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RESEARCH ARTICLE

Matrix composition mediates effects of habitat fragmentation: a modelling study

Jordan Chetcuti · **William E. Kunin** · **James M. Bullock**

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Abstract

Context Habitat loss has clear negative effects on biodiversity, but whether fragmentation per se (FPS), excluding habitat loss does is debatable. A contribution to this debate may be that many fragmentation studies tend to use landscapes of fragmented focal-habitat and a single vastly different species-poor intervening land cover (the matrix).

Objectives How does matrix composition influence the effect of FPS on biodiversity?.

Methods Using an individual-based model to investigate the effect of different configurations of the matrix on the relationship between FPS and biodiversity of the focal-habitat. We manipulated the number and quality of land cover types in the matrix, and their similarity to the focal-habitat.

Results Extremely different matrix, caused an order of magnitude stronger effect of FPS on alpha- and gamma-diversity and beta-diversity to decline. Low FPS led to high gamma-diversity. Increasing FPS caused a dramatic decline to low diversity. In contrast landscapes with a more similar matrix had lower diversity under low FPS declining little with increasing FPS. Having few matrix types caused beta-diversity to decline in general compared to landscapes with a larger numbers.

Conclusions The effects of FPS on biodiversity may change depending on the number of matrix types and their similarity to the focal-habitat. We recommend that fragmentation studies should consider a greater variety of landscapes to help assess in which cases FPS does not have a negative impact and allow better predictions of the impacts of fragmentation. We show the importance of having a diversity of matrix land cover types and improving the hospitability of the matrix for species dependent on the focal-habitat.

Keywords Species diversity · Fragmentation per se · Individual-based model · Movement ecology · Matrix habitat · Landscape scale

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-021-01243-5.

J. Chetcuti (✉) · J. M. Bullock
UK Centre for Ecology and Hydrology, Hydrology,
Wallingford, OX, UK
e-mail: chetcutj@tcd.ie

J. Chetcuti · W. E. Kunin
Faculty of Biological Sciences, University of Leeds,
Leeds, UK

J. Chetcuti
Department of Botany, School of Natural Sciences,
Trinity College Dublin, Dublin, Ireland

Introduction

Conversion of natural habitat to human land-uses has been overwhelmingly detrimental to biodiversity (IPBES 2018). It has, however, been argued that the negative effects of this conversion are purely due to the well-known effects of habitat loss, with habitat fragmentation per se (FPS; fragmentation after taking account of, or in the absence of habitat loss), having either no effect or actually causing an increase in species richness (Fahrig 2003, 2017; Fahrig et al. 2019). In reality, fragmentation and loss of habitat are intrinsically linked (Fletcher et al. 2018). Nonetheless, it is important both for conservation actions and ecological understanding to separate the effects of FPS from those of area loss (Isaac et al. 2018). Such an understanding can be achieved by assessing the impacts of dividing a fixed habitat area into more smaller patches and assessing under what circumstances this FPS leads to higher or lower species diversity.

The impacts of FPS have occasioned much debate, and one suggestion has been that studies at the patch scale showing fragmentation has a negative impact on biodiversity (alpha-diversity) (Sisk et al. 1997; Haddad et al. 2015; Fletcher et al. 2018), may not be replicated in landscape-scale biodiversity changes (gamma-diversity) (Fahrig 2017; Fahrig et al. 2019). Patch-scale studies do not allow for potentially positive mechanisms of FPS, such as competitive release, spreading of risk, increased functional connectivity, and higher land cover diversity as these act at the landscape scale, through increasing beta-diversity (Fahrig et al. 2019; Rybicki et al. 2019). The difference between patch-scale and landscape-scale findings may also be due to differences in the study designs used at these two scales of study. Most patch-scale empirical studies, as well as many modelling studies, are conducted on binary landscapes. These binary landscapes have a fragmented focal-habitat and a single type of intervening matrix that is of an extremely different land cover to the focal-habitat, and typically one that is less species-diverse (Ewers et al. 2011; Haddad et al. 2017; Damschen et al. 2019; May et al. 2019; Thompson et al. 2019). This study design also prevents examination of some of the positive mechanisms of FPS, increased land cover diversity and positive edge effects (Fahrig et al. 2019). Examples of this large difference between matrix and focal-habitat are grassland focal-habitat surrounded by plantation forestry (Damschen et al. 2019) or natural woodland surrounded by arable fields (Crawford et al. 2016). Some landscapes will show this type of extreme contrast, with a focal-habitat of conservation value and a matrix of intensive anthropogenic land-use (Wintle et al. 2019). Therefore, studies using this extreme paradigm have been and will continue to be useful in identifying the negative effect of fragmentation in such landscapes. However, does the effect of fragmentation hold true for different, possibly less extreme landscapes such as those where native woodland sits among plantations and scrub, or heathlands lie among acid grasslands? Furthermore, what effect will having a matrix that is less species-diverse have on the effect of FPS? Having a species-poor matrix may lead to a reduced effect of competition on focal-habitat-species (Miller-Rushing et al. 2019) or allow focal-habitat species to access to sub-optimal habitats (Jacob et al. 2017), and therefore reduce the effect of FPS. Will a matrix with higher species diversity therefore lead to a greater effect of FPS due to increased competition?.

Unlike oceans in the theory of island biogeography, even an anthropogenic matrix is not entirely hostile to all species that live in the focal-habitat (Tscharntke et al. 2012). The quality of the matrix has been identified as an important factor in the survival of species in the matrix and consequently the movement of species between focal-habitat patches (Fahrig 2001, 2017; van der Hoek et al. 2015). The matrix influences species persistence in the landscape by subsidizing resources, and facilitating movement where it is more similar to the focal-habitat (Driscoll et al. 2013). It has, as a consequence of these qualities, been suggested that FPS may have a lesser effect if the matrix includes land covers that are of a similar type to the focal-habitat (Miller-Rushing et al. 2019). Matrix heterogeneity may also help maintain variation in species across landscapes (beta-diversity) and offset negative effects of FPS on gamma-diversity (Neilan et al. 2018). As mentioned, land cover diversity and positive edge effects have been identified as potential positive mechanisms of FPS (Fahrig et al. 2019). At the landscape scale, beta-diversity may increase and counteract negative mechanisms such as negative edge effects from tourist species (Magurran 2004) and increases per-patch extinction rates, which lead to reductions in alpha-diversity. If the effect of matrix intensity and heterogeneity on the relationship of diversity to FPS can be identified then this will allow for a more accurate analysis of the effect of habitat loss and fragmentation (Bueno et al. 2018; De Camargo et al. 2018). It may then be possible to estimate the effects of FPS in different landscapes (Fahrig et al. 2019).

