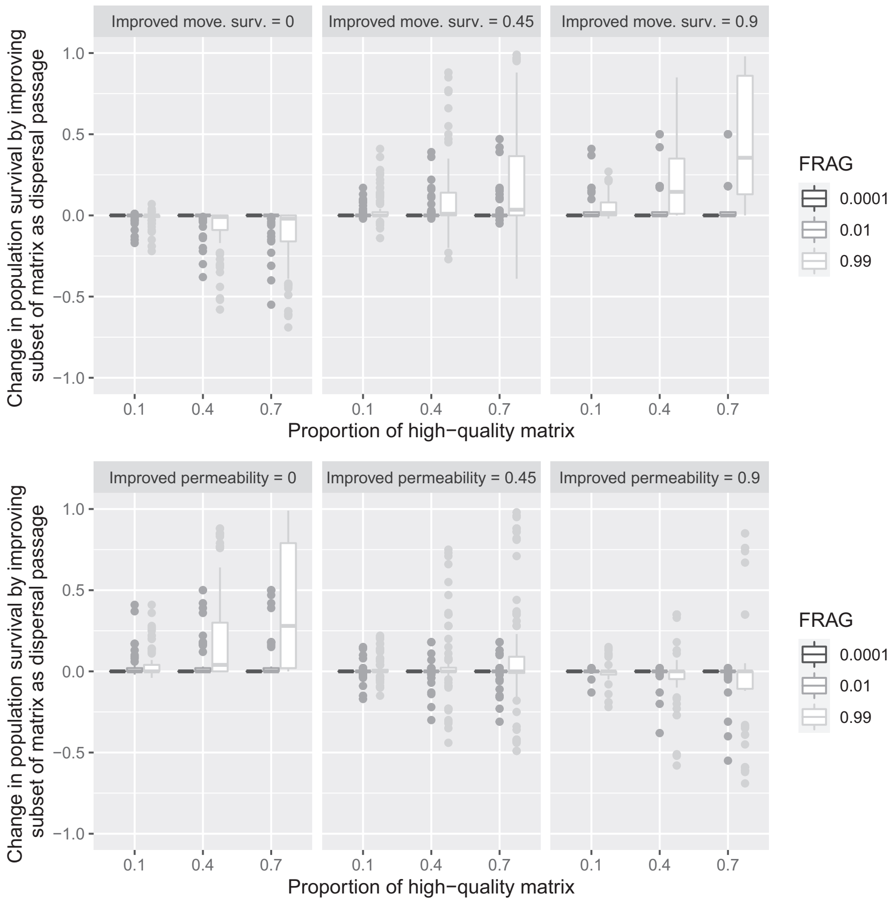

FIGURE 3 Effects of matrix improvement as dispersal passage on population survival (experiment 2). Matrix improvement was evaluated by comparing landscapes with/without improved high-quality matrix; negative value indicates matrix improvement reduced population survival. Effects are shown separately by either increased values of matrix movement survival (top row) or those of matrix permeability (bottom row). Left-end panels show improvement effects of another matrix property while holding the focal property constant

that movement survival rather than matrix permeability determined population vital rates under pronounced habitat loss and fragmentation. This would have occurred because most dispersers had to emigrate from remnant habitats with high edge to core area ratio and had to enter the matrix, which made movement survival through the matrix critically important in this context.

4.2 | Improving permeability versus movement survival

Our second experiment showed the situation of a dispersal trap (Vasudev et al., 2015). Matrix improvement to increase matrix permeability while holding movement survival constant decreased all three population vital rates. High permeability does not always coincide with high movement survival (and vice versa). For example, dispersers may change movement behaviour to avoid predation once they enter a matrix with high predation risk (permeability is low but survival is moderate: Zollner & Lima, 1999). Conversely, amphibians and reptiles are either attracted to, or do not avoid roads, and incur high mortality due to collisions with vehicles (Fahrig & Rytwinski, 2009).

