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Species' movement influence responses to habitat fragmentation

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Abstract

Aim: Human conversion of land leads to habitat loss and fragmentation. The effects of habitat loss are well-established, but the effects of fragmentation beyond those of habitat loss, "fragmentation per se" (FPS), are intensely debated. One area of debate is how different species might respond to FPS. We will answer whether FPS have more negative effects on species that spend more time in the matrix and less on species with higher potential patch encounter rates.

Location: Virtual landscapes.

Methods: We simulated the effects of FPS on multiple species with different movement characteristics. All species moved with a random walk (RW), a correlated RW (CRW), or a habitat-dependent walk (HDW). Species also had increasing habitat bias which caused individuals to have a higher probability of moving into a more suitable habitat. The walk type modified the rate at which species encountered habitat patches. Increased bias caused individuals to spend more time in suitable habitats and less time in the matrix between patches. All species experienced higher mortality in less suitable habitats. We analysed FPS effects on species for whom the fragmented focal habitat was the most suitable.

Results: With bias, the species diversity of RW species declined with FPS, while FPS had little effect on the species diversity of species moving by CRW. For HDW species, spending less time in the matrix (moderate movement bias) caused species diversity to increase with FPS, but to decline with high bias.

Main conclusions: These results suggest that even for species that are dependent on fragmented habitat, FPS does not have a unidirectional effect. FPS can have a positive effect on species with high patch encounter rates (HDW with moderate bias) as their functional connectivity increases. These results help to explain why different studies show contradictory effects of FPS on biodiversity.

KEYWORDS
fragmentation per se, individual-based model, movement bias, movement ecology, site fidelity, species diversity

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1 | INTRODUCTION

Many landscapes have experienced large-scale habitat loss and fragmentation through conversion to different land covers and uses (IPBES, 2018; Lawton et al., 2010). While habitat loss and fragmentation are associated in reality, nonetheless different patterns of habitat loss can leave remaining habitat in a range of configurations from a single contiguous patch to many tiny fragments, so that any given total area of habitat can display widely different levels of fragmentation. These different levels of fragmentation for a fixed total habitat area are referred to as "fragmentation per se" (FPS; Fahrig, 2003). While habitat loss has clear negative effects on the diversity of species associated with that type of habitat (Fahrig, 2003; Loke et al., 2019), there is debate over whether FPS always has a negative effect on biodiversity (Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018). While much of the debate about biodiversity responses to FPS revolves around how individuals and species are partitioned among habitat patches (Fahrig, 2020), a full understanding of FPS effects must take account of movement ecology, that is, the ability of individuals to move between patches and over the landscape (González-Fernández et al., 2019). Such movement is critical in determining the degree to which remaining habitat patches are connected in practice, and thus the ability of a species to persist in a fragmented landscape. The relationship of FPS to connectivity concepts is somewhat complex. Structural connectivity, the physical connectedness of habitat in a landscape, can be seen as the inverse of FPS (Auffret et al., 2017; Bélisle, 2005). By contrast, functional connectivity is dependent on the ability of species to move between patches (Auffret et al., 2017; Taylor et al., 1993; Tischendorf & Fahrig, 2000). FPS could increase functional connectivity if the resulting smaller patches are closer together and spread through the landscape than under lower FPS, allowing species to move more easily between patches than between larger but more distantly spaced patches (Fahrig, 2017; Galán-Acedo et al., 2019). A modelling study by Thompson et al. (2019) considered connectivity by measuring individuals' abilities to disperse through fragmented landscapes. For the generic species simulated within their study, fragmented landscapes were more functionally connected than were less fragmented landscapes. Functional connectivity is, however, an attribute of a species' movement characteristics and its interactions with the landscape it is in. This raises the questions as to how the type of movement a species or community of species employs affects the response to FPS, which relates to the hypothesis that responses to FPS depend on the characteristics of the species studied (De Camargo et al., 2018; Valente & Betts, 2019).

Simulation studies of animal responses to habitat fragmentation have generally created species that move with a random walk (RW) (Fahrig, 2001; Rayfield et al., 2011) or a correlated RW (CRW) (Boone & Hunter, 1996; Jepsen & Topping, 2004; Johnson et al., 1992; McIntire et al., 2013; Table 1). These movement types might be criticized as being too simple and unrealistic. In reality, an animal may use different walks in different circumstances; for

TABLE 1 Description of the three main walk types used by the simulated species in this study

Walk	Abbreviation	Description	Turning angle distribution	Example
Random walk	RW	An individual always moves in a random direction with no reference to a previous step. As a result, an individual will move slowly away from its starting point. A group of individuals will diffuse gradually outward from a starting location	Uniform distribution	Moving without memory as in some simple insects (Potgieter et al., 2015)
Correlated random walk	CRW	An individual has a higher probability of continuing to move in the direction it is already moving than of changing direction. An individual can turn sharply, or back on itself, but this is uncommon. A group of individuals will move more rapidly outwards than under RW as fewer will return the way they came than will move away	Gamma distribution	Persistent movement such as the migration of caribou (Bergman et al., 2000)
Habitat dependent walk	HDW	An individual moves differently depending on the habitat or land cover in which it finds itself. When in a highly suitable habitat the individual moves with a random walk. As the habitat becomes less suitable the individual moves in a straighter path (more similar to a correlated random walk) (Kuefler et al., 2010)	Maximum turning angle is defined by habitat with a negative exponential function relating the habitat to the angle (see Figure 3)	Species that alter their movement depending on habitat to more quickly pass through unsuitable habitats (Conradt & Roper, 2006; Kuefler et al., 2010)

Note: All movements are step by step rather than continuous (Codling et al., 2008; Turchin, 1998).