Allowing more complex matrix configurations has been criticised for similar reasons to suggestions of a move away from considering simplistic landscapes. The worry is that non-habitat can provide resources and so landscapes may not be fragmented from a species perspective, which may obscure the effects of habitat fragmentation (Fletcher et al. 2018). Land managers and researchers generally use a human perspective when measuring and mitigating FPS, by classifying a land cover as a habitat and then looking at its fragmentation. This perspective fails to consider that each species has a different association with the different land cover types across the landscape; that is, individual species are not associated solely with one, human-defined, land cover, and each species has an individual set of habitat associations (Bollmann et al. 2005; Betts et al. 2014; Brodie and Newmark 2019; Chetcuti et al. 2019, 2020). Some species typically associated with the land cover being fragmented may use or move through matrix land covers readily. For these species, increasing FPS may not lead to a reduction in connectivity. They then may have access to a greater diversity of land cover types and have meta-populations in the new fragments of habitat. Here, we continue to consider the fragmented habitat from the perspective of a human classified land cover, but also utilise a benefit of individual-based modelling (IBM) by allowing species-level perspectives, with different species having different associations with the focal-habitat and the different matrix land cover types.

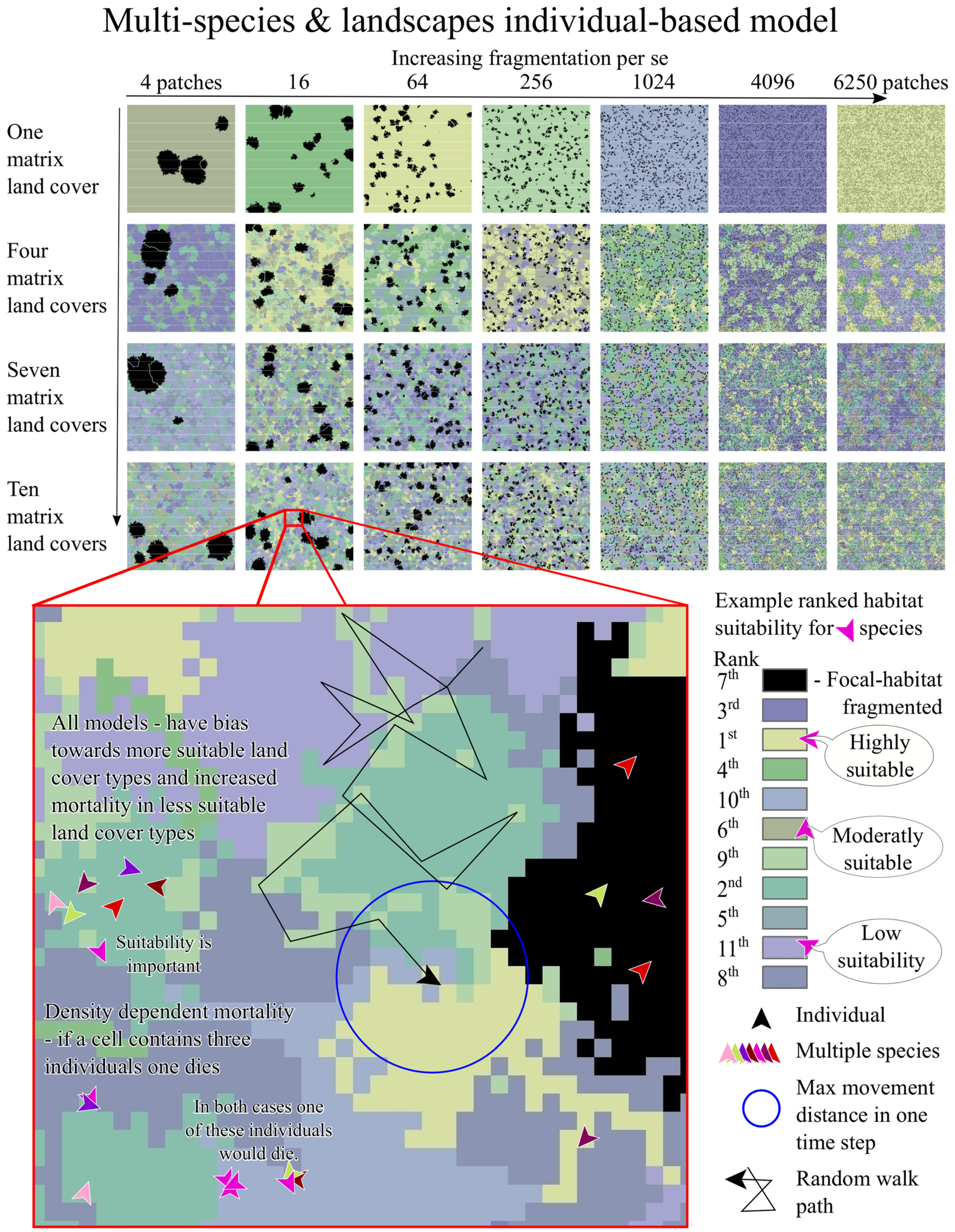
We have created a multi-species and landscapes simulation in the form of an IBM, in which we focus on the species diversity in patches of the fragmented focal-habitat (Chetcuti et al. 2020). Because FPS acts differently on different components of biodiversity, we use our simulation to look at the emergent alpha-, beta-, and gamma-diversity that results from individuals of species with different habitat associations moving through landscapes with varying levels of FPS, represented by the number of patches of a focal-habitat. In this paper, we configure the matrix in ifferent ways by varying the number, the associated species diversity, and the similarity of the matrix land covers compared to the focal-habitat. We test the following hypotheses. (1) A matrix which is more dissimilar to the focal-habitat will lead to a stronger negative effect of FPS while a more similar matrix will lead to higher alpha- and gamma-diversity but lower beta-diversity of focal-habitat patches and a lesser effect of FPS. (2) Matrix land cover types which support more species will lead to FPS causing a strong decline in gamma-diversity of the focal-habitat-species because of greater influxes of tourist species into the patches as they become fragmented. (3) An increase in the number of matrix land cover types increases gamma-diversity due to higher beta-diversity. Under low FPS this will lead to there being more land cover types and therefore higher beta-diversity and gamma-diversity. As FPS increases, more species will be able to utilise different parts of the landscape and gain access to more of the different matrix land covers, leading to increasing beta-diversity with FPS and so a lesser decline in gamma-diversity.

Methods

Our multi-species and landscapes simulation (Fig. 1) was built using NetLogo software (v6.0.4) (Wilensky 1999). The NetLogo simulation parameters were set up, run and the outputs analysed using R version 3.5 (R Core Team 2018). The model is presented in Chetcuti et al. (2020) and has been described in detail following the ***Overview, Design concepts, Details*** (ODD), protocol for describing individual- and agent-based models (Grimm et al. 2006, 2010). To aid the readability of these Methods, the ODD is placed in the supplementary materials. Each model and landscape configuration was repeated 50 times. This resulted in 7000 simulation runs.