Increased movement survival was required to achieve intended conservation outcomes. It is therefore desirable to understand whether suggested management practices such as tree retention in farmlands, agroforestry, low input agriculture (e.g. Arroyo-Rodríguez et al., 2020) and green tree retention in forestry (Betts et al., 2021), can increase movement survival and not only permeability. Installing physical barriers (e.g. fences) and animal detection systems along roads (Rytwinski et al., 2016) and providing food and concealment cover in dispersal passages (Zollner & Lima, 2005) are expected to increase movement survival. Reducing hunting pressure and other mortality events such as fatal collisions with buildings outside of protected areas also would be useful (Nyhus, 2016; Van Doren et al., 2021). We advocate moving beyond matrix improvement and connectivity modelling based solely on matrix permeability to focus on issues of promoting movement survival across landscapes.

4.3 | Improving matrix to support population sinks

By definition, a sink population cannot persist in isolation (Pulliam, 1988). Benefits of matrix upgrading from dispersal passage to a sink population would therefore arise from increased colonization via lowered dispersal mortality and surplus individuals (floaters) as well as provision of asynchronized populations (Howe et al., 1991). Compared to matrix improvement supporting only dispersal passage for population survival, we found clear advantages of upgrading the matrix to support a sink population when habitat was fragmented and intermediately abundant. When habitat is contiguous, increased colonization would be sufficiently achieved by improvement of dispersal passage. Conversely, when habitat is scarce, this strategy would be insufficient to increase colonization rates given strong

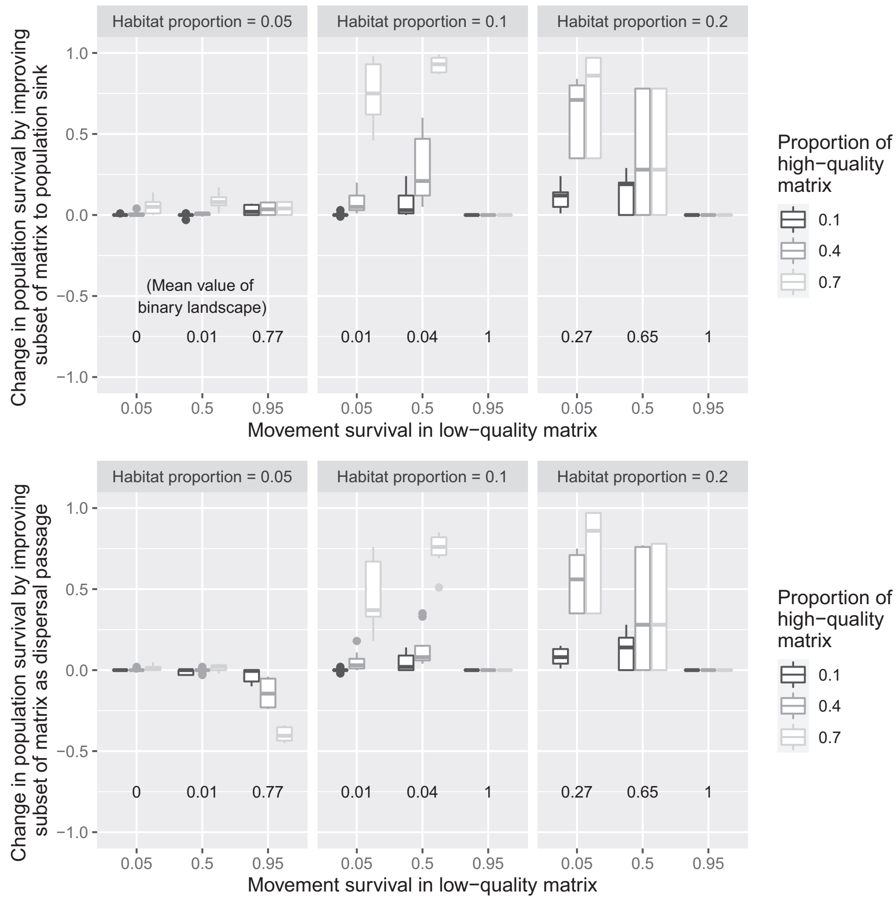

FIGURE 4 Effects of matrix improvement supporting population sink on population survival (experiment 2). To elicit the effects of providing for population sink, population sink scenario (top row) and the best-quality dispersal-passage cases (bottom row) are shown for the comparison. Subsets with intense habitat fragmentation (FRAG = 0.99) are only shown. Negative value indicates matrix improvement reduced population survival. Mean values of population survival without any high-quality matrix (binary landscape) are also described as the reference at the lower part of the panels

habitat fragmentation. These results suggest that when habitat is abundant, the matrix can be improved for dispersal passage while protection/restoration of source habitat would be prioritized subject to scarce habitat. Otherwise, matrix upgrading to population sinks would have merits (see also Appendix S5).