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example, it may employ RW behaviour when searching within a habitat patch (Heinrich, 1979) and CRW when travelling towards a food patch (Osborne et al., 1999) or away from danger (Nathan et al., 2008). The walk employed may also be influenced by topography, resources, landscape features, and perception of danger (Ma et al., 2018; Nottebrock et al., 2017; Schmid et al., 2016; Teckentrup et al., 2019). Species also exercise choice over whether to enter or exit a particular area of habitat or land cover. The combinations of the programmed walks and the choices made may result in an emergent walk that may be best described as a Levy walk (Benhamou, 2007). We have not sought here to exhaustively explore all possible walks, but simply to highlight how changes in how species move, even in our simple case, can change how species are impacted by FPS. Our study does not describe how species will be affected by FPS but illustrates how differences in movement could contribute to differences in observed effects of FPS.

Some species are more or less bold and therefore have different site fidelity or tendency to remain in their current habitat patch (Harris et al., 2020). Species may also differ in their ability to detect suitable habitats, remember the landscape, and the distance over which they can do so (Aben et al., 2021; Lewis et al., 2021; Schlägel & Lewis, 2014). It may be more realistic to represent individuals as moving differently depending on the habitat in which they find themselves (Kuefler et al., 2010; Palmer et al., 2011; Wang, 2019) and therefore showing a habitat-dependent walk (HDW), for which we characterize a simple form in Table 1. Each modelled walk type is likely not a bad model for movement, but each may represent the movement behaviours of different types of species (Bérces & Růžičková, 2019; Da Silveira et al., 2016; Fletcher et al., 2019; Thomaes et al., 2018) or at different places or times (Morales et al., 2004). We explore here whether differences in movement behaviour could lead to differences in the effect of FPS.

In landscapes with an extremely hostile matrix, the cost of moving between patches within the landscape is high and FPS has an extremely negative effect on species diversity, however, FPS is far less detrimental in more common moderate landscapes (Chetcuti et al., 2021). Moving between patches of suitable habitat by crossing the matrix can be costly in terms of time lost from other activities and the risks of increased mortality (Bonte et al., 2012). Individuals spending more time in the less suitable habitat should spend less time reproducing and will incur higher mortality due to the lower food availability, injury or loss of condition, and predation. Thus, FPS might have negative effects if it increases the amount of time individuals of a species spend outside suitable habitats. Species who leave suitable habitat patches less often should be more successful, and in the short term, FPS should affect them less if they can survive in small patches. Such species may however experience longer-term effects of isolation such as inbreeding depression if individuals of the species are unable to move between habitat patches (Cosgrove et al., 2018). Having more small patches that are closer together may lead to a higher encounter rate of individuals with these patches when moving over the landscape and therefore spending less time in the matrix (Fahrig, 2017) while benefitting from the spread of risk and competitive release by being able to access new patches and for genetic flow between patches. Species existing in a single population in one patch are potentially at risk from extinction in the landscape as a result of the destruction of this single population and are safer by having multiple sub-populations spread among different patches which are connected via dispersal (Fahrig et al., 2019; Rybicki et al., 2019). Species may also benefit from competitive release through different competitor species occupying different patches at different times (Resasco et al., 2017) or by patches acting as refuges from predation (Hovel et al., 2001).

Alpha-, beta-, and gamma-diversity are defined in Socolar et al. (2016) as the number of species in a patch; the difference in species composition between patches, giving a measure of species heterogeneity and with reduction analogous to homogenization; and the diversity of all of the patches collectively. Species with a tendency to spend time in the matrix have higher boldness or lower patch fidelity. The species can then also have a low or high encounter rate of patches. If an individual finds a patch of their focal habitat with low fidelity/high boldness they can then leave a patch again. Fahrig (2017) proposed several mechanisms by which FPS may affect species gamma-diversity, and we address two here that relate to movement ecology. First, we predict that FPS will have a greater negative effect on gamma-diversity if the species tend to spend a greater time in the matrix between patches of the fragmented "focal habitat." Second, we predict that FPS should have either no effect or a positive effect on gamma diversity when the species have higher patch encounter rates, due to being able to traverse the landscape more easily. The second of these, if true, would support the idea of increased functional connectivity for such species with species moving more easily between patches. We address these hypotheses by simulating species that move more or less directionally, with CRW, HDW, or RW (more to less directionality respectively), and by changing the degree of bias in the movement towards a more suitable habitat (the walks become more biased for each of CRW, HDW, and RW). These increases in functional connectivity could not compensate for the negative effects of extremely poor-quality matrix habitat, but in more moderate landscapes, may cause FPS to have a positive effect (Chetcuti et al., 2021).

In this paper, we use an individual-based model (IBM; Chetcuti et al., 2020) with multiple species to consider how differences in species' movement characteristics affect gamma-diversity under FPS. We do not attempt to fully explore every possible way species can move and the effect FPS has on these species. Instead, we explore specifically how movement can influence the effect of FPS, attempting to test the effects suggested within the literature. To address the first hypothesis, we modified the degree of biased movement towards a more suitable habitat which led to different amounts

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of time spent in the matrix. To address the second hypothesis, we created different patch encounter rates by changing how the species move, from RW, through HDW to CRW. RW species do not move rapidly across the landscape. HDW species can be parameterized to move in a straighter path in the matrix and CRW species to move in a straighter path in both matrix and suitable habitat leading to rapid movement across the landscape. The HDW and CRW species do not move purposefully towards a new patch, but because they are passing through the landscape more rapidly, in general, they encounter more patches of habitat. Our study was designed specifically to test these proposed mechanisms and does not explore the full range of possible movement. The study may however act as an example of how movement could cause FPS to have a different effect, although our study is a simple model.

2 | METHODS

Our IBM (Figure 1) was built using the NetLogo software (v6.0.4) (Wilensky, 1999). The NetLogo simulations parameters were set up, run, and the outputs analysed using R version 3.5 (R Core Team, 2018). The model is described in detail following the *Overview*, *Design concepts*, *Details* (ODD) protocol for describing individual- and agent-based models (Grimm et al., 2006, 2010) in Appendix S1.