FPS and matrix land cover diversity

In this study, we simulated land covers and their configuration using the R package ‘LcvGen’ (Chetcuti 2020) in which we created different levels of fragmentation of the landscape by increasing the number of patches of focal-habitat while keeping the total focal-habitat area constant (Fig. 1). Chetcuti et al. (2020) showed that FPS had the same effect on biodiversity with 10% and 40% focal-habitat cover. We therefore used 10% focal-habitat cover in all of our


Multi-species & landscapes individual-based model
Increasing fragmentation per se
4 patches
16
64
256
1024
4096
6250 patches
One matrix land cover
Four matrix land covers
Seven matrix land covers
Ten matrix land covers
All models - have bias towards more suitable land cover types and increased mortality in less suitable land cover types
Suitability is important
Density dependent mortality - if a cell contains three individuals one dies
In both cases one of these individuals would die.
Example ranked habitat suitability for species
Rank
7th - Focal-habitat fragmented
3rd
1st
4th
10th
6th
9th
2nd
5th
11th
8th
Highly suitable
Moderatly suitable
Low suitability
Individual
Multiple species
Max movement distance in one time step
Random walk path

◀**Fig. 1** A figurative description of the individual-based model, showing how we represented FPS by increasing the number of patches of the focal-habitat (in black) while keeping its total area the same and that we looked at a differing number of matrix land cover types. We give an example of the ranked suitability for the different land covers on the right for one species and an example of a random walk in the middle. Not all species like the focal-habitat the best as can be seen from the legend. All individuals interact with the different land cover types according to their assigned suitability, with habitat-modified mortality and individuals showing biased movement

landscover as this gave a reasonably large amount of matrix cover. We created increasing FPS by simulating land covers with 4, 16, 64, 256, 1024, 4096 and 6250 focal habitat patches of the 1000 × 1000 cells of land cover. We also varied the number of land cover types in the spaces in-between the focal-habitat patches, i.e. the matrix. We did this by creating 1, 4, 7 or 10 matrix land cover types. Combining variation in FPS (7 treatments) and the number of matrix land covers (4 treatments) gave 28 different landscape types. For every landscape simulated, we also created a dataset that defined patches in that landscape. We defined each patch as a contiguous area, including those connected diagonally by corner cells, of a land cover type. The landscape for every one of the 7000 simulation runs was different as we generated each landscape and corresponding patch dataset individually for each replicate and model scenario. We did this to avoid idiosyncrasies in results that might arise by using a limited set of each landscape type.

Simulation

We defined the species in the simulation differently for different scenarios, but we always created them randomly or stratified randomly (focal-habitat-species and non-focal-habitat-species each being associated with different random land covers) and they did not represent any particular taxon. The only characteristic of these species was that they move and are each differently suited to the different land cover types in the landscape. We focus on how species relationship to the matrix configuration will influence the effects of habitat fragmentation. We defined each distinct species by how suitable it found each of the different land cover types in the landscape. To do this, we defined each species in terms of suitability for the 11 land cover types irrespective of the number of matrix land cover types in a particular run of the simulation (1, 4, 7, or 10). We defined this habitat suitability by ranking each of the 11 land cover types with values between one and either 11 or 23 depending on the experimental scenario. One of the scenarios used a ranking of the 11 land covers from one to 23 to increase differences between land cover types, we explain this in the description of that scenario. We generated species randomly as there are too many combinations of suitability for different land cover types to create species to represent all ways of defining species. By randomly creating species, we captured the critical variation across different types of species. We generated the species separately for each replicate and landscape. We define focal-habitat-species as those species for whom the focal-habitat is most suitable (habitat suitability rank one). The huge range of possible species within this simulation, is further justification for keeping the species simple as adding in further complexity would lead to difficulty in interpreting results.

All organisms moved with a habitat-biased random-walk. Each individual counted the cells of each habitat in the circle around it defined by the maximum movement distance of five cells (Fig. 1) and multiplied these by the bias multiplier. Each habitat was assigned a proportion of values between zero and one. A random number was generated between zero and one selecting a habitat. The individual, then moved to a random point in that habitat. As a result, individuals were more likely to choose to move into more preferred habitat. Individuals had a 5×10^{-4} chance of reproducing by creating another individual with its characteristics during a time-step based on allometry that make them realistic for a range of different species with this movement distance scaling across scales (Chetcuti et al. 2020). The individuals also had habitat-modified mortality. We defined both the habitat-biased movement and habitat-modified mortality multipliers as logistic curves that related habitat suitability to a value between zero and one that increased the probability of choosing a preferred land cover type and increasing mortality in less suitable land cover types. We use suitability to represent both preference (i.e. movement choices) and suitability in this study, noting that they can be different in reality (e.g. ecological traps). The curves had midpoints of six or 12 and slopes of 0.75 or 0.341 depending on the scenario (Fig. 2). We chose a

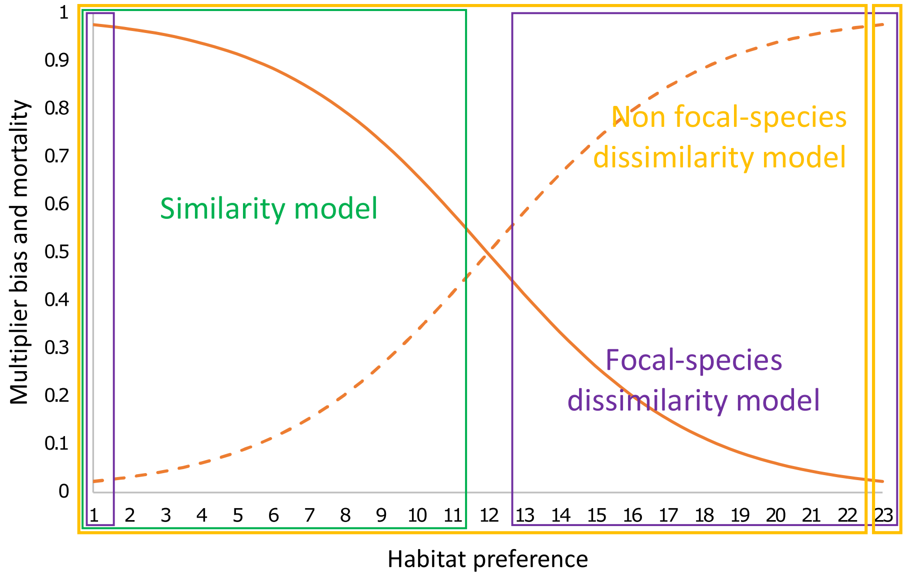


Fig. 2 Values used for the logistic slope within each experimental scenario for habitat-biased movement and mortality. The baseline model and the two models in the matrix diversity scenario used the curves in blue with a midpoint of six and a slope of 0.75. The two models in the focal/matrix similarity scenario used the orange curves with a midpoint of 12 and a slope of 0.341, to make the matrix land covers more similar or dissimilar to the focal-habitat. The graph shows the effect the slopes have on the multiplying values used to bias the movement towards more suitable land cover types and to increase mortality in less suitable land cover types. There are general mortality rates through density-dependence and when the whole simulation goes over the carrying capacity for individuals in the landscape. The habitat-biased mortality is additional to the general levels. To link levels of added mortality to that of the reproductive rate, we multiplied the habitat mortality multipliers by the reproduction rate 5 × 10–4 to give the additional probability of mortality

carrying capacity of 4000 individuals in the landscape which increased the chance of dying for all individuals when numbers were over the carrying capacity. See parameters in the supplementary materials.