4.4 | Interaction between habitat and matrix management

Simultaneous increases in landscape-scale reproduction and dispersal success could synergistically promote population survival. Our third experiment identified positive interactions between the amounts of habitat and improved matrix. Since habitat amount and configuration had nonlinear effects on population survival (Figure 5), manipulating the amount and configuration of remaining habitat may yield diminishing returns. When habitat management is costly, the largest conservation returns may be obtained by investing in management of (limited) core habitats and the surrounding matrix. Since the amount of improved matrix is a key factor in increasing population vital rates, the economic costs of matrix improvement are relevant to promoting conservation benefits. For example, we extended the model to consider the cost performance of habitat and matrix management based on Figure 5d (Appendix S7). When we increased the economic cost of habitat restoration relative to matrix improvement, a mixture (hybrid) of habitat restoration and matrix improvement had higher cost effectiveness than habitat restoration alone (Appendix S7).

4.5 | Spatial configuration of high-quality matrix

Our results suggest that buffering and connecting habitats by improving the matrix can yield additional conservation benefits (Figure 5e,f) although this configuration effect was not large (Table 1b–d). Benefits of matrix improvement indeed increased with pronounced habitat fragmentation (Figure 3). However, these positive effects were found when high-quality matrix supported population sinks or movement survival increased (Table S4-2). Otherwise, contiguous permeable matrix would leak individuals from habitat, leading to negative population outcomes through being a dispersal trap. When matrix improvement increases movement survival, buffering and connecting habitat remnants through a high-quality matrix would be beneficial via enhanced dispersal success as previously suggested (Franklin, 1993).

4.6 | Habitat loss and fragmentation

Our model provides insights into situations where habitat fragmentation may become very important. We found strong habitat fragmentation effects on population survival and density when habitat