In the IBM simulations, we create multiple competing species. Each of the species finds the 11 habitat types of our simulated land cover to have different levels of suitability, giving each species a different overall preference. One of these 11 habitats was chosen as a focal habitat, so we varied in terms of FPS and examined the diversity of the species for whom this habitat was most suitable. Reduced suitability is simulated by increasing mortality in less suitable habitats above background mortality. This suitability can also be used to give the species bias to choose to move into a more suitable habitat. Within the simulations, we have both modified habitat bias and movement type and then looked at the effect FPS has on the response of the species. We only look at the species that find our focal habitat most suitable (focal species) patches (FPS). The species are not defined as universally specialists across the landscape as Chetcuti et al. (2020) found that specialization did not lead to a difference in the effect of FPS. In local areas of the landscape, some species would be specialists as the focal patch may contain habitats that they have no affinity for. Species differ from each other in their preferences for all of the habitats within the landscape similar to the real-world difference shown between species (Chetcuti et al., 2019).

2.1 | Land cover generation

We did not use real land cover data in this study, as in such data, the level of focal-habitat fragmentation, the area of focal habitat, and the number and area of other habitats are correlated (Cushman et al., 2008; Fletcher et al., 2018). To allow for exploration of FPS independent of habitat area, we simulated land covers over which we

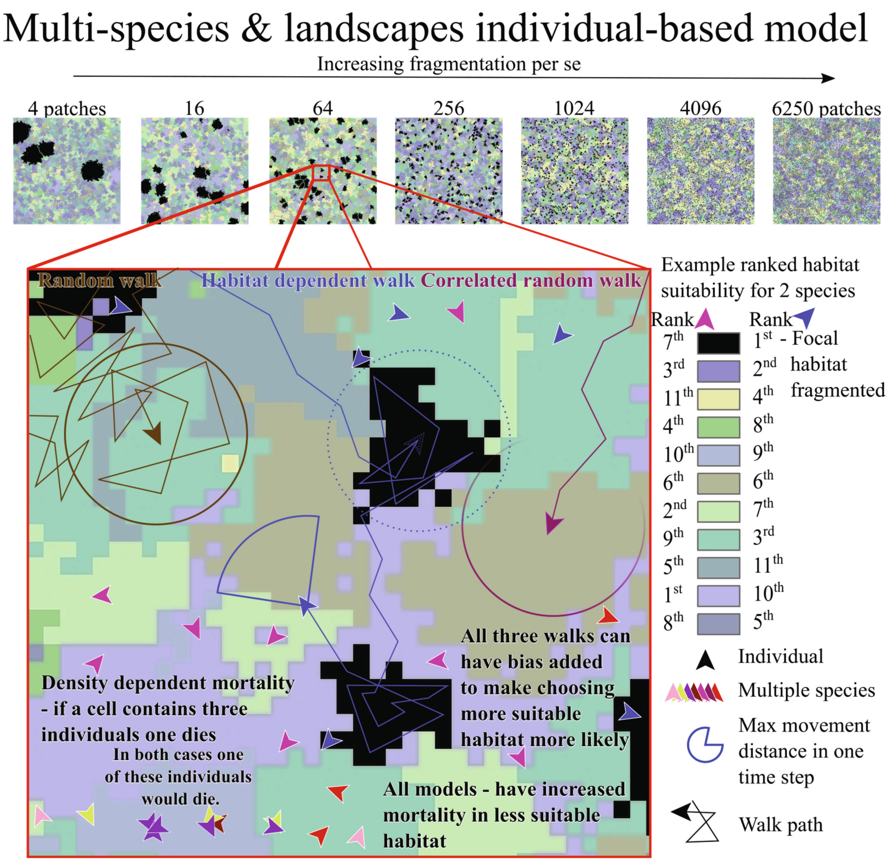

FIGURE 1 A figurative description of the individual-based model, showing how we represented FPS by increasing the number of patches of the focal habitat (in black) while keeping its total area the same. We give two examples of the ranked suitability for habitats on the right for a non-focal-habitat species on the left and a focal-habitat species on the right. We used three types of movement, random walk (RW), correlated random walk (CRW), and habitat-dependent walk (HDW). We included more variation in walks by modifying the rate of individuals' transition to a more directed walk within the HDW. All individuals interact with the habitats according to their assigned suitability, with habitat-modified mortality. We varied bias in moving towards habitat to make choosing a more suitable habitat more likely. These biases ranged between no bias (zero) and high bias (two).

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had precise control, using the R package "LcvGen" (Chetcuti, 2020). To accommodate computational limitations the landscapes were generated 500 × 500 cells in size and then scaled up to 1000 × 1000 cells in size. Hence, the minimum distance between patches was two cells. Following Fahrig (2003) FPS was represented by the number of patches, with more fragmented landscapes having more patches of focal habitat (Figure 1). These focal-habitat patches were not necessarily of the same size, with the size of each patch taken from a uniform distribution. The focal habitat covered 10% of the landscape, as responses to FPS are the same irrespective of the fixed area of the focal habitat unlike the suggestion of the fragmentation threshold hypothesis (De Camargo et al., 2018; Fahrig, 2017; Parker & Mac Nally, 2002; Swift & Hannon, 2010). This was also found in another study using our model to look at FPS at 10% and 40% focal habitat but not differing species movement (Chetcuti et al., 2020). The matrix habitats between focal-habitat patches comprised a mixture of 10 different habitats, to reflect the fact that the matrix in the real world is not uniformly low-quality habitat, and that each species has a specific set of habitat preferences (Betts et al., 2014; Chetcuti et al., 2019). The number of patches of each of the matrix habitats varied, chosen from a uniform distribution between 1 and 200 patches for each. The area of each habitat was also randomly generated to be a proportion of the available space in the matrix. The exception was the last habitat generated which filled all remaining space. Because it included the space between patches it includes more linear features and could have any number of patches. The matrix habitats were generated in a random order so that the last generated was not always the same habitat type. Each focal habitat and matrix habitat patch (except the last generated), was randomly located within the landscape, but at least two cells apart from any patch of the same habitat type. Each patch was then grown until the habitat covered the specified area while remaining separate from another patch of the same habitat by at least two cells. For the matrix habitats, if a habitat could be grown no further, that habitat was considered finished and the next habitat was grown.