The boundary was toroidal with individuals able to cross over the edge and reappear on the other side of the landscape. At the edge of the simulated landscape, we added a ten cell-wide strip to each side of the landscape, with each cell randomly assigned a land cover type to avoid the land cover on the other side of the landscape influencing species into crossing over the edge or not.

Experimental scenarios

We applied two scenarios to the 28 types of landscape that varied according to focal-habitat FPS and number of matrix land cover types. We compared the model outputs for both scenarios to the same baseline model. For the baseline model we specified that each matrix land cover type would have the same number of species associated as did the focal-habitat and that each land cover type in the matrix could be more or less similar to the focal-habitat entirely randomly. The first scenario, the focal/matrix similarity scenario, contrasted: (1) all of the matrix land cover types being similar to the focal-habitat; with (2) all of the matrix land cover types being dissimilar to the focal-habitat. The second scenario, the matrix diversity scenario, contrasted: (1) half as many species associated with each matrix land cover type as with the focal-habitat; with (2) double the number of species associated with each matrix land cover type (Fig. 3). We ran the simulations for 200,000 time-steps and present outcomes for the end of the simulations. Using this number of time-steps allowed the simulations to approach an equilibrium number of species (Chetcuti et al. 2020).

Baseline model

In the baseline model, the midpoints of the logistic functions used for the habitat-modified movement and mortality were six and the slopes were 0.75 (Fig. 2). Each land cover type had 40 species which were most

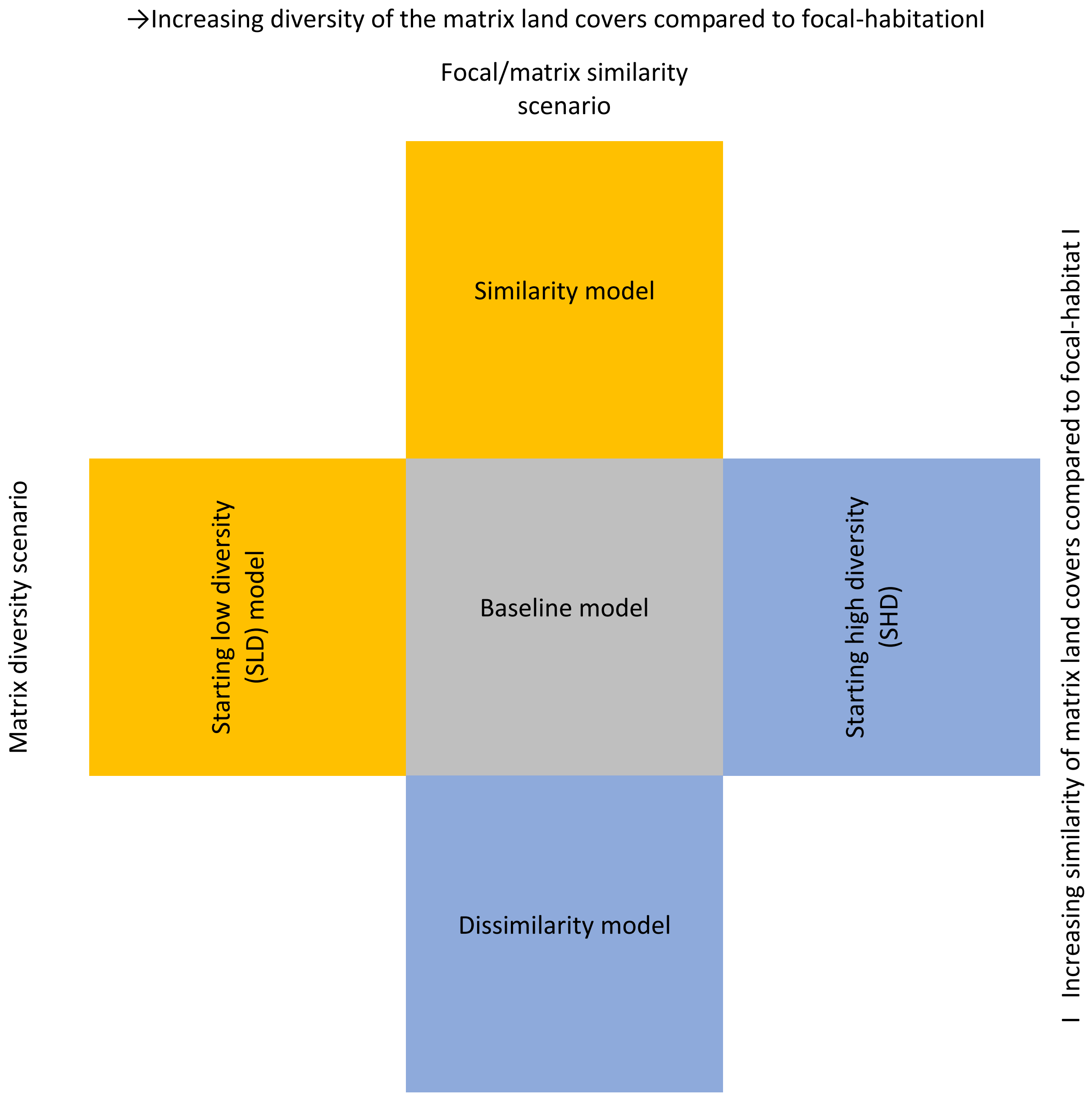


Fig. 3 The four models of the two scenario in contrast to the baseline, with each scenario only changing either the similarity of the matrix land covers to the focal-habitat, or the starting diversity of the matrix land covers compared to the focal-habitat. Colours correspond to those in the graphs in the results

strongly associated with that land cover type, being species for which that land cover type had a habitat suitability of rank one (and the ranking for other land cover types randomly assigned inclusively between two and 11). This gave 440 species at the beginning of the simulation. Because we assigned a random ranking for the 11 land covers to each species, the focal-habitat and matrix land covers were not universally similar nor dissimilar.

Focal/matrix-similarity scenario

The focal/matrix-similarity scenario contrasted two models, the Similarity and Dissimilarity models.