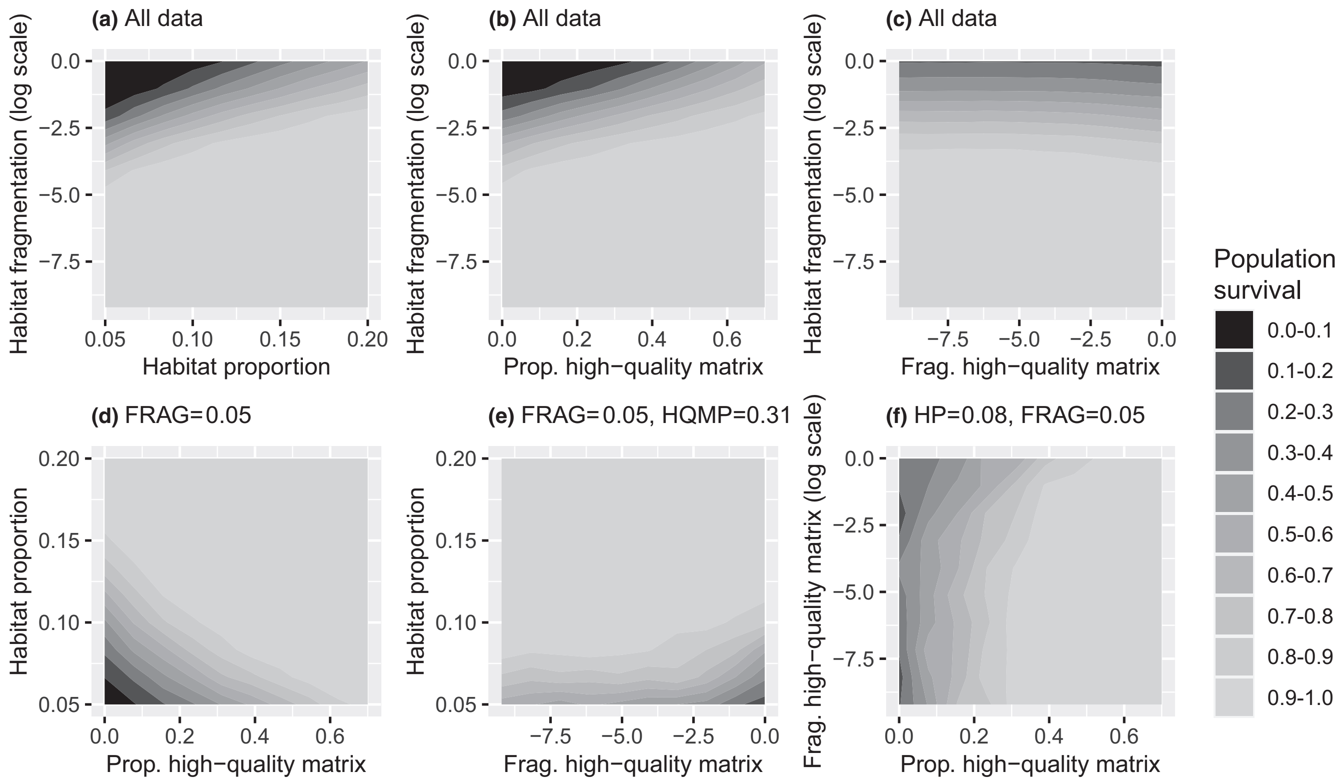

FIGURE 5 Interactive effects of habitat amount, fragmentation and matrix improvement supporting dispersal passage on population survival (experiment 3). Experimental factors were changed by 10 levels and the degree of fragmentation is represented at log scale (0.0001–0.99 is represented by −9.2 to −0.01). (a–c) All data pooled and summarized. (d–f) Only subsets of factors are used to show major interactions. Abbreviations: HP, habitat proportion; HQMP, high-quality matrix proportion

was scarce (Table 1b–d, Figures 2 and 5, Appendix S4). However, previous modelling and empirical studies have found only limited fragmentation effects (Fahrig, 2002, 2017). According to our model (Appendix S6), we suggest that weak fragmentation effects identified in previous studies are likely due to the following reasons: (a) habitat was abundant, (b) movement survival in the matrix was high, (c) the degree of habitat fragmentation was limited or (d) the range of habitat fragmentation considered was narrow. These context dependencies may help explain why there is conflicting evidence and views about the roles of habitat fragmentation (Fletcher et al., 2018; Fahrig et al., 2019).

4.7 | Challenges and prospects

Our modelling approach using circuit theory has challenges to overcome. First, dispersers were assumed to follow random walks and have no memory about the previous movement steps (McRae et al., 2008). Such memory effects can be considered as correlated random walks using individual-based models (Bocedi et al., 2014) or Markov chain theory, of which circuit theory is a special case (Fletcher et al., 2019). Another issue is long computation time for landscapes with many habitat cells, which can be effectively addressed by dividing the landscape into smaller areas (Marx et al., 2020), using parallel computing (Hall et al., 2021) and calculating current flow at coarse resolution (McRae et al., 2008) within a specific distance (McRae et al., 2016).

This study provides an efficient means to evaluate not only addition/removal of particular patches for population vital rates but also improvement/degradation of the particular matrix (Appendix S8). Wiens (1995, 1997) suggested that the complexity of landscape mosaics makes landscape ecology difficult to develop predictive models, although theory linking landscape patterns to their consequences should be kept simple. Our modelling framework represents demographic parameters and dispersal rates of heterogeneous landscapes as mathematical matrices in a concise and tractable manner. This may be useful to shift reserve management to 'mosaic management' (sensu Wiens, 1997) not only for biodiversity conservation but also for humanity's development (Kremen & Merenlender, 2018; Ellis, 2019).

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CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTIONS

Y.Y., R.J.F., S.J.L. and D.L. conceived the ideas and designed methodology; Y.Y. and M.H. collected and analysed the data; Y.Y., R.J.F. and D.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.1rn8pk0v3 (Yamaura et al., 2022).

ORCID

Yuichi Yamaura https://orcid.org/0000-0001-9355-4413
Robert J. Fletcher Jr https://orcid.org/0000-0003-1717-5707
Steven J. Lade https://orcid.org/0000-0001-9719-9826
Motoki Higa https://orcid.org/0000-0003-3406-999X
David Lindenmayer https://orcid.org/0000-0002-4766-4088

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