2.2 | Species simulations

All individuals of all generic species could reproduce, generating an additional individual with a probability of 5×10^{-4} during a time step, and could move up to a maximum of five cells from their current location during a time step. These values were only applicable to generic species but approximate real species at different scales. For example, based on allometric equations (Sibly et al., 2013) this could be on an approximate sliding scale with size: 5 m per minute and 260 offspring a year, similar to invertebrates; or 5 km per hour and four offspring a year similar to birds or mammals (Hirt et al., 2018). However, all generic species within the simulations were at the same spatiotemporal scale as each other and therefore do not encompass some species moving at 5 m and others at 5 km for example. Only reproductive individuals, females, were simulated and the simulations did not include sex ratios or male-limited reproduction with reproduction independent of density. To simulate density-dependent mortality, an individual died if there were two other individuals of any species in the same cell including their own. There was an overall carrying capacity of 4000 individuals in the landscape. Above this, all individuals had a slightly higher probability of dying within a time step proportional to how many individuals over the simulation there were. The simulations iterated through individuals in random order. This random order was important when the population was over the carrying capacity and when assessing density-dependent mortality. Those assessed first were more likely to die.

Each species had an individual set of ranks for the 11 habitats in the land cover, which specified how suitable that species found each habitat, and this defined that species. These ranks were randomly assigned to each of the species. All species had increased mortality in less suitable habitats. This additional habitat mortality was specified using a logistic equation to relate the rank for habitats to a multiplying value between zero and one. To increase the mortality within a time step in a less suitable habitat the values between zero and one were normalized by the overall rate of reproduction, to give a similar order of magnitude value to reproduction (Figure 2). This multiplication meant the highest additional density-independent mortality equalled the reproduction probability.

In this paper, we only focus on the group of focal-habitat-species. The focal-habitat species are species that rely most on our focal habitat. This is the habitat that we fragmented and these are thus the species that are most susceptible to FPS (Chetcuti et al., 2020; Fletcher et al., 2018). We define focal-habitat species as those for whom the focal habitat is the most suitable (habitat suitability rank one). To test the effects of the group of focal-habitat species spending more time in the matrix habitats and being able to move between patches more readily, we simulated 24 scenarios. The 24 scenarios encompassed different walk types (Figure 1 and Table 1) and biases in the movement towards suitable habitat ("movement bias," Figure 2). The movement bias was represented by logistic curves that converted the habitat suitability rank to a value between zero and one (Figure 2), representing four levels of movement bias; none, low, medium, and high. These values between zero and one were then converted to a probability by stacking values for all habitats and normalizing the values (Chetcuti et al., 2020). The probability was used along with the area of each habitat that the species could possibly move into in that step, to decide which habitat an individual did move to. This bias results in an increase in the probability of a species choosing to move into more suitable habitat in a step. We used six different walks, a RW, CRW, and four types of HDWs. Strictly speaking, these movements are truly RW, CRW, and HDW only when bias is zero; otherwise they are properly termed biased-random-walk, biased-correlated-random walk, and biased-habitat dependent walk. For simplicity and comparability, we refer to them as RW, CRW, and HDW with or without bias. All individuals with all walks could move up to a maximum of five cells. The

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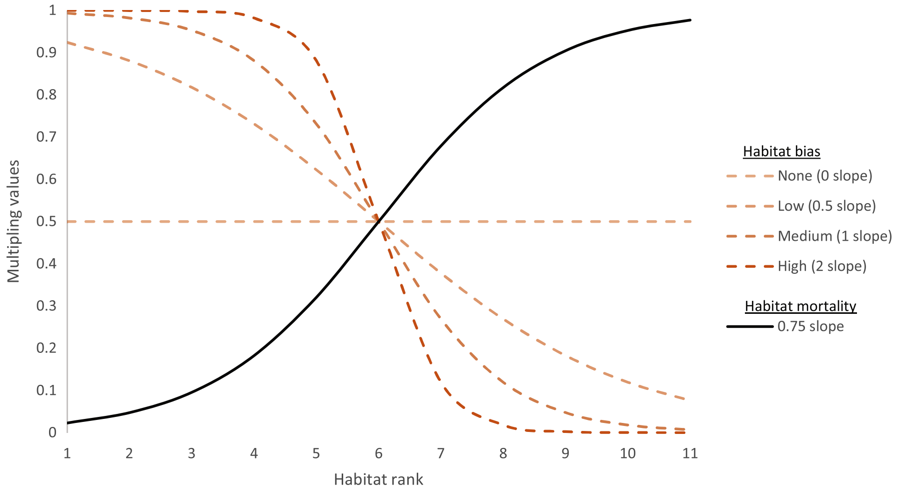

FIGURE 2 Shows how logistic equations were used to relate the habitat suitability rank, one to eleven, to both increased habitat mortality in less suitable, and bias towards more suitable, habitats. The same additional mortality slope was used for all species in all scenarios. Habitat bias towards more suitable habitat varied from none to high bias. To give increased mortality the multiplying values were multiplied by the reproductive rate to give additional mortality that was of a similar magnitude to reproduction. In the case of bias towards a more suitable habitat the multiplying values were used to modify the probability of choosing a more suitable habitat.