Specifying the two models of this scenario was more complex than for the other scenarios. For land covers to be similar, species had to have similar multiplying values derived from the logistic equation for habitat-biased movement and habitat-modified mortality, and for dissimilar land cover types to have very different values (Fig. 4). To do this we allowed the suitability for the 11 land covers to range between 1 and 23 instead of 1 and 11. The midpoint of the logistic function was changed to 12 and the slope to 0.341, so that the value derived from the equation that we used to specify habitat-biased movement and habitat-modified mortality, remained approximately the same (0.98 and 0.02 respectively) (Fig. 2). For the Similarity model, we assigned a rank to each species for each habitat suitability between 1 and 11 (but in this case maximum dissimilarity has a rank of 23, not 11 like in the baseline) so that species would find the land cover types to be more similar to each other (Fig. 4).

In the dissimilarity model, the focal-habitat-species had a rank of one for the focal-habitat. The habitat suitabilities for the other land covers (the matrix) were chosen from values 13 to 23 inclusively (Fig. 4). This means that for the focal-habitat species the matrix land covers were very dissimilar to the focal-habitat and so the bias in movement towards them was very low and the mortality in them was very high. For the other species (i.e. other than the focal-habitat species), each had a rank of one for one of the matrix land cover types. For the other nine matrix land cover types, we assigned ranks between 2 and 22 for each of these other species. All non-focal-habitat species had a rank of 23 for the focal-habitat. The nine other matrix land cover types were given ranks of 2 to 23, because although the matrix land covers were dissimilar to the focal-habitat, they were not necessarily dissimilar to each other. This dissimilarity model is an extreme example and with two fundamental types of species in the focal-habitat, species for whom the focal-habitat had high suitability (focal-habitat species) or low suitability (all other species). Table 1 gives an example of suitabilities for the land covers for similar matrix and focal-habitat and dissimilar matrix and focal-habitat.

Matrix-diversity scenario

As in the baseline, the midpoint of the logistic function used for the habitat-biased movement and habitat-modified mortality was six and the logistic slope was

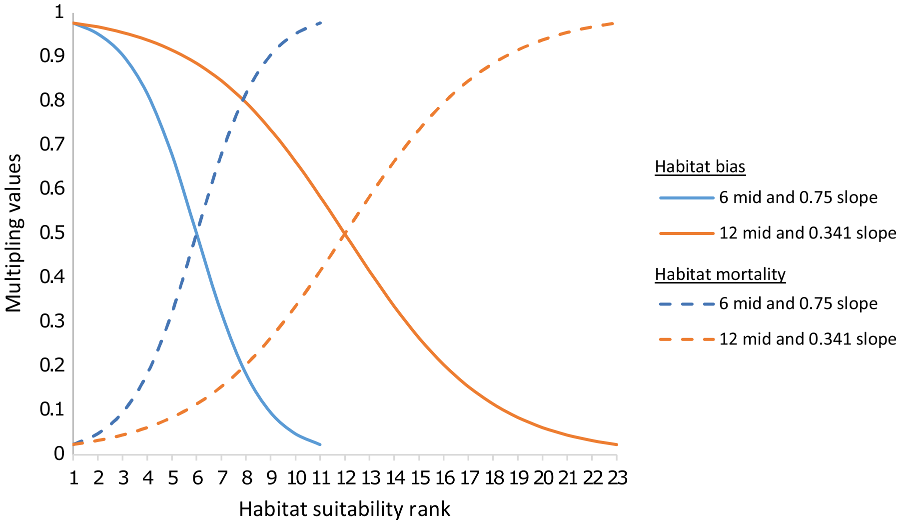


Fig. 4 For the similarity model, the ranking for the 11 land covers was chosen from between one and 11 inclusively, shown in green, this meant the bias in solid orange and mortality in dashed orange were less different between the land covers. The dissimilarity model had focal-habitat species who had a rank of one for the focal-habitat and other ranks chosen between 13 and 23 for the other land covers as these land covers were very different (purple). This then meant the bias in movement away from and mortality in these land covers was higher. The non-focal-habitat species (yellow) all had a rank of 23 for the focal-habitat as it was very different. The other land covers had values chosen between one and 22, as the land covers could be similar to each other or not

Table 1 An example of the habitat suitability ranks for different species, resulting in the focal and matrix land covers becoming more similar or dissimilar

Land cover	1	2	3	4	5	6	7	8	9	10	11
Similarity model											
Species 1	1	3	8	9	4	11	10	7	6	5	2
Species 2	11	5	3	2	9	2	4	7	8	6	3
Species 3	5	7	9	2	3	1	4	8	11	10	6
Dissimilarity model											
Species 1	1	15	16	13	17	23	22	19	18	20	14
Species 2	23	1	5	22	9	23	4	3	8	6	11
Species 3	23	19	9	2	3	1	15	8	11	10	6

Species 1 is a focal-habitat species in both examples. Land cover 1 is the focal-habitat

0.75 (Fig. 2). The matrix-diversity scenario included two models in which we changed the number of species for whom the each matrix land cover type had a suitability rank of 1: (1) the Starting Low Diversity (SLD) model, where each matrix land cover type had a lower species diversity at the beginning of the simulation than the focal-habitat and than in the baseline model, vs. (2) the Starting High Diversity (SHD) model, where each matrix land cover type started the simulation with a higher species diversity than the focal-habitat and than in the baseline model. In the SLD model, each matrix land cover type was associated (i.e. suitability = 1) with half as many species, 20 compared to the 40 in the focal-habitat; giving 240 species at the beginning of the simulation (10 × 20 + 40 in the focal-habitat). In the SHD model, 80 species were associated with each of the matrix land cover types, giving a starting number of species of 840. We loaded these freshly generated 240, 440 or 840 species into each run of the simulation regardless of how many matrix land covers the simulation had.

Alpha-, beta- and gamma-diversity

At the end of each simulation run, we recorded the individuals in each focal-habitat patch, analysing the focal-habitat only as this is the focus of fragmentation studies. We calculated mean alpha-diversity per patch, mean pairwise (i.e. between pairs of patches) beta sim diversity (Barwell et al. 2015) and gamma-diversity of the focal-habitat using the R package 'vegan'(Oksanen et al. 2019). We calculated alpha-, beta- and gamma-diversity for focal-habitat-species only. We define the focal-habitat-species as the species for whom the focal-habitat is most suitable and who are dependent on focal-habitat. We focus on the effect of treatments on the focal-habitat-species because they are the species most strongly affected by increasing the FPS of their habitat (Chetcuti et al. 2020).