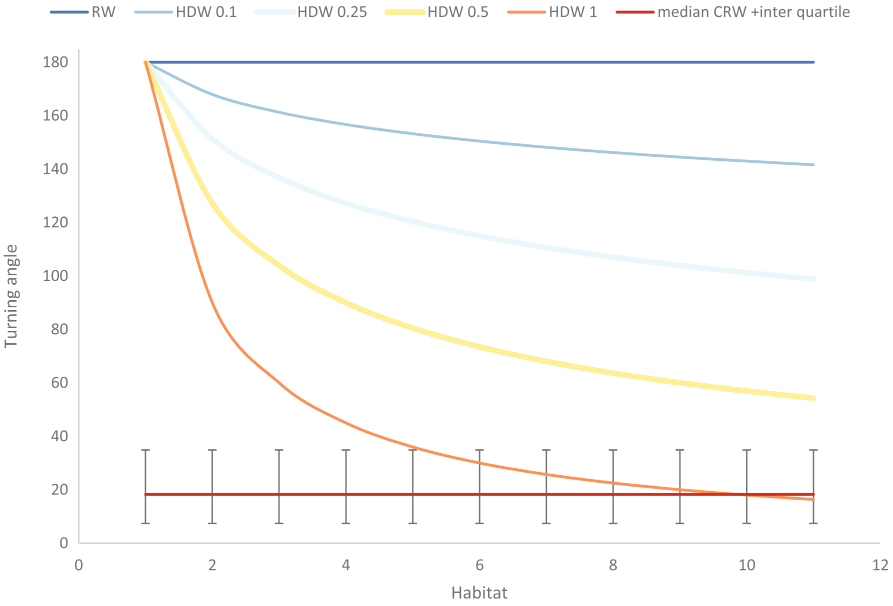

FIGURE 3 Shows how the angle defining where the species can move to (turning angle) changes with the ranked habitat suitability of the species for the habitat-dependent walk (HDW) compared to the random walk (RW) and correlated random walk (CRW). RW species can turn completely around. CRW species can turn through any angle, but the angle is defined by a gamma distribution and therefore the median angle is 36°, with a lower probability for obtuse turning angles. The HDW species can turn completely around in suitable habitat like the RW species and move more directly in a less suitable habitat.

RW individuals could move in any direction. The CRW individuals could turn within an angle centred on where they were facing after their last step, which was defined by a gamma distribution of alpha = 1 lambda = 2 multiplied by 3600, giving a median turn of 36° but the ability to turn occasionally through big angles. This angle defined a sector of a circle the individual could move into up to the maximum distance. The HDW walk was defined by a negative exponential function that related the habitat suitability rank to a turning angle for a species for each habitat (Figure 3). The four HDW walks had exponents of 0.1, 0.25, 0.5, and 1, which gave walks that deviate progressively more from an RW, with movement in the least suitable habitat eventually becoming like a CRW, but always remaining an RW in suitable habitat. RW species did not move directly through the landscape. HDW walks with progressively higher exponents moved more directly across the matrix between patches. CRW always moved directly across both the matrix and patches of suitable habitat. HDW movement combined elements of both RW and CRW, with HDW species able to turn readily with an RW within suitable habitat patches but to traverse less suitable habitats like the CRW.

2.3 | Multi-species and landscapes model description

The simulations loaded the habitat map and 10 individuals of each of 400 species. Each individual had a random starting location within the 1000×1000 cell simulations. The simulations were toroidal, meaning individuals who passed out of one edge reappeared on the other side of the landscape. Using a toroidal design, we assumed

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each simulation run was part of a wider landscape that was configured the same as the simulation. To avoid the other side of the landscape attracting individuals that were moving with bias, we added a bounding area around the edge of the landscape of 10 cells wide with each cell in the area being randomly assigned a different habitat (Chetcuti et al., 2020). The simulations were run for 200,000 time steps, which depending on the scale (minutes or hours) would be between 100 and 8000 years. Using a high number of time steps allowed the number of species to reduce within the simulations to approach an asymptotic number of species. At the end of the simulations, the patch (defined as the contiguous area of habitat using eight nearest neighbours) and species of every individual in the focal habitat were recorded. Each species' movement type and level of FPS were repeated 50 times. This resulted in 8398 simulation runs (two runs failed).

2.4 | Alpha-, beta-, and gamma-diversity

Using the information on focal-habitat species in each focal-habitat patch, we calculated mean focal-habitat patch alpha-diversity, mean pairwise patch (i.e., between pairs of focal-habitat patches) beta sim diversity (Barwell et al., 2015) and overall gamma-diversity of the focal habitat using the R package "vegan" (Oksanen et al., 2019) (Figure 4).

2.5 | Analysis of results

We analysed the results by constructing generalized linear models for alpha-diversity (with a gamma distribution with a log link), gamma-diversity (with a Poisson distribution with a log link), and beta-diversity using beta regression (index values bound between zero and one) against the number of focal-habitat patches, which represented FPS. Due to the simulation nature of our study, using p-values is not advisable (White et al., 2014). We instead focus on effect sizes and 95% confidence intervals. The effect size is usually calculated over an increase of a unit of the independent variable. In our study, this would be the change in the diversity of adding a single patch, but the addition of a single patch is a tiny change in FPS. It is more appropriate to consider the effect size over the range of FPS simulated (change in diversity between 4 and 6250 patches). We calculated the effects over the range of FPS using the R package "effects" (Fox, 2003; Fox & Weisberg, 2019).

3 | RESULTS

Movement bias had the largest influence on whether FPS affected overall species diversity. With bias, walk then made a difference in how species diversity responded to FPS. We present the results below first looking at the result in the simulations where none of the specie in the simulations had a bias towards choosing preferred habitat, then looking at the effect of having bias, and then moving with an RW, CRS, and HDW. Alpha-, beta-, and gamma-diversity are plotted against an increasing number of habitat patches representing FPS in Figure 5a–c.