Analysis of model outputs

We performed regression analyses of how alpha-, beta- and gamma-diversity responded to an increasing number of focal-habitat patches, which represented FPS. We used generalized linear models for gamma- (with a Poisson distribution with a log link) and alpha-diversity (with a gamma distribution with a log link). We used beta regression for beta-diversity ('betareg') (Cribari-Neto and Zeileis 2010). Beta sim values range between zero and one inclusively while beta-regression only allows above zero and below one. To perform beta regression, we therefore scaled the values to be greater than zero and less than one (0.001 to 0.991). Where gamma-diversity values were zero we excluded the zero beta-diversity value as meaningless. We did this because with the zero values the fitted relationships of beta-diversity did not match the datapoints and because including them suggested a much larger difference between the SHD, SLD and baseline models. Ultimately the results were very similar but reduced in magnitude. We also excluded missing beta-diversity values. These missing values arose when only one patch had species. To calculate alpha-diversity with a gamma distribution, we added 0.001 to the values to remove zeros. We tested differences between pairs of models by including both scenarios and creating interaction terms. Due to the simulation nature of our study using p-values was not advisable (White et al. 2014). We instead focused on effect size and 95% confidence intervals. The effect size is typically considered over an increase of a single unit of the independent variable, which would be a patch in this study. This approach is not very meaningful in our study, and it is more appropriate to consider the effect size over the range of fragmentation values simulated. We obtained predicted values for each of the number of patches used in our study to determine an effect sizes by using the R packages 'effects' (Fox 2003; Fox and Weisberg 2019).

Results

For the focal-habitat species, increasing FPS by increasing the number of patches of focal-habitat always led to a decrease in alpha-diversity. Beta- and gamma-diversity variously increased or decreased in the different models, although in the case of gamma-diversity any increase was negligible. Alpha-diversity approached zero with high FPS in all cases. Making the focal-habitat and matrix land covers more (similarity model) or less (dissimilarity model) similar, changing the starting diversity of the matrix land covers to be more (SHD model) or less (SLD model) diverse than the focal-habitat, or increasing the number of matrix land cover types, did not change overall trends in alpha- or gamma-diversity of the focal-habitat -species. There were, however, differences in amounts and rates of diversity change with FPS between scenarios, some of which were extreme. Beta-diversity was strongly influenced by the scenario used, being either positively, not or negatively affected by FPS. We will first present the results of the focal/matrix-similarity scenario which have the most extreme results, then the matrix-diversity scenario, and finally assess the difference the number of matrix land covers made to model outcomes.

Focal/matrix-similarity scenario

In the models of the focal/matrix-similarity scenario (Fig. 5), alpha-diversity decreased with increasing FPS in all models, but most steeply in the dissimilarity model. When the matrix was similar to the focal-habitat (the similarity model), beta-diversity increased (0.09–0.16). When the matrix was dissimilar to the focal-habitat (the dissimilarity model), beta-diversity decreased (−0.48 to −0.33). In the baseline model, where the matrix was neither completely similar nor dissimilar, beta-diversity was unaffected by FPS (between −0.01 and 0.02), except when there were ten matrix land covers, where beta-diversity increased marginally with FPS (0.07). The resulting effect on gamma-diversity was that it usually declined with FPS, but the effect was weak for the similarity model and sometimes reversed, whereas gamma-diversity declined strongly in the dissimilarity model. The baseline model, as found for beta-diversity, showed a weak decline in gamma-diversity with FPS where there were few matrix land covers, and gamma-diversity decreased more strongly with more matrix land covers.

Matrix-diversity scenario

Starting the simulation with the focal-habitat having 40 associated species, and each of the 10 matrix land covers having 20, 40, or 80 associated species (less, equal, or more diverse for SLD, baseline, or SHD models), led to differences in the species composition at the end of the simulations (Fig. 6). As in the previous scenario, alpha-diversity always declined with FPS. With more starting species, the alpha-diversity was higher under low FPS (SHD > Baseline > SLD models). Also, with more starting species (SHD model), beta-diversity rose with increasing FPS (0.10–0.14). The beta-diversity of the baseline model, as seen in the focal/matrix-similarity scenario, was unaffected by FPS, except when there were ten matrix land covers, in which case it increased. This was similar for the SLD model, although beta-diversity declined slightly with few matrix land covers (−0.02) and increased slightly with ten matrix land covers (0.02). These patterns again resulted in an overall decline in gamma-diversity with FPS, but this only became apparent at high FPS. Gamma-diversity was higher when there were more initial starting species, again with the SHD model having the most, then the baseline model and the lowest with the SLD model.

Number of matrix land covers

Increasing the number of matrix land cover types increased the alpha-diversity (by 0.53–3.81 species) and gamma-diversity (by 0.98–2.61 species) when FPS was low. Because of these higher levels of diversity with low FPS, the alpha- and gamma-diversity values then declined more steeply than with a low number of matrix land cover types. Increasing the number of matrix land cover types also caused

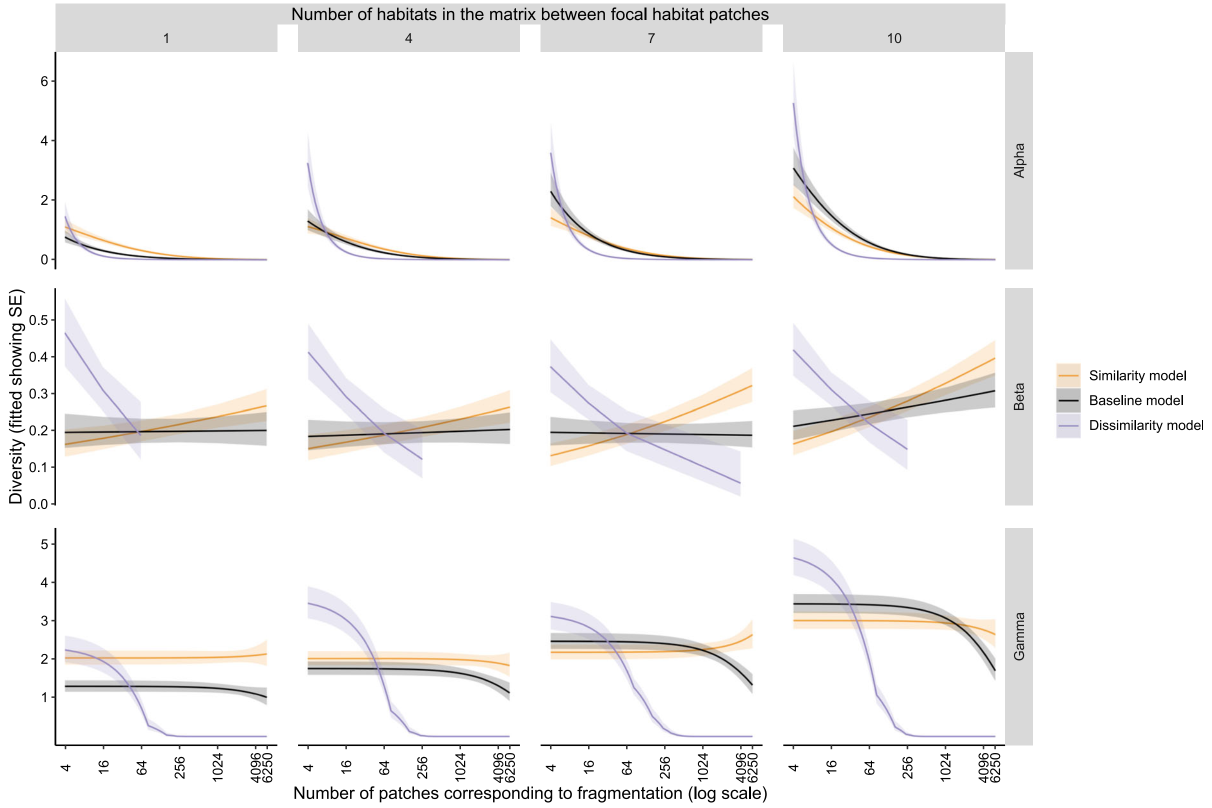


Fig. 5 Change in alpha-, beta-, and gamma-diversity of the focal-habitat with FPS, for the focal-habitat species, being those for whom the focal-habitat was most suitable. The panels show the fitted results with standard errors for the similarity, baseline (neither similar nor dissimilar) and dissimilarity models with increasing FPS from left to right

beta-diversity to increase, or increase more strongly in the case of the similarity and SHD models, with FPS, except in the dissimilarity model in which beta-diversity always declined.

Discussion

Our study showed that FPS had a consistently negative effect on alpha- and gamma-diversity for species associated with the focal-habitat. But the magnitude of this FPS effect was much increased when the focal-habitat and matrix were very different from each other in terms of suitability of focal-habitat species. Study designs using a very dissimilar matrix and focal habitat are often used for experimental landscapes in field and simulation fragmentation studies (Ewers et al. 2011; Haddad et al. 2017; May et al. 2019). However, a study of forest fragments found that changes in bird communities were decreased where fragments bordered matrix habitat that was more similar to the forest (Hatfield et al. 2020). Given our results, studies with an extreme focal-habitat vs. matrix design could conceal cases where positive FPS mechanisms could cause either no relationship of diversity to FPS or a positive one, and imply wrongly that FPS will always have a strongly negative effect. Alongside variation in findings due to which species (e.g. all *vs* those dependent on the fragmented habitat) are considered (Miller-Rushing et al. 2019; Chetcuti et al. 2020), this could be another reason why patch-scale studies (Sisk et al. 1997; Haddad et al. 2015; Fletcher et al. 2018) consistently show negative effects of FPS, while landscape-scale studies sometimes show neutral or positive changes in diversity (Fahrig 2017; Fahrig et al. 2019). In these patch-scale studies,

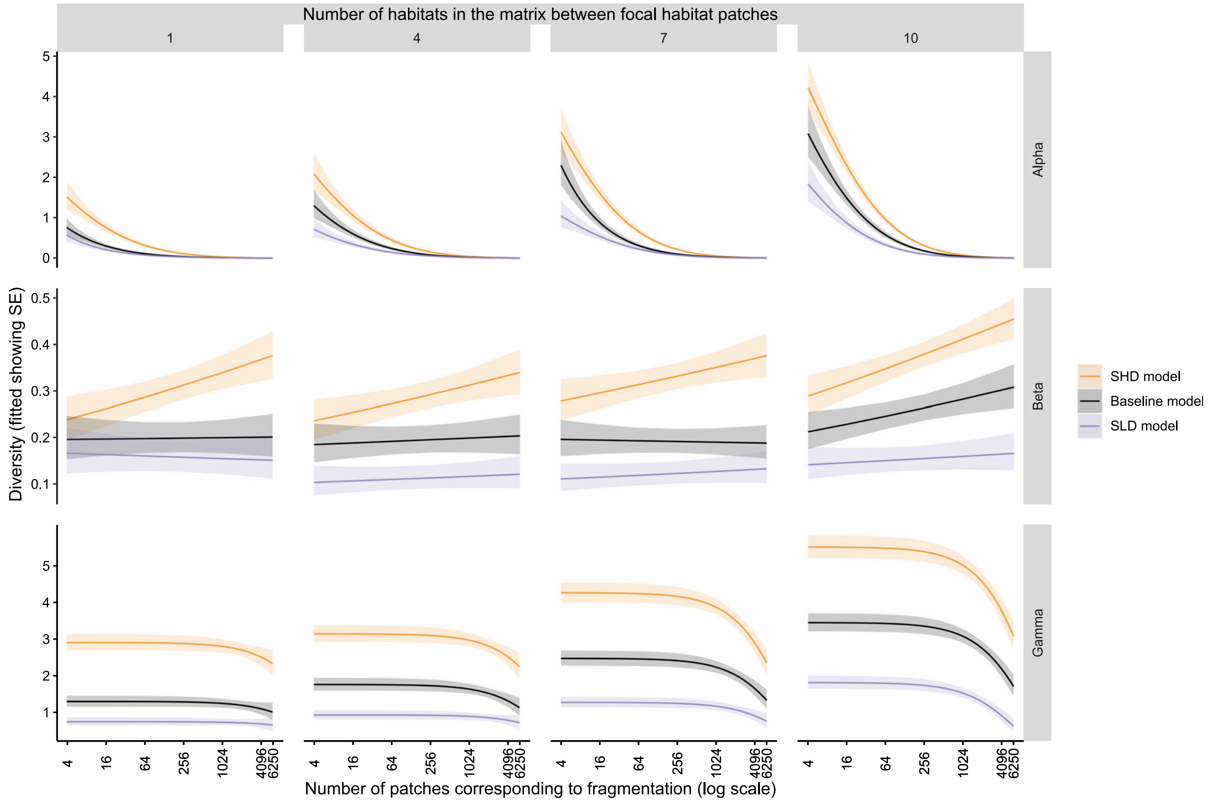


Fig. 6 Change in alpha-, beta-, and gamma-diversity of the focal-habitat-species (for whom the focal-habitat was most suitable) with FPS of the focal-habitat. The panels show the fitted results with standard errors for the Starting Low Diversity (SLD), baseline (starting equally diverse) and Starting High Diversity (SHD) models with increasing FPS from left to right

increases in beta-diversity caused by the positive mechanism of FPS, increased land cover diversity, cannot be accounted for. Where the matrix is species-poor, and very dissimilar to the focal-habitat, this further increases mortality, and drives down alpha-diversity. Chetcuti et al. (2020) showed that gamma-diversity is unaffected by FPS in certain circumstances; in that case for focal-habitat-species, but which were split into specialists and generalists.