3.1 | No bias

Where there was no movement bias, the gamma-diversity of the focal habitat species was unaffected by FPS for all the walk types, with effect sizes between −0.47 and 0.23 species over the full range of FPS (see Table S3). Alpha-diversity decreased less with a straighter walk across the total range of FPS, from RW through the HDW scenarios to CRW (−2.22 to −0.84 species; see Table S1). Beta-diversity increased with FPS in all cases, but not by a large amount (between 0.06 and 0.11; see Table S2). The alpha- and beta-diversity

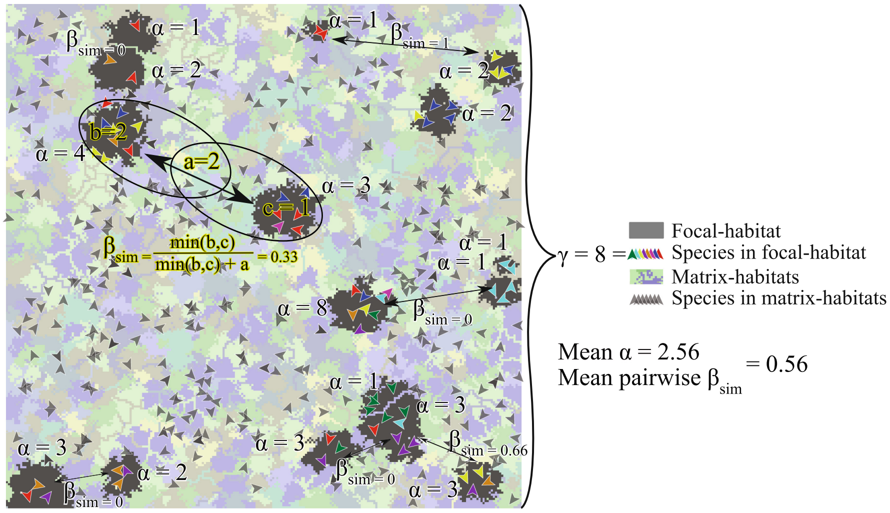

FIGURE 4 An explanation of alpha- (α), beta- (β), and gamma- (γ) diversity for species within a focal habitat across a landscape. Beta-diversity is shown using the measure beta sim (Koleff et al., 2003) and explained in terms of a, b, and c for two patches in the middle of the landscape. a represents shared species, b species only in the left patch, and c only those in the right patch.

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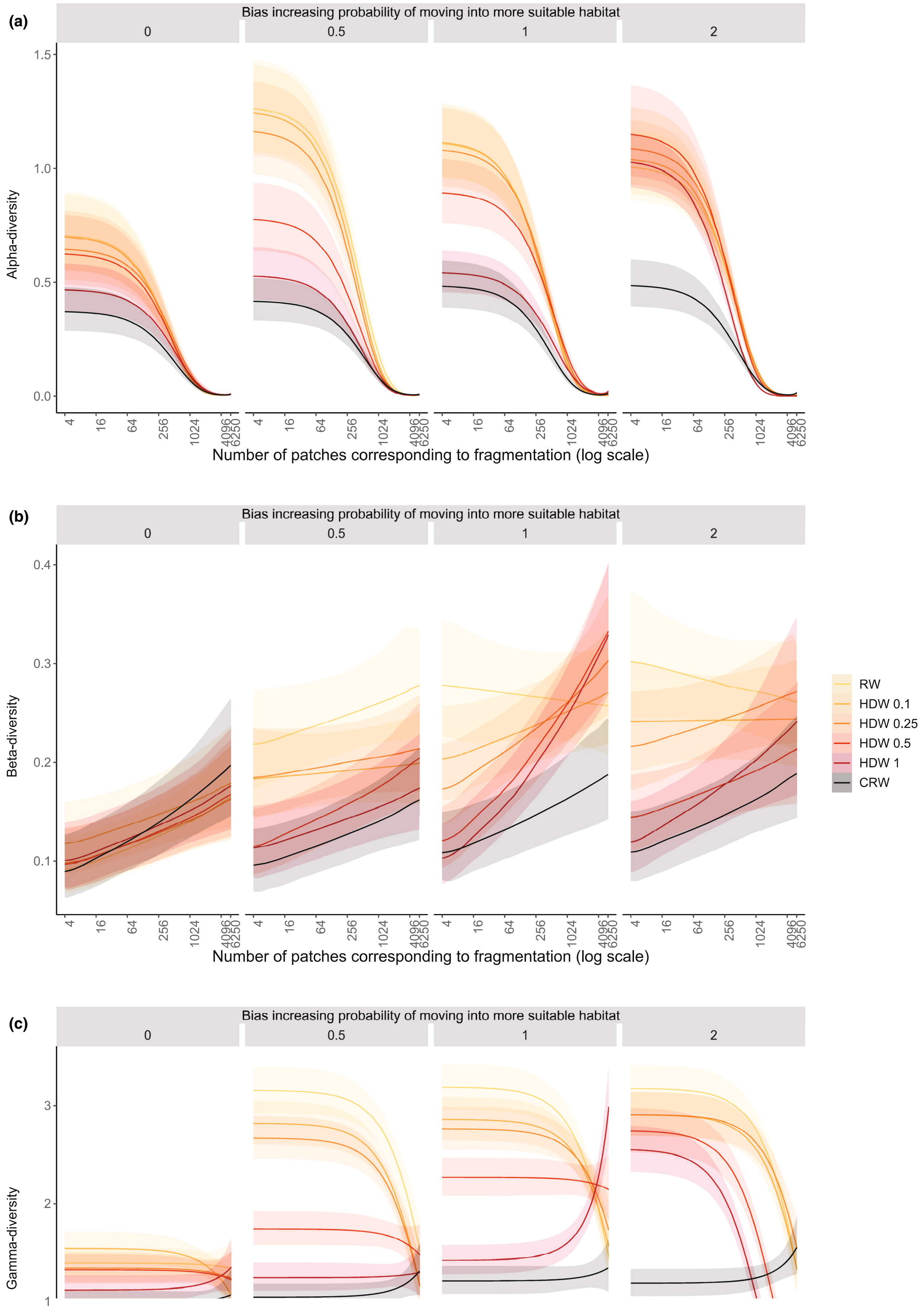

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FIGURE 5 (a) alpha-, (b) beta-, and (c) gamma-diversity changes with increasing FPS represented by the number of patches of focal habitat for species with individuals moving with different walks, random walk (RW), habitat-dependent walk (HDW), and correlated random walk (CRW) and with different movement bias towards more suitable habitat (0 = no bias, 2 = high bias). There are four types of HDW, increasing in the straightness of movement path in less suitable habitats (HDW 0.1 is more similar to RW and HDW 1 to CRW). SE is shown as the shaded area on either side of the lines.

of the focal habitat species almost completely balanced each other, explaining the limited change in gamma-diversity.