As might have been expected, making the matrix more hospitable by making it more like the focal-habitat reduced the effect of FPS. Therefore, modifying the matrix between focal-habitats to make it more hospitable to the species that depend on the focal-habitat and to include a greater diversity of land covers might lessen the effect of FPS. Modifying the matrix is one potential way of increasing functional connectivity (Hunter-Ayad and Hassall 2020). Other ways are by including stepping-stones or corridors (Haddad et al. 2014). Stepping-stones or corridors of the same land cover or similar land covers could also have a similar effect to making the matrix more similar. Landscapes exist along a continuum of levels of difference, from highly modified urban, industrial or industrial-scale farming, through smaller patchworks of gardens, pasture, semi-natural grassland, scrub and hedgerows, to more natural heathland, scrub and forestry. Given our results, classifying how extreme a landscape is, could be a means of determining what the impact of fragmentation of remaining habitat in that landscape would be and assist conservation planning in particular landscapes.

We found changing the species diversity of the matrix compared to the focal-habitat led to little difference in the effect of FPS. This suggests that controlling for differences in species-diversity of the matrix land covers compared to the focal-habitat in field studies is not very important. Within any particular matrix diversity design the effect of FPS on diversity was similar. Despite that, increasing the species diversity of the matrix did cause the alpha- and gamma-diversity of the focal-habitats to be higher. We had expected the opposite effect as we had hypothesised that more species in the matrix would also mean more of them would be "tourists" in the focal-habitat patches. We expected a reduction in the number of focal-habitat-species due to competition as more of the tourist species would find the focal-habitat partially suitable. This was not the case and the reason for this is not clear. Despite there being the same number of individuals due to the fixed carrying capacity, there was a greater diversity of non-focal species of the possible ca. 36 million non-focal species. These non-focal species had therefore a greater diversity of different rankings for different land cover types. This could mean that there were more small areas occupied by species well suited to a particular mix of land covers in that area. Different focal-habitat-species may do better with different neighbours, therefore, although species in this simulation did not exploit each other, they were more competitive or less competitive compared to each other depending on the land cover they are in. This could result in species inhabiting certain sub-optimal parts of the landscape (Jacob et al. 2017; Orme et al. 2019). With fewer matrix species, say, one species could occupy a large area of the matrix, and only the focal-habitat-species that does well against that species would survive. With a higher diversity of matrix species, two or more species may occupy the same area, and therefore two or more focal-habitat-species may be better able to compete against these species leading to a higher diversity of the focal-habitat.

We showed that a greater diversity of matrix land cover types led to increased beta- and gamma-diversity of species that depend on the focal-habitat, by allowing for a greater diversity of species with different dependencies on secondary habitats. This supports the conservation idea that habitat quality and diversity of the matrix should be conserved and enhanced (van der Hoek et al. 2015). It also shows that taking into consideration the effect different matrix land cover types have on focal-habitat species is important in fragmentation and connectivity research and planning (Fletcher et al. 2019). Having more matrix land cover types reduced the effect of FPS in the dissimilarity model, but not to the degree of the baseline, similarity, SHD or SLD models. Having few matrix land cover types was detrimental to beta-diversity, preventing it from increasing with FPS. Assessing the impact of having more matrix land cover types may be important when conducting field studies, particularly when investigating if there are positive effects of FPS. We therefore agree with the call to move away from binary landscape studies, as suggested by Valente and Betts (2019). Beta-diversity has also been suggested as important at a larger scale in supporting multiple ecosystem functions (Mori et al. 2018). Therefore, a diversity of matrix land covers may be important in supporting beta-diversity in a fragmented landscape.

Given the influence of the diversity of matrix land cover types on the effect size of FPS on gamma-diversity, it may be useful to record more information on the landscapes used in empirical studies of fragmentation (Miller-Rushing et al. 2019; Thompson et al. 2019). This could include information on the matrix and on species, for example by calculating species habitat association for the different species found in the landscape (Chetcuti et al. 2019). This would allow researchers to place studies within a framework of meta-information, allowing for consideration of context or to consider more factors when performing a meta-analysis of the effects of fragmentation. This meta-analysis should also include the definition being used for fragmentation (Thompson et al. 2019). Such information could then be used to make better predictions of what effect fragmentation would have in a particular sort of landscape (Fahrig et al. 2019; Brodie and Newmark 2019).

One issue we did not look at in this study and that could be looked at in future work, is the effect of the different physical structure of different land covers that could affect the ability of species to move through different matrix land covers (Keeley et al. 2017; Thompson et al. 2019). Our species experienced differences in mortality and movement bias in different land covers. So, for example, a grassland species may experience higher mortality in woodland, and would more often move towards a grassland land cover (Haddad et al. 2017). But our species did not differ in their ability to move through different land cover types. Using the example again of a grassland species, this species may be unable to move through dense woodland, or a woodland species may turn back at a woodland edge and avoid travelling across an open matrix. Future research could achieve this by changing the movement rates of species in different land covers

(Brodie and Newmark 2019), changing the level of movement bias and therefore habitat fidelity and by modifying the walk from a random walk to either a correlated-random-walk or habitat dependent walk and again looking at the configuration of matrix land covers. Additionally future studies could look at distance that species will travel through different matrix types, either choosing not to enter matrix if unable to see new habitat (Aben et al. 2021), moving a distance before returning to a known patch (Fronhofer et al. 2013) or mortality increasing the longer the individual spent in sub-optimal habitat matrix. Our modelling could also be extended into real landscapes including seasonality and cycles of landscape management (Nabe-Nielsen et al. 2010).

Our study has important implications for how to conduct future research into fragmentation. In this study, different configurations of matrix land cover types did not change results as to whether fragmentation had positive or negative effects on alpha- and gamma-diversity; but did have different effects on beta-diversity. This suggests the potential for finding further inconsistencies in the effect of fragmentation on biodiversity. The effect size of fragmentation on gamma-diversity was much higher in the dissimilar focal-habitat and matrix model than in all the other models. This suggests that this popularly used research landscape could dominate more nuanced patterns. Some of the results showing different relationships of diversity to FPS could be explained by more moderate matrix land cover than the worst-case scenario used in many studies. Researchers could potentially assess this difference, even at a patch scale, by using landscapes that are more varied with a diversity of matrix land cover types. Further, this study supports the need to safeguard the diversity of matrix of land cover types and species within the landscape to lessen any negative effects of habitat fragmentation by safeguarding and improving matrix quality.

Author contributions JC did the analysis and wrote the first draft of the manuscript. JB wrote parts of the text. JB and WK provided guidance on the building and parameterization of the simulation and provided significant guidance and editing of the manuscript.

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Data availability Input data was randomly generated. Output data was generated in simulations (the code for which is provided below). This created a huge amount of data. This data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Code availability The NetLogo simulation can be found at: https://zenodo.org/badge/latestdoi/289454188 and the R package LcvGen at: https://zenodo.org/badge/latestdoi/205820444.

Declarations

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Consent for publication All authors contributed to the article and approved the submitted version.

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