3.2 | Movement bias

Increasing the movement bias led to cases where FPS affected gamma-diversity. With increased bias, the gamma-diversity of species with individuals moving with different walks showed both negative (reducing by as much as 2.58 species) and positive (increasing by as much as 1.56 species) relationships of gamma-diversity to FPS (see Table S3). With increasing FPS the effect size of alpha-diversity always decreased by between −0.84 and −3.39 (see Table S1), while effect sizes of beta-diversity changed by between −0.02 and 0.20 (to give an idea of scale, possible beta-diversity values range between zero and one, therefore decreasing by 2% and increasing by 20%; see Table S2).

3.3 | Random walk

With movement bias, the gamma-diversity of RW species always declined with increasing FPS, as they were unable to pass readily between patches of the focal habitat. With bias, these species would have spent less time in the matrix, and the gamma-diversity was higher than with no bias (+1.75 with four patches but only +0.17 with 6250; see Table S3). With increasing movement bias, beta-diversity declined (from 0.07 to −0.02; see Table S2) but alpha-diversity decreased less (see Table S1), and therefore the gamma-diversity declined with increasing FPS was similar. The lesser decrease in alpha-diversity was probably due to fewer individuals leaving the focal habitat under higher movement bias and therefore their risk of mortality was lower and fewer species went extinct.

3.4 | Correlated random walk

Gamma-diversity of CRW species, who turned infrequently and therefore traverse the landscape rapidly, increased with FPS when movement bias was introduced, although only by a very small amount (between +0.13 and +0.36; see Table S3). Increasing bias had little effect on alpha- (between −0.89 and −1.19; see Table S1), beta- (between +0.07 and +0.08; see Table S2) and gamma-diversity (the black lines in Table S3). This very low increase in gamma-diversity with FPS for the CRW species was likely due to the inability of individuals to stay within the focal-habitat patches having encountered them, especially when the patches were small. The CRW species encountered patches more frequently due to the landscape having higher functional connectivity for them with high FPS, but the increase in bias was not enough to keep them in patches.

3.5 | Habitat dependent walk

We looked at four forms of the HDW species by varying the exponent of the negative exponential relationship from 0.1 to 1. With the 0.1 exponents, individuals turn through a large range of angles in the matrix and with an exponent of 1 they turn through a smaller angle and therefore move in a straighter path (Figure 3). With movement bias, the HDW species with an exponent of 0.1 had a relationship of alpha, beta, and gamma-diversity to FPS that was similar to the RW (two lightest lines in Figure 5). As the HDW straightened in less suitable habitat (with higher exponents), for low and moderate movement bias, the relationship of gamma-diversity to FPS changed from negative (low bias −1.66 and moderate bias −1.29), to positive (low bias +0.05 and moderate bias +1.56) (see Table S3). The increase with low bias was very small but larger with moderate bias (bias 1 column of Figure 5c). Alpha-diversity decreased less with a straighter walk than a more RW for both low (−3.24 most RW like HDW to −1.40 most directional HDW) and moderate bias (−2.64 most RW like HDW to-1.24 most directional HDW) (see Table S1 and Figure 5a). Beta-diversity increased with the more directed walks (Figure 5b). This change with more direct walks was very small with low bias (+0.02 to +0.06) but changed by a larger amount with moderate bias (+0.06 to +0.20) (see Table S2). This small change with low bias and larger change with moderate bias was similar to the difference between low and moderate bias for gamma-diversity.

3.6 | High movement bias

In contrast to the changing relationship of gamma-diversity to FPS from negative to positive with more direct walks under moderate bias, having high movement bias (bias exponent of 2) did not cause gamma-diversity to increase with more direct walks. With high bias, individuals would have a very high chance of choosing preferred habitat. They would therefore rarely leave patches of habitat. Gamma-diversity declined more with straighter walks (going from −1.58 to −2.54; see Table S3). Alpha-diversity reduced less, as it had done with the low and moderate bias, but

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not by as much (from −2.47 to −1.83; see Table S1). Beta-diversity increased less (+0.01 to +0.12; see Table S2), and the declines in alpha-diversity explained the declines in gamma-diversity (Figure 5).

4 | DISCUSSION

Our results (with only minor exceptions) confirm that the fragmentation of habitat decreases alpha-diversity but increases beta-diversity (Chetcuti et al., 2020; Damschen et al., 2019; Fletcher et al., 2018; Haddad et al., 2015). The effect on alpha-diversity is probably partially (but not entirely) fuelled by patch sizes—as diversity is being measured at patch scale, and highly fragmented landscapes have much smaller patches on average. By contrast, our chosen beta-diversity index (beta sim) is insensitive to sample size. Gamma-diversity is driven by both alpha- and beta-diversity, and we have shown that the net result of these two opposing measures can produce either positive or negative responses of gamma-diversity to fragmentation. It is notable that we found positive effects of fragmentation under some circumstances, even though we focussed exclusively on species that favour the focal habitat. It would not be surprising for species that prefer matrix habitats to be better represented in patches of their less preferred habitat under higher FPS, because of higher encounter rates. Our results, however, show that even specialists can benefit from the fragmentation of their favoured habitat. This is shown in some of the bird species studied by Devictor et al. (2008) and in the desert lizards of Attum et al. (2006).

Our results show that spending less time in the matrix, through having a movement bias and therefore patch fidelity, can be beneficial to species that are able to move readily across the less suitable habitats. Critically, too high a movement bias and therefore high patch fidelity or low likelihood of leaving a patch can cause alpha- and gamma-diversity of species that could otherwise move between patches to decline with FPS. This is because they find themselves in progressively smaller patches and they do not move to other patches. With no movement bias, as might be the case with some passive dispersers, such as seeds or some insects, FPS had no effect in our study. Our results showed both negative and positive effects of FPS on the gamma-diversity of the focal habitat species (the species for whom the focal habitat is most suitable). This suggests that it is possible to find negative impacts of FPS at a landscape scale, and so results from patch scale studies (Fletcher et al., 2018; Haddad et al., 2015), may be applicable at landscape scales in some cases, particularly given the strong influence of alpha-diversity on gamma-diversity. But FPS does not always have a negative effect on gamma-diversity, with positive mechanisms of FPS such as increased functional connectivity, higher habitat diversity, and competitive release causing beta-diversity to increase strongly. Those species that can move between patches directly experience lower mortality due to less time in the matrix. Because of higher functional connectivity, beta-diversity likely increases due to competitive release as different species can survive in different patches and move between patches.

Calls for additional landscape-scale analysis of FPS (Fahrig, 2017, 2019; Fahrig et al., 2019) are relevant and these studies are needed. But field studies at landscape-scale studies are not always possible and are costly. There is value in patch-scale analysis; for example, it should be possible to investigate if there are less negative effects of FPS on the alpha-diversity of species that are able to cross less suitable habitats, as we have seen in this simulation. It would be difficult to infer, however, whether this lower decline in alpha-diversity would be enough for landscape-scale gamma-diversity to increase with FPS. Unlike our study, which looked at the effect of FPS on the diversity of multiple species, there are examples of studies on individual species with their individuals moving with a random walk and being negatively affected by fragmentation. One such case is a study of an endangered ground beetle which generally moved with a biased random walk (Bérces & Růžičková, 2019). Likewise, there are cases of a species that move more directly and appear to be unaffected by fragmentation, as in the case of pandas that showed no genetic differentiation caused by fragmentation (Ma et al., 2018). However, further examples are difficult to come by specifically because the way species move is not considered when looking at the effects of fragmentation. Further research is required on the effects of fragmentation rather than assuming, as much research on species movement does, that fragmentation will have a negative effect (Thomaes et al., 2018). Da Silveira et al. (2016) tested how starlings moved through landscapes, hypothesizing they would move in a similar way to how we have characterized HDW. They instead found the birds turned more randomly than expected, often switching direction sharply, and the authors suggested that the starlings may have adapted to fragmentation through behavioural plasticity. A mode of movement that we have not included, but which may have different effects, is foray loops or prospecting, which are being found to be used by an increasing number of species (Bauduin et al., 2016). Foray loops would seem to suggest some memory of previous locations (Grant et al., 2018) and we would expect these species to respond more like the HDW species, looping out and back if they do not find a new patch of habitat and benefiting from fragmentation in that new patches are more often found. Indeed, species' ability to gather information beyond their immediate location is an important area of research (Aben et al., 2018, 2021). In this particular study, we used multiple different habitats that vary continuously in their suitability for the species within the simulation. In our Chetcuti et al. (2021) study using the same model but only RW, the effect of matrix composition was explored including landscapes with fewer or a single hostile matrix. We showed that in these cases the decline in diversity was dramatic. It is possible that species with the ability to move directly through such a hostile matrix may be less affected by the extreme landscapes. However, future

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empirical work is necessary to explore whether such species are less affected.

Our study did not sweep across the full range of possible values for each parameter and did not seek to simulate specific species, but still found a range of effects of FPS on gamma-diversity. Our results show that it is possible to find different effects of FPS as a result of simulating species with different movement characteristics. A next step could be to investigate how common these different sorts of species are in real landscapes and run simulations with variations between species. Are species more able to move between patches and have moderate fidelity levels in landscapes or habitats that are historically fragmented? Are species with passive dispersal more likely to be unaffected by FPS, and how is this dependent on the degree of habitat-dependent mortality? Further simulations could test this last idea by focusing on species without movement bias and sweeping over a greater range of mortalities. This could be done possibly using an exponential relationship instead of the logistic relationship used in this study to allow mortality to remain the same in the focal habitat while increasing it in matrix habitats. Can species adapt to fragmented landscapes by reducing site fidelity, possibly by becoming bolder through plasticity or utilizing intra-species variation in behaviour (Villegas-Ríos et al., 2018)? Does this lead to bet-hedging and reduced fitness in non-fragmented landscapes (Olofsson et al., 2009)? Another possibility for species to adapt to FPS is by becoming better dispersers exploiting intraspecific variation and increasing the proportion of the population that is adapted to dispersal, such as wing dimorphism in insects, where it has been shown that a higher proportion of the population has wings in fragmented landscapes (Chapman et al., 2005).

5 | CONCLUSIONS

We have shown that variation in the movement characteristics of species could contribute to explaining some of the different effects of fragmentation that are reported in the literature (Fahrig, 2017; Fahrig et al., 2019). Depending on which studies are included in an analysis, fragmentation could overall have a positive or negative effect on gamma-diversity. Defining fragmentation as the converse of connectivity is troublesome as the functional connectivity of any landscape will differ among different sorts of species. As we show, increased FPS can lead to both reduced and increased functional connectivity, landscapes should be assessed for the species in them when making decisions on planning conservation. The safest recommendation in the absence of information on specific species, such as through specific connectivity analysis, would be to variously conserve large patches of habitat in some areas while putting effort into conserving many small patches in other areas. This will give a diversity of different landscape configurations and therefore species across the landscape.

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DATA AVAILABILITY STATEMENT

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. Other inputs and outputs can be found at: https://doi.org/10.5281/zenodo.6025702.

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Author contributions: J.C. did the analysis and wrote the first draft of the manuscript. J.B. wrote parts of the text. J.B. and W.K. provided guidance on the building and parameterization of the simulation and provided significant guidance and editing of the manuscript. All authors contributed to the article and approved the submitted version.

SUPPORTING INFORMATION

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

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